

Seasonal Patterns of Body Composition
and Gut Morphology of Beaver (Castor canadensis)

by

Daniel W. Soprovich

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Master of Science, Zoology
in
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SEASONAL PATTERNS OF BODY COMPOSITION AND GUT
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BY

DANIEL W. SOPROVICH

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements for the degree of

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ABSTRACT

Seasonal changes in body composition and gut morphology were studied in 22 kit and 45 adult (>1 year old) beaver (Castor canadensis) from southern Manitoba. Fat accounted for 0.9-16.7% and 0.6-15.0% of ingesta-free body mass in kits and adults, respectively. Adult beaver were leanest during the period 16 May - 8 July, when mean ($\pm$ SE) body fat content was $2.49 \pm 0.32\%$ in females and $1.36 \pm 0.66\%$ in males. The fat content of adults increased from mid-summer until well after freeze-up, reaching peak levels in mid-winter. During the period 22 December - 17 February, mean fat content was $14.31 \pm 0.35\%$ in females and $12.02 \pm 0.97\%$ in males. Fat levels did not decline until late winter - early spring. Following break-up, adult females were considerably fatter than adult males. The body fat content of kits was comparable to that of adults from fall to mid-winter. For adult females, body protein was lowest in late spring and early summer, and body minerals were lowest from late summer to fall. My findings imply that energy derived from body fat is most critical during and after spring break-up, and that fat and protein reserves are essential for defraying reproductive costs in females.

I hypothesized that beaver adjust their gut morphology seasonally as a means to improve the digestibility of winter diets. The masses of the cecum, large intestine and small intestine of adult beaver were heaviest during winter and lightest in summer. As predicted, the body fat content and

cecal mass of adult males were positively correlated. These adjustments are consistent with the need to optimize extraction of energy from a high-fiber winter diet, and to secure the uptake of highly digestible components from this forage.

Predictive models for body nutrient levels were developed for skinned and whole beaver carcasses. On the basis of depot and index measurements, the tail fat depot was saturated prior to subcutaneous and coelomic reserves, and coelomic reserves were the last to be saturated. Consequently, precision improved when several depots and/or indices were used to estimate total fat reserves. The mass of an abdominal depot, the total kidney fat index, and a heart mass-corrected perirenal index were related to total body fat content by logarithmic functions. Body fat content was directly related to an index of subcutaneous fat reserves. Ingesta-free mass and the mass of the M. plantaris both appeared to model dynamic body protein variation, and estimates of body protein mass were most precise if multivariate models included one of these measures. As an index of total body protein, the M. plantaris mass was superior to the heart or kidney mass. Estimates of body mineral mass were most precise when predicted from ingesta-free mass and structural measures.

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Abbreviations used in the Text

ABDOMFT	abdominal fat depot mass
ADF	acid detergent fiber
ALEKIND	heart mass-corrected kidney fat index
CECMAS	cecal mass
DATE	Julian date of collection
DMAF	dry matter accounted for
FAT	body fat content (% dry matter)
GUTMAS	total gut mass
HEARTWT	heart mass
HINDFT	hind foot length
IFMASS	ingesta-free body mass
KIDFT	mass of perirenal fat
KIDIND	total kidney fat index
KIDWT	mass of kidneys
LENGTH	total body length
LINTMAS	large intestine mass
LWT	lean body mass
MAND1	incisor length
MAND2	mandible length
MUSCPERC	<u>M. plantaris</u> dry matter content
MUSCWT	<u>M. plantaris</u> mass
PROT	body protein mass
PROTASH	body protein and ash content (% dry matter)
SINTMAS	small intestine mass
STOMAS	stomach mass
SUBBRISK	brisket subcutaneous fat index

SUBMID1	midventral subcutaneous fat index 1
SUBMID2	midventral subcutaneous fat index 2
SUBPELVI	pelvis subcutaneous fat index
SUBRMPEL	rump-pelvis subcutaneous fat index
SUBTAIL1	backfat subcutaneous fat index
SUB1	cumulative subcutaneous fat index 1: SUBBRISK + SUBMID1 + SUBMID2
SUB2	cumulative subcutaneous fat index 2: SUB1 + SUBPELVI
SUB3	cumulative subcutaneous fat index 3: SUB2 + SUBTAIL1
SUB4	cumulative subcutaneous fat index 4: SUB3 + SUBRMPEL
TAILFAT	tail fat index
TAILSTN1	standard tail length
TAILTHIK	tail thickness
TAILUND	tail length
TAILVOL	tail volume
TAILWIDT	tail width
TAILWT	tail mass
TIB	tibia length
ULNARND	whole-beaver ulna length
ULNASKIN	skinned-beaver ulna length
VISCFT	visceral fat mass
ZYGRND	whole-beaver zygomatic width
ZYGSKIN	skinned-beaver zygomatic width

General Introduction

Winter poses critical nutritional and energetic challenges for many northern mammals. With plant senescence, nutrient levels and digestibility decline, making it difficult for a herbivore to acquire sufficient nutrients from its food. Perhaps the principle means by which these mammals have adapted is the scheduling of energy- and nutrient-intensive events like reproduction to periods of high food quality and moderate climatic conditions. However, herbivorous mammals also demonstrate the capacity to modify their digestive tract in response to changing food quality (eg., Virgl and Messier 1992a; Hammond 1993). Furthermore, northern mammals demonstrate numerous physiological and behavioral adaptations to mitigate the effects of their extreme winter environment.

The beaver, Castor canadensis, is the largest North American rodent, and is a common resident of northern lakes and streams. To exploit these environments, beaver have adapted to winters during which streams and lakes are covered by thick ice for extensive periods. One of the most obvious adaptations is their well-known habit of caching food resources in the vicinity of the lodge. Another behavioral adaptation is the construction of lodges which provide beaver with access to a thermoneutral microclimate (Buech et al. 1989; Dyck and MacArthur 1993a).

Despite considerable study of this species (see Novak 1987), the means by which beaver provide for their winter metabolic requirements remains unclear. Foods stored in the

cache are generally of low quality compared to the beaver's summer diet (Aleksiuk 1970a; Skinner 1984), and appear to be poorly digestible (Buech 1987). Furthermore, the quantity of nutrient resources in the cache does not appear adequate for the beaver's metabolic requirements (Novakowski 1967), particularly when foraging and digestion costs are considered (Dyck and MacArthur 1993b). Cache resources might be adequate if the winter metabolic rate of this species is depressed, as suggested by Aleksiuk and Cowan (1969a). However, recent studies have failed to document a substantive drop in deep body temperature in winter (Smith et al. 1991; Dyck and MacArthur 1992). Beaver are also known to store energy in the form of body lipids (Aleksiuk and Cowan 1969b), and Novakowski (1967) suggested that the shortfall of energy in the winter food cache might be provided by these tissue reserves. Beaver may also supplement the energy resources of the cache by selectively feeding on the rhizomes of aquatic plants (eg., Nash 1951; Jenkins 1981). However, the significance of these items to the beaver's winter energy budget is poorly understood.

Information on the body fat dynamics of beaver is restricted to one study of the variation in fat indices of immature animals (Aleksiuk and Cowan 1969b). In that study, it was uncertain if beaver utilized fat energy between freeze-up and break-up. Furthermore, indices often predict body fat resources poorly (eg., Torbit et al. 1988; Watkins et al. 1991). Therefore, studies of body composition are necessary

to evaluate the role of fat reserves in the beaver's winter energy budget. Although other rodents appear to compensate for low digestibility diets through adjustments to their gut, it is not known if beaver respond to their winter diet in this manner. Body protein and mineral reserves are known to vary seasonally in other mammals (Huot 1989; Batzli and Esseks 1992; Virgl and Messier 1992a), but there is no comparable information for beaver. Finally, predictive models which permit precise and simple assessment of body composition are lacking for this species.

This study investigates several of the options by which beaver might provide for their winter metabolic requirements, examines the dynamics of body fat, protein and mineral reserves, and develops functions to predict the levels of these body nutrients in carcasses. To address the role of fat reserves in the bioenergetics of beaver, Part I examines these reserves in relation to season, sex and age. The variation of protein and mineral reserves are similarly examined. Part II investigates seasonal adjustments in the digestive tract of beaver. To assist further research, Part III develops predictive models of body composition which provide accuracy, precision and flexibility.

PART I

Variation in the body composition of the
beaver, Castor canadensis

INTRODUCTION

In several mammalian taxa, the storage of body fat represents an important component of their adaptive response to seasonal shortfalls in dietary energy. The ability of an individual to assimilate and store energy as fat can have a direct bearing on its future survival. For example, depletion of fat reserves can lead to starvation of a substantial portion of an ungulate population (Kucera 1976; Clutton-Brock 1985; Depperschmidt et al. 1987), and it has been suggested that survival of these animals relates to the amount of fat acquired prior to winter (Mautz 1978; Hobbs 1989). The probability of death by accident (O'Gara and Harris 1988) or predation (Allen 1979) may increase if body fat reserves are low. For small rodents with high mass-specific metabolic rates, fat reserves appear to function mainly to enhance survival during brief periods of adverse environmental conditions (Perrin 1979; Millar 1981). Fat reserves are also critical to overwinter survival in small hibernators, and are important to successful migration in many species (Young 1976).

Among cervids, the impact of lactation on fat resources may delay ovulation by several weeks (Cothran et al. 1987) or even a year (Clutton-Brock 1985). For Peary caribou, Rangifer tarandus pearyi, winters are sometimes so severe that several years are required to acquire the fat resources necessary for pregnancy (Thomas 1982). Menarche can be delayed and ovulation may cease when fat reserves are low in humans

(Frisch 1988). In an extremely resource-limited environment, body condition may also influence the sex of progeny in a polygynous species (Clutton-Brock 1985). Clearly, it is sometimes not profitable for an individual to become pregnant and the amount of stored fat may be integrally involved in determining this event. In males of various species, fat resources may offset the energetic demands of breeding (Young 1976). In contrast, although fat resources may vary with reproductive status in small rodents (Millar et al. 1991; Batzli and Esseks 1992), stored body fat often appears to contribute little to the cost of reproduction in these mammals (eg., see Millar 1979).

In wild populations of cervids and rodents, body protein levels have also been observed to vary seasonally (Huot 1989; Virgl and Messier 1992a). The often considerable seasonal variation in body mass (eg., Bozinovic et al. 1990) also suggests that body protein is dynamic in some species of small rodents. Similarly, seasonal variation in mineral levels have been reported for several species of rodents under natural conditions (Batzli and Esseks 1992; Virgl and Messier 1992a). For brown lemmings, Lemmus sibiricus, Barkley et al. (1980) predicted that pure natural diets of low mineral content would lead to body mineral deficiencies. Finally, King and Murphy (1985) postulated that the annual protein cycles reported in endotherms could result from episodes of active protein storage, and they suggested that minerals, vitamins and other nutrients might also be held in reserve.

The beaver, Castor canadensis, is the largest North American rodent. Consequently, among non-hibernating North American rodents, fasting endurance and body fat content should theoretically be highest in this species (Lindstedt and Boyce 1985; Millar and Hickling 1990). However, the extent to which northern beaver depend on the energy stored in adipose tissue remains unknown. This is due, in part, to the fact that previous estimates of body fat resources are limited to studies of three individuals collected in two locations (Pitts and Bullard 1968). Although Aleksiuk and Cowan (1969b) documented temporal variation in fat indices, the ability of these indices to model total body fat is questionable (see Part III). Therefore, more complete data on fat resources of beaver are essential to assess the role of endogenous tissue reserves during the annual cycle.

The principal objective of this study was to document temporal, sex- and age-related variation in the fat resources of beaver. On the basis of the variation in the fat indices adopted by Aleksiuk and Cowan (1969b), it was hypothesized that the fat reserves of beaver should be minimal and stable during summer. I also predicted that beaver would accrue fat prior to and while restricted beneath the ice, and that fat reserves would be maximal during winter. I expected beaver to mobilize fat during the months immediately preceding spring break-up, when food quality (Skinner 1984) and/or quantity (Aleksiuk 1970a) may be in decline.

The protein content of the beaver's diet appears to vary

considerably between seasons (Aleksiuk 1970a), and may decline prior to spring break-up (Skinner 1984). Therefore, it was hypothesized that body protein reserves might also vary seasonally. If dietary protein becomes limiting, this should be particularly apparent in females due to the considerable protein synthesis required for reproductive tissue and fetuses. I predicted that beaver with low body fat would also be deficient in protein reserves.

The amount of calcium, phosphorus, and other minerals in the beaver's diet also may decline over the winter (Skinner 1984), and likely differs between winter and summer forages (eg., Flanagan and Van Cleve 1983; Skinner 1984). Furthermore, the high Ca:P ratio of bark in the cache (Skinner 1984) might adversely affect body pools of both minerals (Barkley et al. 1980). Therefore, it was hypothesized that the body mineral reserves of beaver might vary over time.

STUDY AREA

Beaver for this study came principally from the Cooks Creek ($49^{\circ}57'N$ - $50^{\circ}09'N$ Lat.; $96^{\circ}41'W$ - $96^{\circ}55'W$ Long.) and southern Netley Marsh ($50^{\circ}15'N$ - $50^{\circ}19'N$ Lat.; $96^{\circ}50'W$ - $97^{\circ}00'W$ Long.) areas of Manitoba, Canada. One beaver originated from a drainage ditch northeast of the Cooks Creek area ($50^{\circ}17'N$ Lat.; $96^{\circ}25'W$ Long.) while another was from a shallow lake in northern Netley Marsh ($50^{\circ}24'N$ Lat.; $96^{\circ}54'W$ Long.).

Of the 44 beaver collected from the Cooks Creek area, 38 were from Cooks Creek and its tributaries, 5 from Devil Creek

and its tributaries, and 1 from Birds Hill Park. Although the majority of these beaver came from relatively undisturbed riparian habitat, a few of the animals were collected from channelized creek or drainage ditch habitat. With the exception of Birds Hill Park, the principal land use in the area is cereal crop production, and wooded cover is limited principally to the riparian habitat adjacent to creeks and tributaries. The habitat is dominated by bur oak (Quercus macrocarpa), Manitoba maple (Acer negundo) and trembling aspen (Populus tremuloides), with substantial amounts of emergent vegetation (Carex sp., Scirpus fluviatile, Typha latifolia) and submergent vegetation present in most of the areas sampled. Soils originate from lacustrine parent material and are highly fertile throughout the Cooks Creek and southern Netley Marsh areas (Ellis 1938). Additionally, both areas are subject to the input of nutrients by runoff from agricultural fields and cattle operations, and from various other sources. Streams within the Cooks Creek area are subject to strong seasonal variation in flow, and were ice-covered from approximately mid-November to early April during the period of study. The beaver from this area typically construct dams across the relatively narrow creeks and tributaries.

The 21 beaver from southern Netley Marsh came from Goldeye Creek, Mink Creek, Netley Creek, Wavy Creek, and other creeks and channels within the marsh. Netley Creek and Wavy Creek are relatively wide in the western portion of this area, and land use is primarily cereal crop production with lesser

amounts of forage production and grazing. This region is characterized by a sometimes extensive and rich riparian habitat dominated by green ash (Fraxinus pennsylvanica), Manitoba maple, trembling aspen, choke cherry (Prunus virginiana), high bush-cranberry (Viburnum opulus), and red-osier dogwood (Cornus stolonifera). A band of emergent vegetation (T. latifolia and other species) typically occurs adjacent to the riparian habitat, and open water with submergent vegetation is extensive. In contrast, the eastern portion of the area is a floodplain-wetland consisting of large shallow lakes dominated by submergents, large expanses of emergent vegetation, creeks, and levees (Janusz and O'Connor 1985). Willow (Salix sp.) often dominates the low levees of small creeks and channels which meander throughout the marsh. Common emergent vegetation found in southern Netley Marsh includes S. acutus, S. fluviatile, S. validus and T. latifolia, while common species of submergents are bladderwort (Utricularia vulgaris), pondweeds (Potamogeton sp.) and water-milfoil (Myriophyllum spicatum). Janusz and O'Connor (1985) provide a comprehensive list of plants native to the region. As a floodplain-wetland, this area is subject to considerable seasonal variation in flow. Unlike the Cooks Creek area, beaver in Netley Marsh do not build dams. Although lakes in the region typically freeze to the bottom during winter, this does not occur in creeks and channels owing to their greater average depth (Janusz and O'Connor 1985). Additionally, the water level below the ice is

sometimes affected by regulation of Lake Winnipeg. During the period of study, channels and creeks in the Netley Marsh area were ice-covered from approximately late November to mid-April.

METHODS

Animal Collection

The sampling dates encompassed all seasons; however, greatest effort was allocated to anticipated periods of fat mobilization and accretion. The storage and mobilization of fat should ultimately be determined by plant phenology, which should correlate to some extent with break-up and freeze-up dates. Therefore, in view of the relatively long Manitoba summer, it was anticipated that the mobilization phase would end earlier, and the accretion phase begin later, than is typically the case for Arctic beaver (Aleksiuk and Cowan 1969b). Several commercial trappers and a fur buyer supplied the specimens which were either caught in Conibear traps or were shot with a small-caliber rifle. Often, several beaver were collected from one lodge or location prior to the collection of further specimens. The initial objective was to obtain all specimens from the Cooks Creek area; however, it became necessary to collect from other areas as well. A total of 67 beaver, of which 22 were kits, were collected from 25 October 1988 to 24 June 1990.

Conibear traps were usually checked daily, and the date

of collection has typically been treated as the date of death. Soon after collection, specimens were placed in plastic bags and temporarily stored in a freezer (or outdoors if ambient temperature was $<-20^{\circ}\text{C}$). Shortly thereafter, specimens were weighed to the nearest 1 g on a Sartorius electronic balance, or to the nearest 15 g on a Toledo scale for 2 beaver >26 kg. They were then either stored in a freezer at ca. -24°C or were immediately dissected. Necropsy provided tissue samples for further processing, as well as the measurements required to examine gut dynamics (see Part II) or to predict body nutrient levels (see Part III). Teeth were removed by chipping away adjacent bone with a hammer and chisel and then using a dental elevator to pry them loose. The deciduous premolar clearly indicated age for kits while lower premolars and molars were retained to age older beaver according to Van Nostrand and Stephenson (1964) and Larson and Van Nostrand (1968).

Body Composition

Specimens were stored at ca. -24°C after the above measurements and samples had been collected. Fetuses and associated tissues were included in estimates of body composition for pregnant females. A Hobart Model 5012 bandsaw was used to cut beaver into pieces of variable length which were ca. 2.5 cm^2 . All visible tissue that adhered to the saw table, blade and blade housings was collected, and the amount of tissue lost in this process was insignificant. The previously removed teeth were broken into small pieces with a

rock crusher. These were combined with the carcass sections, the adherent tissue, and those parts removed during initial dissection. The entire carcass was then passed through a Hobart Model H600 mixer/grinder twice. A plate with 9.5-mm (ID) holes was used for the first pass, while a plate with 3.2-mm (ID) holes was utilized for the second pass. Following the second pass, the mixer attachment was used to homogenate the tissue to a consistent color and texture. Six replicates, each of 450 g, were then randomly sampled from the homogenate. Replicates were stored at ca. -24°C until dried; however, some samples were partially thawed due to freezer failure and then refrozen. Additionally, any tissue which had not gone through the plates after the second pass was collected and frozen separately.

Initially, three replicates per beaver were thawed and spread over aluminum pans, and then dried to constant mass at 60°C in a Fisher Isotemp Model 176 forced-air oven. The dried tissue was removed from the pans, double-bagged, stored at ca. -24°C , and later homogenated to a fine consistency with a Black and Decker Model CBM100 coffee bean grinder. Although most samples were allowed to warm to room temperature prior to grinding, it was necessary to take samples with high levels of fat directly from a freezer and grind immediately. Otherwise, the tissue could not be finely ground and fat tended to adhere to various parts of the grinder, including the blades. The tissue which had remained in the Hobart grinder after the second pass was also dried at 60°C in the oven, and was then

ground with a tool designed for crushing small rock samples. Prior to homogenization with the bean grinder, this latter tissue (along with any teeth removed for aging purposes) was added to each replicate in proportion to its contribution to total dry matter. Throughout tissue preparation and assays for body composition, samples were weighed to document and allow adjustment for changes in moisture content. For example, storage of single-bagged samples in one laboratory led to an increase in tissue water content (paired t test, $t = -8.28$, $df = 38$, $P < 0.001$). The water content of samples was also found to increase by a small, variable amount during storage or occasionally grinding. Small amounts of tissue were lost during removal of tissue from the drying pans, through adhesion of lipids to the bean grinder, and as dust during grinding of samples with a low fat content. In those circumstances when mass decreased after the final homogenization, the weight prior to this step was used to calculate final dry matter.

The following assays of body composition were made for each replicate. To determine crude protein, nitrogen was assayed via macro-Kjeldahl with a Tecator Kjeltac Auto 1030 Analyzer. Ash was assayed by combustion at 500°C for 12 hours in a Thermolyne 30400 muffle furnace. Fat was extracted with petroleum ether in a Soxhlet apparatus according to the following protocol: (1) Thimbles were dried at 90°C for 2 hours and then placed in a desiccator for ≥ 1 hour. (2) Each thimble was then weighed and filled with 10.0 ± 0.1 g of

sample. (3) Thimbles with sample were dried at 90°C for 2 hours, then placed in a desiccator for ≥ 1 hour, and weighed. (4) A volume of 175 ml of petroleum ether and 4-5 glass beads were placed in each 250-ml Soxhlet flask. (5) No. 4 filter paper (7 cm) was folded into a cone, the end of the cone snipped off, and the cone was mounted in the top of the thimble containing the sample. (6) Thimbles with sample were placed in the Soxhlet apparatus and extraction begun. (7) Extraction was performed for 8 hours per day, over 2 consecutive days, with the Soxhlet apparatus turned off overnight. (8) After the extraction period, thimbles with extracted sample were removed to a fume hood until petroleum ether fumes were no longer detected (approximately 3 hours). (9) Thimbles with extracted sample were dried at 90°C for 2 hours, then placed in a desiccator for ≥ 1 hour, and weighed.

Partway through the assays, it was recognized that fat and/or an unidentified gummy residue was sometimes extracted and deposited within the thimble or filter paper. Thereafter, those samples in which fat visibly adhered to the thimble and/or filter paper were further extracted, sometimes with new solvent. Whenever possible, estimates of fat were also adjusted for mass changes in the thimble from pre- to post-extraction. This adjustment increased the mean fat content (% dry matter) of 13 kit estimates by 0.19% (range = -0.99% - 1.02%) and 40 adult estimates by 0.35% (range = -1.37% - 1.97%). Data were discarded if there was evidence that they were incorrect due to extraction difficulties.

The combined assays for ash, fat and protein generally accounted for 87-98% of the dry matter of adults (Fig. 1-1) and kits (Fig. 1-2). However, in a few cases, substantial discrepancies existed (eg., the combined assays accounted for only 69.23% of dry matter for Kit No. 13). The principal cause of these discrepancies was the incomplete extraction of neutral lipids in very fat specimens (see Appendix I). To determine if my protocol was directly responsible for the incomplete extraction of fat, assays of 8 samples were conducted at an independent laboratory. When standard AOAC procedures were followed at the Food Analysis Section Laboratory, Manitoba Department of Agriculture, the resulting mean fat estimates were 0.68-5.70% lower (% dry matter) than those obtained using the above protocol (Adult No. 11, Kit Nos. 10, 13). Consequently, the fat resources of five of the adults (Nos. 11-14, 38) were predicted from the relationship:

$$[1] \quad \text{FAT} = 90.276 - 0.958 \text{ PROTASH}$$

($F_{1,31} = 695.21$, $P < 0.001$, $S_{Y/X} = 1.92\%$), where FAT is the adjusted fat content (%), and PROTASH is the combined protein and ash content (%) of the dry matter. Similarly, the fat resources of seven of the kits (Nos. 7-13) were predicted from the relationship:

$$[2] \quad \text{FAT} = 88.910 - 0.955 \text{ PROTASH}$$

Figure 1-1. The proportion of dry matter accounted for by the combined assays for ash, fat and protein (%) in adult (>1 year old) Castor canadensis. Each adult number represents a unique animal.

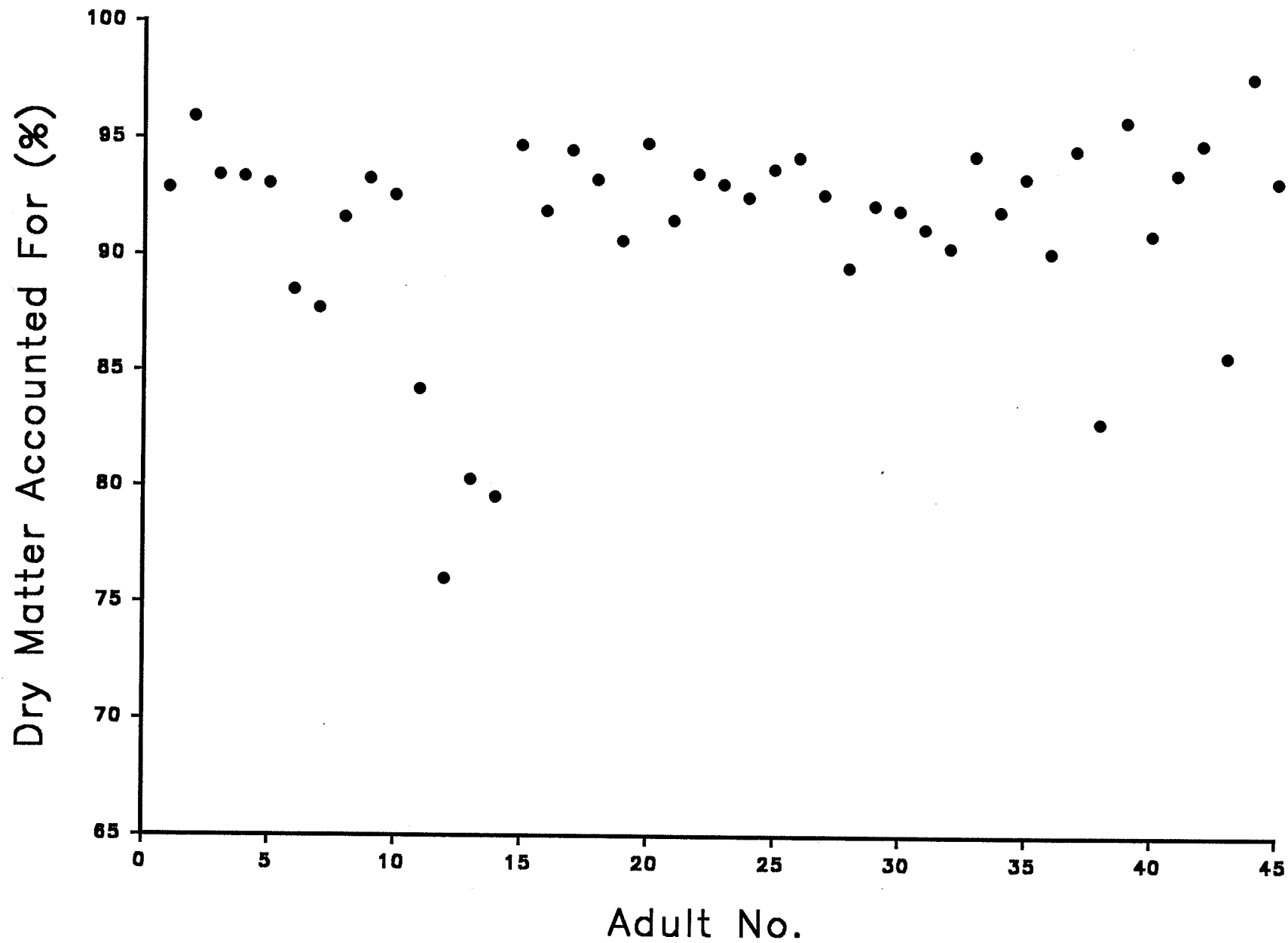
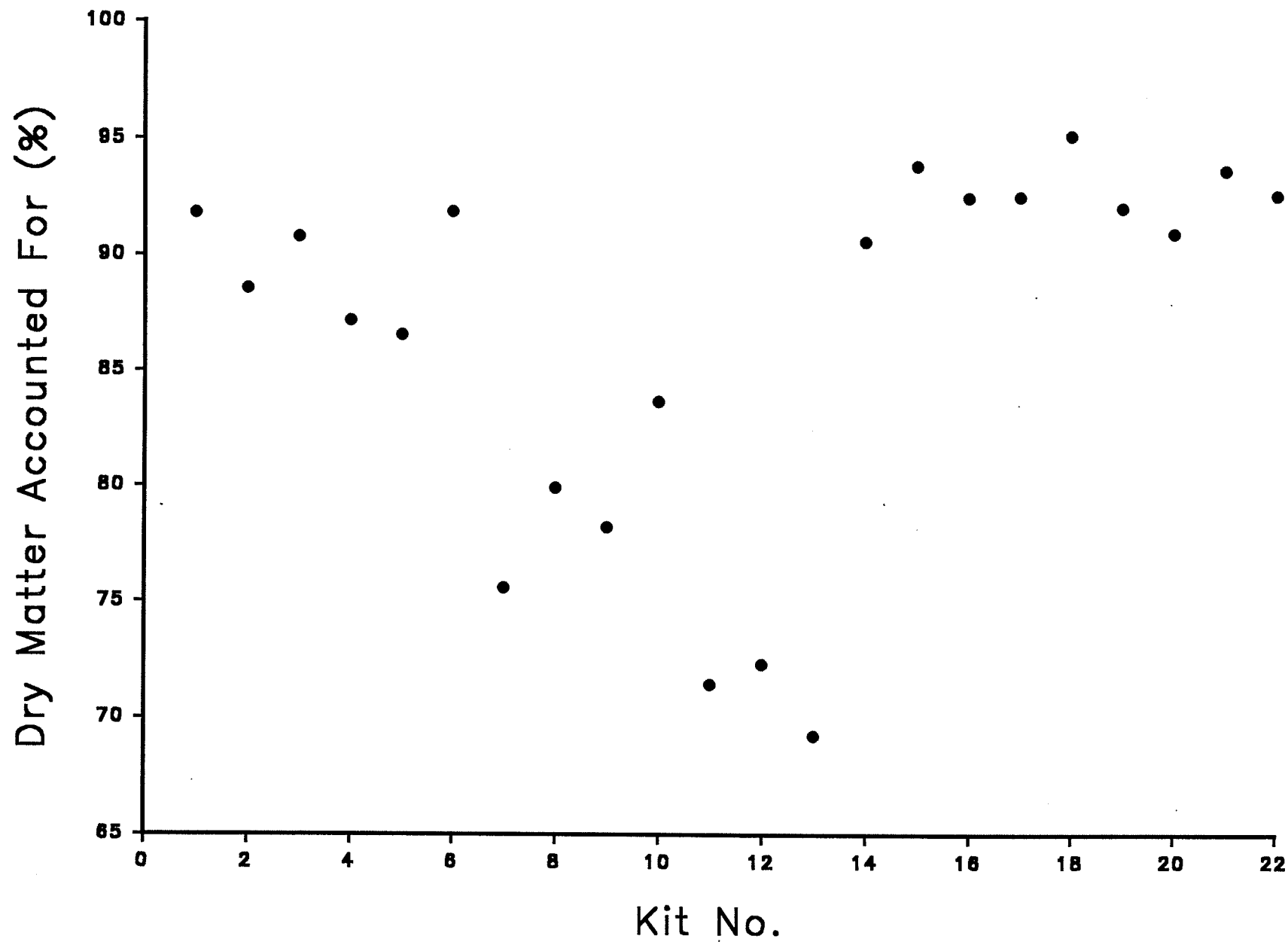


Figure 1-2. The proportion of dry matter accounted for by the combined assays for ash, fat and protein (%) in kit Castor canadensis. Each kit number represents a unique animal.



($F_{1,11} = 128.06$, $P < 0.001$, $S_{Y/X} = 2.34\%$). I chose to utilize these predicted values because the individuals were among the fattest beaver sampled, and were therefore particularly important to the study objectives. Furthermore, the error in predicting FAT was low, relative to its variation. These 12 beaver were collected from 8 December to 17 February, 9 from one lodge in the Cooks Creek area and 2 from an adjacent lodge. Homogenate samples from most of these beaver changed color and texture during storage, and were among those which had partially thawed.

Percentage water in the tissue was defined as $100 - \% \text{ final dry matter}$. The fat content of tail tissue was predicted from the water content of tissue samples (see Part III), according to the relationship reported by Aleksiuk (1970b).

Statistical Analysis

For each animal, ash, fat, protein and dry matter content were estimated as the mean of the three initial replicate measurements. For ash, fat and protein, the estimate was of acceptable precision if the SE was $\leq 1\%$ of dry matter. If an estimate did not meet this precision criterion, further samples of the initial replicates were assayed. If it was necessary to sample additional replicates, then the SE was calculated with the larger n .

Inspection of a plot of % body fat against time suggested that body fat content was reasonably stable within each of

four discrete sampling periods (16 May - 8 July, 29 July - 2 December, 22 December - 17 February, 19 March - 27 April), but differed between sampling periods. The effects of sampling period and sex on % body fat were evaluated via ANOVA and Fisher's LSD test. In addition, temporal variation in body fat resources was modeled with PROC NLIN (PC-SAS) as a continuous line segment (Seber and Wild 1989) incorporating two distinct phases. Preliminary inspection suggested that the data generally fit this model. The significance of more complex models, or size and sex effects, were tested with a partial F approach for improvement of the two-phase model (eg., Kleinbaum and Kupper 1978; Seber and Wild 1989).

To examine temporal variation in protein and mineral resources, it was necessary to control for the considerable size variation of beaver. Therefore, body crude protein mass and body mineral mass were predicted from structural variables in multiple regression analyses. Descriptions of the measurement of these structural variables are provided in Part III. Body protein mass was related to total body length (LENGTH), tail width (TAILWIDT) and tail length (TAILUND) in males ($R^2 = 0.96$), and to LENGTH and TAILWIDT in females ($R^2 = 0.93$). Body mineral mass was related to LENGTH, incisor length (MAND1) and whole-beaver ulna length (ULNARND) in males ($R^2 = 0.93$), and to LENGTH and TAILWIDT in females ($R^2 = 0.83$). For kits, body protein mass was related to LENGTH and TAILWIDT ($R^2 = 0.91$), and body mineral mass to hind foot length (HINDFT) and TAILWIDT ($R^2 = 0.91$). The residuals from these

morphometric-based predictive equations represented those protein and mineral resources which were not explained on the basis of size variation, and it was these residuals which were examined for temporal and other variation. As the predictive equations incorporated only morphometric variables which were significant at $P \leq 0.05$, this procedure almost certainly utilized only the structural aspects most responsible for describing size. The separate predictive equations used for male and female beaver emphasizes the structural variation within each of these groups, and should improve the ability to detect other sources of variation. Temporal variation was assessed from plots of residuals against Julian date, using simple linear and polynomial regression analyses of the residuals, or stagewise regression (Draper and Smith 1966), as well as tests of time effects within multivariate models.

I chose to examine fat dynamics on the basis of % body fat, expressed as the percentage of ingesta-free wet mass. Although this derived variable may reflect variation in other body nutrients, I rejected using residuals from a body fat mass-to-size relationship for several reasons. Firstly, a plot of adult body fat mass against ingesta-free mass clearly showed that parameter estimates would be biased. This was principally due to a lack of independence between adult size and collection date in the sample. As a consequence, this sampling effect had a direct bearing on the observation that the five adults with the highest % body fat ($\bar{x} = 13.96\%$) were also considerably longer ($\bar{x} = 112.2$ vs 102.3 cm) than the five

leanest adults ($\bar{x} = 1.74\%$). Similarly, parameter estimates for kits would be representative of fat individuals, as only one kit in the sample had $<5.31\%$ body fat. Furthermore, the body fat mass-to-body length relationship for kits was weak ($P = 0.043$) and the precision of the slope poor ($B_1 = 31.7$, $SE = 17.5$). Secondly, for the linear regression of body fat mass on ingesta-free mass in adults, the absolute value of the residual increased with mass ($F_{1,41} = 10.57$, $P = 0.002$). This demonstrates that the assumption of homoscedasticity is violated (Kleinbaum and Kupper 1978). Furthermore, an ANCOVA or residual analysis approach assumes that slope effects do not exist, and this is clearly incorrect. To address size effects adequately, it was necessary to transform body fat mass such that the homoscedastic assumption is not violated. Division of total body fat by ingesta-free mass largely accomplishes this.

Sex effects were examined with a test of coincidence (Kleinbaum and Kupper 1978) for simple linear models. The type III partial SS of PROC GLM (PC-SAS) were used to test individual terms for multivariate models. Means are generally reported ± 1 SE. With the exception of estimates of s and SE, and tests of partial correlation for group effects (including those for two-phase models), statistical tests and probability levels were calculated according to PC-SAS Version 6.03 (SAS Institute Inc., Cary, NC, USA). Tests for outliers (Appendix I) were made according to Grubbs and Beck (1972).

RESULTS

Fat Dynamics

The body fat content of adult beaver (Table 1-1) varied with sampling period ($F_{3,40} = 28.57$, $P < 0.001$) and sex ($F_{1,40} = 6.80$, $P = 0.013$). For males, fat content decreased with time during the 19 March - 27 April sampling period ($F_{1,6} = 7.62$, $P = 0.033$), and % body fat was estimated to be $8.48 \pm 0.87\%$ at the midpoint of this period (8 April). This temporal effect was responsible for an inability to detect a sex effect for this particular sampling period ($P = 0.207$), despite the greater body fat content of females during the period 13 April to 27 April ($\bar{X}_{\text{Females}} = 9.66\%$, $\bar{X}_{\text{Males}} = 5.99\%$, $P = 0.020$). Temporal variation in body fat content was not apparent within other sampling periods ($P \geq 0.097$).

Adult beaver were lean during the sampling period 16 May - 8 July, particularly the two males sampled on 16 and 29 May (0.60% and 0.80% body fat, respectively). By the period 29 July - 2 December, the % body fat of adults had increased (Table 1-1, $P < 0.001$). Adults demonstrated maximum % body fat in the sampling period 22 December - 17 February. However, it should be noted that the four beaver with the highest % body fat in this sample were collected from one lodge in the Cooks Creek area. Body fat subsequently declined during March and April, although beaver retained high fat levels from 19 March through 2 April ($\bar{x} = 10.68 \pm 0.69\%$, $n = 4$). It was not until 12 April that an adult was caught with

Table 1-1. Seasonal variation in body fat concentration (%), residual protein (g) and residual ash (g) of kit and adult (>1 year old) beaver. Means are presented with ± 1 SE and sample sizes are given in parentheses.

Body reserve	Group	Sampling period ^a			
		16 May- 8 July	29 July- 2 December	22 December- 17 February ^b	19 March- 27 April
Fat	Adult male	1.36 $\pm$ 0.66 (3)	6.60 $\pm$ 0.73 (8)	12.02 $\pm$ 0.97 (3)	7.63 $\pm$ 1.22 (8) ^c
	Adult female	2.49 $\pm$ 0.32 (3)	8.02 $\pm$ 0.66 (10)	14.31 $\pm$ 0.35 (3)	9.56 $\pm$ 0.67 (7)
	Kit	0.92 (1)	9.05 $\pm$ 0.59 (12) ^c	14.69 $\pm$ 0.51 (6) ^c	9.35 $\pm$ 2.17 (3)
Protein	Adult male	-7 $\pm$ 126 (3)	-10 $\pm$ 85 (8)	141 $\pm$ 68 (3)	-46 $\pm$ 12 (7)
	Adult female	-81 $\pm$ 130 (3)	122 $\pm$ 53 (9)	-6 $\pm$ 157 (3)	-140 $\pm$ 59 (6)
	Kit	68 (1)	7 $\pm$ 12 (12)	20 $\pm$ 13 (6)	-89 $\pm$ 45 (3)
Ash	Adult male	-13 $\pm$ 36 (3)	-14 $\pm$ 18 (6)	30 $\pm$ 9 (3)	5 $\pm$ 17 (7)
	Adult female	0 $\pm$ 62 (3)	-24 $\pm$ 22 (9)	31 $\pm$ 3 (3)	20 $\pm$ 12 (6)
	Kit	33 (1)	-2 $\pm$ 3 (12)	1 $\pm$ 8 (6)	-3 $\pm$ 11 (3)

^aKits were sampled from 27 September to 29 May.

^bAll kits and adult females, and one adult male, were trapped from the same lodge.

^cBody reserve increased with time ($P < 0.05$) within sampling period.

substantially reduced body fat (3.72%). Most adult beaver sampled, particularly females, exhibited significant levels of body fat (3.67-13.09%) near the end of April. However, by mid-May to mid-June, adults had depleted the majority of their remaining body fat (Table 1-1).

The two-phase model which described temporal changes in the % body fat of adults was significant ($R^2 = 0.62$, $F_{3,41} = 21.97$, $P < 0.001$), and was improved with inclusion of a sex effect ($R^2 = 0.71$, $F_{4,37} = 2.82$, $P < 0.05$). The sex effect was apparent for the fat mobilization phase of the model ($P < 0.05$), but not for the accretion phase ($P < 0.25$). These models (Fig. 1-3) demonstrate the increase in % body fat from a lean condition in late spring (eg., 30 May: J.Date = 150) through to peak fat levels in winter (eg., 4 February: J.Date+365 = 400), followed by a decline in body fat, particularly in males, by 27 April (J.Date+365 = 482). A rapid decline in the body fat content of males relative to that of females was also apparent. The fit of the data to this model was reasonably strong for both females ($R^2 = 0.71$, $S_{Y/X} = 2.06\%$, $F_{3,19} = 15.59$, $P < 0.001$) and males ($R^2 = 0.67$, $S_{Y/X} = 2.32\%$, $F_{3,18} = 12.35$, $P < 0.001$). In contrast to total body fat, the predicted fat content of tail tissue showed little temporal variation (Fig. 1-4).

The body fat maxima for males (16 March: J.Date+365 = 440) appeared to be strongly influenced by the steep negative slope of the fat mobilization portion of the cycle (Fig. 1-3). Furthermore, the % body fat of males sampled from 13 January

Figure 1-3. Temporal variation in body fat concentration (% ingesta-free wet mass) of adult (>1 year old) female (closed circle) and male (open triangle) Castor canadensis from southern Manitoba, 1988-1990. The two-phase model was fitted by a non-linear regression procedure.

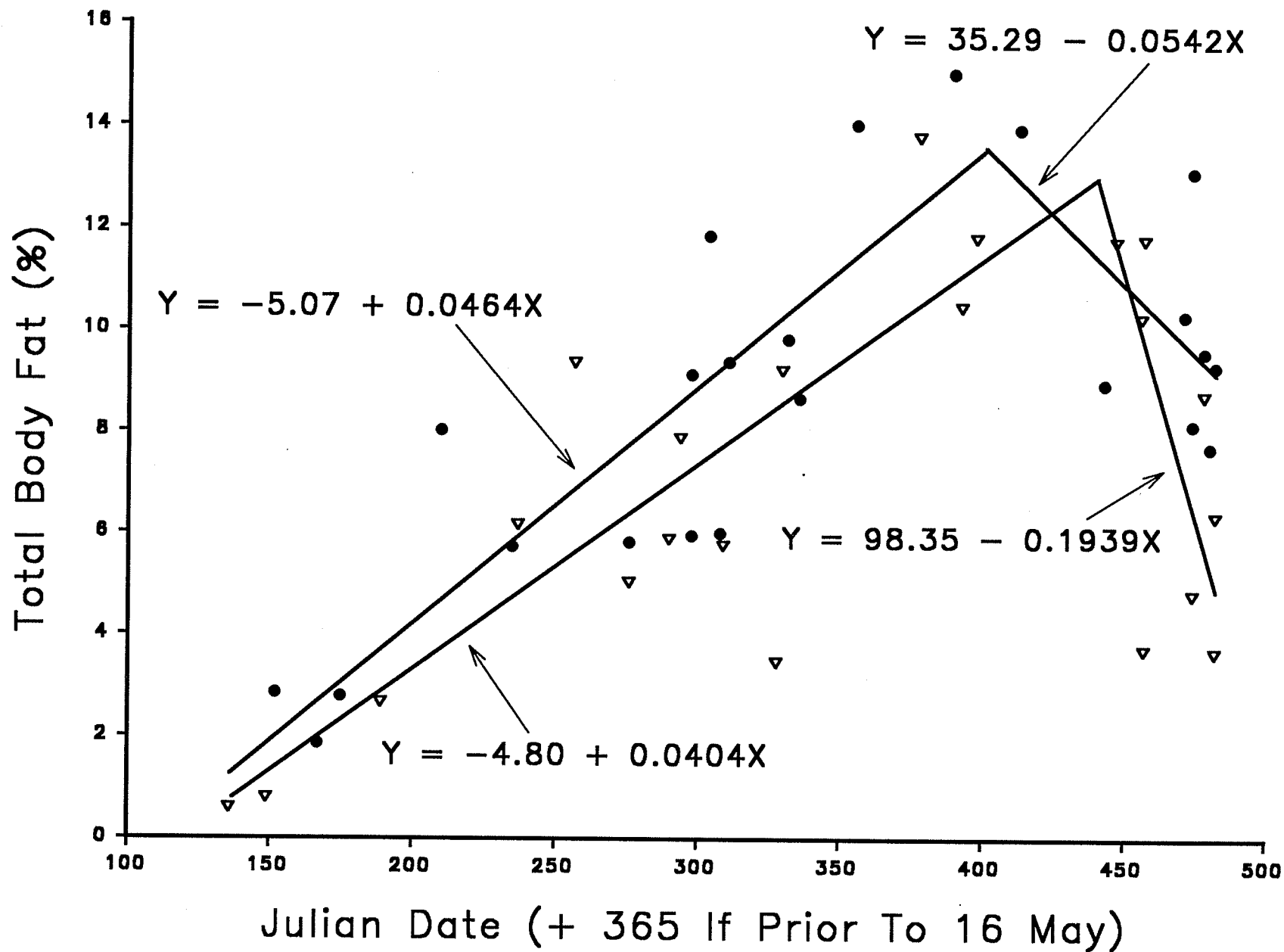
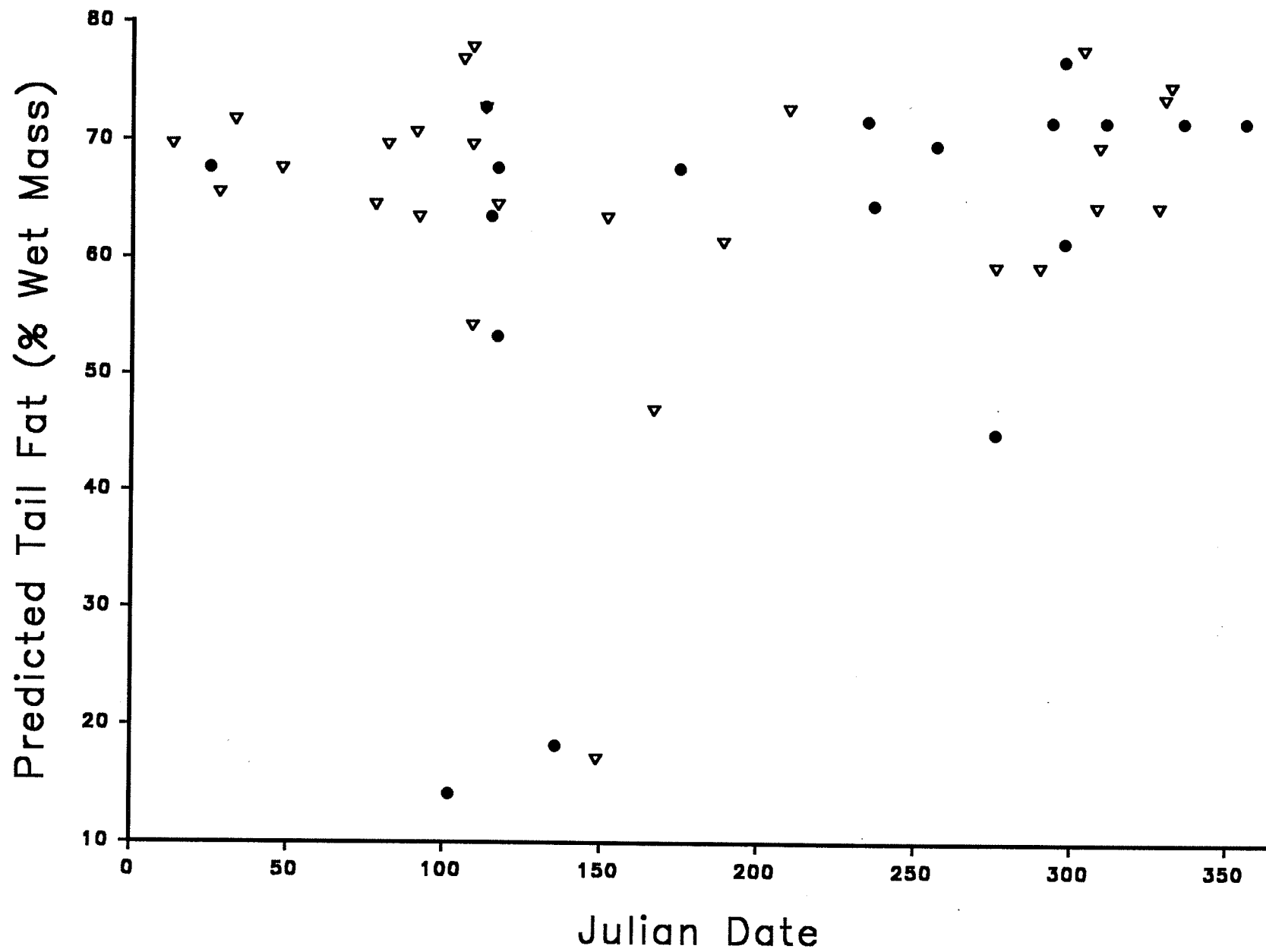


Figure 1-4. Temporal variation in the predicted fat content of tail tissue (% wet mass) for adult (>1 year old) Castor canadensis from southern Manitoba, 1988-1990. Beaver >2 years old denoted by open triangle.



to 2 February ($\bar{x} = 12.02 \pm 0.97\%$, $n = 3$) was similar to that of males sampled from 23 March to 2 April ($\bar{x} = 11.26 \pm 0.51\%$, $n = 3$), suggesting that fat resources may have been stable between these periods.

Residuals were similar for the pregnant ($\bar{x} = -0.27 \pm 1.06\%$, $n = 5$) and non-pregnant (0.12% and 0.19% , $n = 2$) adult females sampled between 19 March and 27 April. Among the three pregnant females with negative residuals, one was a small (13.46 kg) 2-year-old with one fetus ($e_i = -1.58\%$), and the other was a mature (6+ years old) female which had emerged from beneath the ice to forage in late March, and had two embryos ($e_i = -2.34\%$). The adult with the highest residual among all females was >6 years old and had 6 fetuses ($\bar{x} = 360.0$ g).

Neither the residuals from the two-phase models ($P \geq 0.441$) nor their absolute values ($P \geq 0.059$) were directly related to body length or ingesta-free mass in either females or males. Therefore, these analyses do not provide support for an influence of physical size on % body fat. Obvious relationships were not apparent when residuals were plotted against age.

Seasonal variation in the % body fat of kits was similar to that of adults (Table 1-1; $F_{2,17} = 14.97$, $P < 0.001$), but a sex effect was not apparent ($F_{1,17} = 1.51$, $P = 0.236$). Temporal variation existed within the 29 July - 2 December ($F_{1,10} = 9.06$, $P = 0.013$) and 22 December - 17 February ($F_{1,4} = 15.35$, $P = 0.017$) sampling periods. The first kit was

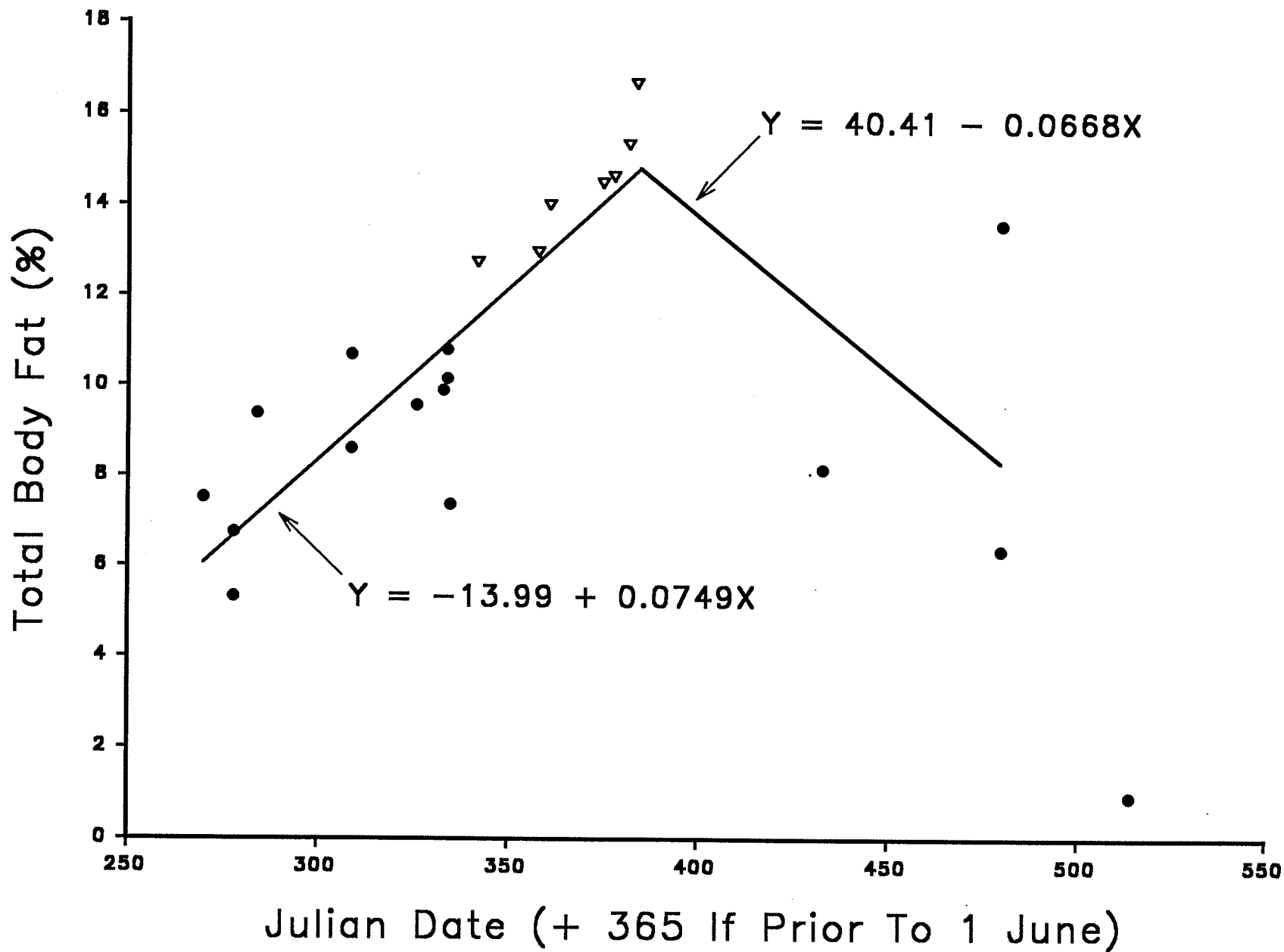
collected on 27 September, therefore age classes were compared over the period 27 September to 2 December. The predicted % body fat of kits at the midpoint of this sampling period (30 October: $8.63 \pm 0.47\%$) was similar to that of adult females ($\bar{x} = 8.30 \pm 0.78\%$, $n = 8$), but greater than for adult males ($\bar{x} = 6.21 \pm 0.83\%$, $n = 6$). For the sampling period 22 December - 17 February, all six kits and four of the adults were from the same lodge. The % body fat of kits (Table 1-1) did not differ from that of the adults trapped from this lodge ($\bar{x} = 14.18 \pm 0.28\%$).

For the period 27 September - 25 April, the % body fat of kits was described by a two-phase model (Fig. 1-5; $R^2 = 0.65$, $S_{y/x} = 2.01\%$, $F_{3,17} = 10.32$, $P < 0.001$). A sex effect was not apparent for the fat accretion phase of the model ($F_{2,14} = 1.75$, $P > 0.10$). Size effects were not obvious over this phase, as neither the residual nor its absolute value were directly related to length or ingesta-free mass ($P \geq 0.078$). The predicted fat content of tail tissue from kits varied between 42.92% and 66.61% ($n = 8$) for the period 16 October - 15 December, and was 31.59% in the beaver sampled on 29 May. The body water mass comprised a greater percentage ($t = 7.64$, $df = 60$, $P < 0.001$) of the combined mass of ash, protein and water in kits ($\bar{x} = 75.4\%$) compared to adults ($\bar{x} = 73.1\%$).

Protein Dynamics

The residual protein mass of adult males did not vary directly with Julian date ($F_{1,19} = 0.60$, $P = 0.448$). The

Figure 1-5. Temporal variation in body fat concentration (% ingesta-free wet mass) of kit Castor canadensis from southern Manitoba, 1988-1990. Open triangles denote values estimated from protein and ash, as a % of dry matter. The two-phase model was fitted by a non-linear regression procedure.



residuals appeared to be low for males sampled from 23 March to 16 May ($\bar{x} = -67 \pm 24$ g), but the structurally-based model was not improved by inclusion of this group effect ($F_{1,16} = 1.84$, $P = 0.194$). Residual protein did not differ among the sampling periods in Table 1-1 ($P = 0.510$).

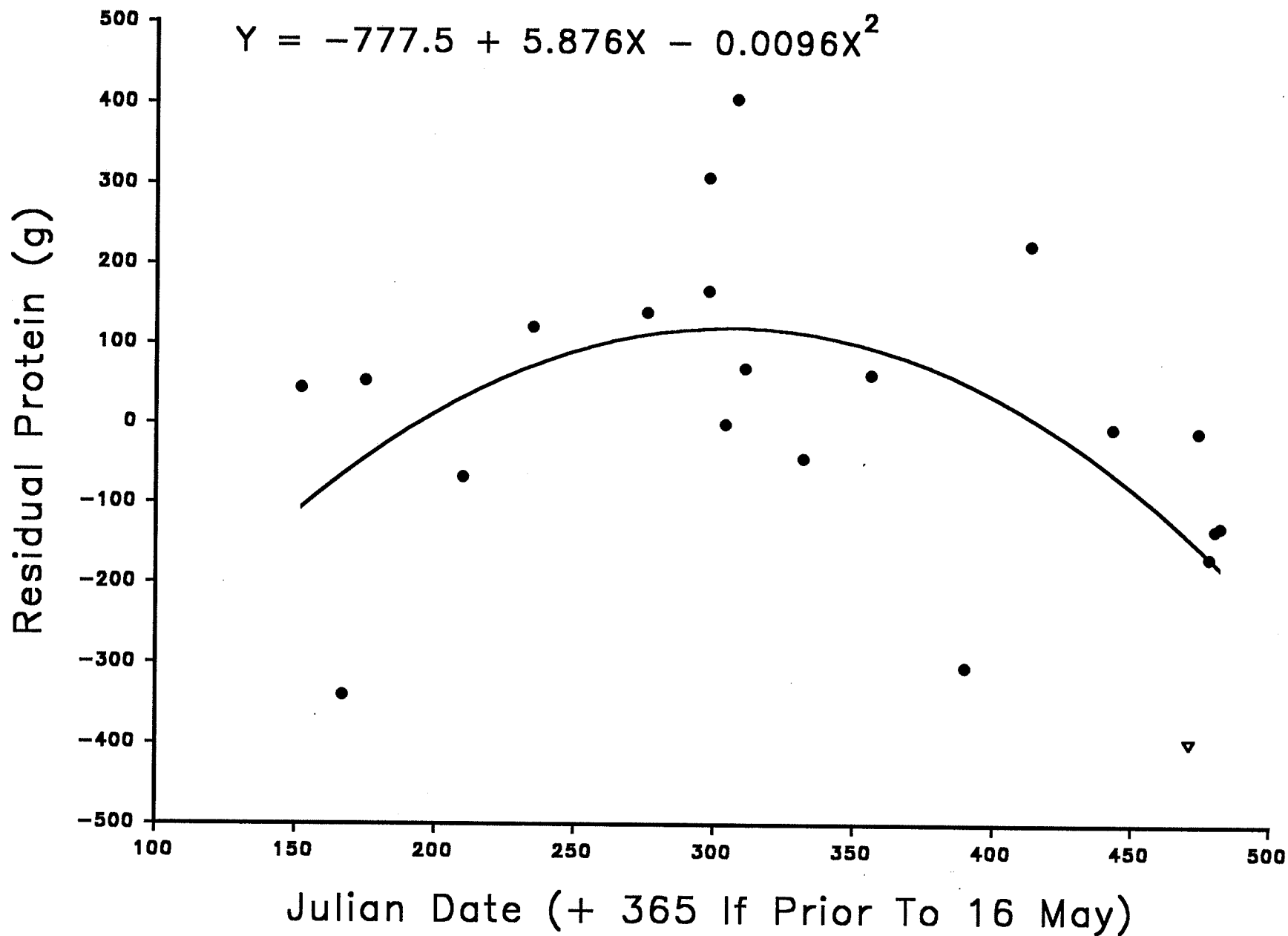
Examination of protein variation over the same time frame as % body fat revealed the existence of a temporal quadratic relationship for adult females (Fig. 1-6; $F_{2,18} = 4.43$, $P = 0.027$). The prediction of body protein mass from structural variables was improved by the addition of a time effect ($F_{2,16} = 4.24$, $P < 0.05$), and the relationship was described by:

$$[3] \quad \text{PROT} = -8292 + 7.936 \text{ LENGTH} + 17.125 \text{ TAILWIDT} \\ + 5.789 \text{ DATE} - 0.00965 \text{ DATE}^2,$$

where PROT is the total protein mass in g, LENGTH is in mm, TAILWIDT is in mm, and DATE is the Julian date on which the beaver was collected (+365 if prior to 16 May). Residual protein did not vary among the sampling periods listed in Table 1-1 ($P = 0.072$), but did differ between the 29 July - 2 December and 19 March - 27 April periods ($P = 0.014$).

Generally, it was pregnant or lactating females which exhibited the lowest residuals. One of the two lactating females had a residual protein of -340 g, and a total protein mass which was 89.5% of that predicted on the basis of structural characteristics. The direct relationship expected between residual protein and residual body fat was not

Figure 1-6. Temporal variation in protein reserves of adult (>1 year old) female Castor canadensis from southern Manitoba, 1988-1990. Open triangle denotes Adult No. 43.



observed in either female ($P = 0.864$) or male ($P = 0.577$) beaver.

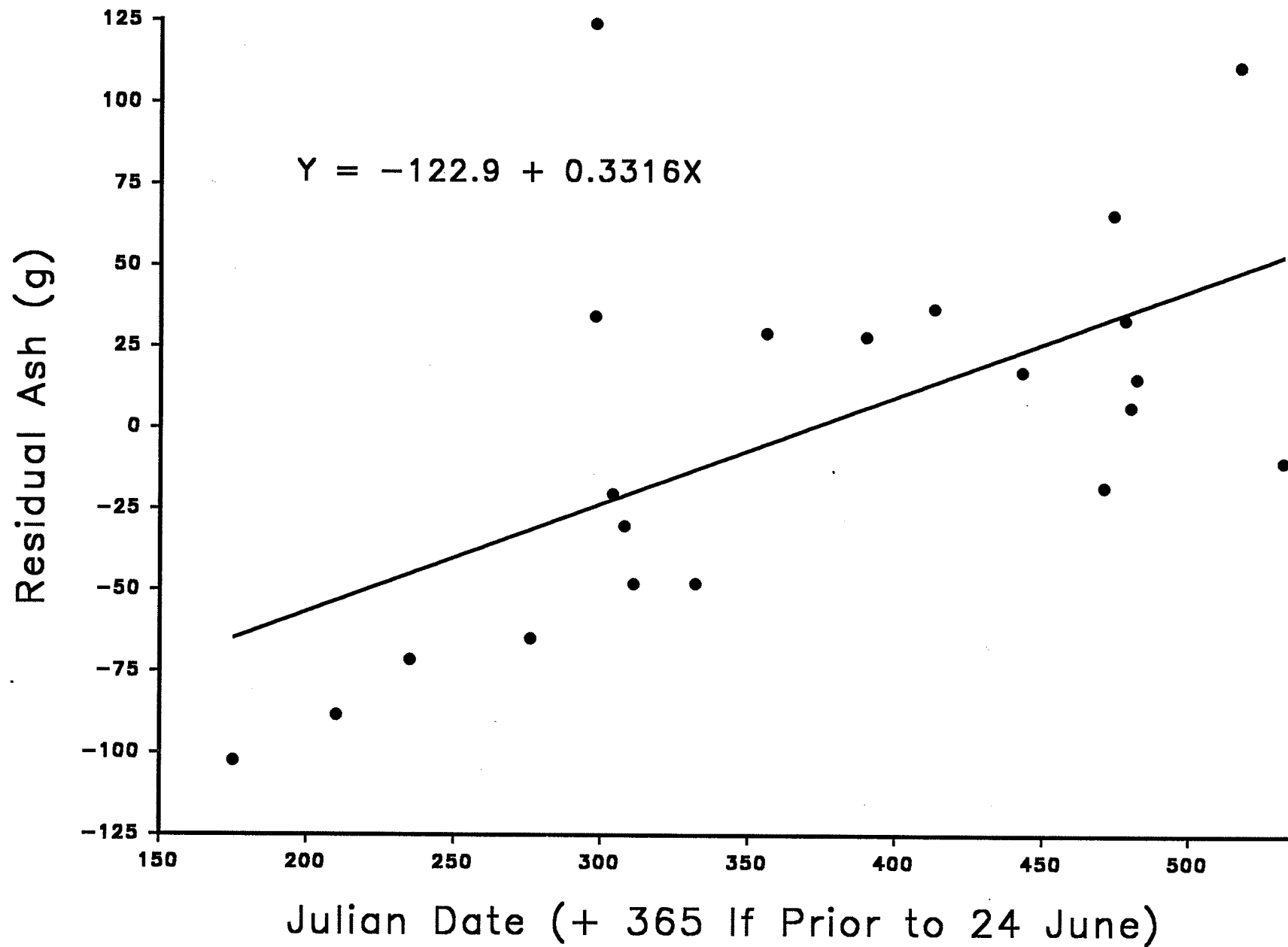
For kits, there was no evidence of a direct relationship between residual protein mass and time ($F_{1,20} = 0.36$, $P = 0.553$). Comparison of sampling periods (Table 1-1) indicated a time effect ($F_{2,18} = 6.39$, $P = 0.008$), with kits from the 19 March - 27 April period having lower protein reserves than kits sampled in the other two periods ($P < 0.005$). A direct relationship between residual protein and residual body fat was not observed in kits ($P = 0.210$).

Mineral Dynamics

Comparison of residual ash mass for the sampling periods in Table 1-1 did not reveal temporal effects for adult males ($F_{3,15} = 0.76$, $P = 0.537$), adult females ($F_{3,17} = 0.96$, $P = 0.432$), or kits ($F_{2,18} = 0.09$, $P = 0.915$). A group effect was not apparent in the adult data set which combined the sexes ($F_{3,36} = 1.77$, $P = 0.170$); however, residual ash differed ($P = 0.047$) between the periods 29 July - 2 December ($\bar{x} = -20 \pm 15$ g) and 22 December - 17 February ($\bar{x} = 31 \pm 4$ g).

A plot of residual ash mass vs Julian date suggested temporal variation in adult females. To examine this variation beginning from females with low residuals, Julian date was adjusted by the addition of 365 if the date were < 175 (24 June). Residual ash was directly related to this adjusted time scale (Fig. 1-7; $F_{1,19} = 10.07$, $P = 0.005$). For adult males, residual ash mass did not relate directly to Julian

Figure 1-7. Temporal variation in mineral reserves of adult (>1 year old) female Castor canadensis from southern Manitoba, 1988-1990.



date ($F_{1,17} = 3.68$, $P = 0.072$), nor to the adjusted Julian date ($P = 0.152$), although the trend was similar to adult females. For the 27 September - 29 May period, the residual ash of kits did not relate directly to time ($F_{1,20} = 1.15$, $P = 0.296$).

DISCUSSION

Fat Dynamics

Accretion and maintenance in adults

Various authorities have suggested that the cache represents the primary, if not sole source of food available to a colony in winter (Novakowski 1967; Aleksiuk 1970a). On this basis, Novakowski (1967) estimated that, in three out of five colonies, the energy resources of the cache were inadequate for beaver to maintain energy balance. However, Novakowski (1967) assumed high digestibility coefficients (eg., 52.4-60.1%; see Buech 1987) and grossly overestimated the amount of energy available to beaver from a cache (Aleksiuk 1970a). Novakowski (1967) also did not consider the potentially high metabolic costs of digestion and foraging in cold water (Dyck and MacArthur 1993b). Therefore, studies to date suggest that the beaver's winter metabolic requirements far exceed the energy provided by the cache.

As in the Arctic (Aleksiuk and Cowan 1969b), beaver in southern Manitoba continue to store lipids after permanent ice formation, when their activity is confined to lodges, bank dens, air pockets, and near-freezing water. In both regions,

maximum body fat levels appear to be achieved in mid-winter. Even after a winter during which streams are ice-covered for 4-5 months, the fat reserves of beaver from southern Manitoba were similar in magnitude to those observed prior to freeze-up. My models predict a % body fat for females of 9.75% on 15 November and 9.80% on 15 April, compared with values of 8.09% and 7.22% for male beaver on the same dates. Therefore, beaver do not appear to mitigate shortfalls of energy in the cache through significant mobilization of stored body fat.

Several factors could account for the ability of beaver to increase their fat resources after freeze-up and to generally maintain high fat levels throughout winter. First, there is evidence to suggest that beaver will supplement food stored in the cache with items likely to be high in digestible energy. For example, the rhizomes of yellow pond-lily (Nuphar variegatum) are commonly found in caches, and can constitute a major food item for beaver (Nash 1951). Interestingly, Jenkins (1981) reported that the rate of tree cutting during fall was minimal for a colony with access to yellow pond-lily and fragrant water-lily (Nymphaea odorata) rhizomes, and he suggested that this trend was related to the use of these aquatic plants for food. MacArthur and Dyck (1990) provided evidence to suggest that beaver will forage on emergent vegetation beneath the ice, presumably in situations where they can utilize the rhizomes of species like cattail (Typha sp.). Given the large size of some aquatic rhizomes (Northcott 1972) and the likelihood that they are high in

digestible energy (Campbell and MacArthur 1994), I suggest that such food items should constitute a highly preferred forage of beaver during winter. It is noteworthy that the majority, if not all beaver from this study would have had access to aquatic rhizomes.

Another strategy for achieving high body fat levels in winter may be for beaver to extract nutrients more efficiently from available food resources, particularly the bark and twigs of the cache. Beaver apparently have a poor ability to digest aspen bark in late spring (Buech 1987). However, since beaver in winter increase the mass of their lower digestive tract (Part II), it is likely that the digestibility of aspen bark and other fibrous items improves during this season. Furthermore, the increase in the mass of the beaver's small intestine in winter (Part II) may also be associated with an increase in the uptake rate of highly digestible nutrients (Bozinovic and Itturi 1990). An increase in digestive and assimilation efficiencies would not only reduce forage biomass requirements, but could additionally serve to minimize the metabolic costs of foraging in cold water.

Aleksiuk and Cowan (1969a) reported that the mass of the thyroid exhibited considerable seasonal variation, reaching a minimal value in winter, and they suggested that metabolic rate may follow a similar circannual rhythm. To date, metabolic trials have been conducted principally on yearlings and young adults, during periods when beaver typically grow and/or incur the metabolic costs associated with body fat

storage and cache construction (MacArthur 1989; Dyck and MacArthur 1993b). Thus, there exists a distinct possibility that the winter metabolic rate is depressed below current estimates derived from laboratory studies (see Dyck and MacArthur 1993b). Certainly, any depression in metabolism would reduce maintenance requirements, and could allow for a surplus of energy to be stored as fat.

Mobilization phase in adults

In this study, female beaver appeared to mobilize fat from mid-winter to spring break-up. However, it should be noted that few data were collected over this period. For males, the major decline in body fat appeared to occur just prior to, or during, spring break-up. The mobilization of fat by adults during late winter would coincide with a period when beaver may exhibit limited motor activity (Dyck 1991; Dyck and MacArthur 1992). For example, between 16 and 20 February, Dyck (1991) found that one adult beaver spent an average of 13.7 minutes/day outside of the lodge. Although data on winter foraging efficiency does not exist, I suggest that this level of activity would generally be insufficient to provide for daily nutrient requirements, and that fat reserves were likely mobilized at this time. A decline in the quality of bark in the cache (Skinner 1984) may adversely influence energy balance, especially in late winter. Another factor that might contribute to a decrease in fat resources in late winter is the decline in cecal mass (Part II), which suggests a lower fiber digestibility at this time.

The few beaver examined from late winter in this study did not demonstrate an obvious decline in the mass of ingesta. This is not surprising, as current estimates of metabolic requirements dictate that beaver must continue to forage during this period. For example, the model developed for female beaver predicts that fat reserves of a 20-kg (17.202 kg ingesta-free) animal would decline by 643 g between 5 February and 15 April. At basal requirements (MacArthur 1989) and assuming an energy equivalent of 39.3 KJ/g of fat (Schmidt-Nielson 1979), this same beaver would require 4265 g of fat over the above period. Although it appears that beaver must continue to provide most of their energy requirements during late winter through foraging, this does not preclude the possibility that activity might be reduced to a minimum level, thereby substantially decreasing energy demands.

At spring break-up, or shortly thereafter, beaver from southern Manitoba rapidly mobilize their considerable fat reserves. Some of the vegetation available to beaver at this time is actively growing and should be highly digestible. For example, sedges can initiate growth beneath the ice (Gorham and Gibson Somers 1973) and likely provide beaver with a high-protein food at an early date in southern Manitoba (Campbell and MacArthur 1994). It would appear, then, that food quality is not the primary reason for the rapid depletion of fat reserves in the spring. However, if beaver were to continue to forage primarily on bark at this time, as the data of Svendsen (1980a) suggest, then fat resources might be

critical, given the low digestibility of bark (Buech 1987).

Although foods of high digestibility and protein content become available in early spring, this is also a time when floods may be disruptive to beaver (Novak 1987). Consequently, it is possible that an increase in the level of motor activity is largely responsible for the spring decline in fat resources. Dispersal (Svendsen 1980b; Novak 1987), somatic growth, social interactions (Novak 1987), and the high metabolic costs of gestation incurred by females in late pregnancy (eg., Oftedal 1985), may all impose additional energy costs at this time.

The substantial fat resources of beaver at spring break-up likely represent an adaptation for coping with an energetically costly stage in the annual cycle (King and Murphy 1985; Huot 1988). However, this may not be the circumstance during a typical year in which floods are minor and beaver are able to forage on emergent or submergent vegetation, and access an abundant supply of woody vegetation. The apparent surfeit of body fat in late spring suggests that beaver from southern Manitoba might be adapted to atypical years when these animals encounter severe energy deficits. Such a year might include a long or unusually cold winter with thick ice, delayed growth of new vegetation in spring, and/or severe spring flooding. Under these conditions, a reserve of body fat could prove critical to overall fitness.

Influence of sex and age

Adult females typically had greater fat reserves than

males during the mobilization phase of the annual cycle, particularly in late spring. This result is not surprising, since female mammals often exhibit larger fat stores than males (Young 1976). Although female beaver were generally fatter than males during accretion, it was not possible to statistically demonstrate an influence of sex. Due to the high costs of gestation (Oftedal 1985), the metabolic rates of most females, particularly those near parturition, were likely greater than those of males in mid-spring. On the basis of fetal growth rates (Pilleri et al. 1985), several of the pregnant females collected would have been close to parturition, including one beaver estimated to be 13 days from parturition.

Fat resources must be considered in the context of both present and future demands for energy (King and Murphy 1985; Huot 1988). Therefore, the greater fat reserve of adult females in spring is likely a consequence of predictable metabolic costs of reproduction which presumably exceed those of males. It is noteworthy that in mid-spring, the average body fat content of 2-year-old females (8.83%) was similar to that of adult females, but greater than in 2-year-old males (3.67%, 3.72%). The relatively high fat content of these young females may represent a contingency resource in the event that they become pregnant. The additional stored energy available to females might also be critical to successful reproduction in years characterized by unusually stressful springs.

Temporal variation in the body fat levels of kits was consistent with that of adults. Kits were already quite fat by early fall, with predicted body fat levels of 9.90% on 15 November, 14.77% at the mid-winter peak on 19 January, and 9.03% on 15 April. It appeared that kits, like adults, increased their fat resources after the formation of persistent ice; however, further data are required to verify this trend. As body fat content was collected from few kits between mid-winter and spring, and the cache of one of these kits was apparently removed by ice, the prediction of % body fat over this period is imprecise and should be treated cautiously.

Comparison with other populations

Due to Aleksasuk and Cowan's (1969b) use of indices, comparison of the fat dynamics of southern Manitoba beaver with those of Arctic beaver is difficult (see Part III). Furthermore, Aleksasuk and Cowan (1969b) did not treat females and males separately, and only reported on immature beaver. Despite these differences in methodology, the body fat cycle of beaver from southern Manitoba is generally consistent with that reported for Arctic beaver (Aleksasuk and Cowan 1969b). Beaver from both areas are lean during the spring and early summer, and gain fat from mid-summer until freeze-up. Similarly, beaver from the Arctic continue to deposit substantial amounts of fat while restricted by ice cover, and these reserves peak at approximately the same time for both populations. In contrast to southern Manitoba populations,

the mobilization of fat reserves may end some 2-3 weeks later in beaver from the Arctic.

A perirenal index was one of the indices used by Aleksiuk and Cowan (1969b) to model fat dynamics. If it is assumed that the index was determined according to the methods in this study (see Part III), then beaver from southern Manitoba store considerably more fat than do Arctic beaver. For example, nearly 75% of the beaver I examined had indices which exceeded the maximum documented by Aleksiuk and Cowan (1969b). Furthermore, the relationship developed in Part III predicts a body fat content of only 6.47% for the fattest Arctic beaver. Given Aleksiuk and Cowan's (1969b) speculation that Arctic beaver were comprised of "... perhaps 30-40% fat.", differences in formulation of the index may have been responsible for this apparent geographic distinction.

For beaver ≤ 2 years of age, Aleksiuk (1970b) reported strong seasonal variation in the fat content of tail tissue. In contrast, I found that tail fat was depressed only infrequently in beaver > 1 year old. Therefore, the seasonal mobilization of lipids from the tail depot observed in Arctic beaver (Aleksiuk 1970b) is neither widespread nor temporally protracted among adults from southern Manitoba. As the fat resources of the tail depot are among the last to be mobilized (Aleksiuk 1968; Part III), the evidence suggests that beaver from the Arctic may often exhaust a greater proportion (perhaps the majority) of their fat resources prior to the end of winter. This conjecture is consistent with Aleksiuk's

(1970a) observation that one month prior to break-up, beaver from as many as half of the colonies he studied cut holes in the ice and emerged to forage.

The predicted % tail fat of kits was greater than that observed by Aleksiuk (1970b) for Arctic beaver of similar age. As the fat content of the tail reflects total fat resources (Part III), kits from southern Manitoba appear to have larger lipid stores than do kits from the Arctic. Perhaps as a consequence of the shorter growing season and/or later parturition dates, Arctic kits may not be able to acquire the fat reserves of kits from more southern latitudes. As further support for the existence of constraints on nutrient acquisition in Arctic beaver, the kits in this study were much larger than those collected by Aleksiuk (1968).

Beaver from the Cooks Creek and southern Netley Marsh areas were subject to commercial trapping, and the population density of the Cooks Creek area was low as a consequence. Exploitation rate may influence female growth rate, the age at which females conceive, and age of dispersal (Boyce 1981; Storm and Tzilkowski 1982). The removal of beaver during winter may also increase the abundance and quality of available food resources to remaining members of the colony. In both of these areas, primary production would have been high and habitat quality good. Therefore, the models developed in this study may reflect the combined effects of the exploitation rate and habitat quality on body fat reserves.

Protein and Mineral Dynamics

It was principally pregnant and lactating females that had low protein reserves. In this context, it is important to note that the body protein levels of pregnant females included the often considerable protein mass of the uteri and fetuses. For example, based on the protein content of fetuses and newborns of other species (Huot 1989; Virgl and Messier 1992b), and the mass of fetal tissue, fetuses might have represented $\geq 6\%$ of the total body protein of the female nearest parturition. Therefore, temporal variation in body protein, exclusive of that invested in reproductive tissue, should be even greater than that reported herein.

During pregnancy, female beaver apparently maintain the growth of fetal tissue at the expense of their own body protein. This body protein deficit also appears to exist in post-partum lactating females. These findings imply that forage protein levels prior to, or soon after, parturition might be crucial, and suggest that stored body proteins play a key role in female reproduction. It is relevant to note that a decrease in protein levels was not apparent in adult males, further suggesting that the response in females was linked to reproduction.

As suggested by King and Murphy (1985), female beaver may effectively store body protein in anticipation of the predictable events of gestation and lactation. Adult females exhibited high body protein reserves from late fall through early winter, with the body protein level predicted to peak on

2 November. It is likely that female beaver build these reserves while they have access to high-protein foods, prior to being restricted to lower quality winter forage.

Although the protein reserves of kits appeared to be low in spring, this finding was due principally to the very low residual protein of a kit whose food cache had apparently been destroyed by ice movement. Consequently, it is premature to infer temporal variation in this age class. Nonetheless, this study did demonstrate that several individual kits were in relatively poor condition with respect to their body protein reserves.

The hypothesis that beaver with relatively low protein reserves were also those low in body fat, was not supported by the data. This suggests that the ability to maintain body protein is generally independent of the amount of stored fat, and that the beaver examined in this study did not catabolize significant amounts of protein when in a negative energy balance.

The body ash reserves of adults appeared to be relatively low from mid-summer to freeze-up. For females, this trend was particularly apparent for the period from 24 June - 8 October, when ash reserves were well below average (Fig. 1-7). This suggests that the diet of female beaver may not provide for their mineral requirements during this time of active somatic growth. Body mineral reserves were above average from mid-winter until the beginning of summer, suggesting that winter food provides a more than adequate source of the principal

body minerals.

Summary

In this study, beaver did not appear to require substantial amounts of body fat to supplement shortfalls of energy in the cache. Rather, these reserves appeared to serve principally as a source of energy during spring. Due to high reproductive costs, body fat and protein reserves appear particularly important for females in spring. Future studies should focus on the factors responsible for these sex-related differences in body composition. Seasonal variation in the nutrient content of ingesta should also be examined, to assess the role of diet quality in body nutrient cycles.

PART II

Temporal and sex-related variation in the gut of the
beaver, Castor canadensis

INTRODUCTION

In northern ecosystems, the biomass and quality of forage consumed by herbivores are often subject to strong seasonal fluctuations. Of particular importance, the fiber content of forage often increases with plant senescence, thereby limiting the extent to which herbivores can digest these foods. As well, the requirement for energy fluctuates in response to seasonal variation in microclimate and to significant life history events like reproduction.

Laboratory studies have clearly established that the gut of small herbivorous rodents responds morphologically to changes in dietary fiber (Woodall 1989; Hammond and Wunder 1991; Nagy and Negus 1993) or energy demand (Hammond and Wunder 1991; Derting and Bogue 1993; Nagy and Negus 1993). The gut generally lengthens and/or becomes heavier if diet quality is poor or intake high. However, such findings must be viewed with caution, as small rodents are often under minimal nutritional challenge in the laboratory environment, and experimental treatments may not reflect natural conditions (eg., Woodall 1989; Hammond 1993). Although the magnitude of variation may be less than in laboratory trials, size and mass of the gut have been shown to vary seasonally in natural populations (Bozinovic et al. 1990; Virgl and Messier 1992a; Hammond 1993).

The beaver, Castor canadensis, is a "choosy generalist" which selects food from a wide range of plant species found in its habitat. From late spring until the end of summer, the

diet of this large rodent includes grasses, forbs, aquatics, and the leaves and apical portions of shrubs and trees. For the remainder of the year, the diet appears to be dominated by bark and terminal twigs (Aleksiuk 1970a; Svendsen 1980a; Novak 1987). The winter food cache may also be supplemented by, or occasionally, may consist entirely of aquatic rhizomes (Nash 1951; Jenkins 1981). However, the contribution of rhizomes to the winter diet is not clear, and it is reasonable to assume a winter diet which is generally dominated by bark.

Jenkins (1981) indicated that the fiber content of bark is much greater than for green vegetation. Furthermore, nutrients of high digestibility may leach while the fiber proportion increases in bark stored over the winter (Skinner 1984). Consequently, the ability of beaver to access energy from fiber may become more important as winter progresses. Although beaver can digest natural fiber (Hoover and Clarke 1972), a winter diet of bark and twigs should nevertheless constitute a formidable digestive challenge to this species. Therefore, I hypothesized that beaver might adjust their digestive tract in response to seasonal variation in food quality. The principal objective of this study was to examine temporal and sex-related variation of the beaver gut. It is well known that the cecal mass of rodents increases in response to increased dietary fiber (Hammond and Wunder 1991; Loeb et al. 1991), a response that enhances the ability of these animals to extract energy from this dietary constituent. Therefore, I also hypothesized that body fat resources should

relate to cecal mass in beaver.

METHODS

Details concerning the study areas, sampling regime, processing of specimens, and determination of body composition are provided in Part I. Soon after collection, beaver were weighed to the nearest 1 g on a Sartorius electronic balance, or to the nearest 15 g on a Toledo scale for 2 beaver >26 kg.

During necropsy, the stomach, small intestine and cecum were removed. The colon, from the cecum to a point ≈ 2 cm anterior to the interior longitudinal folds of the rectum, was removed and defined as the large intestine. The remainder of the colon, including the anus, was then excised. With the exception of this last section of the colon, all adipose tissue and associated mesentery were removed from the gut. Organs with ingesta were weighed, cleared of ingesta, and then re-weighed to determine ingesta mass. Tissues were weighed to the nearest 0.1 g on an Ohaus Dial-o-gram triple-beam balance.

Lean body mass was defined as ingesta-free mass less mass of body fat (estimated in Part I). I chose to use lean body mass to control for size variation because ingesta-free mass incorporates mass changes which are independent of size. Residual fat was defined as the residual from the two-phase model for temporal fat dynamics (see Part I). It is a measure of the fat content, on an ingesta-free, wet mass basis, corrected for temporal variation. The total gut was defined as all gut segments exclusive of the posterior colon and

rectum.

Most of the statistics were calculated with PC-SAS Version 6.03 (SAS Institute Inc., Cary, NC). Relationships were examined with simple linear, polynomial and multiple regressions, and dependent and independent variables were ln-transformed as appropriate. Individual terms in multivariate models were tested with the Type III partial SS of PROC GLM. The basis for model selection among simple regressions was the calculation of the root mean square error ($RMSE = S_{Y/X}$), and inspection of residual plots to detect violations of test assumptions. If the dependent variable had been ln-transformed, predicted values were retransformed to the original base₁₀ scale to calculate the RMSE (Anderson-Sprecher 1994). Sex effects were examined with a test of coincidence (Kleinbaum and Kupper 1978) or, for multivariate models, with Type III partial SS and backward elimination of effects for each term. For linear regressions, the standard error of Y at X_0 was estimated according to Kleinbaum and Kupper (1978), and means are reported ± 1 SE. Relationships between organ mass and lean body mass were determined, and temporal variation in organ mass was examined via stagewise regression (Draper and Smith 1966) of lean body mass-corrected residuals vs Julian date, and by tests of time effects in full models. Test acceptance was set at a type I error of ≤ 0.05 .

RESULTS

Lean body mass of adult beaver varied from 10.27 to 23.84

kg (Table 2-1). Cecal mass related directly to lean body mass ($F_{1,41} = 20.00$, $P < 0.001$), and the residuals exhibited a strong temporal quadratic relationship (Fig. 2-1; $F_{2,40} = 19.44$, $P < 0.001$). The mass of the cecum was relatively low from late spring to fall, as evidenced by the negative residuals for beaver sampled between 16 May (J. date 136) and 3 October (J. date 276). Inclusion of lean body mass and temporal quadratic effects in one model yielded the relationship described by:

$$[1] \text{CECMAS} = 149.7 + 4.781 \text{LWT} - 1.262 \text{DATE} + 0.003336 \text{DATE}^2$$

($R^2 = 0.70$, $F_{3,39} = 29.83$, $P < 0.001$), where CECMAS is the mass of the cecum in g, LWT is the lean body mass in kg, and DATE is the Julian date on which the beaver was collected. According to this model, cecal mass was maximal on 1 January and minimal on 8 July (118.5 g below maximum). The cecal masses on Julian dates 1 and 365 were similar enough to conclude that the quadratic model was reasonable. Sex effects were not found for any term in the model ($P \geq 0.110$); however, the variance of the residuals was greatest for males ($F_{20,21} = 2.66$, $P = 0.031$). Residual body fat was directly related to residual cecal mass in males (Fig. 2-2; one-tailed test, $t = 1.93$, $df = 19$, $P = 0.034$) but not in females (one-tailed test, $t = -0.25$, $df = 20$, $P = 0.597$).

The mass of the large intestine varied directly with lean body mass ($F_{1,41} = 38.28$, $P < 0.001$), and the residuals

Table 2-1. Physical characteristics of adult (>1 year old) beaver from southern Manitoba, 1988-1990.

Characteristic	Sex ^a	$\bar{x}$	s	Range
Lean body mass (kg)	F	15.01	3.16	10.51-22.57
	M	15.36	3.49	10.27-23.84
Cecum mass (g)	F	141.6	37.1	61.4-215.3
	M	136.8	50.2	71.6-275.6
Large intestine mass (g)	F	254.2	63.3	132.4-410.2
	M	239.6	74.9	145.3-384.6
Small intestine mass (g)	F	198.0	57.2	125.1-329.8
	M	175.8	52.3	84.9-276.9
Stomach mass (g)	F	129.3	23.3	91.3-186.9
	M	118.0	30.7	65.2-182.7
Total gut mass (g)	F	723	154	443-1120
	M	670	195	393-1078

^aSample included 22 female and 21 male beaver.

Figure 2-1. Temporal variation in the mass of the cecum of adult (>1 year old) Castor canadensis from southern Manitoba, 1988-1990.

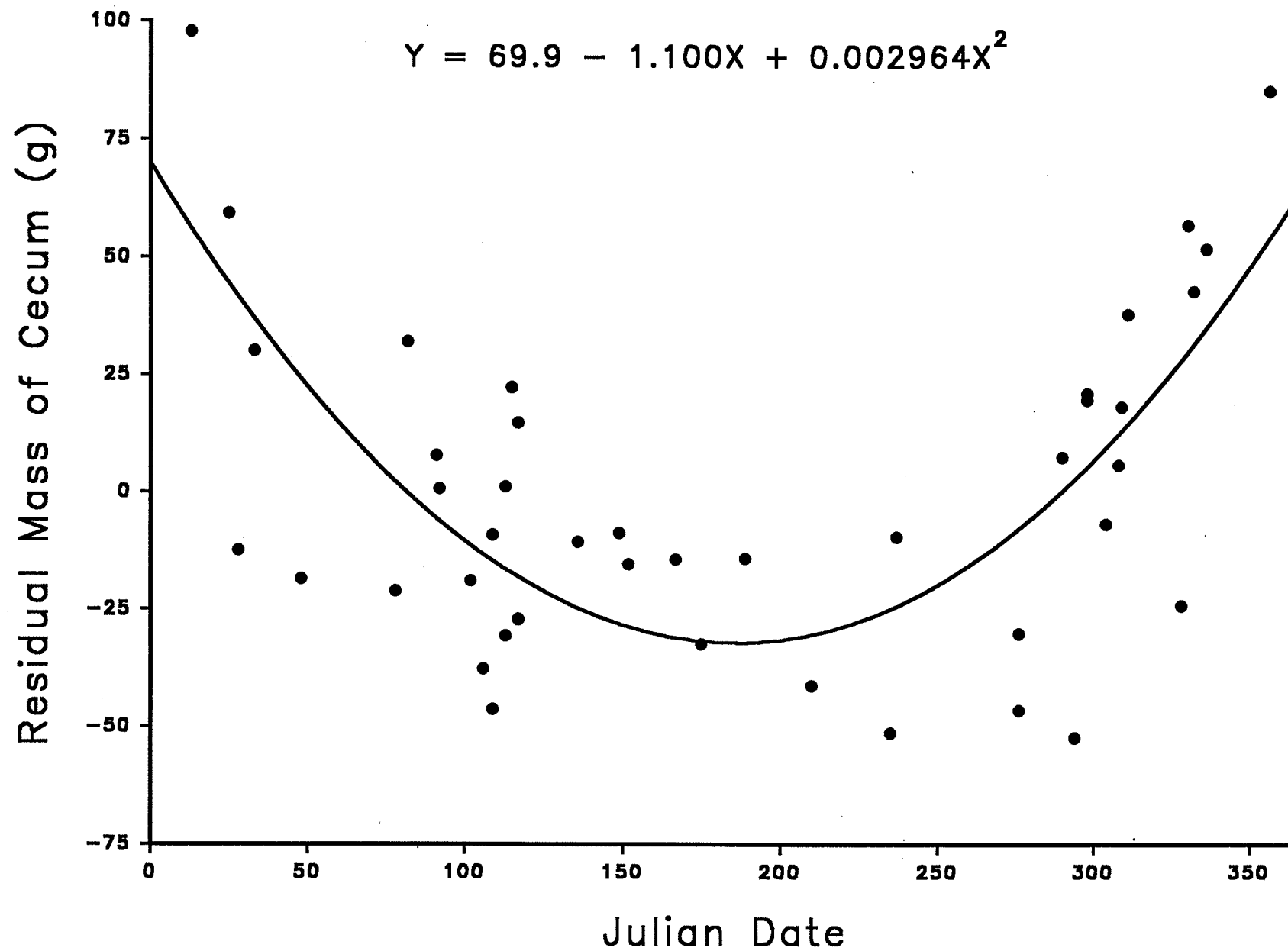
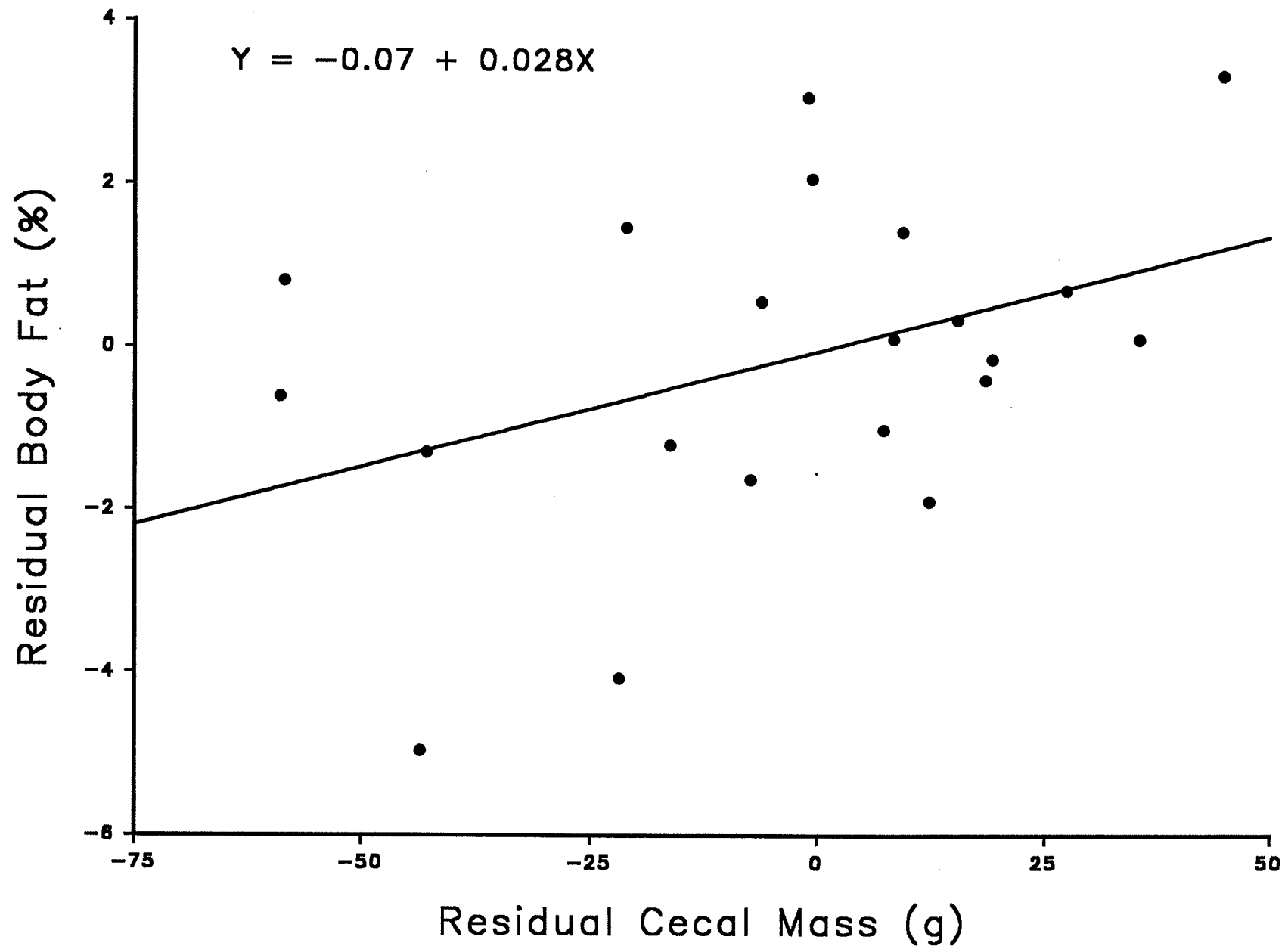


Figure 2-2. Linear relationship between body fat (residuals from two-phase model for temporal fat variation, % wet mass) and mass of cecum (residuals from cecal mass vs lean mass and time, g) for male adult (>1 year old) Castor canadensis from southern Manitoba, 1988-1990.



exhibited a quadratic temporal pattern similar to that observed for cecal mass (Fig. 2-3; $F_{2,40} = 15.38$, $P < 0.001$). The relationship with lean body mass and time effects was described by:

$$[2] \text{ LINTMAS} = 141.2 + 12.044 \text{ LWT} - 1.352 \text{ DATE} + 0.003844 \text{ DATE}^2$$

($R^2 = 0.72$, $F_{3,39} = 33.34$, $P < 0.001$), where LINTMAS is the mass of the large intestine in g. A sex effect was not detected for any of the model terms ($P \geq 0.105$). On the basis of the above model, it was estimated that the mass of the large intestine was maximal on 31 December and minimal on 5 June (137.5 g below maximum).

The mass of the small intestine was directly related to lean body mass ($F_{1,41} = 23.27$, $P < 0.001$), and the residuals for this segment of the gut also exhibited a quadratic temporal effect (Fig. 2-4; $F_{2,40} = 11.26$, $P < 0.001$). The model based on lean body mass and temporal effects was improved by a sex effect for lean body mass ($F_{1,38} = 4.61$, $P = 0.038$). The relationship for females was described by:

$$[3] \text{ SINTMAS} = 91.8 + 9.823 \text{ LWT} - 0.870 \text{ DATE} + 0.002632 \text{ DATE}^2$$

($R^2 = 0.64$, $F_{4,38} = 16.02$, $P < 0.001$), where SINTMAS is the mass of the small intestine in g. For males, the model was identical, except that the regression coefficient for lean body mass was 8.320. On the basis of these relationships, the

Figure 2-3. Temporal variation in the mass of the large intestine of adult (>1 year old) Castor canadensis from southern Manitoba, 1988-1990.

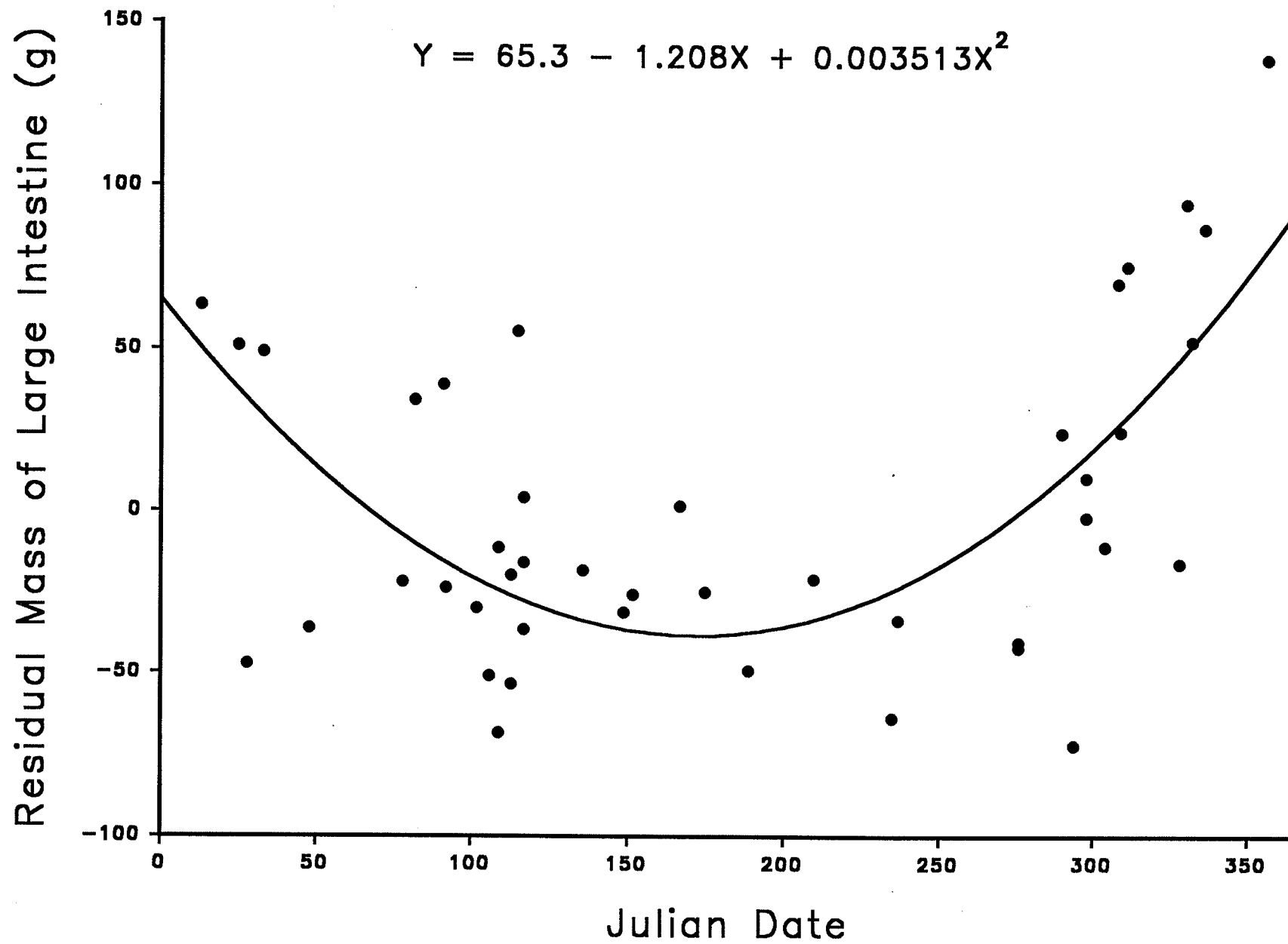
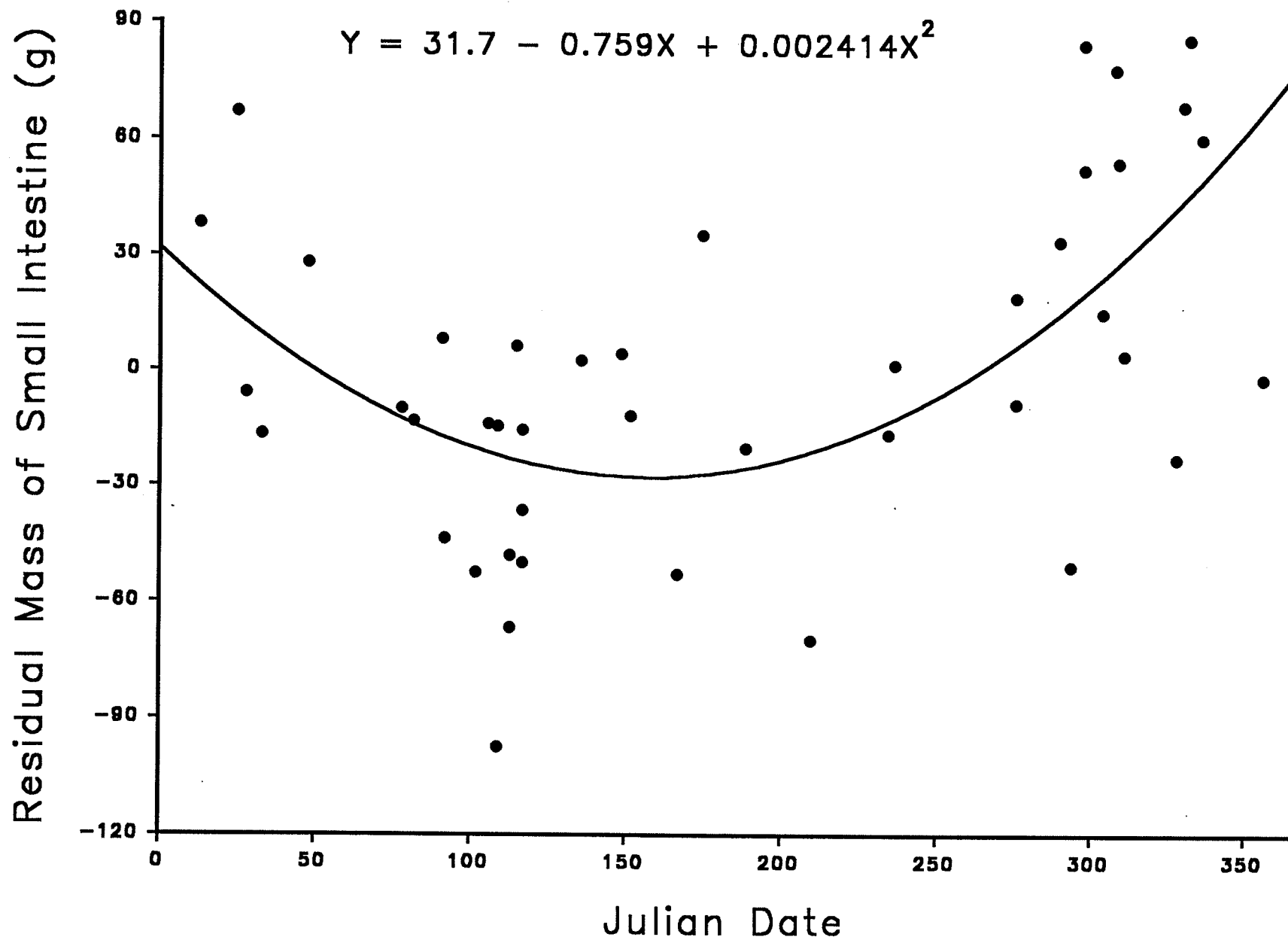


Figure 2-4. Temporal variation in the mass of the small intestine of adult (>1 year old) Castor canadensis from southern Manitoba, 1988-1990.



small intestine was predicted to be 15.4-35.8 g heavier in females. Small intestine mass was estimated to be maximal on 31 December and minimal on 14 June (105 g less than maximum).

The mass of the stomach was directly related to lean body mass ($F_{1,41} = 41.34$, $P < 0.001$) and varied with sex (Fig. 2-5; $F_{2,39} = 4.57$, $P < 0.025$). The stomach mass of small adults was greater in females than in males (eg., F: $\hat{Y}_{11} = 111.8 \pm 6.7$ g; M: $\hat{Y}_{11} = 85.5 \pm 6.0$ g). However, stomach mass did not differ for larger animals (eg., F: $\hat{Y}_{17} = 138.0 \pm 4.9$ g; M: $\hat{Y}_{17} = 130.2 \pm 4.1$ g). A linear relationship was apparent between the residuals of stomach mass corrected for sex and lean body mass effects, and time (Fig 2-6; $F_{1,41} = 5.95$, $P = 0.019$). In theory, stomach mass should be almost equivalent on 1 January and on 31 December. Therefore, the data suggest the existence of a complex temporal pattern in stomach mass that does not conform to a simple quadratic model. The time effect improved the model ($F_{1,38} = 6.10$, $P = 0.018$). With all of these effects incorporated, the model for females was described by:

$$[4] \text{ STOMAS} = 43.1 + 4.876 \text{ LWT} + 0.064 \text{ DATE}$$

($F_{4,38} = 17.83$, $P < 0.001$), where STOMAS is the mass of the stomach in g. The model was identical for males, except that B_0 was -13.0 and the regression coefficient for LWT was 7.844.

Total gut mass (cecum, large intestine, small intestine, stomach) related directly to lean body mass ($F_{1,41} = 43.40$, $P < 0.001$), and the residuals exhibited a strong quadratic time

Figure 2-5. The relationship between stomach mass and lean body mass for adult (>1 year old) female (solid circles) and male (open triangles) Castor canadensis from southern Manitoba, 1988-1990.

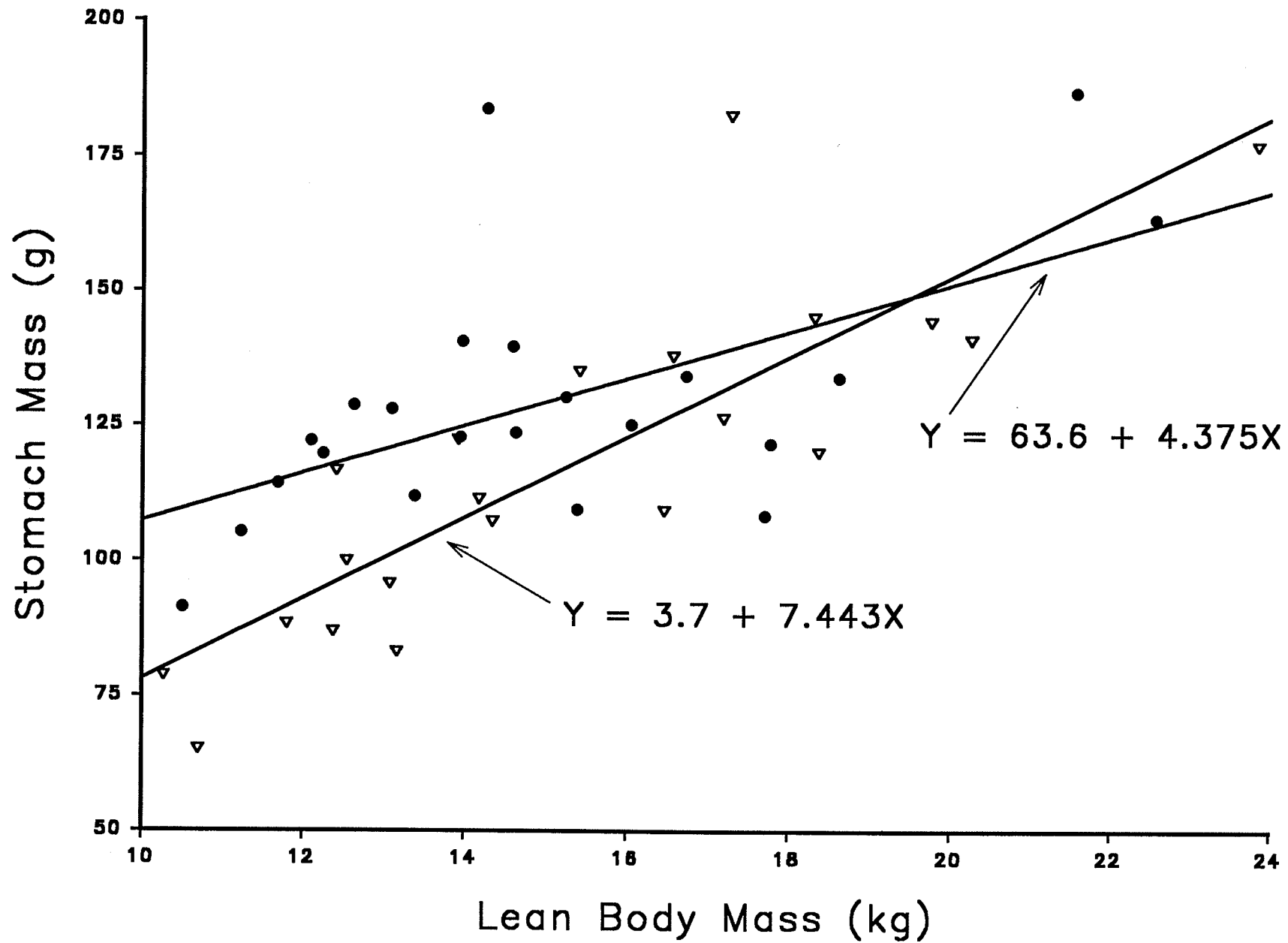


Figure 2-6. Temporal variation in the mass of the stomach of adult (>1 year old) Castor canadensis from southern Manitoba, 1988-1990.

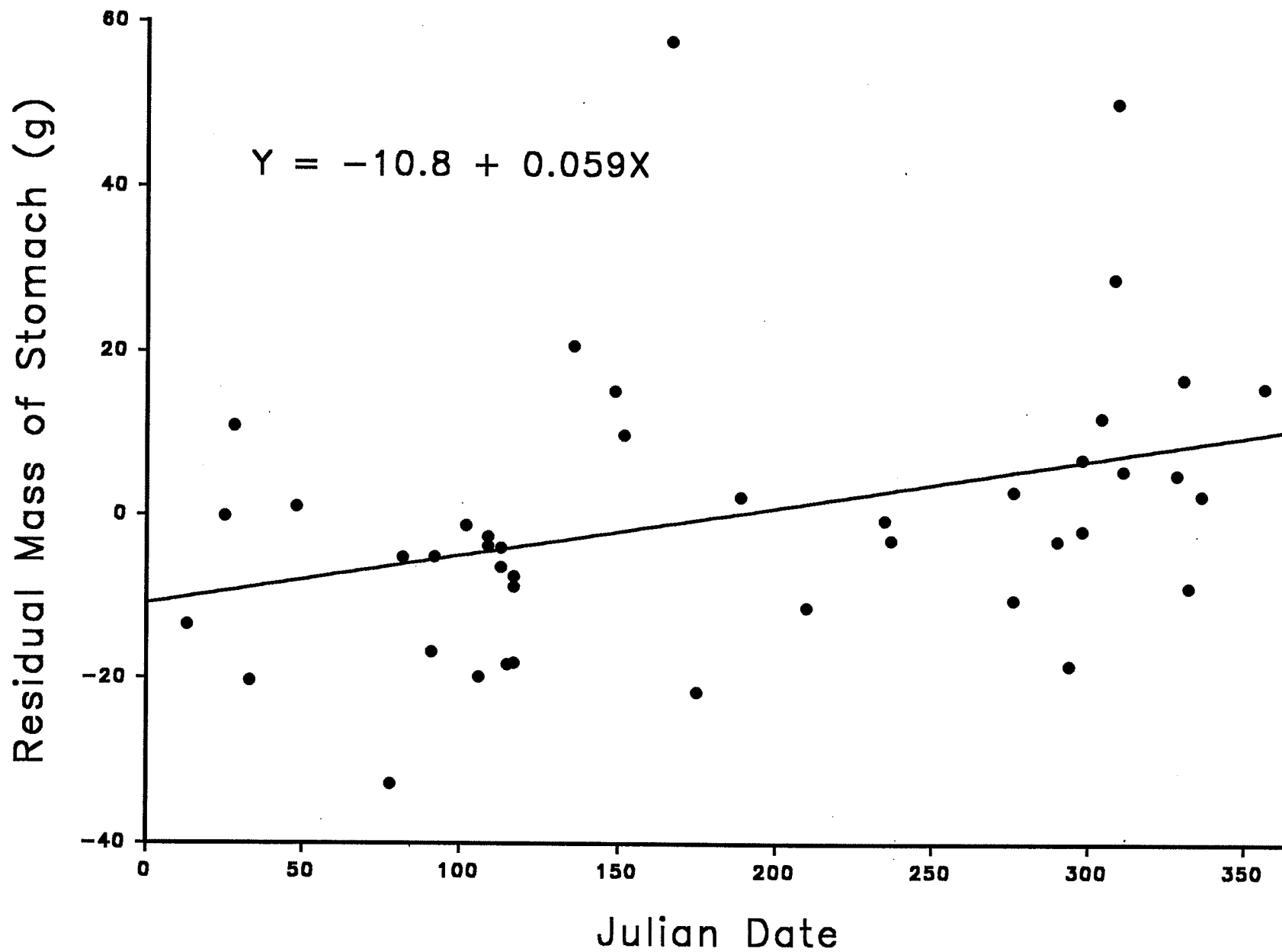
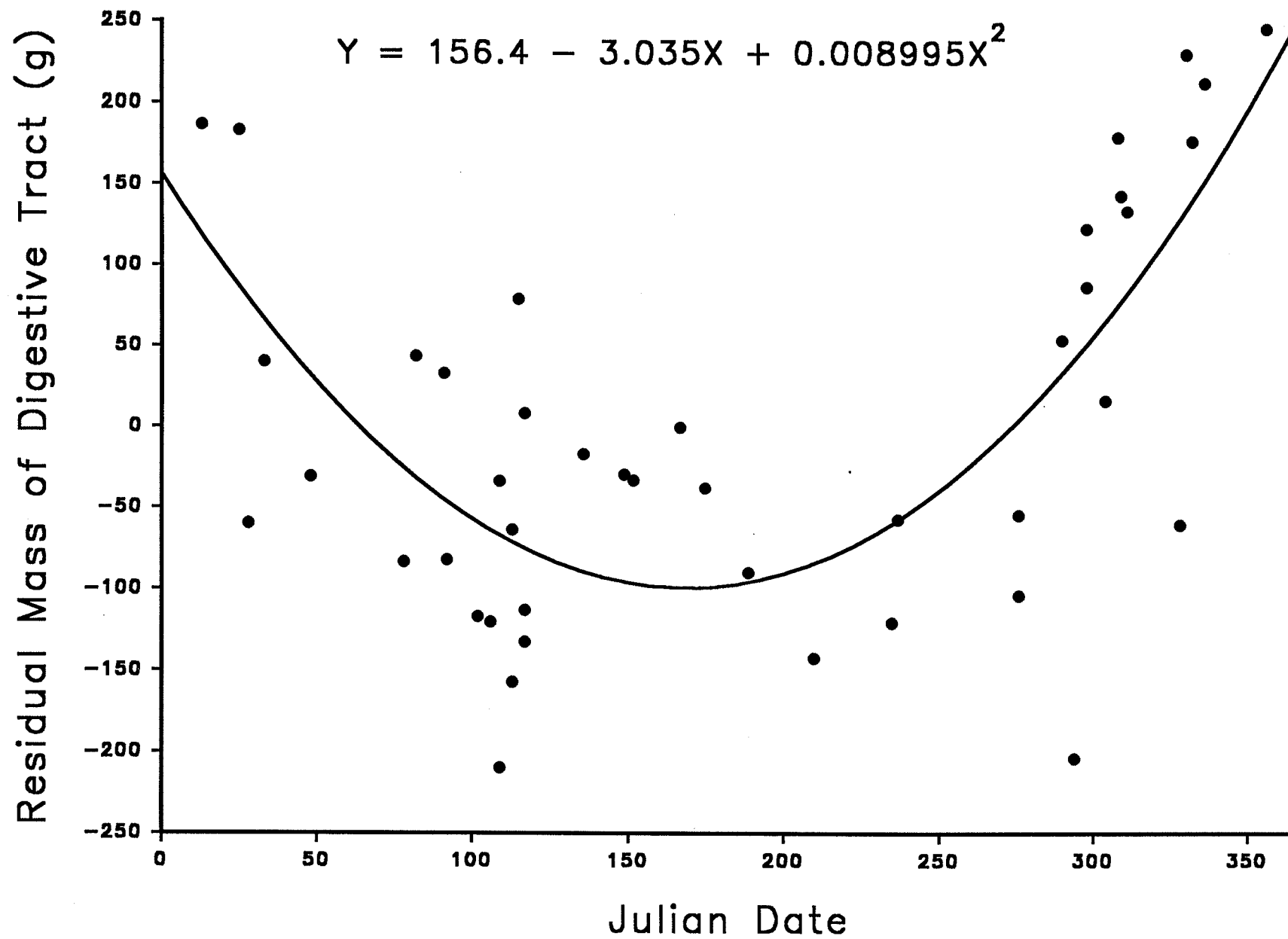


Figure 2-7. Temporal variation in the mass of the digestive tract (cecum, small intestine, large intestine, stomach) of adult (>1 year old) Castor canadensis from southern Manitoba, 1988-1990.



effect (Fig. 2-7; $F_{2,40} = 20.06$, $P < 0.001$). The relationship of total gut mass to lean body mass and time was improved by a sex effect for the intercept ($F_{1,38} = 4.60$, $P = 0.039$), and the model with all of these effects was significant ($R^2 = 0.79$, $F_{4,38} = 36.31$, $P < 0.001$). The relationship for females was described by:

$$[5] \text{ GUTMAS} = 428.8 + 32.326 \text{ LWT} - 3.451 \text{ DATE} + 0.009844 \text{ DATE}^2,$$

where GUTMAS is the total gut mass in g. The intercept was 373.0 g for adult male beaver. The model predicted that gut mass would be maximal on 31 December and minimal on 24 June (354.2 g below maximum).

DISCUSSION

This study has clearly demonstrated that beaver increase the mass of their cecum and large intestine from summer to winter, a morphological response consistent with an increase in dietary fiber. Combined with coprophagy (Buech 1984), fermentation in the cecum and upper colon allows beaver to exploit the energy and protein resources of a high-fiber diet (Kitts et al. 1957; Currier et al. 1960; Hoover and Clarke 1972). Natural seasonal variation in the mass or dimensions of the cecum and large intestine has also been reported in several other rodents (Bozinovic et al. 1990; Hammond 1993), as well as the rabbit, Oryctolagus cuniculus (Sibly et al. 1990). For the muskrat, Ondatra zibethicus, Virgl and Messier

(1992a) provided data to suggest that the cecum responds to natural changes in dietary fiber.

Unfortunately, experimental data on the composition and digestibility of the natural foods of beaver are limited and somewhat conflicting. In trials involving a single beaver, Buech (1987) found the apparent dry matter digestibility of a diet composed principally of water-lily leaves (66.5%) to exceed that of herbaceous foliage (58.9%), aspen bark and leaves (58.9%), or aspen bark alone (37.5%). In contrast, Doucet and Fryxell (1993) reported that the true dry matter digestibility of aspen leaves, twigs and bark (57.5%) exceeded that of water-lily leaves and stems (38.7%). Furthermore, as digestibility usually varies inversely with fiber content, the estimates of Doucet and Fryxell (1993) are surprising, given that acid detergent fiber (ADF) represented 40.5% of the aspen diet, compared to only 18.5% of the water-lily diet. Clearly, the available data on digestibility are seriously limited by sample sizes (Buech 1987) and/or imprecise estimates (Doucet and Fryxell 1993).

The high ADF of leaves, twigs and bark (Doucet and Fryxell 1993), as well as some natural summer diets (Hoover and Clarke 1972), suggest that fiber constitutes a significant fraction of the beaver's diet throughout the year. Although diet quality was not determined in this study, my findings suggest that adult beaver modify their cecum and large intestine to improve their ability to digest a high-fiber, bark-dominated, winter diet. These organs represent the

primary sites of fermentation and absorption of volatile fatty acids in hindgut fermenters (Hoover and Clarke 1972; Hume 1989), and this morphological response is consistent with the need to defend digestibility in an environment where food quality is in decline (Hammond 1993).

The hypothesis that relative fat resources would relate directly to cecal mass after correction for body mass and time effects, was supported for male, but not for female beaver. This finding suggests that cecal mass may have an important bearing on the energetics of male beaver. Failure to detect a similar relationship for females may have related to the lower variability in their residual cecal mass. Perhaps female beaver maintain their cecum within relatively narrow tolerances, owing to their greater energy requirements for reproduction.

The small intestine was heaviest when beaver were on a diet likely to be high in fiber, but lightest when food quality was presumably optimal. This response is somewhat puzzling, as laboratory studies of rodents have generally demonstrated that the mass of the small intestine responds mainly to energy demand (Hammond and Wunder 1991; Derting and Bogue 1993), rather than to dietary fiber (Loeb et al. 1991; Hammond and Wunder 1991). Loeb et al. (1991) suggested that herbivores should not enlarge their small intestine when dietary fiber is high, because fiber digestion in the small intestine is limited. Nevertheless, at least one laboratory study has reported a large increase in small intestine mass in

response to a high-fiber diet, under conditions of high energy demand (Nagy and Negus 1993). Furthermore, significant digestion of hemicellulose and cellulose in the small intestine has been documented in domestic hindgut fermenters (Hintz et al. 1971; Millard and Chesson 1984), and Barboza and Hume (1992) reported that wombats (Vombatus ursinus and Lasiornhinus latifrons) may digest neutral detergent fiber in their stomach and/or small intestine.

Other studies of mammals existing under natural conditions suggest that the seasonal changes in the small intestine of beaver are not atypical. For example, the mass of the small intestine of the prairie vole, Microtus ochrogaster, appears to be greatest during cold months when food is of low quality (Hammond 1993). Similarly, Bozinovic et al. (1990) reported that the mass of the small intestine of the South American field mouse, Abrothrix andinus, was greatest during winter, although seasonal variation in body mass confounded their analyses. Bozinovic and Iturri (1990) also reported that the rates of uptake of glucose and alanine by the small intestine were greatest in winter, and suggested this was a response to a period of high energy demand and poor food quality.

In a nutritional environment where highly digestible nutrients may be scarce and/or comprise a low fraction of ingesta, beaver might increase the mass of their small intestine to ensure that these nutrients are secured. Given the substantial cost of foraging in cold water (MacArthur and

Dyck 1990), beaver may attempt to maximize digestion of high-energy items like pond-lily rhizomes. Moreover, increasing the mass of the small intestine might ensure that nutrients made available through coprophagy are assimilated, particularly the amino acids derived from microbial protein. Recovery of microbial protein may be especially critical, given that foods in the cache are low in crude protein (Skinner 1984). Finally, an increase in the mass of the small intestine might also indicate enhanced fermentation activity in this segment during winter. Clearly, it must be advantageous for beaver to maintain their small intestine at high mass while on their winter diet.

Although the stomach of beaver demonstrated little plasticity in comparison to other regions of the digestive tract, it is known that the length (Hammond 1993) and mass (Sibly et al. 1990) of this organ may vary in other species. The large cardiac gland of the beaver stomach (Kitts et al. 1957) contributes substantially to stomach mass, and perhaps direct comparison with some species is inappropriate. Although no clear trend was apparent, my data suggest that the beaver's stomach is heaviest late in the year, and that it may increase in mass during a period when body fat is stored (see Part I).

In other rodents, the mass of the small intestine (Bozinovic et al. 1990; Virgl and Messier 1992a) or entire digestive tract (Millar et al. 1991) is greater in females than in males during the reproductive season. Similarly,

female wild rabbits maintain the mass of their digestive organs throughout the year, whereas males exhibit seasonal decreases (Sibly et al. 1990). In this study, the mass of the small intestine, stomach, and total gut were greatest in female beaver. It is likely that female beaver invest greater resources in their digestive system to accommodate the substantial costs of reproduction. The heavier digestive system of females is also consistent with their greater body fat content during most of the ice-bound period (Part I).

The above morphological adjustments have important implications for previous tests of digestive efficiency in beaver. For example, Buech (1987) tested a winter diet of aspen bark at a time when beaver in southern Manitoba would have altered their digestive tract, presumably in preparation for a summer diet. Therefore, existing estimates of dry matter digestibility for aspen bark (Buech 1987) may not accurately reflect the digestive capabilities of this species in winter. The reported inability of beaver to maintain their mass on an aspen diet (Buech 1987; Dyck and MacArthur 1993b) may also relate, at least in part, to the state of their digestive tract at the time of testing.

In this study, the decrease in the gut mass of beaver in late winter is noteworthy. Was this a response to an environmental limitation such as a decline in food quality, or do beaver decrease their intake as they begin to mobilize stored fat energy? Future studies of the beaver gut should focus on seasonal variation in dimensions (eg., length,

width), and the precise nature of the morphological variation observed in this study.

PART III

Prediction of body composition in the beaver,
Castor canadensis

INTRODUCTION

Adequate body nutrients are integral to survival and reproduction, hence accurate measures of body condition are fundamental to developing an understanding of the relationships between a species and its environment. Unfortunately, practical considerations dictate that studies of large mammals typically do not assess body composition on the basis of chemical determinations. Body condition, or the influence of ecological factors on condition, has generally been assessed on the basis of variation in discrete fat depots or indices (Ransom 1967; Aleksiuk and Cowan 1969b; Todd 1985).

Implicit to this approach is the assumption that selected depots or indices will reflect variation over the complete range of body conditions. However, these measures frequently are not adequate for this purpose. For example, the relationship between the femur fat and kidney fat indices is asymptotic in white-tailed deer, Odocoileus virginianus (Ransom 1965), and therefore each is relevant to different ranges of body fat. Mech and DelGiudice (1985) concluded that the value of the femur fat index is limited for white-tailed deer, because marrow lipids are not mobilized until total body fat reserves are nearly exhausted. Utility is also compromised by relationships between indices which differ with age class (Monson et al. 1974). Most critically, the curvilinear or asymptotic relationship often observed between body fat concentration and each of these indices (Finger et al. 1981; Torbit et al. 1988; Watkins et al. 1991) severely

limits their usefulness as indirect comparative measures. For example, when total body fat is high in white-tailed deer fawns, it becomes insensitive to changes in the kidney fat index (Watkins et al. 1991). For these reasons, knowledge of the relationship between an index or depot and the variable it attempts to model is crucial (Finger et al. 1981; Watkins et al. 1991).

Previous studies of body fat dynamics of beaver are limited to the early work by Aleksiuk and Cowan (1969b). Unfortunately, the usefulness of this earlier study of Arctic beaver is seriously constrained because these authors measured only depots and indices. As the body composition of beaver can vary with season, age and sex (see Part I), relationships which predict body composition for whole beaver and skinned carcasses should be valuable to future studies of the bioenergetics and body composition dynamics of this species. Therefore, the principal objective of this study was to determine the relationships between standard measures of body condition and selected fat depots and indices in beaver. Because the nature of specimens collected may vary considerably (eg., it may often be impossible to determine ingesta-free mass from carcasses), I chose to predict the mass and concentration of body fat, in order to ensure that estimates of both variables could be readily obtained from any specimen.

METHODS

Sampling Regime and Body Composition Determinations

The study areas, sampling regime, processing of specimens, and determination of body composition are detailed in Part I. Extraction of lipids was incomplete in samples from five adult (>1 year old) beaver and, in these cases, fat was estimated from ash and crude protein. Data from these five animals were not used to develop predictive equations for fat mass and concentration. Body fat was predicted from ash and protein for seven kits; however, these data were included in analyses to increase the sample size and variation. Preliminary analysis indicated that inclusion of these data was necessary for the development of reasonable models, and that residuals of the other data were not increased or distorted by the use of these estimates. Body fat concentration was defined as the percentage of ingesta-free wet mass that was accounted for by fat, and lean body mass was defined as ingesta-free wet mass less fat mass.

Morphometrics, Fat Depots and Indices

A 20 X 61 X 2 cm board fixed at a 90° angle to a 61 X 122 X 2 cm board was used to measure total body length. Beaver were oriented parallel to the long axis of the larger board, with their nose placed against the smaller board, and LENGTH was defined as the distance from the small board to the tip of the tail. If the tip of the tail was outside the sagittal

plane, that point on the plane directly medial to the most distal part of the tail was defined as the tip. With the foot flattened along the ruler portion and the calcaneum positioned against the vertical arm of a combination square, HINDFT was measured as the distance from the calcaneum to the end of the claw on digit IV. The maximum distance between the tip of the lower incisor and the interface of gum and incisor (MAND1) was measured from the anterior aspect of the incisor. The shortest distance between the tip of the angular process and the interface of gum and lower incisor (MAND2) was measured from the buccal side of the mandible. Maximum skull width was measured from one zygomatic arch to the other, before (ZYGRND) and after (ZYGSKIN) removal of the skin. The ulna, from the olecranon to the notch where the ulna and radius meet (near the base of the lateral styloid process), was measured before (ULNARND) and after (ULNASKIN) removal of the skin. Measurements were taken from the dorsal aspect with the forearm in an anterior position, and muscle tissue was scraped away from the bone prior to measurement of ULNASKIN. Tibia length (TIB) was measured ventrally, as the distance from the nearly flat anterior part of the tuberosity to the small notch lateral to the medial malleolus. A flexible ruler was used to measure the distance from the tip of the tail to the depression between the sacrum and first caudal vertebrae (TAILSTN1), and the distance between the tip of the tail and the cranial end of the scaly tail hair on the midventral tail surface (TAILUND). The maximum width of the tail was measured

(TAILWIDT). The tail was then removed along the line of demarcation where scaly hair begins, and its mass (TAILWT), volume by water displacement (TAILVOL), and maximum thickness (TAILTHIK) were measured.

Where appropriate, measurements were collected from both sides of a beaver. It was difficult for a right-handed person to measure accurately the right ulna on a whole specimen, and it was hypothesized that the resulting measurement was inflated. This hypothesis was supported for both kits (H_A : $ULNARND_{LEFT} < ULNARND_{RIGHT}$, $P = 0.02$) and adults (H_A : $ULNARND_{LEFT} < ULNARND_{RIGHT}$, $P = 0.02$). Measurements from the left and right sides did not differ ($P > 0.05$) for HINDFT, MAND1, MAND2, ULNASKIN, or TIB. Measurements from the left side were subsequently used in all analyses. With the exception of ULNARND, the measurement from the right side was substituted only if that from the left side could not be taken.

The masses of the kidneys (KIDWT) and perirenal fat (KIDFT) were used to calculate a total kidney fat index (KIDIND), according to Monson et al. (1974). To remove kidneys and fat, perirenal fat was scraped away from the body cavity lateral, anterior and posterior to each kidney. Included with the fat depot were parietal peritoneum, mesentery, connective tissue, a small portion of the ureter, and renal vessels. Kidneys were isolated, and perirenal fat mass was calculated as the difference between the mass of the kidneys with and without the fat depot. In fatty specimens, it was difficult to distinguish between the perirenal depot

and adipose tissue associated with the ovary and, in these cases, it was necessary to lift the ovary and cut the mesentery which encompasses this depot.

Visceral fat (VISCFT) associated with the stomach, small intestine, cecum, large intestine, spleen, and their respective mesenteries was removed and weighed. The contiguous depot which extends from the xiphisternum to the pelvic girdle within the abdominal cavity (ABDOMFT) was removed, along with associated parietal peritoneum, and weighed. In lean specimens, the VISCFT and KIDFT depots contain minimal amounts of adipose tissue, and are comprised almost entirely of mesentery. Following excision, all adipose tissue was wiped against the pelage to remove excess water.

Tissue samples were removed from the tail at sites midway between the tip and the point where the pelage begins, directly adjacent to the medial ridge. For kits, additional samples were collected 5 mm anterior to the previous two samples. At each location, a tail core was extracted with the use of a 1.27-cm ID leather punch. The skin was removed and the tissue stored in a plastic bag at ca. -24°C . Samples were later dried to constant mass by freeze-drying or at 60°C in a convection oven, and the tail fat index (TAILFAT) was defined as the percent dry matter of the tissue. A strong inverse relationship exists between the fat and water contents of this tissue (Aleksiuk 1970b), hence TAILFAT should constitute an excellent index of the fat content of this depot.

Thickness of the midventral subcutaneous fat depot was

measured between the anterior and posterior ends of the sternum (SUBBRISK), and also at a point 2 cm caudad to the anterior end of the pubis (SUBPELVI). The SUBPELVI measure incorporated a thin muscle layer within the depot but excluded muscle tissue adjacent to the skin. Additional measurements were taken along the median at sites located one-third (SUBMID1) and two-thirds (SUBMID2) of the distance between SUBBRISK and SUBPELVI. The thickness of the rump-pelvis depot (Stribling et al. 1984) was measured at the point 3 cm to the left of the spine between the last thoracic vertebrae and the posterior end of the sacrum (SUBRMPEL). It was necessary to cut through a muscle layer adjacent to the skin to access this depot. Thickness of the backfat depot (Huot 1988) was measured 2 cm from the start of a line which began at the intersection of the sacrum and first caudal vertebrae, and ran caudally at 45° from the spinal column (SUBTAIL1). Measurements of subcutaneous fat thickness were summed to create the following variables: $SUB1 = SUBBRISK + SUBMID1 + SUBMID2$; $SUB2 = SUB1 + SUBPELVI$; $SUB3 = SUB2 + SUBTAIL1$; $SUB4 = SUB3 + SUBRMPEL$.

The M. plantaris (Young 1937), from its origin on the lateral epicondyle of the femur to the point where the muscle inserted on the tendon, was removed from both legs. Superficial fat was removed and the muscle was weighed (MUSCWT), stored in a plastic bag at ca. -24°C, and later freeze-dried to constant mass to estimate dry matter content (MUSCPERC). A strong inverse relationship exists between the

water and fat concentrations of muscle tissue (Rhee et al. 1988), hence dry matter content should be an excellent indicator of the fat content of this muscle. As the body fat levels of cervids are strongly correlated with the fat content of skeletal muscles (eg., Ringberg et al. 1981; Watkins et al. 1991), it was hypothesized that the body fat content of beaver would relate directly to MUSCPERC. The heart was removed and all associated vessels trimmed away. The heart was opened and wiped against the pelage to remove internal blood and clots, and was subsequently weighed (HEARTWT). A second kidney fat index, similar to that of Aleksasuk and Cowan (1969b), was calculated as: $ALEKIND = (\text{perirenal fat mass} \times 1000) / \text{heart mass}$.

Unless indicated otherwise, morphological measurements were made with a ruler calibrated in 1-mm increments or with dial calipers accurate to 0.01 mm (MAND1, MAND2, ZYGRND, ZYGSKIN, ULNARND, ULNASKIN, TIB and TAILWIDT). Subcutaneous fat measurements <1 mm were given a value of 0, and all other linear measures were rounded to the nearest mm. Tissues were weighed to the nearest 0.1 g on an Ohaus Dial-o-gram triple-beam balance. Water displaced by the tail was measured in a graduated cylinder calibrated in 10-ml increments.

Statistical Analysis

Other than tests for sex effects, statistics were calculated with PC-SAS Version 6.03 (SAS Institute Inc., Cary, NC). Morphometrics from the left and right sides were

compared with a paired t -test. Body composition was related to independent variables by means of linear regression and forward multiple linear regression models. As appropriate, dependent and independent variables were $\ln$ -transformed to estimate bivariate relationships. Models were selected on the basis of the calculation of the root mean square error (RMSE = $S_{Y/X}$) for precision, inspection of residual plots to detect violations of test assumptions, and absence of strong interaction among independent variables. If the dependent variable had been $\ln$ -transformed, predicted values were retransformed to the base₁₀ scale to calculate the RMSE (Anderson-Sprecher 1994). Variables from non-linear bivariate relationships were tested in both their transformed and raw forms in multiple regression analyses. Individual terms in multivariate models were tested with the Type III partial SS of PROC GLM. Sex effects were examined with a test of coincidence (Kleinbaum and Kupper 1978), and asymptotic models were estimated by PROC NLIN. Alternate hypotheses were generally one-sided for simple regression analyses, and test acceptance was set at a type I error of ≤ 0.05 . Models were selected for display on the basis of precision, practical considerations relative to the type of specimen, and availability and characteristics of predictor variables.

RESULTS

Mass of beaver varied from 5.480 to 10.347 kg in kits, and from 12.31 to 29.38 kg in adults (Table 3-1). Body fat

Table 3-1. Physical characteristics of kit and adult (>1 year old) beaver from southern Manitoba, 1988-1990.

Characteristic	Kit				Adult			
	n	$\bar{x}$	s	Range	n	$\bar{x}$	s	Range
Mass (kg)	22	8.027	1.352	5.480-10.347	40	18.65	4.08	12.31-29.38
Ingesta-free mass (kg)	21	6.712	1.099	4.462-8.494	42	16.57	3.84	10.67-26.22
Lean body mass (kg)	21	5.999	0.923	4.162-8.059	42	15.13	3.31	10.27-23.84
Fat mass (g)	22	698	341	75-1416	40	1200	710	80-3560
Fat concentration (% wet mass)	21	10.36	3.89	0.92-16.67	38	6.95	3.28	0.60-14.00
Fat concentration (% dry mass)	21	29.1	9.0	3.5-42.3	38	20.0	8.3	2.2-35.8
Crude protein mass (g)	22	1163	190	805-1540	44	3340	780	2250-5250
Mineral mass (g)	22	246	52	165-357	43	670	150	410-1010
Length (mm)	22	811	40	729-886	42	1055	69	944-1216
Abdomft (g)	22	20.8	13.9	1.6-55.2	40	31.5	26.3	0.5-128.4
Kidft (g)	22	26.8	15.6	7.4-64.8	40	41.4	28.9	1.8-137.2
Kidind (%)	21	54.4	27.9	9.8-109.5	36	40.1	22.1	2.0-93.5
Tailfat (%)	22	59	12	36-83	40	70	15	22-84
Sub3 (mm)	22	22.1	9.0	3-35	38	19.4	10.3	0-39
Alekind (%)	33 ^a	1092	529	301-2561	37	864	465	45-2006
Muscwt (g)	22	38.1	7.4	24.6-54.6	42	116.3	26.9	61.4-195.1
Muscperc (%)	22	22.6	0.6	21.1-25.0	40	23.5	0.9	20.7-25.5

^aSample included kits and beaver <2 years old.

concentration ranged from 0.92 to 16.67% in kits, and from 0.60 to 14.00% in adults. Appendix II contains data on additional physical characteristics used to predict body nutrient reserves.

Mass and Concentration of Body Fat

For adult beaver, body fat mass related poorly to ingesta-free mass (IFMASS) and ZYGRND (Table 3-2). For carcasses, total fat mass related strongly to the ABDOMFT depot, and the model with ABDOMFT and TAILFAT provided the greatest precision. The precision of single-variable models which incorporated cumulative indices of subcutaneous fat ($RMSE \geq 430$ g) was improved by the inclusion of LENGTH in the model (Table 3-2). Fat mass was predicted best by ABDOMFT and TAILFAT combined with either SUBBRISK or SUB3. For three-variable models, individual coefficients were significant at $P \leq 0.009$ with SUB3 and $P \leq 0.022$ with SUBBRISK. For kits, fat mass related directly to the ABDOMFT depot, and precision improved with the addition of TAILFAT to the model (Table 3-3). As with adults, precision was relatively low for models with single indices of subcutaneous fat, and improved only slightly for those with cumulative indices.

Curvilinear relationships ($P < 0.001$) were found between the body fat concentration of adult beaver and ABDOMFT (Fig. 3-1), VISCFT, KIDFT and KIDIND. Body fat content correlated most strongly to ABDOMFT or KIDIND ($r^2 = 0.75$), and less strongly to KIDFT ($r^2 = 0.65$). Similar curvilinear

Table 3-2. Simple and multiple linear regressions of body fat mass (g) on selected fat depots and indices available from skinned carcasses or whole adult (>1 year old) beaver.

Independent variable(s)	Equation	r ² or R ²	n	P	RMSE ^a
Ifmass (g), zygrnd (mm)	$Y = 7679.6 + 0.28692(IF) - 110.512(Z)^b$	0.48	28	<0.001	470
Abdomft (g)	$\ln(Y+1) = 4.326 + 0.804\ln(AF+1)$	0.85	40	<0.001	273
Tailfat (%)	$\ln(Y+1) = 3.879 + 0.043(TF)$	0.66	40	<0.001	509
Abdomft, tailfat	$Y = -328.6 + 21.820(AF) + 12.027(TF)^c$	0.91	40	<0.001	220
Abdomft, tailfat, subbrisk (mm)	$Y = -204.7 + 20.245(AF) + 6.497(TF) + 57.269(SB)^d$	0.94	40	<0.001	188
Sub2 (mm), length (mm)	$Y = -4204.7 + 52.229(S2) + 42.377(L)^c$	0.76	38	<0.001	364
Sub3 (mm), length	$Y = -4049.1 + 50.739(S3) + 40.496(L)^c$	0.78	38	<0.001	344
Abdomft, tailfat, sub3	$Y = -234.4 + 18.637(AF) + 6.974(TF) + 18.285(S3)^e$	0.94	40	<0.001	182

^aRoot mean square error.

^bIndividual coefficients significant at $P < 0.005$.

^cIndividual coefficients significant at $P < 0.001$.

^dIndividual coefficients significant at $P < 0.05$.

^eIndividual coefficients significant at $P < 0.01$.

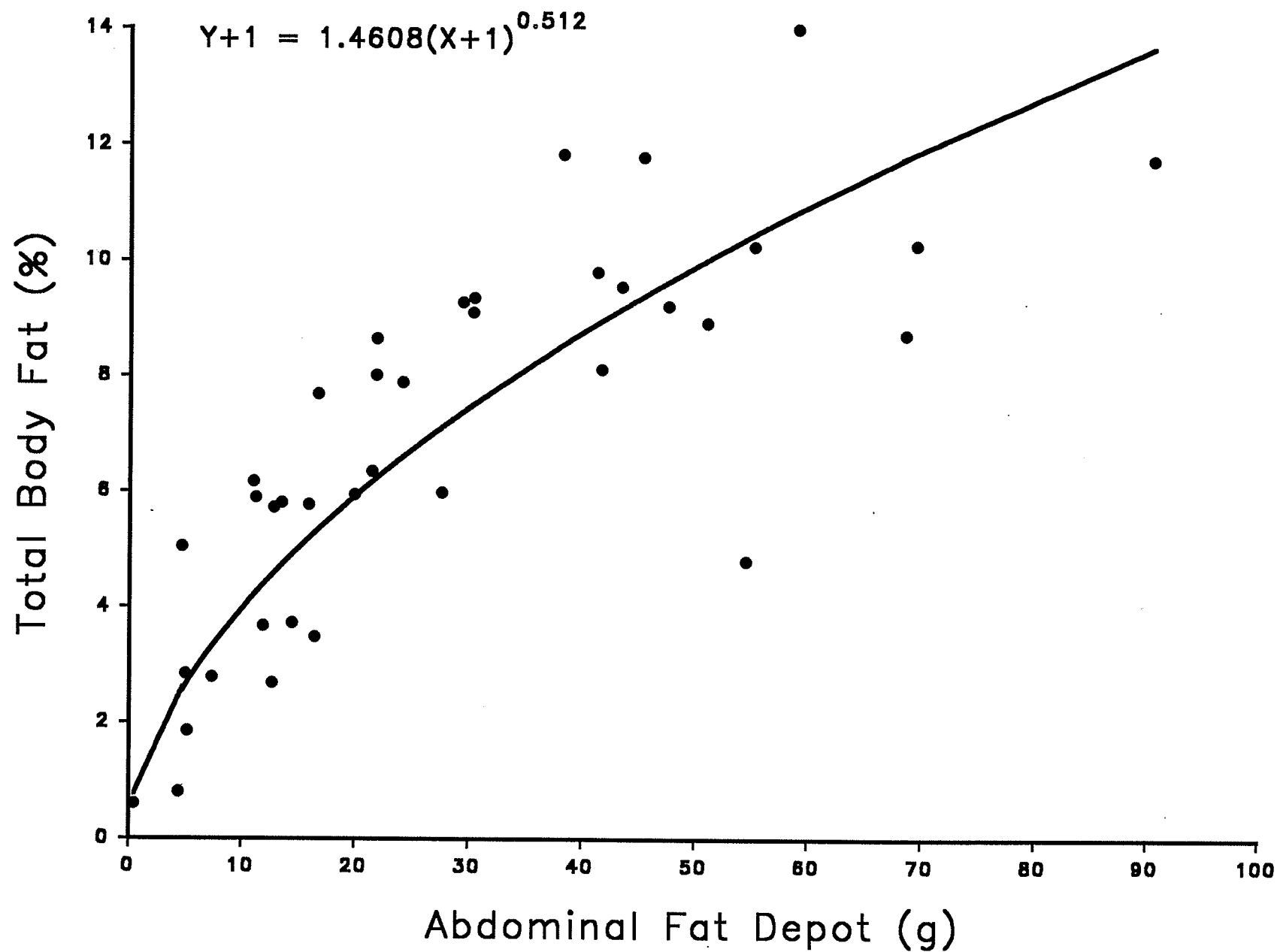
Table 3-3. Simple and multiple linear regressions of body fat mass (g) on selected fat depots and indices available from skinned carcasses or whole kit beaver.

Independent variable(s)	Equation	r ² or R ²	n	P	RMSE ^a
Abdomft (g)	Y = 211.1 + 23.384(AF)	0.91	22	<0.001	106
Tailfat (%)	Y = -601.2 + 22.041(TF)	0.57	22	<0.001	230
Abdomft, tailfat	Y = -141.9 + 19.485(AF) + 7.366(TF) ^b	0.95	22	<0.001	83
Sub2 (mm)	Y = -19.4 + 35.479(S2)	0.75	22	<0.001	174
Sub3 (mm)	Y = -41.8 + 33.434(S3)	0.78	22	<0.001	163

^aRoot mean square error.

^bIndividual coefficients significant at P<0.005.

Figure 3-1. The relationship between total body fat concentration (% ingesta-free wet mass) and the mass of the abdominal fat (ABDOMFT) depot of adult (>1 year old) Castor canadensis from southern Manitoba, 1988-1990.



relationships were found between body fat content and VISCFT, KIDFT and KIDIND. The precision increased with introduction of the morphometric variable MAND2 to these models, and the resulting regression coefficient was negative as expected (Table 3-4). The hypothesis that body fat concentration would increase with MUSCPERC was not supported in either adults ($t = 1.18$, $df = 36$, $P = 0.123$) or kits ($t = 1.35$, $df = 19$, $P = 0.097$). Although body fat content related to TAILFAT according to a curvilinear model, the fit was poor (Fig. 3-2), and the variables were not directly related at $>7.2\%$ fat ($P = 0.728$; $\bar{x}_{TAILFAT} = 77.8\%$). The model with TAILFAT, ABDOMFT and MAND2 produced the best precision for carcasses.

Direct relationships were found between body fat content and most subcutaneous depot indices; however, intercepts differed from zero (eg., $B_0 = 5.23\%$ for SUBTAIL1, $B_0 = 5.80\%$ for SUBRMPEL). Of the single- and two-variable models examined, body fat concentration was most strongly related to cumulative indices of subcutaneous fat, and relationships between these variables were strongly linear (Fig. 3-3). Precision was greatest for the multivariate models for whole beaver, and the four-variable model had highly significant individual coefficients, the lowest RMSE, and the best distribution of residuals.

Strong curvilinear relationships were found between percent fat and both ABDOMFT and KIDIND in kits (Table 3-5). Unlike the situation in adults, MAND2 did not enter any of the relationships between percent fat and ABDOMFT, VISCFT, KIDFT

Table 3-4. Simple and multiple linear regressions of body fat concentration (% ingesta-free wet mass) on selected fat depots and indices available from skinned carcasses or whole adult (>1 year old) beaver.

Independent variable(s)	Equation	r ² or R ²	n	P	RMSE ^a
Abdomft (g), mand2 (mm)	$\ln(Y+1) = 3.519 + 0.596\ln(AF+1) - 0.034(M2)^b$	0.87	36	<0.001	1.43
Kidft (g), mand2	$\ln(Y+1) = 3.740 + 0.707\ln(KF+1) - 0.042(M2)^b$	0.79	36	<0.001	1.77
Kidind (%), mand2	$\ln(Y+1) = 1.738 + 0.692\ln(KI+1) - 0.022(M2)^c$	0.79	36	<0.001	1.76
Tailfat (%)	$\ln(Y+1) = 0.123 + 0.027(TF)$	0.59	38	<0.001	2.25
Abdomft, tailfat, mand2	$\ln(Y+1) = 2.682 + 0.474\ln(AF+1) + 0.009(TF) - 0.028(M2)^b$	0.91	36	<0.001	1.30
Abdomft, subbrisk (mm), length (mm)	$Y = 11.02 + 0.075(AF) + 0.713(SB) - 0.0097(L)^d$	0.90	36	<0.001	1.09
Sub2 (mm)	$Y = 1.42 + 0.310(S2)$	0.82	38	<0.001	1.41
Sub3 (mm)	$Y = 1.26 + 0.296(S3)$	0.85	38	<0.001	1.31
Abdomft, tailfat, sub3, length	$Y = 9.74 + 0.056(AF) + 0.040(TF) + 0.192(S3) - 0.0104(L)^d$	0.93	36	<0.001	0.92
Alekind (%)	$\ln(Y+1) = -2.056 + 0.611\ln(AI)$	0.57	37	<0.001	2.15
Alekind (%) ^e	$\ln(Y+1) = -2.504 + 0.694\ln(AI)$	0.73	33	<0.001	1.89

^aRoot mean square error.

^bIndividual coefficients significant at P<0.001.

^cIndividual coefficients significant at P<0.01.

^dIndividual coefficients significant at P<0.005.

^eSample included kits and beaver <2 years old.

Figure 3-2. The logarithmic relationship between total body fat concentration (% ingesta-free wet mass) and the tail fat index (% dry matter of tail tissue) for adult (>1 year old) Castor canadensis from southern Manitoba, 1988-1990.

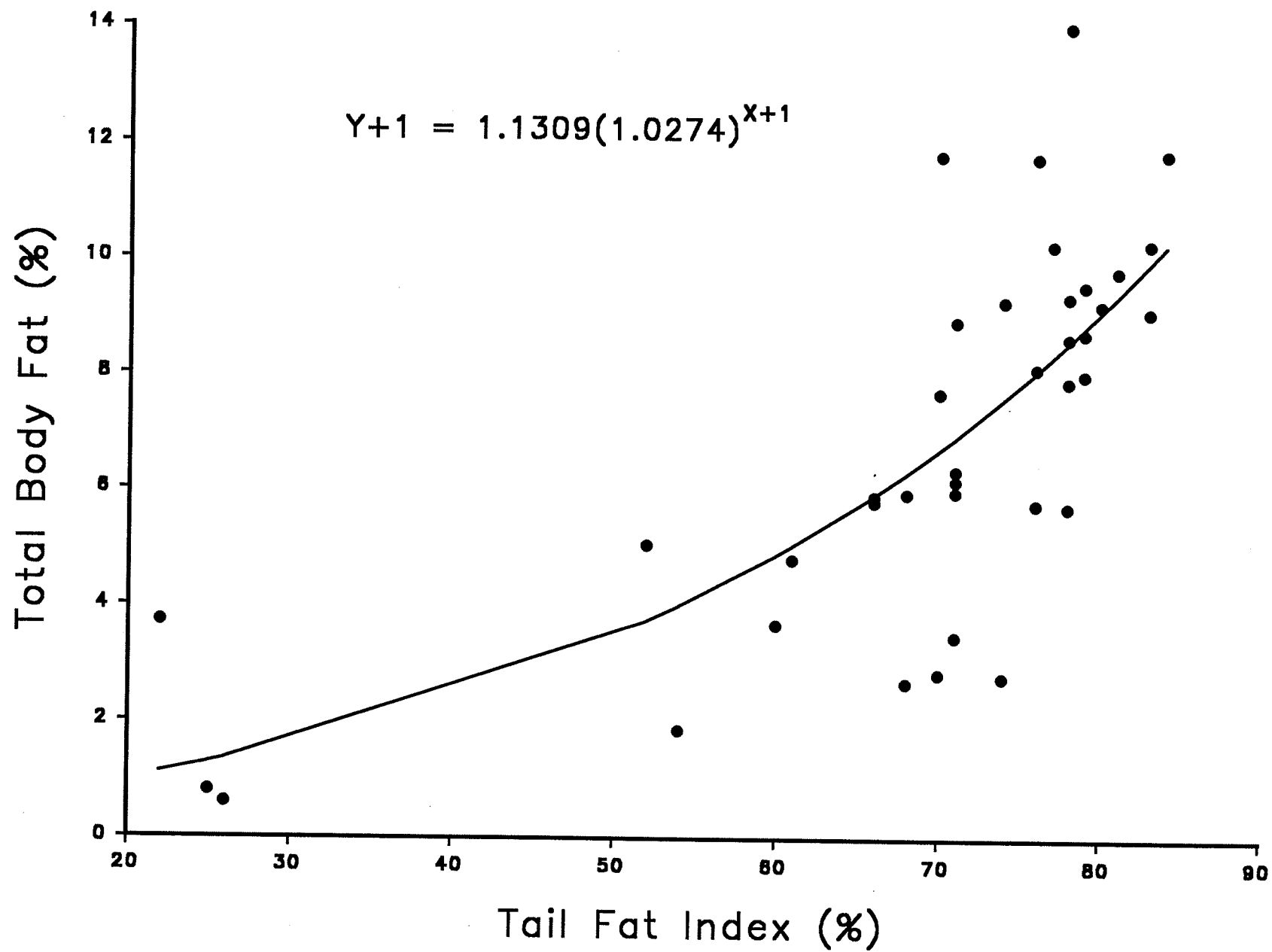


Figure 3-3. The relationship between total body fat concentration (% ingesta-free wet mass) and the SUB3 index of subcutaneous fat for adult (>1 year old) Castor canadensis from southern Manitoba, 1988-1990.

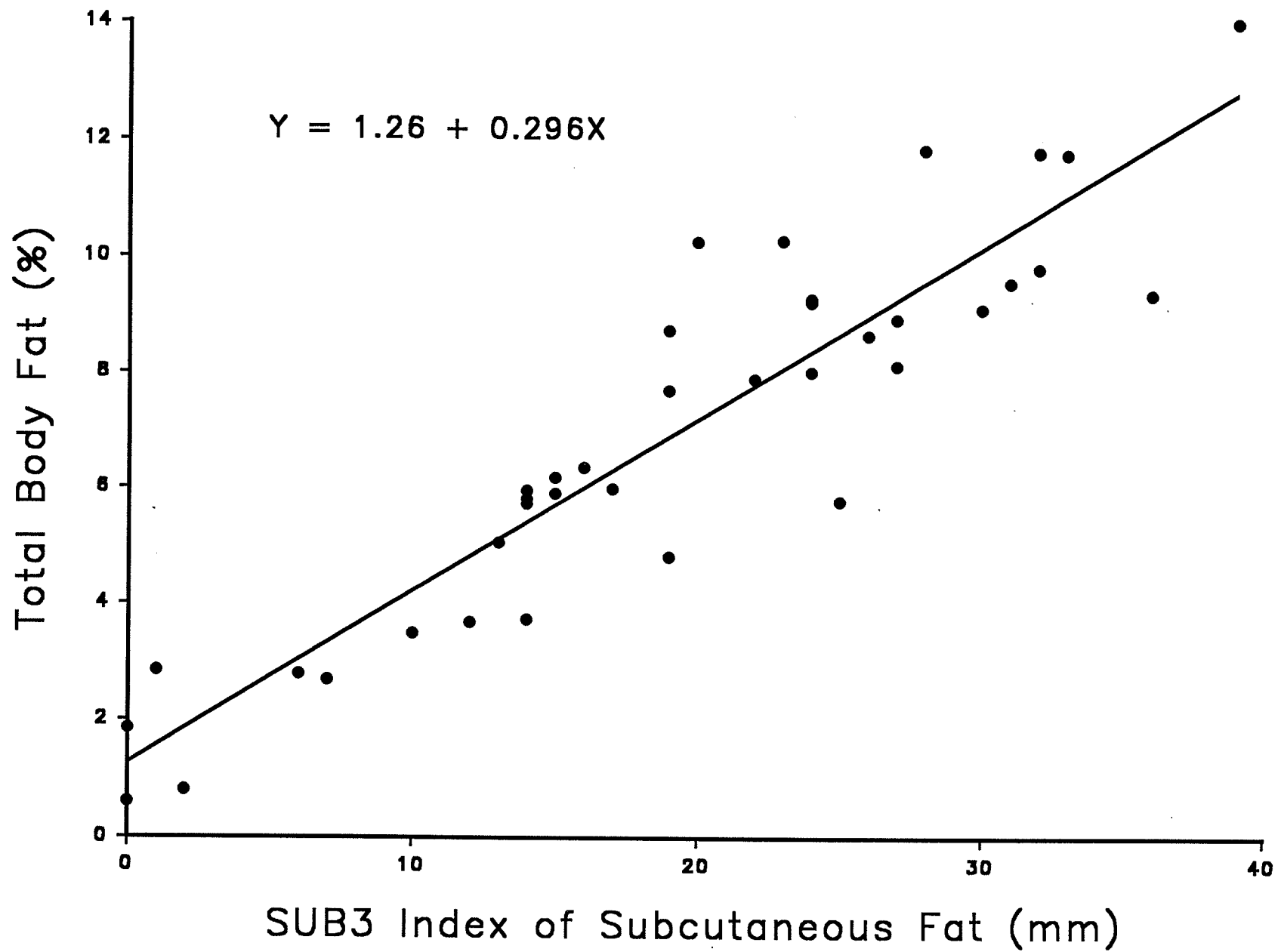


Table 3-5. Simple and multiple linear regressions of body fat concentration (% ingesta-free wet mass) on selected fat depots and indices available from skinned carcasses or whole kit beaver.

Independent variable(s)	Equation	r ² or R ²	n	P	RMSE ^a
Abdomft (g)	$Y = -3.50 + 4.826\ln(AF+1)$	0.87	21	<0.001	1.42
Kidft (g)	$Y = -9.78 + 6.281\ln(KF+1)$	0.83	21	<0.001	1.64
Kidind (%)	$Y = -14.20 + 6.336\ln(KI+1)$	0.88	21	<0.001	1.40
Tailfat (%)	$Y = -45.89 + 13.807\ln(TF+1)$	0.58	21	<0.001	2.59
Kidind, viscft (g)	$Y = -19.54 + 4.612\ln(KI+1) + 3.327\ln(VF+1)$ ^b	0.92	21	<0.001	1.18
Kidind, viscft, subpelvi (mm)	$Y = -16.76 + 3.324\ln(KI+1) + 2.643\ln(VF+1) + 2.604\ln(SP+1)$ ^c	0.94	21	<0.001	1.06
Sub2 (mm)	$Y = 1.79 + 0.416(S2)$	0.79	21	<0.001	1.81
Sub3 (mm)	$Y = 1.46 + 0.394(S3)$	0.83	21	<0.001	1.63
Abdomft, tailfat, length (mm)	$Y = 23.25 + 0.217(AF) + 0.117(TF) - 0.0300(L)$ ^d	0.93	21	<0.001	1.10

^aRoot mean square error.

^bIndividual coefficients significant at $P < 0.01$.

^cIndividual coefficients significant at $P < 0.05$.

^dIndividual coefficients significant at $P < 0.001$.

and KIDIND of kits ($P \geq 0.749$). Precision was best for the model with KIDIND, VISCFT and SUBPELVI; however, individual coefficients were significant at $P \leq 0.031$ in comparison to $P < 0.001$ for the model with ABDOMFT, TAILFAT and LENGTH.

The rate of increase of body fat content with SUB2 was greater in kits than in adults ($P < 0.001$). For adults, the percent fat vs SUB2 model was not improved by inclusion of LENGTH ($F_{1,33} = 0.04$, $P = 0.836$) or ingesta-free mass ($F_{1,34} = 0.21$, $P = 0.652$), implying that the relationship is independent of body size within this group.

Body fat concentration and ALEKIND were related according to a curvilinear model (Table 3-4) for adult beaver ($F_{1,35} = 70.64$, $P = 0.001$) and for beaver < 2 years old ($F_{1,31} = 72.46$, $P = 0.001$). The heart mass of adult beaver related directly to lean body mass ($F_{1,40} = 67.26$, $P = 0.001$), and the intercept differed from zero ($B_0 = 4.892$ kg, $P = 0.001$).

Interrelationships of Fat Depots

An asymptotic model best described the relationship between the TAILFAT and ABDOMFT depots of adult beaver (Fig. 3-4; $F_{3,41} = 18.33$, $P < 0.001$). A similar relationship was observed between the TAILFAT depot and the subcutaneous depot index, SUB3 (Fig. 3-5; $F_{3,41} = 16.87$, $P < 0.001$). The relationship between the SUB3 and ABDOMFT depots was also modeled as asymptotic (Fig. 3-6; $F_{3,41} = 44.94$, $P < 0.001$), since B_1 for the stable portion of the model was not different from zero ($\underline{t} = 1.14$, $df = 18$, $P = 0.135$).

Figure 3-4. The relationship between the tail fat index (% dry matter of tail tissue) and the mass of the abdominal fat (ABDOMFT) depot for adult (>1 year old) Castor canadensis from southern Manitoba, 1988-1990.

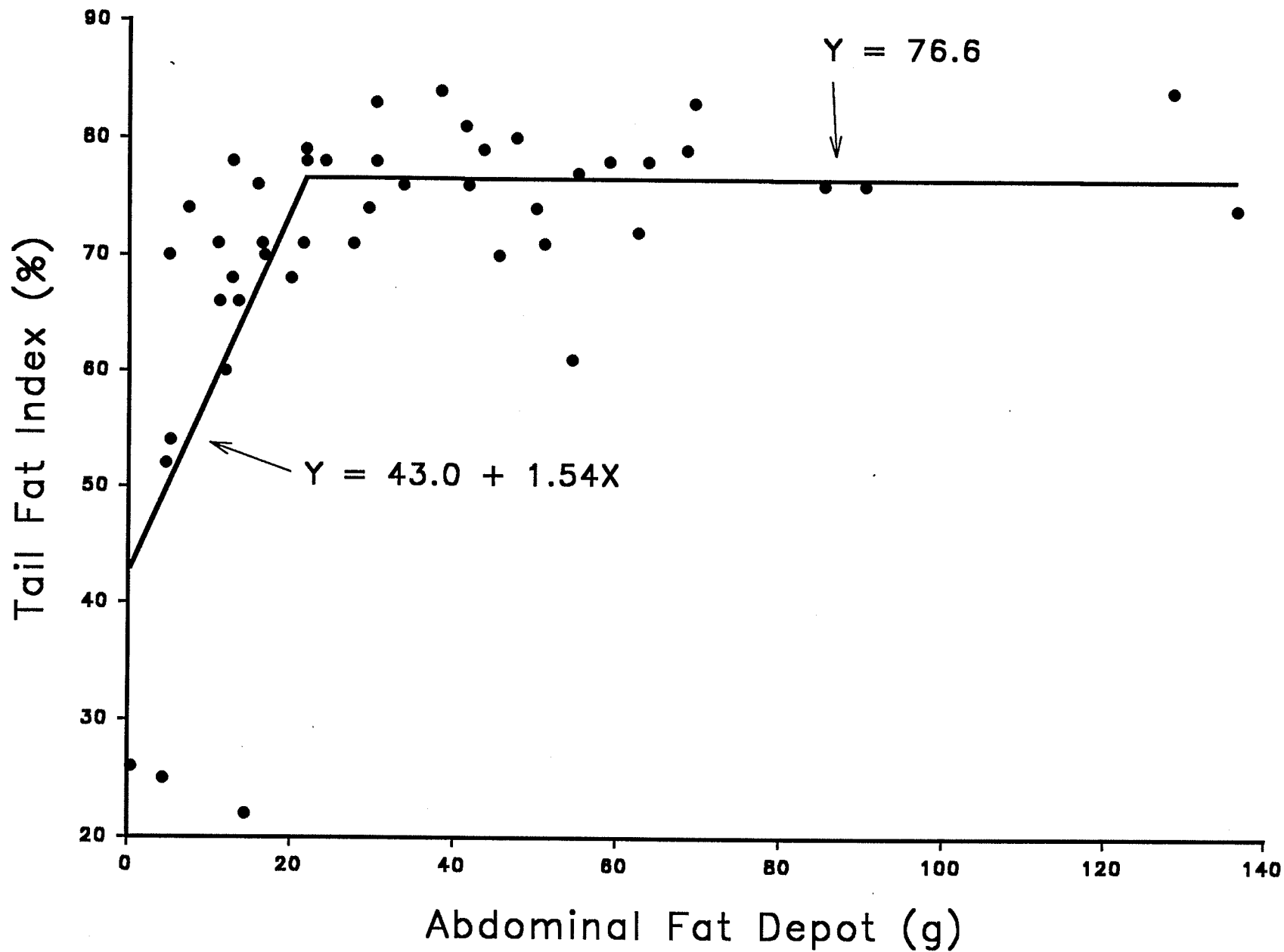


Figure 3-5. The relationship between the tail fat index (% dry matter of tail tissue) and the SUB3 index of subcutaneous fat for adult (>1 year old) Castor canadensis from southern Manitoba, 1988-1990.

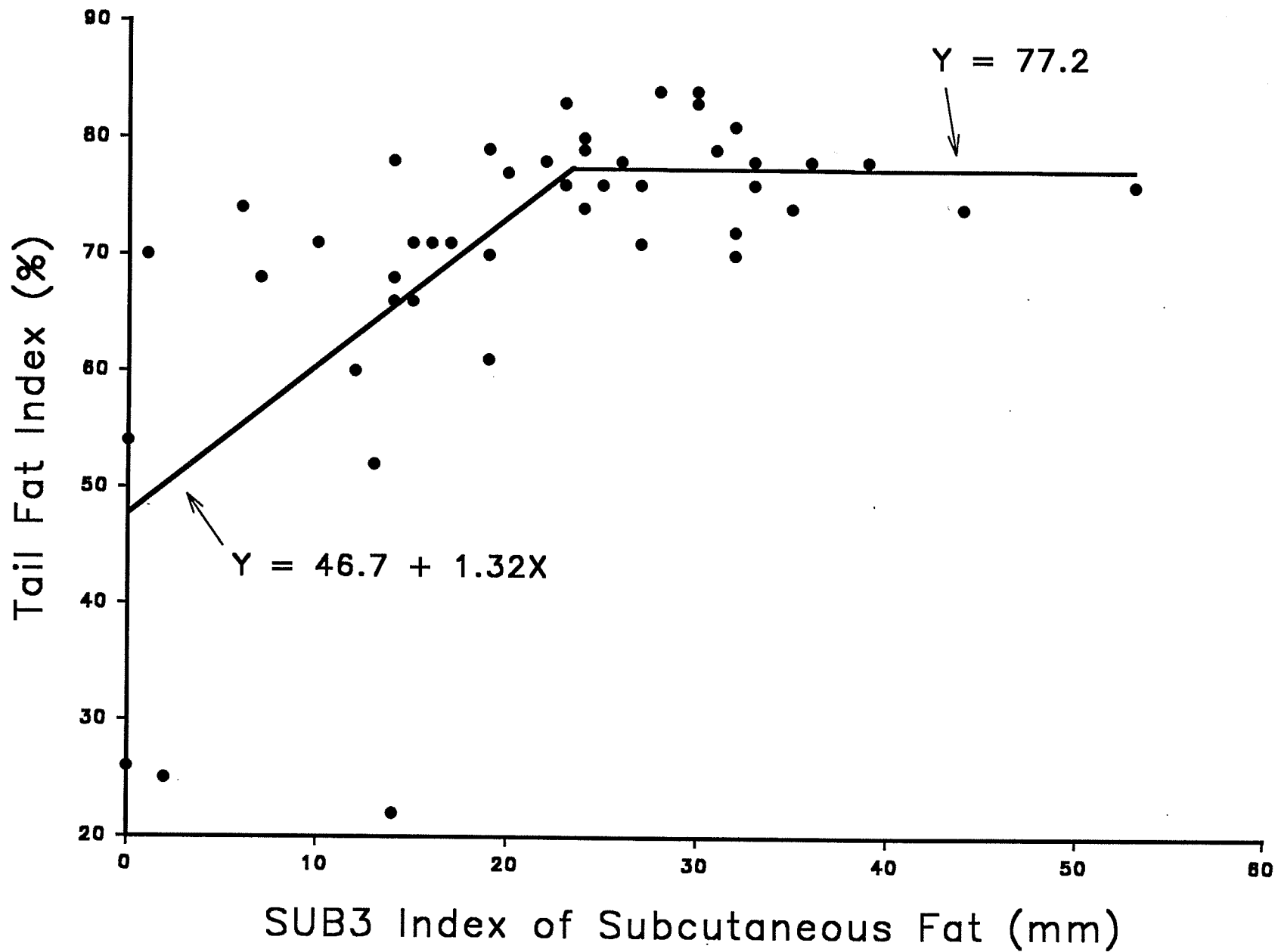
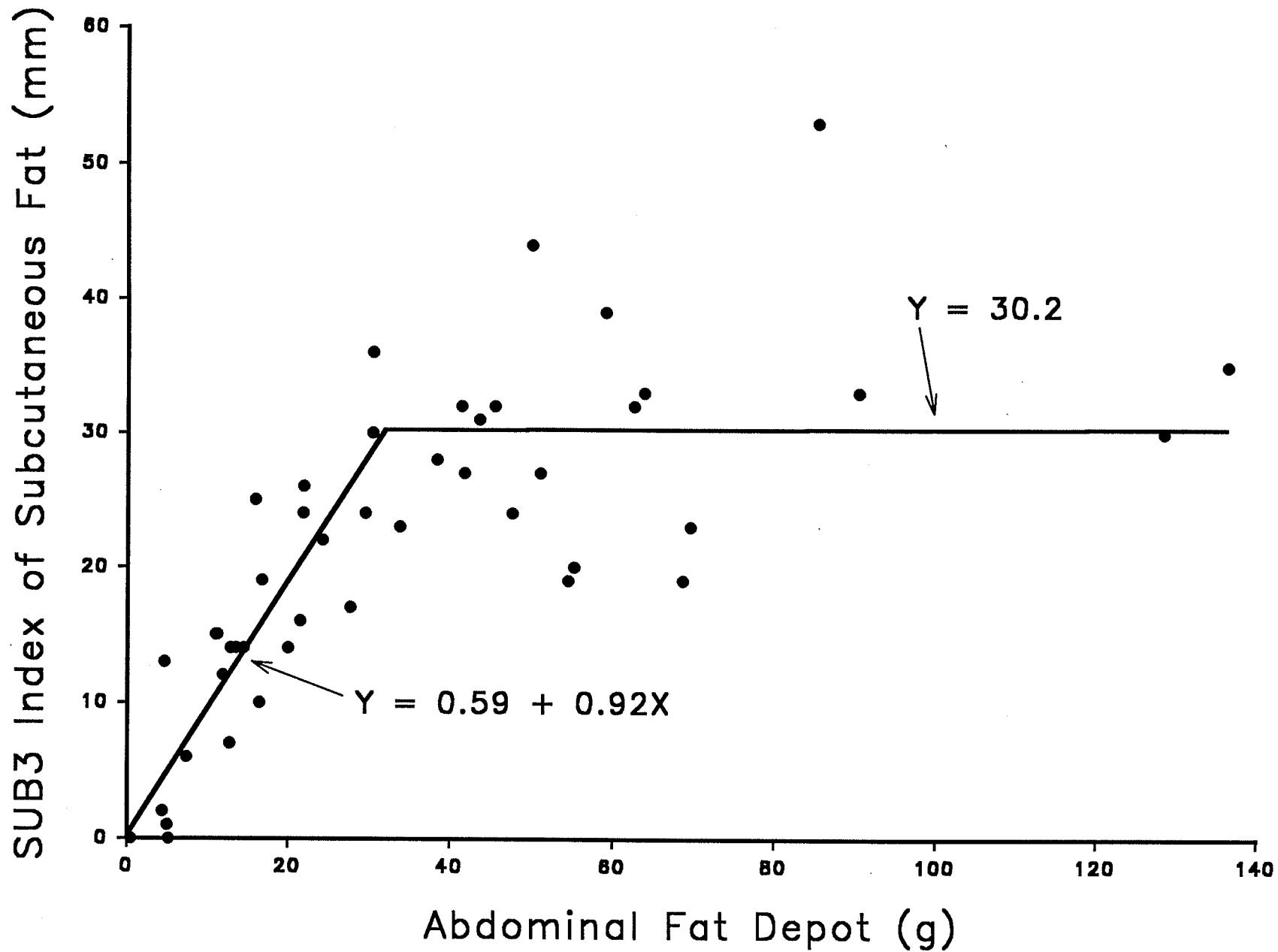


Figure 3-6. The relationship between the SUB3 index of subcutaneous fat and the mass of the abdominal fat (ABDOMFT) depot for adult (>1 year old) Castor canadensis from southern Manitoba, 1988-1990.



Body Crude Protein Mass

For kits, crude protein mass was predicted best from MUSCWT and HINDFT for carcasses, and from LENGTH, TAILWIDT and IFMASS for whole animals (Table 3-6). With the data for Kit Nos. 14 and 16 excluded, the RMSE decreased to 40 g for the model based on LENGTH and TAILWIDT, and to 52 g for the model based on MUSCWT and HINDFT. Linear relationships were relatively weak for body crude protein vs KIDWT or HEARTWT ($\text{RMSE} \geq 124$). Intercepts differed from zero for protein mass vs KIDWT ($B_0 = 342 \text{ g}$, $P = 0.037$), HEARTWT ($B_0 = 428 \text{ g}$, $P = 0.031$) and MUSCWT ($B_0 = 240 \text{ g}$, $P = 0.003$).

Among the variables available for adult carcasses, crude protein mass was best predicted from ZYGSKIN, and inclusion of TAILWT and TIB in the model improved the precision (Table 3-6). Body protein mass was directly related to MUSCWT ($\text{RMSE} = 390$, $P < 0.001$), KIDWT ($\text{RMSE} = 488$, $P < 0.001$) and HEARTWT ($\text{RMSE} = 450$, $P < 0.001$). The intercept of these relationships differed from zero for HEARTWT ($B_0 = 840 \text{ g}$, $P = 0.004$), but not for MUSCWT or KIDWT ($P \geq 0.132$). In whole adults, body crude protein was most strongly related to IFMASS, and IFMASS and LENGTH. For the model based on LENGTH and TAILWIDT, a sex effect was found for LENGTH ($P = 0.018$). Sex effects were also apparent for body crude protein vs IFMASS ($F_{2,38} = 5.78$, $P < 0.01$), and IFMASS and LENGTH ($F_{3,34} = 5.31$, $P < 0.005$). However, as LENGTH did not enter the model for females ($t = 1.60$, $df = 17$, $P = 0.128$), I chose to include this variable only in the model for males (Table 3-6).

Table 3-6. Simple and multiple linear regressions of body crude protein mass (g) on selected physical characteristics available from skinned carcasses or whole kit and adult (>1 year old) beaver.

Age class	Independent variable(s)	Equation	r ² or R ²	n	P	RMSE ^a	
Kit	Hindft (mm)	Y = -2266.9 + 22.604(HF)	0.80	22	<0.001	88	
	Tib (mm)	Y = -1364.9 + 26.405(TI)	0.78	22	<0.001	91	
	Hindft, tailwt (g)	Y = -1321.4 + 14.043(HF) + 1.842(TM) ^b	0.91	22	<0.001	60	
	Muscwt (g)	Y = 239.7 + 24.239(MW)	0.90	22	<0.001	63	
	Muscwt, hindft	Y = -744.2 + 8.247(HF) + 17.217(MW) ^c	0.93	22	<0.001	54	
	Length (mm), tailwidt (mm)	Y = -2239.8 + 3.624(L) + 5.052(TW) ^c	0.91	22	<0.001	60	
	Ifmass (g)	Y = 149.9 + 0.15324(IF)	0.88	21	<0.001	64	
	Length, tailwidt, ifmass	Y = -1414.2 + 2.363(L) + 3.191(TW) + 0.05631(IF) ^d	0.96	21	<0.001	40	96
Adult	Zygskin (mm)	Y = -7236.6 + 110.613(ZS)	0.85	34	<0.001	313	
	Tib	Y = -8592.6 + 92.846(TI)	0.78	44	<0.001	366	
	Zygskin, tib	Y = -8945.3 + 72.823(ZS) + 41.463(TI) ^b	0.90	34	<0.001	263	
	Zygskin, tib, tailwt	Y = -6130.6 + 51.465(ZS) + 27.171(TI) + 1.964(TM) ^e	0.95	34	<0.001	188	
	Mand2 (mm), tib, muscwt	Y = -6693.4 + 46.948(M2) + 29.959(TI) + 12.554(MW) ^f	0.91	42	<0.001	237	
	Zygskin, tib, tailwt, muscwt	Y = -5109.6 + 45.669(ZS) + 19.426(TI) + 1.541(TM) + 6.440(MW) ^c	0.96	34	<0.001	164	
	Zygrnd (mm)	Y = -7523.5 + 107.000(Z)	0.88	34	<0.001	287	
	Length, tailwidt	Y = -7326.6 + 7.886(L) + 15.918(TW) ^b	0.93	F ^g	<0.001	211	
		Y = -7326.6 + 8.041(L) + 15.918(TW) ^b		M			
	Ifmass	Y = 203.1 + 0.18284(IF)	0.95	F ^g	<0.001	179	
		Y = 129.2 + 0.19805(IF)		M			

Table 3-6. ..cont'd

Ifmass, length	$Y = 203.1 + 0.18284(IF)$	0.93	F^h	<0.001	187
	$Y = -3517.1 + 4.561(L) + 0.12734(IF)^b$	0.98	M	<0.001	114

^aRoot mean square error.

^bIndividual coefficients significant at $P < 0.001$.

^cIndividual coefficients significant at $P < 0.025$.

^dIndividual coefficients significant at $P < 0.05$.

^eIndividual coefficients significant at $P < 0.005$.

^fIndividual coefficients significant at $P < 0.01$.

^gSample included 21 female and 21 male beaver.

^hSample included 21 female and 20 male beaver.

Table 3-7. Simple and multiple linear regressions of body mineral mass (g) on selected physical characteristics available from skinned carcasses or whole kit and adult (>1 year old) beaver.

Age class	Independent variable(s)	Equation	r ² or R ²	n	P	RMSE ^a
Kit	Hindft (mm)	Y = -717.4 + 6.350(HF)	0.85	22	<0.001	21
	Tib (mm)	Y = -484.5 + 7.632(TI)	0.88	22	<0.001	18
	Tib, mand2 (mm)	Y = -644.4 + 5.272(TI) + 4.648(M2) ^b	0.90	21	<0.001	15
	Hindft, tailwidt (mm)	Y = -651.1 + 4.673(HF) + 2.056(TW) ^c	0.91	22	<0.001	16
	Tib, ifmass (g)	Y = -346.8 + 4.828(TI) + 0.01965(IF) ^c	0.93	21	<0.001	14
Adult	Mand2	Y = -1800.5 + 24.432(M2)	0.77	41	<0.001	76
	Tib	Y = -1532.6 + 17.107(TI)	0.70	43	<0.001	84
	Mand2, tib	Y = -1881.0 + 16.365(M2) + 6.957(TI) ^b	0.80	41	<0.001	71
	Mand2, tailwidt	Y = -1516.7 + 15.636(M2) + 4.261(TW) ^c	0.85	41	<0.001	62
	Length (mm)	Y = -1239.8 + 1.784(L)	0.82	F ^d	<0.001	68
	Length, mand1 (mm), tailwidt	Y = -1717.3 + 2.285(L)		M		
		Y = -1484.5 + 1.035(L) + 14.588(M1) + 3.545(TW) ^e	0.87	41	<0.001	58
	Ifmass	Y = 151.2 + 0.02945(IF)	0.84	F ^d	<0.001	61
	Ifmass, mand2	Y = 68.3 + 0.03752(IF) + 13.220(M2) ^c	0.89	M	<0.001	51

^aRoot mean square error.

^bIndividual coefficients significant at P<0.05.

Table 3-7. ..cont'd

^cIndividual coefficients significant at $P < 0.001$.

^dSample included 21 female and, for Length: 20 male beaver, for Ifmass: 19 male beaver.

^eIndividual coefficients significant at $P < 0.005$.

Body Mineral Mass

For kits, the best single predictors of mineral mass were TIB and HINDFT (Table 3-7). Use of multiple predictor variables led to slightly improved precision. For adult beaver carcasses, body mineral mass was directly related to MAND2 and TIB, with increases in precision for multivariable models, particularly if TAILWIDT was included (Table 3-7). For whole adult animals, the best precision among single predictor variables was found for LENGTH or IFMASS. Sex effects were found for the relationships between mineral mass and both LENGTH ($F_{2,37} = 3.99$, $P < 0.05$) and IFMASS ($F_{2,36} = 4.77$, $P < 0.025$).

DISCUSSION

Mass and Concentration of Body Fat

For several species of birds, lipid energy resources can be predicted accurately from body mass and structural characteristics (Johnson et al. 1985; Castro and Myers 1990). This ability would be of immense value in ecological or physiological studies of live beaver. Although body fat mass could be estimated from ingesta-free mass and zygomatic width in adult beaver, precision was sufficiently poor to limit the usefulness of this procedure.

The abdominal fat depot was the best single predictor of body fat in adult beaver, and is recommended because it can be measured quickly and yields estimates of high precision. As

the abdominal fat depot and the various indices of tail and subcutaneous fat can each vary independently, inclusion of these variables in multivariate models led to improved precision. Although the significance of the individual terms was greatest with SUB3 in the three-variable model, use of SUBBRISK provides the practical advantage that it can be collected without pelt damage.

The body fat mass of kits was predicted best from depots and indices available from skinned carcasses, with no apparent advantage to the collection of subcutaneous depot indices. Since models were derived from a sample in which only one kit had a body fat content $<5.31\%$, estimates of fat reserves for lean kits should be treated cautiously. The model based on the abdominal fat depot and the tail fat index is recommended, due to its high precision and potential to accurately predict body fat in lean kits.

The percent body fat of adult beaver was estimated precisely from the abdominal fat depot and a measure to control for size variation. As the fundamental relationship is not linear, use of the depot by itself, rather than predicted values, would produce inaccurate assessments of body fat reserves. The lipid resources of tail tissue were both mobilized and saturated at lower body fat levels. Consequently, the model based on the tail fat index is weakly predictive for beaver with a high fat content in their tail tissue.

Body fat content related strongly to several individual

indices of subcutaneous fat; however, the fat content of lean adult beaver would be overestimated by these relationships. Similar to the situation in cervids (Huot 1988; Watkins et al. 1991), deposition of fat in the backfat and rump-pelvic depots of beaver began after substantial amounts had been stored elsewhere. Therefore, as reported for other mammals (Anderson et al. 1972; Stribling et al. 1984), the predictive value of these depots is extremely limited for beaver. As a single predictor, the SUB3 cumulative index has a number of positive attributes. Body fat content related strongly and directly to this predictor, and the relationship was not influenced by the physical size of adults, although estimates might be slightly biased for lean beaver. The evidence suggests that use of this index by itself might allow for comparison at the interval level (Kleinbaum and Kupper 1978). However, it would not be correct to compare kits and adults, and as with all indirect measures, it is recommended that predicted values be used for comparative purposes.

Unlike the situation for adults, size did not influence relationships between body fat content and the kidney fat or abdominal fat depots of kits. Failure to detect a size effect was likely due to a lack of independence between kit size and time, and the limited variation of fat content within the sample. Therefore, all predictive relationships for the body fat resources of kits are tentative. Because the kidney fat index should at least partially control for size variation, this variable should be used to predict body fat content from

carcasses. Strong precision was found with the subcutaneous index SUB3 as the predictor, although estimates for lean kits would likely be biased.

For adults, the multivariable models based on the abdominal fat depot and length, with either SUBBRISK or TAILFAT and SUB3, are strongly recommended to predict body fat content. Examination of residuals suggested that bias might occur in other multivariate models. Although some limited bias was suggested for the model with SUBBRISK, practical advantages of the model include ease of data collection and avoidance of damage to the pelt. The model which predicted fat content from the abdominal fat depot, length and TAILFAT is recommended for kits. The influence of length on the model, as well as the relationship between the abdominal fat depot and the tail fat index, were similar in both kits and adults, and individual coefficients were highly significant. Therefore, although the sample of kits was small, model elements behaved as expected in relation to the results for adult beaver, thereby suggesting a fundamentally sound model.

The form of the relationship between % body fat and TAILFAT of kits differed from that of adults, apparently due to concurrent maturation of this and other depots in kits. This relationship might have been quite different if kits had been sampled at the same time. In these respects, and because the maximum fat content is less in kits (Aleksiuk 1970b, this study), the age effect apparent for the fat content of tail tissue is similar to that for the femur marrow of cervids

(Cheatum 1949; Torbit et al. 1988). The curvilinear relationship between body fat content and the kidney fat index of beaver is similar to that of cervids (Finger et al. 1981; Torbit et al. 1988; Watkins et al. 1991). Body fat content was predicted better by the kidney fat index than by the mass of kidney fat, a finding consistent with the practise of using kidney mass to control for size variation.

Heart mass-corrected kidney fat indices of Arctic beaver (Aleksiuk and Cowan 1969b) were substantially lower than those of beaver from this study. Description of their methodology is sparse, but there is no indication that Aleksiuk and Cowan (1969b) used less than complete kidney fat depots from both kidneys to construct their indices. If this is so, then perirenal fat mass and body fat content were much greater in the southern beaver. Nevertheless, the possibility persists that indices differed in their basic formulation, and are therefore not comparable.

Contrary to the assumptions of Aleksiuk and Cowan (1969b), the rate of increase in % body fat with the heart mass-corrected index was not constant. In particular, % body fat was relatively constant from mid to high index values in young beaver. Given the curvilinear relationship between % body fat and mass of the kidney fat depot in beaver and other species, this index would be expected to model fat content rather poorly. However, weak linear models may be appropriate for index values $<1000 \text{ mg} \cdot \text{g}^{-1}$ in young beaver (D. W. Soprovich, Unpublished data). Therefore, if indices in both studies were

determined with the same formula, the index used by Aleksiuk and Cowan (1969b) may have been suitable to indicate relative differences in body fat content between samples. Contrary to the assumption of Aleksiuk (1968), heart mass was a poor indicator of lean body mass in adult beaver, and thus the index used by Aleksiuk and Cowan (1969b) was not independent of size. Clearly, inferences based on such an index should be treated cautiously.

If the distribution of body fat is independent of size, small beaver should have more body fat for a given thickness of subcutaneous fat than large beaver. As predicted, the relationship of % body fat to the subcutaneous index SUB2 was affected by size when kits and adults were analyzed together. In contrast, and despite considerable variation in body size, the relationship of % body fat to subcutaneous depots in adults was not affected by size. Although the statistical power of the test was low, this suggests that small and large adults with the same average thickness of subcutaneous fat will have a similar body fat content. Therefore, it appears that smaller adult beaver may allocate a greater proportion of their fat to subcutaneous depots, perhaps to mitigate thermoregulatory costs in water. To beaver in northern environments, cold water presents a formidable challenge to body temperature control (MacArthur and Dyck 1990). Exposure to cold water forces beaver to incur an energetic cost beyond maintenance in a thermoneutral environment, and subcutaneous fat is an effective means of insulation in this medium

(Scholander et al. 1950). As rate of cooling is size-dependent (MacArthur and Dyck 1990), storage of subcutaneous fat could be particularly important to smaller adults.

Total body fat relates poorly, if at all, to the fat content of the M. plantaris in beaver. This contrasts with the strong relationships reported between % body fat and the fat content of the M. gastrocnemius and M. biceps femoris of cervids (Ringberg et al. 1981; Watkins et al. 1991). Although % body fat was similar, the dry matter content of the M. plantaris of beaver was considerably less than that of the M. gastrocnemius in white-tailed deer fawns (Watkins et al. 1991). Inclusion of the Achilles tendon by Watkins et al. (1991) might have been partially responsible for this divergence. There was little separable fat on, or between, the muscles of the posterior tibial superficial group (Young 1937) in beaver. Conversely, white-tailed deer can allocate >50% of their fat to inter- and intramuscular locations, and store only minor amounts of fat in subcutaneous depots (McCullough and Ullrey 1983). As a mechanism to reduce body heat loss, storage of subcutaneous fat may have been strongly selected for in beaver.

Interrelationships of Fat Depots

The deposition and mobilization of fat among depots was similar for beaver from southern Manitoba and those from the Arctic (Aleksiuk 1968). The fat resources of the tail were mobilized after considerable depletion of other depots, and

the greatest accrual of subcutaneous fat, and particularly coelomic fat, occurred after the tail tissue was saturated. Coelomic depots continued to increase in mass after the saturation, or near-saturation, of subcutaneous depots, and mobilization occurred in the reverse order.

Pond (1978) suggested that thermal benefits, though frequently invoked, are generally not responsible for the distribution of fat in the majority of mammals. For beaver, I concur with the suggestion by Aleksiuk (1968) that the evolution of patterns of fat deposition and withdrawal among depots is related to energetic considerations. By itself, the fur of beaver may be responsible for only a portion of the total insulation in cold water. Since this species may incur a substantial thermoregulatory cost in water (MacArthur and Dyck 1990), the timely deposition of subcutaneous fat in appropriate locations could augment pelage insulation, and thereby mitigate the cost of submersion.

In contrast to terrestrial mammals (Pond 1978), beaver begin utilizing abdominal fat stores prior to accessing subcutaneous depots. This physiological divergence is consistent with the energy mitigation hypothesis for a species which must forage in cold water during winter. That the distribution of fat relates to energetic constraints is also supported by an apparent preferential allocation of fat to subcutaneous sites in smaller adult beaver, and limited or no fat storage in muscle tissue.

Body Crude Protein Mass

Of the individual measures available from whole or skinned kits, total crude protein mass was predicted best from wet M. plantaris mass. Condition indices for mammals have often incorporated kidney mass (Finger et al. 1981; Torbit et al. 1988) or heart mass (Aleksiuk and Cowan 1969b), predicated on the assumption that these variables strongly model body mass. However, the M. plantaris mass modeled the crude protein mass of beaver, particularly kits, much better than did either kidney or heart mass. Therefore, to control for size variation, or to provide an indirect measure of metabolic demand, use of M. plantaris mass introduces the least random error. However, with the possible exception of M. plantaris and kidney masses of adults, indices constructed from these measures would still be mass-dependent because of their non-zero intercepts, and the problems associated with this characteristic (Blem 1984) would limit their usefulness.

Among potential indicators of structural size that are readily available from the carcasses of kits, length of the tibia or hind foot are recommended, because both are good predictors. In contrast to the multivariate model based on M. plantaris mass, the size-based multivariate model was sensitive to individuals which had almost certainly catabolized protein reserves. Such sensitivity is expected for a model which predicts protein reserves from skeletal indicators, and the insensitivity of the other model suggests that M. plantaris mass was responsive to dynamic variation in

body protein. A similar dichotomy was apparent when the body protein mass of adult females was modeled from ingesta-free mass versus skeletal measurements (D.W. Soprovich, Unpublished data). Multivariate models with ingesta-free mass or M. plantaris mass are recommended due to their predictive capability and apparent ability to model protein dynamics.

Body crude protein of adult beaver was estimated precisely from ingesta-free mass. The influence of body length in males but not females, and the more precise estimates of males, appear to relate to temporal variation in female protein resources (Part I) and the ability of ingesta-free mass to integrate this dynamic protein variation. Body protein of males was greater than that of females for beaver of the same length and tail width, although temporal variation in females, together with differences in other structural characteristics, likely had some bearing on this difference. Furthermore, the contrast between sexes would have been greater if crude protein had not incorporated fetuses and reproductive tissue. Precise estimates of crude protein are possible from carcasses if a number of characteristics are measured; however, the simple and multivariate models with ingesta-free mass are recommended due to their highly significant individual coefficients and potential to model dynamic protein variation. If tail mass or zygomatic width cannot be measured, mandible length is a generally available characteristic which allows for reasonably precise estimates.

Body Mineral Mass

Of the single variables examined, tibia length best predicted the body mineral mass of kits. The precision improved if ingesta-free mass was incorporated in a multivariate model with tibia length. For adults, body minerals were predicted from structural measures with similar precision for both carcasses and whole beaver. The most precise estimates were achieved for a model based on ingesta-free mass and mandible length.

Recommendations

By themselves, depots and indices are often poor indicators of the amount of body fat and other nutrients in beaver. As suggested by Watkins et al. (1991), use of predicted values is strongly recommended over the use of raw indices or depots. The predictive functions in this study were developed in a hierarchial fashion, such that precision often relates directly to available variables. Practically, one can select a function to balance precision requirements with constraints such as cost, time, and/or specimen availability. These predictive functions provide an opportunity to use large samples to test hypotheses on bioenergetics or other aspects of the biology of beaver. If one chooses to use predictive functions outside the range for which they were developed, serious errors can result (eg., Castro and Myers 1990). Therefore, estimates should be treated cautiously for any beaver which are smaller or larger

than those from this study. If body mass is measured prior to pelt removal, it is possible to determine ingesta-free mass and thereby apply those functions which require this measure.

Summary and Conclusions

In this study, kit and adult beaver were clearly able to remain in positive energy balance after freeze-up, thereby achieving peak body fat levels in winter. Furthermore, beaver generally maintained high levels of body fat throughout the winter, with kits attaining fat levels similar to those of adults. This ability to accrue and sustain body fat while restricted to a sub-ice environment, suggests that foods of highly digestible energy may form a significant component of the beaver's winter diet. Contrary to suggestions by other researchers, the fat stores of beaver apparently do not function as a significant energy source to mitigate shortfalls in cache nutrients. However, the substantial body fat resources of adult beaver at spring break-up suggests that this source of energy could be critical during severe winters or springs, particularly for pregnant females. Due to their investment in fetal tissue, and perhaps as a consequence of a late winter diet low in digestible protein, adult females experienced a protein deficit during gestation. Although the body mineral reserves of adult females varied seasonally, the factors responsible for this fluctuation are presently unclear.

Beaver adjusted the mass of their digestive tract seasonally, a finding which strongly suggests that they respond to a poor quality diet by increasing their digestive efficiency. This strategy for the provision of energy and other nutrients could be strongly selected for. By more fully

extracting nutrients from available forage, beaver should minimize the time and metabolic costs associated with foraging in cold water. Furthermore, this strategy allows for maximum utilization of resources during a period when foods are generally thought to be limited and of poor quality. Conceivably, this strategy also allows for a smaller cache of stored foods, thereby decreasing foraging costs and perhaps the risk of predation. The heavier digestive tracts of females compared to males, likely relates to the greater reproductive costs of females and perhaps also their need to process more ingesta than males. Finally, a heavy and presumably efficient cecum may be important to the maintenance of fat reserves in beaver.

Smaller adult beaver appear to allocate body fat preferentially to subcutaneous depots. Furthermore, inter- and intramuscular fat storage appears minimal in beaver, and stores in the abdominal cavity are mobilized prior to subcutaneous reserves. These findings suggest that the high metabolic costs of activity in cold water may have influenced the dynamics and distribution of body fat in this species.

The predictive functions developed in this study allow precise estimates of body nutrient reserves from skinned carcasses and whole beaver. Because depots appear to vary independently, use of several measures produced the most precise and accurate estimates. Since curvilinear models often best described relationships between body nutrient reserves and specific depots and indices, and because the

intercept of most linear models failed to pass through the origin, predicted values are preferable to the sole use of indices.

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Appendix I. Precision of estimates and the identification and handling of data which received special treatment.

Precision of Estimates

Despite further sampling and pooling within replicates, and assay of additional replicates, five fat estimates failed to meet the precision tolerance criterion (Table A1-1). Final dry matter estimates were precise, suggesting that imprecise fat estimates were not due to variation among replicates. For example, the SE of the final dry matter estimate for Kit No. 13 was 0.59 g (CV = 0.3%), demonstrating that the homogenate was uniformly mixed.

Identification of Data to Receive Special Treatment

In the following text, the term "dry matter accounted for" (DMAF) refers to the proportion of the dry matter which was accounted for by the sum of the three assays. The dry matter of the mammalian body consists almost entirely of ash, protein and fat (Robbins 1983). Because assays for these components should account for considerably more than 80% of the dry matter, I chose to treat observations with DMAFs of $\approx 80\%$ or less as "problem data". To further identify problem data, one-tailed tests of significance for outliers were conducted (Grubbs and Beck 1972), with the reduced data set re-examined following deletion of outliers.

The removal of kits with DMAF $< 80\%$ left 16 observations in the data set. The observation with the lowest DMAF in this data set was not a significant outlier ($t = -2.39$, $df = 14$, P

Table A1-1. Estimates of body composition, and precision of the estimates, of kit and adult (>1 year old) beaver.

Body component	Precision of estimate (SE)						
	Estimate			Observations which did not meet tolerance criterion ^a			
	n	$\bar{x} \pm s$	Range	$\bar{x} \pm s$	Beaver number	Estimate	SE
Ash (% dry matter)	67	11.53 $\pm$ 1.96	8.58-17.58	0.40 $\pm$ 0.22	Adult-5	11.13	1.02
Protein (% dry matter)	67	56.64 $\pm$ 8.45	40.22-78.17	0.50 $\pm$ 0.23			
Fat (% dry matter) ^b	22	23.85 $\pm$ 6.31	4.45-35.49	0.63 $\pm$ 0.60	Kit-3	28.42	1.25
					Kit-8	24.59	1.91
					Kit-10	29.53	1.73
					Kit-13	20.43	1.97
	45	20.36 $\pm$ 7.80	1.97-36.38	0.33 $\pm$ 0.29	Adult-14	22.73	2.71
Final dry matter (g/450 g wet matter)	67	165.2 $\pm$ 16.6	129.8-193.2	0.4 $\pm$ 0.3 ^c			

^aTolerance criterion was a SE $\leq$ 1% of dry matter.

^bEstimates not adjusted for change in thimble mass; n = 22 for kits, n = 45 for adults.

^cBased on n = 65; final dry matter of two observations calculated from two replicates.

≈ 0.07). However, this observation was treated as a problem datum because of its large residual ($e_i = -7.23\%$), the low power of the statistical test, and because its DMAF was less than for some adult problem data. Observations with DMAF $< 80.30\%$ were excluded from the adult data set. Examination of this data set for outliers led to the deletion of Adult Nos. 38 ($P < 0.025$), 11 ($P < 0.025$) and 43 ($P < 0.05$). With problem data excluded, the mean DMAF was 91.37% ($s = 2.42\%$) and 92.79% ($s = 2.01\%$) for kits and adults, respectively. The mean precision of the fat estimates of problem data was 1.12% ($s = 0.76\%$) and 0.76% ($s = 0.40\%$) for kits and adults, respectively.

The DMAF should be independent of the water content of a homogenate; however, this was not true for kits or adults (Figs. A1-1, A1-2). The problem data were among those with the lowest water content. A strong inverse relationship is typical for the fat and water contents of whole body homogenates (eg., Campbell and Leatherland 1980; Robbins 1983). Therefore, this indicates that homogenates with a high fat content constituted the problem data. Plots of DMAF against the dry matter ash or protein content supported this conclusion. Furthermore, despite extensive sampling and the high precision of ash, protein and dry matter estimates, the poor precision of fat estimates suggests that the assay for fat was responsible for the incomplete extractions in these cases.

Because dry matter is comprised almost entirely of ash,

Figure A1-1. The proportion of dry matter accounted for by the combined assays for ash, fat and protein (%) in relation to the body water content (% ingesta-free wet mass) of kit Castor canadensis. The fat estimate is not adjusted for change in the thimble mass.

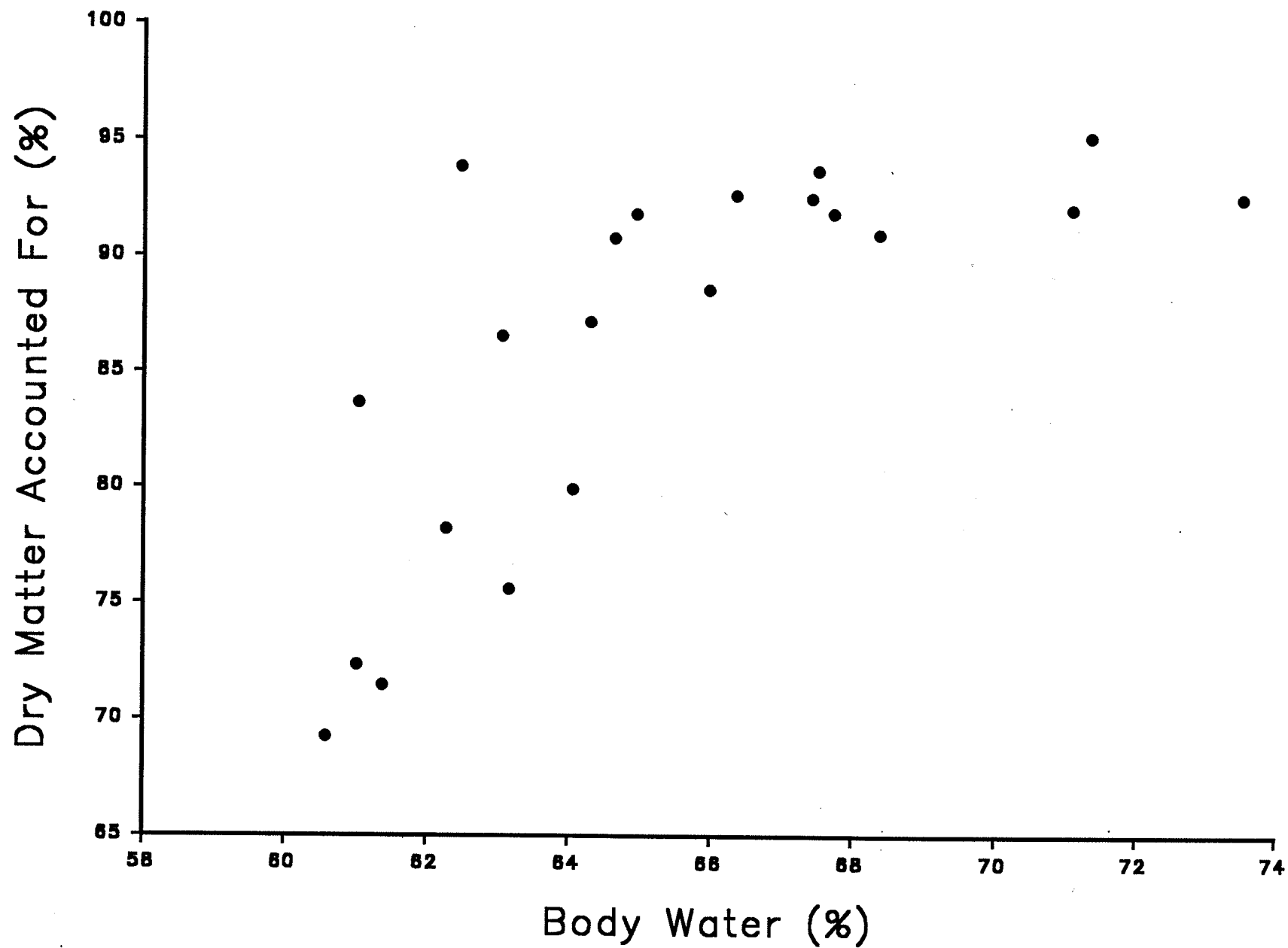
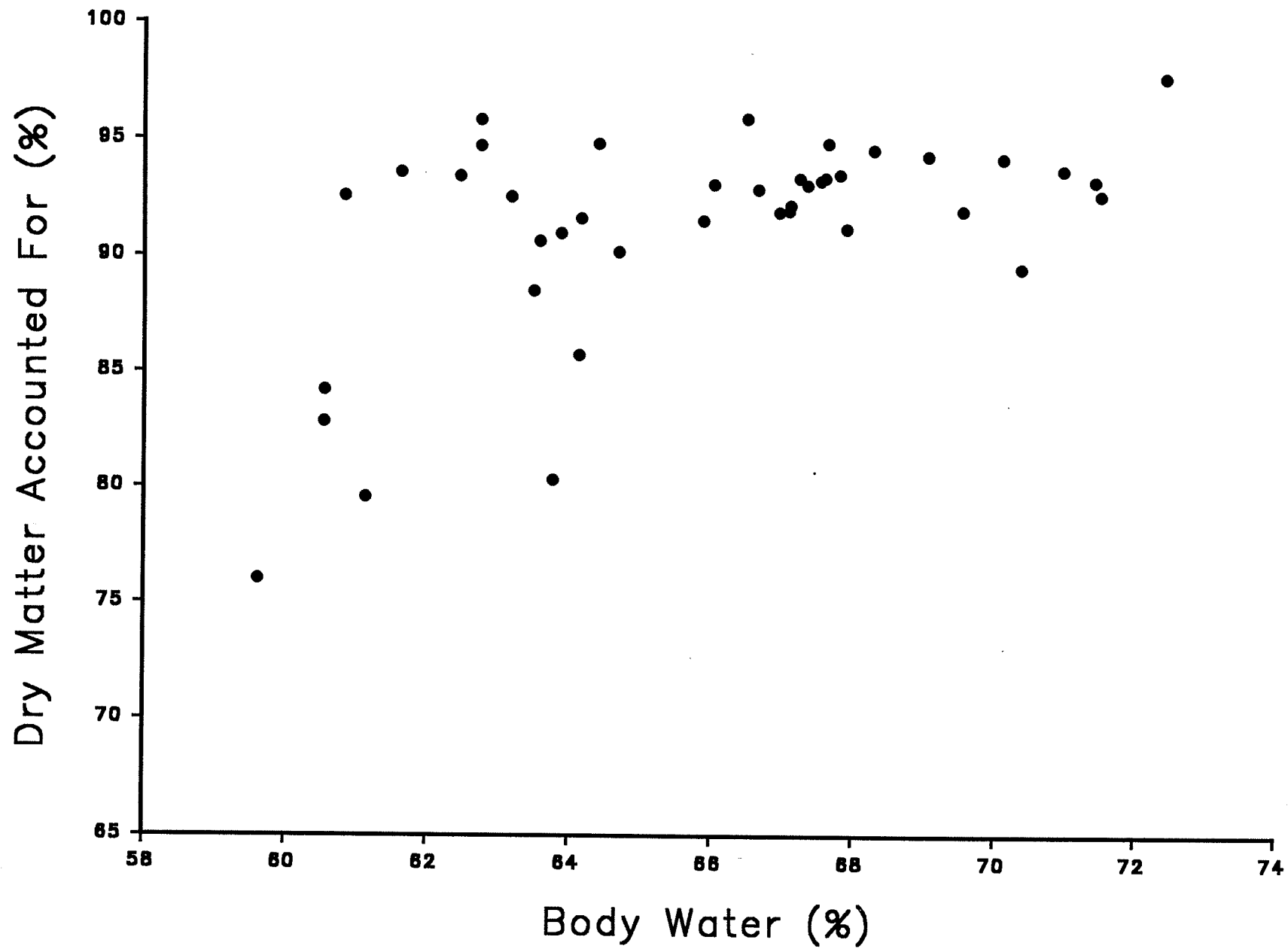


Figure A1-2. The proportion of dry matter accounted for by the combined assays for ash, fat and protein (%) in relation to the body water content (% ingesta-free wet mass) of adult (>1 year old) Castor canadensis. The fat estimate is not adjusted for change in the thimble mass.



protein and fat, the dry matter ash plus protein content should vary directly with body water content. The existence of strong linear relationships for kits and adults (Table A1-2) indicates that the assays for ash and protein were not responsible for the problem data. Furthermore, if the assay for protein was inaccurate, estimates of body protein mass from skeletal measurements (Part III) would have been extremely low for observations with very low DMAF. However, large negative residuals were not observed for these observations. Finally, dry matter ash and protein values for problem data were similar to those of other observations with similar water content.

For adults, dry matter fat content varied inversely with body water content (Fig. A1-3; $r^2 = 0.64$, $P < 0.001$) and five of the problem data had low fat estimates for their water content. Exclusion of problem data greatly improved the model fit ($r^2 = 0.83$), further suggesting an inaccurate fat estimate for these data. The assay for fat did not appear responsible for the low DMAF of one problem datum (Fig. A1-3). For this adult (No. 43), adjustment for the change in thimble mass increased the DMAF to 87.31%, and the initial protein estimate decreased by 3.09% with additional sampling. Therefore, the fat estimate for this observation was accepted.

The water content of fat-free tissue in young mammals declines to a constant proportion as the animal grows (Robbins 1983). Although the relationship between body fat and water contents may vary with age, an inverse trend should exist.

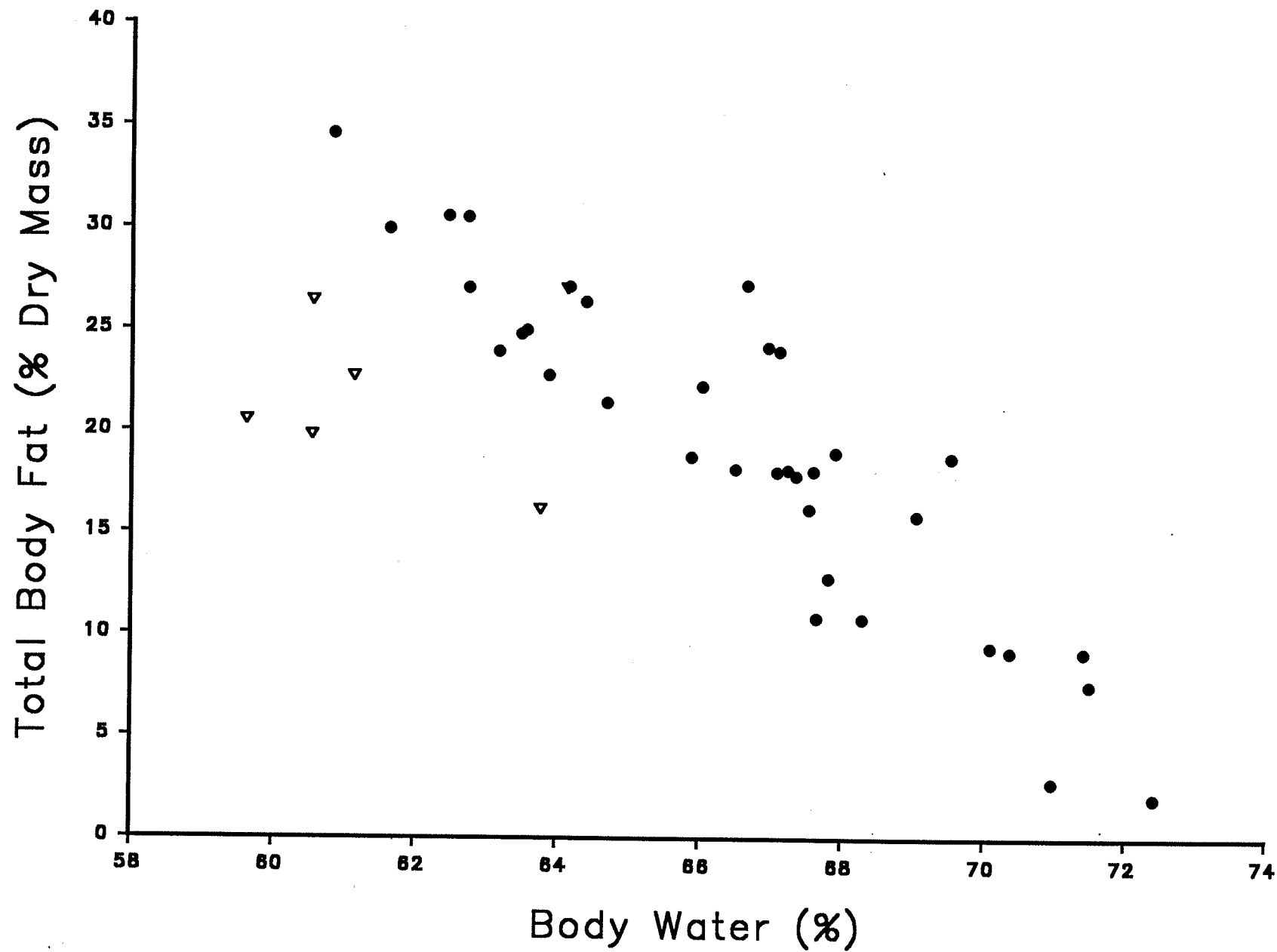
Table A1-2. Prediction of dry matter ash plus protein content (%) and dry matter fat content (%) from body water content (% ingesta-free wet mass) of kit and adult (>1 year old) beaver.

Dependent variable	Age group	Equation	r ²	n	P	RMSE ^a
Ash plus protein	Kit	$Y = -93.28 + 2.38(\%W)$	0.89	21	<0.001	3.17
	Adult	$Y = -99.02 + 2.59(\%W)$	0.82	41	<0.001	4.12
Fat ^b	Kit	$Y = 71.81 - 0.73(\%W)$	0.17	21	<0.05	6.03
		$Y = 93.24 - 1.08(\%W)$	0.25	17	<0.025	6.23
		$Y = 149.89 - 1.87(\%W)$	0.67	14	<0.001	4.45
	Adult	$Y = 194.91 - 2.57(\%W)$	0.90	10	<0.001	2.82
		$Y = 139.92 - 1.83(\%W)$	0.64	41	<0.001	4.62
		$Y = 181.69 - 2.44(\%W)$	0.83	35	<0.001	3.37

^aRoot mean square error.

^bEstimates not adjusted for change in thimble mass.

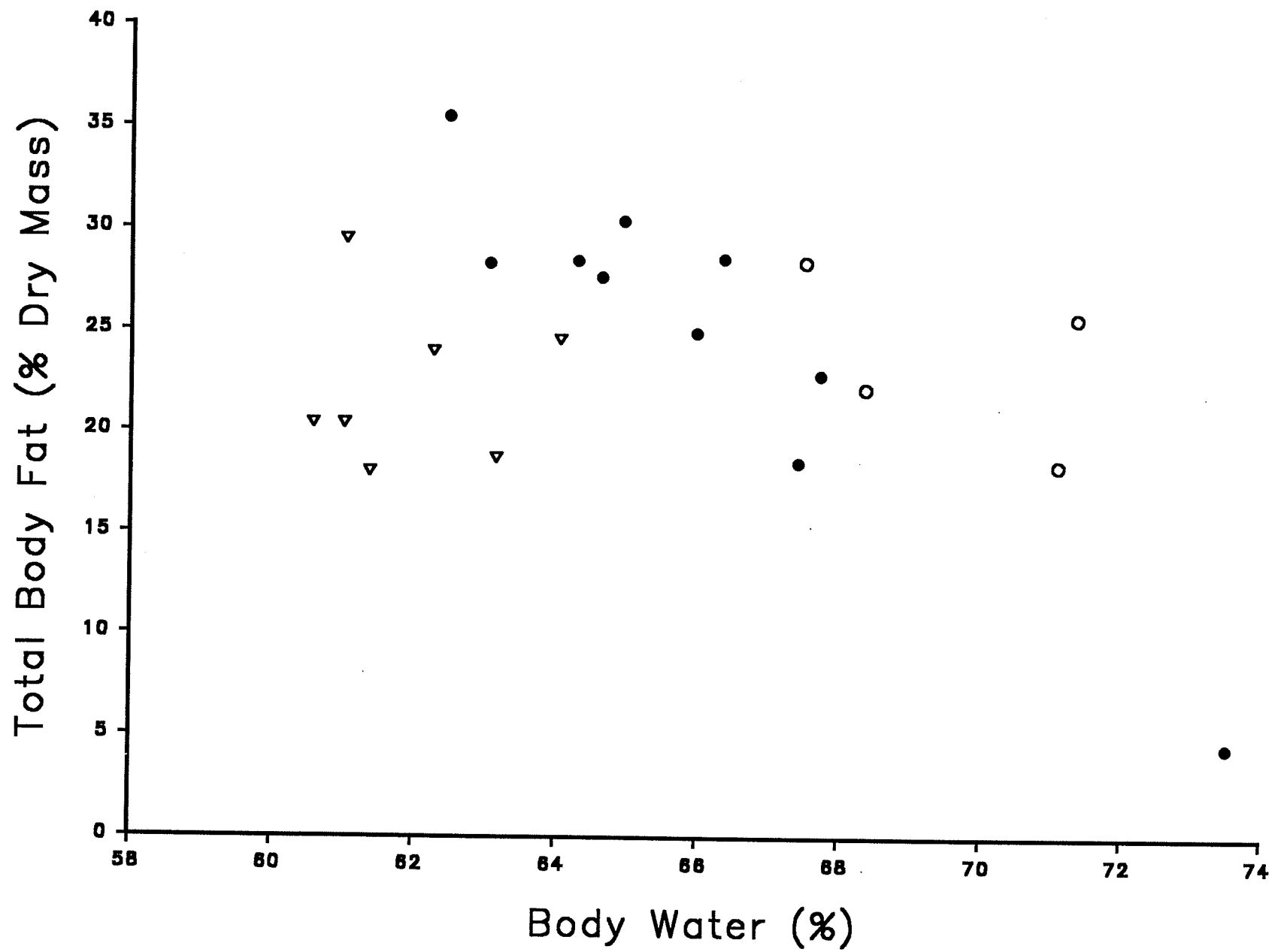
Figure A1-3. The estimate of body fat concentration (% ingesta-free dry mass) in relation to the body water content (% ingesta-free wet mass) of adult (>1 year old) Castor canadensis. The fat estimate is not adjusted for change in the thimble mass. Observations denoted by open triangle are problem data.



Dry matter fat content related poorly to body water content for kits (Fig. A1-4; $r^2 = 0.17$, $P = 0.030$). The water content of the fat-free tissue [(mass of water)/(mass of water + ash + protein)] decreased with time ($F_{1,19} = 6.98$, $P = 0.016$). This finding was due principally to the higher water content ($P < 0.001$) of 4 kits sampled prior to 12 October ($\bar{x} \pm SE = 76.79 \pm 0.005\%$, $n = 4$), in comparison to kits sampled after 4 November ($\bar{x} \pm SE = 75.07 \pm 0.002\%$, $n = 17$).

Due to their high water content of fat-free tissue, earlier-sampled kits also had a high dry matter fat content for their body water content. With these four data excluded, the water content of fat-free tissue was not inversely related to time ($F_{1,15} = 0.90$, $P = 0.359$). Furthermore, after controlling for the influence of this age-related variation, the relationship between the body fat and water contents did not improve (Table A1-2; $n = 17$). As with adults, the fat estimates of the problem data were typically low for their water content. The fit to the inverse model improved considerably with the problem data excluded from the complete data set ($r^2 = 0.67$), or from the data set which did not include younger kits ($r^2 = 0.90$). These findings indicate that the assay did not completely extract fat for the problem data. The relationship between dry matter fat content and body water content was similar to that of adults for this last data set (Table A1-2).

Figure A1-4. The estimate of body fat concentration (% ingesta-free dry mass) in relation to the body water content (% ingesta-free wet mass) of kit Castor canadensis. The fat estimate is not adjusted for change in the thimble mass. Observations denoted by open triangle are problem data; observations denoted by open circle are those with a high water content of lean tissue.



Treatment of Problem Data

The analyses suggested that the estimates of ash content and protein content were generally reasonable. Therefore, I chose to use the combined ash and protein content (% dry matter) to predict fat content (% dry matter) for kits and adults separately. To develop these predictive relationships, several data subject to minor errors, data for which thimble weight could not be adjusted and problem data were excluded from analyses. These strong relationships (see Part I) were then used to estimate the dry matter fat content for problem data, exclusive of Adult No. 43.

Appendix II. Variation in some physical characteristics used to predict body nutrient reserves of kit and adult (>1 year old) beaver from southern Manitoba, 1988-1990.

Table A2-1. Data on physical characteristics.

Characteristic	Kit				Adult			
	n	$\bar{x}$	s	Range	n	$\bar{x}$	s	Range
Viscft (g)	22	38.5	16.8	18.5-94.1	40	66.6	31.4	24.1-170.1
Subpelvi (mm)	22	5.5	2.3	1-9	40	4.7	2.5	0-10
Subbrisk (mm)	22	6.4	2.5	1-10	40	5.4	2.8	0-11
Submid1 (mm)	22	4.0	1.7	0-7	40	4.0	2.4	0-8
Submid2 (mm)	22	4.4	2.5	0-9	40	4.0	2.6	0-9
Subtail1 (mm)	22	1.9	1.3	0-4	40	1.5	1.4	0-5
Subrmpel (mm)	19	0.9	0.9	0-3	31	0.2	0.5	0-2
Sub1 (mm)	22	14.8	6.3	1-24	38	13.4	7.7	0-27
Sub2 (mm)	22	20.2	8.3	2-32	38	18.0	9.7	0-36
Sub4 (mm)	19	24.3	9.1	11-37	29	17.6	10.7	0-41
Hindft (mm)	22	151.7	7.5	137-165				
Tib (mm)	22	95.7	6.4	84-109	44	128.5	7.4	115-143
Zygrnd (mm)	19	79.6	3.4	74-87	34	101.9	7.0	94-121
Zygskin (mm)					34	96.0	6.7	87-115
Mand1 (mm)					41	38.3	2.5	34-45
Mand2 (mm)	21	82.4	3.0	76-87	42	101.0	5.5	90-112
Tailthik (mm)	22	26.5	2.8	22-32				
Tailwidt (mm)	22	91.5	9.0	78-119	43	141.4	15.3	113-179
Tailwt (g)	22	191.9	49.3	115.2-332.8	34	547.5	152.6	328.0-950.4
Heartwt (g)	22	21.2	3.7	14.3-27.1	43	45.0	11.6	26.9-71.0
Kidwt (g)	22	50.4	9.0	37.3-75.7	44	101.2	21.4	62.8-159.4