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VARIATIONS ANNUELLES DE LA COMPOSITION CORPORELLE ET DES HORMONES DE REPRODUCTION CHEZ LE RENARD ROUX (*Vulpes vulpes*)

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RÉSUMÉ

Nous avons vérifié s'il existait des variations annuelles de la composition corporelle chez des renards roux (*Vulpes vulpes*) maintenus sur un régime alimentaire constant. Nous avons premièrement développé des modèles prédisant la composition corporelle à partir de renards vivants ou de carcasses, en mettant en relation des mesures pondérales, morphométriques et électriques avec les teneurs en eau, en gras, en protéines et en minéraux obtenues par l'analyse des carcasses. Ces modèles ont permis d'estimer mensuellement la masse des composantes corporelles chez 12 renards gardés en captivité au Jardin zoologique du Québec. Malgré une légère augmentation de la masse corporelle au cours de l'étude, les réserves adipeuses ont diminué de 50% durant l'été. Au contraire, les contenus en protéines, en eau et en minéraux étaient plus élevés en été. Nous avons également quantifié les variations mensuelles de la FSH, de la progestérone, de la testostérone, du phosphore et de l'albumine sanguins.

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INTRODUCTION GÉNÉRALE

La compréhension de la dynamique des composantes corporelles chez les animaux revêt une grande importance pour les études écologiques puisque cette dynamique est liée à la survie (ex. Peterson 1977) et au succès reproducteur des individus d'une espèce (ex. Poulle *et al.* 1995). En effet, la composition corporelle d'un animal renseigne sur sa condition physique, aide à détecter les périodes et les événements critiques dans sa vie et permet d'estimer la qualité de son habitat (Farley et Robbins 1994). Aux fins d'études écologiques, les composantes corporelles normalement retenues sont: l'eau, les lipides, les protéines et les minéraux. La masse et la proportion relative de ces composantes peuvent varier selon le sexe, l'âge, la saison et les conditions environnementales. Chez les animaux adultes, la teneur en minéraux est relativement stable mais il en va autrement des protéines, des lipides et de l'eau. Cependant, bien que le contenu en protéines puisse être partiellement responsable des variations de la composition corporelle (Torbit *et al.* 1985; Buskirk et Harlow 1989; Huot 1989; Poulle *et al.* 1995), la majeure partie des variations est attribuable à l'accumulation ou au catabolisme des réserves adipeuses utilisées comme source d'énergie (Allen 1976) et aux variations du contenu en eau qui est inversement corrélé au contenu lipidique, sur une base relative (Sheng et Huggins 1979; Robbins 1983; Gauthier et Thomas 1990).

Chez les vertébrés, les lipides emmagasinés dans les tissus adipeux peuvent servir de réserve d'énergie, de couche isolante pour conserver la chaleur, de support et de remplissage autour de certains organes (Pond 1978). Les lipides emmagasinés sont catabolisés lors de périodes où la nourriture se fait rare ou lorsque les dépenses énergétiques sont accrues, par exemple lors des périodes de reproduction ou de la migration (Prestrud et Nilssen 1992). Cependant, l'emmagasinage de gras comporte également des inconvénients. En effet, une augmentation de la masse corporelle associée à un contenu lipidique plus élevé entraîne une augmentation de la dépense énergétique durant les activités physiques et un ralentissement des mouvements, ce qui est désavantageux autant pour un prédateur (Prestrud et Nilssen 1992) que pour une proie. La régulation des dépôts de gras possède donc une valeur adaptative, étant donné que le gras ne devrait être accumulé que lorsque nécessaire (Pond 1981), d'où la présence de variations annuelles du gras corporel chez plusieurs espèces animales (Prestrud et Nilssen 1992; Poulle *et al.* 1995).

L'existence chez les grands herbivores des zones tempérées et boréales d'un cycle annuel de croissance, d'accumulation et d'utilisation des réserves corporelles, sous contrôle hormonal est maintenant bien connue (Mitchell *et al.* 1976; Schwartz *et al.* 1984; Tyler 1987). Ainsi, chez les cervidés, l'appétit et la prise alimentaire sont plus grands durant la saison estivale, au moment des pics de lactation ou de croissance. Durant la saison morte, la prise alimentaire volontaire décroît et la croissance cesse. On assiste alors à une mobilisation des réserves corporelles, bien que les femelles en gestation épargnent des réserves lipidiques en prévision du début de l'allaitement (Tyler 1987). Chez les mâles, la prise alimentaire cesse pratiquement durant le rut, de sorte que les animaux utilisent une grande partie de leurs réserves corporelles (ex. Schwartz *et al.* 1984). Ces mécanismes ont notamment été décrits chez le cerf élaphe (*Cervus elaphus* : Mitchell *et al.* 1976) et le caribou (*Rangifer tarandus* : Crête *et al.* 1993). On pensait initialement que le métabolisme basal suivait ce cycle annuel, mais des études récentes chez le cerf de Virginie (*Odocoileus virgianinus*) indiquent que le métabolisme est constant au cours de l'année (Mautz *et al.* 1992).

La bioénergétique des carnivores est beaucoup moins connue que celle des herbivores. Poulle *et al.* (1995) ont observé récemment que les coyotes du sud-est québécois (*Canis latrans*) étaient 28% plus lourds en automne et en hiver qu'en été. Le pourcentage moyen de gras des coyotes dépendait de la saison et doublait presque de l'été à l'automne (10 *versus* 18%). Pour ces coyotes, le printemps et l'été semblaient être des périodes de rareté de nourriture car les animaux des deux sexes avaient perdu entre la fin de l'hiver et l'été 17% de leur masse protéique. Soulignons que les mammifères ne peuvent supporter une baisse de plus de 30% de leur masse protéique sans compromettre leur survie (Cahill 1970, Torbit *et al.* 1985). Selon Poulle *et al.* (1995), les réserves de gras accumulées par les coyotes durant l'automne n'auraient pas pour fonction de leur permettre d'affronter une période prolongée de déficit énergétique mais plutôt de survivre durant les courtes périodes de jeûne auxquelles ils sont régulièrement confrontés au cours de l'hiver. Chez les renards arctiques de Svalbard (*Alopex lagopus*), Prestrud et Nilssen (1992) ont observé que la masse de lipides diminuait durant l'été, mais non celle des protéines. Ils en ont conclu que le patron de déposition du gras chez les renards arctiques est une adaptation pour pallier aux périodes hivernales de rareté de nourriture, pour augmenter la réserve d'énergie nécessaire à la reproduction et pour affronter les basses températures. Après la période hivernale, les réserves corporelles restantes pourraient être utilisées pour la reproduction.

Il est cependant plus facile de comprendre les avantages d'un cycle au niveau des réserves adipeuses que d'expliquer les variations de la masse protéique. Comme l'ont suggéré Poulle *et al.* (1995), la diminution de la masse protéique pendant l'été pourrait être due à une carence alimentaire. Plusieurs études ont démontré (Reimers *et al.* 1982; Torbit *et al.* 1985; Buskirk et Harlow 1989; Huot 1989; Virgil et Messier 1992) que même si le gras est la principale source d'énergie de réserve (Allen 1976), les protéines musculaires sont aussi catabolisées chez des individus qui sont en déficit énergétique. De plus, il est probable que le catabolisme des protéines augmente avec la diminution des réserves adipeuses.

À partir de ces observations, nous pouvons suggérer plusieurs explications pour les variations de la composition corporelle. Premièrement, la diminution du contenu lipidique pendant l'été peut être causée par un manque de nourriture durant cette période, surtout si on observe également une diminution de la masse protéique. Deuxièmement, ces variations peuvent résulter d'une modification dans le régime alimentaire de l'animal, comme, par exemple, le remplacement de la viande par des fruits. Étant donné que les fruits sont pauvres en lipides et en protéines (Pritchard et Robbins 1990), une augmentation de la consommation de fruits accompagnée d'une réduction de la consommation de proies animales pourrait résulter en une diminution des teneurs en gras et en protéines. Troisièmement, ces variations pourraient exister indépendamment du régime alimentaire de l'animal. Dans la présente étude, nous nous attarderons à cette dernière hypothèse.

Les faibles réserves corporelles estivales des coyotes du sud-est québécois s'accompagnent d'un taux de fécondité remarquablement bas autant au Nouveau-Brunswick qu'au Québec (Moore et Millar 1984; Poulle *et al.* 1995). Crête et Lemieux (1994) ont proposé que les coyotes de la péninsule gaspésienne compenseraient le manque de proies animales en consommant des fruits au milieu de l'été, ce qui influencerait les composantes corporelles et indirectement la reproduction future. Chez les renards arctiques, Prestrud et Nilssen (1992) ont démontré que les femelles qui s'étaient reproduites le printemps précédent étaient moins grasses en hiver que celles qui s'en étaient abstenu. Selon eux, le cycle annuel des réserves adipeuses des renards facilite grandement leur succès reproducteur. Plusieurs études (Thomas 1982; Todd et Keith 1983; Thomas 1990) ont d'ailleurs clairement démontré qu'il existe un lien entre les réserves adipeuses et la fertilité. En effet, un minimum de réserves adipeuses serait nécessaire pour qu'une femelle se reproduise. Par exemple, chez les femmes, le pourcentage de gras est important pour le maintien du cycle menstruel normal (peut-être pour le rôle que joue le gras périphérique dans la conversion des androgènes en

oestrogènes; McArdle *et al.*, 1996). Le cycle menstruel souvent perturbé des femmes athlètes en est un bon exemple. Il y aurait cependant d'autres facteurs, pour l'instant peu connus, qui entreraient en ligne de compte. Il devient intéressant de quantifier les variations de la composition corporelle pour reconnaître les teneurs lipidiques critiques pour qu'un animal se reproduise. Cependant, dans une première étape, il est primordial de quantifier le cycle annuel des hormones de reproduction chez des animaux bien alimentés.

De par ses fonctions de transport des nutriments, des déchets métaboliques cellulaires et des hormones, le sang présente un milieu de choix pour puiser des informations sur l'état nutritif et physiologique des animaux (Huot 1988). En suivant des constituants sanguins qui sont reliés au régime alimentaire par exemple, nous pourrions établir une relation entre leurs valeurs et la condition physique des renards roux. Il faut cependant noter que les indices sanguins semblent surtout utiles pour identifier des carences plutôt que pour comparer la condition physique relative d'animaux normaux (Huot 1988). De plus, leur concentration renseigne sur les contenus mais non sur les flux.

La composition corporelle est l'un des meilleurs indicateurs de la condition physique des animaux puisqu'elle permet notamment d'estimer les variations des réserves adipeuses et celles du contenu protéique. Elle est habituellement déterminée en broyant les carcasses d'animaux afin d'obtenir un échantillon homogène pour les analyses (Huot *et al.* 1995) ou par dissection (Adamczewski *et al.* 1987; Ouellet 1992). Parce que ces méthodes sont coûteuses, difficiles à utiliser sur le terrain et qu'elles nécessitent l'utilisation d'animaux morts, il devient intéressant de développer une technique plus rapide qui pourrait s'appliquer à des animaux vivants. Un bon modèle pour prédire la composition corporelle d'animaux vivants fera appel à des mesures simples à obtenir, s'appliquera facilement sur le terrain et sera peu coûteux et rapide.

Chez les carnivores, quelques chercheurs (Prestrud et Nilssen 1992; Pond *et al.* 1994; Poulle *et al.* 1995) ont développé des modèles pour prédire la composition corporelle avec des valeurs obtenues par l'analyse de carcasses, mais peu d'entre eux se sont attardés à développer des modèles pouvant s'appliquer à des animaux vivants (Roby 1991; Farley et Robbins 1994). À l'aide de tels modèles, il devient alors possible de suivre les fluctuations annuelles de la composition corporelle chez un même individu, éliminant ainsi les variations interindividuelles qui peuvent limiter l'interprétation des résultats.

Notre étude a donc deux objectifs qui constituent les deux chapitres de ce mémoire. Le premier chapitre porte sur le développement de modèles de régression multiple pour estimer les différentes composantes corporelles à partir d'indices simples à mesurer sur des carcasses ou des renards vivants. Le deuxième chapitre concerne la vérification de l'existence de variations annuelles de la composition corporelle, des hormones de reproduction et de constituants sanguins chez des renard roux gardés en captivité et maintenus sur un régime alimentaire constant.

Chapitre I

Prediction of body composition of live and post-mortem red foxes (*Vulpes vulpes*)

Cet article étant destiné à la revue *Journal of Wildlife Diseases* pour fins de publication, le format utilisé répond aux exigences de la revue.

Résumé

Nous avons pris une série de mesures (longueurs, circonférences, pinçées de gras sous-cutané, masses et résistance électrique) sur 29 renards roux (*Vulpes vulpes*) avant et après leur mort. Nous avons ensuite déterminé la composition corporelle des carcasses par l'analyse des homogénats des viscères, des carcasses et de la peau. Nous avons développé 8 modèles de régression multiple pour prédire la teneur en eau, en gras, en protéines et en minéraux chez des renards vivants ou morts, en utilisant les mesures corporelles comme variables indépendantes. Tous les modèles étaient très significatifs ($p < 0{,}0001$) et nécessitaient 3 ou 4 variables explicatives. Les coefficients de détermination (r^2) ajustés variaient entre 0,95 pour la masse d'eau et 0,81 pour la masse des minéraux. Les modèles couvraient une large gamme de conditions étant donné que le pourcentage de gras des 29 échantillons variait entre 1,1 et 28,4%. Nos modèles sont rapides à utiliser, peu coûteux et ne nécessitent pas l'euthanasie des animaux.

Abstract

We took a series of measurements (lengths, circumferences, skinfolds, masses and resistance) on 29 red foxes (*Vulpes vulpes*) of both sexes before and after their death. We determined the body composition of each carcass by chemical analysis of homogenized samples of viscera, carcass and skin. We then developed 8 multiple regression models to predict body water, fat, protein, and mineral, using body measurements as independent variables taken on live or dead animals. All final models were highly significant ($p < 0.0001$) and included 3 or 4 explanatory variables. Adjusted coefficients of determination varied between 0.95 for water mass and 0.81 for mineral mass. The models cover a wide range of conditions as percent body fat in the 29 samples varied between 1.1 and 28.4%. Our models can serve for management or research purposes with living or dead red foxes as they are quick, inexpensive and non-destructive.

Introduction

Understanding the dynamics of animal body composition is of great importance for ecological studies, as it can be related to survival (e.g. Peterson, 1977) and reproductive success (e.g. Poulle et al., 1995). The body composition of an animal also reveals its physical condition and can provide cues on habitat quality, in addition to identifying critical times or events in its life cycle (Farley and Robbins, 1994). Many studies (Huot and Picard, 1988; Buskirk and Harlow, 1989; Prestrud and Nilssen, 1992; Poulle et al., 1995) have related indices of body composition with values obtained by chemical extraction, but only few models have been developed for live animals (Roby, 1991; Farley and Robbins, 1994). Obtaining sample sizes adequate for management and research purposes necessitates fast and accurate methods of determining body composition of live and dead animals.

Body composition is usually obtained by grinding an animal to provide an homogenate for sampling and analysis (Huot et al., 1995), or by dissection and weighing (Adamczewski et al., 1987; Ouellet, 1992). However, as these methods are time-consuming, expensive and difficult to use in the field, researchers have relied on indices to estimate body composition. As fat reserves are the primary source of energy in case of nutritional deficiency, most of the indices are related to fat content (Poulle et al., 1995). Qualitative indices based on estimates of fat deposits in different parts of the body (e.g. Hammill, 1983) remain highly subjective and must be used cautiously by different observers (Prestrud and Nilssen, 1992). Body or carcass mass, kidney fat, femur marrow fat, and dorsal fat are the most commonly used indices (Huot, 1988). However, these measurements apply mainly to dead animals, which excludes the possibility to use these methods to monitor the condition of a given animal.

Several non-destructive methods also exist for assessing water and fat contents of mammals and birds: total body electrical conductivity (TOBEC; Van Loan and Mayclin, 1987; Pethig, 1979), near infrared interactance (IRI; Rosenthal, 1986), isotopic water dilution (IWD; Sheng and Huggins, 1979), and bioelectrical impedance analysis (BIA; Kushner, 1992) are the most commonly used. These methods depend on the close inverse relationship existing between body water and fat, and the constancy of the protein and mineral contents of their dry, fat-free mass in mature animals (Robbins, 1983). TOBEC explained 99.1% of the variation in lean body mass of Northern Bobwhites (*Colonus virgianus*) when the birds were normally hydrated and properly restrained (Roby, 1991). However, this method applies only to small animals, available instruments being most accurate in the range of 50-250 g live

mass (Castro et al., 1990). Larger apparatus designed for humans are very expensive and too large for use in the field (Roby, 1991). Although theoretically promising (Rosenthal, 1986), IRI has proven to be disappointing in birds (Roby, 1991).

IWD and BIA are best adapted to mid-size animals. With IWD, body water is estimated by injecting a known dose of isotope, allowing it to equilibrate with the body water, and measuring its specific activity in a sample of body water (Pace et al., 1947; Lukaski, 1987; Gauthier and Thomas, 1990). BIA was originally developed for determining human body composition (Lukaski, 1987). BIA measures the resistance to conduction (in ohms) of a low-level alternating current in an organism. Because the conductivity of body lipids is only 4-5% that of lean tissues, body fluids, and bones (Pethig, 1979), the resistance measured by BIA gives an indicator of body water content (Fiorotto et al., 1987; Walsberg, 1988; Hall, Lukaski and Marchello, 1989).

Body composition has been widely investigated in ungulates but to a lesser extent in mammalian carnivores (Kistner et al., 1980; Huot, 1988; Adamczewski et al., 1995). There is at present no satisfactory indirect method for estimating body components of live and dead red foxes. For carnivores, Buskirk and Harlow (1989) developed models to assess body composition of american marten (*Martes americana*), Prestrud and Nilssen (1992) for the arctic fox (*Alopex lagopus*), and Poulle et al. (1995) for coyotes (*Canis latrans*). They tested the relationships between selected indices and ingesta-free body composition determined by chemical analysis. In the present study, we aimed at developing reliable models for predicting body composition of red foxes from indices readily available on live animals or on carcasses.

Methods

Sampling

Red foxes (16 males and 13 females) were collected by trappers and government personnel within a 250 km radius of Québec City during the autumns of 1994 and 1995. They were captured with padded foot traps (Victor Coil No. 3, Animal Trap Co., Lititz, Pennsylvania) and snares equipped with a safety catch. After catching, foxes were immobilized with a catch pole, carried inside, and then anesthetized by intramuscular injection of a mixture of Rogarsetic® 26.7 $mg \cdot kg^{-1}$ (Rogar STB, London, Ontario) and Rompun® 8.9 $mg \cdot kg^{-1}$

(Bayer Inc., Etobicoke, Ontario) for a series of measurements. This study was approved by the Animal Protection Committee of Université Laval (permit No. 93-276) and the work was conducted in conformity with the guidelines issued by the Canadian Council of Animal Protection.

Measurements on live red foxes

Animals were weighed (total body mass, TBM; Salter model 235, England, graduation: ± 50 g) and measured with a tape (graduation: ± 5 mm; Fig. 1): total length (TL), i.e. the distance between the anterior edge of the muzzle to the tip of the last vertebra, body length (BL), i.e. the distance between the anterior edge of the muzzle to the base of the tail as determined by placing it perpendicular to the back, front limb length (FLL), from the dorsal edge of the scapula to the longest claw of the extended limb, posterior limb length (PLL), i.e from the iliac crest to the last claw of the extended limb, foot length (FL), from the last claw to the tuber calcis, head circumference (HC), just in front of ears, neck circumference (NC), i.e approximately at the level of the third cervical vertebra, chest circumference (CC), i.e. right behind front limbs, thorax circumference (ThC) at the level of the distal part of the xiphoid cartilage of the sternum (Miller, 1962), waist circumference (WC), in front of posterior limbs, and thigh circumference (TC), i.e the proximal part of the thigh. When measuring circumferences, we exerted a tension equivalent to a mass of ≈ 500 g on the tape, measured with a spring scale. We also measured skinfolds with a caliper (Slimguide®, Creative Health Products, Plymouth, Michigan, graduation: ± 0.5 mm) at the following sites (Fig. 1): on the dorsal surface at approximately the third cervical vertebra (skinfold on cervical vertebrae, SCV), 1 cm behind scapulae (SS), between front limbs (SBF), on thorax side (STS), i.e towards the distal part of the xiphoid cartilage, and on the back at the level of the pelvis (SP). For each of these sites, we took three measurements that were averaged for further analyses. The following measurements were taken when the animal was in a sternal position with legs in normal resting position: TL, BL, HC, NC, SCV, SS, and SP. Other measurements were taken when foxes laid in a lateral position.

Bioelectrical impedance analyses

We measured BIA resistance and reactance in the scale 0-1000 and 0-500 ohms, respectively, with a Model 101A instrument (RJL Systems, Detroit, Michigan). We used a consistent positioning of the fox (sternal with legs in normal resting position) and of the electrodes, because BIA readings are strongly affected by limb position and electrode distance (Kushner,

1992). We used snout to tail resistance. The anterior electrode pair was clamped to the upper lip, at the level of the canines, and the posterior electrodes were placed on either side of the anus, making sure that they were not in contact. Good electrical contact was ensured by wetting the electrodes, the lips, and the anus with water.

Isotopic water dilution

We could utilize IWD with only 8 foxes. We first took a blood sample of ≈ 3 ml from the jugular vein of each animal before injection as an individual control. We then injected 250 µl of tritiated water containing ≈ 0.88 MBq into the jugular vein. After 90 min, the estimated equilibration time, we collected ≈ 3 ml of blood from the same vein. We determined the equilibration time at the outset of the experiment with 2 foxes whose blood was sampled every 30 min for 3 h. Blood samples were centrifuged (International Centrifuge, model CM, Boston, Massachusetts) at 1500 RPM for 10 min, and serum samples were collected and frozen for further analysis. From these samples, we pipetted 200 µl and added 10 ml of liquid scintillation cocktail (Ready Safe™, Beckman Instruments Canada Inc., Mississauga, Ontario). The tritiated serum samples were counted with a liquid scintillation counter (LKB Wallac model: 1219 Rackbeta, Turku, Finland) and the tritium activity was expressed in desintegrations per minute (DPM) per ml of water. We estimated total body water content from the quantity of tritium we injected to the fox and its concentration ($DPM \cdot ml^{-1}$) after 90 min.

Measurements on dead red foxes

Foxes were euthanized with T-61® (Hoechst Canada Inc., Regina, Saskatchewan), placed in plastic bags, frozen, and stored at -20°C until analysis. Frozen carcasses were thawed, weighed, skinned, leaving as much subcutaneous fat as possible on the carcass, and weighed again (skinned body mass, SBM). The digestive tract was then cleaned 3 times by making pressure on the tract from the oesophagus to the rectum and weighed again (ingesta-free body mass, IFBM). Fat attached to each kidney (kidney fat mass, KFM) was removed and weighed (Sartorius 1364 MP, Göttingen, Germany, graduation: ± 0.01 g) separately as were the kidneys (kidney mass, KM). Fat attached on the pericardium (heart fat mass, HFM) and the heart (heart mass, HM) were similarly weighed. We calculated a kidney fat index (KFI = KFM x 100/KM) and a heart fat index (HFI = HFM x 100/HM, Huot et al. 1995). The viscera, which comprised all organs in the body cavity including the diaphragm, were removed. The eviscerated carcass was then weighed (ECM). The viscera mass (VM) was

deducted by subtracting ECM from IFBM. Finally, one piece of femur marrow (femur marrow fat, FMF), approximately 5 cm long, was collected, weighed, and dehydrated.

Composition analyses

Before analysis, frozen carcasses were ground twice in a Hobart meat grinder (Model A-200, Hobart Co., Don Mills, Ontario); once through a 6 mm mesh size sieve and once through a 5 mm mesh size sieve. The homogenate was mixed mechanically between and after mincing. Three subsamples of about 100 g from each animal were collected and frozen again for chemical analyses. We followed the same procedure for viscera. Because of its resistance to grinding, hide was analysed separately. Samples of hide were haphazardly chosen, excluding on paws and in front of ears, then shaved, and chopped into small pieces. We aimed at obtaining approximately 50 g of skin samples. Whole body composition was derived by summing carcass, viscera, and skin components and in correcting for their different proportion of the whole body mass.

Water content was determined by freeze-drying the 3 subsamples of the homogenate for 72 h (Labconco No. 5, Kansas City, Missouri). The dried homogenates were ground with a blender and used for all subsequent chemical analyses. Fat was extracted from 1 g samples in a Soxhlet extractor (Soxtec System HT6, Tecator Inc., Herndon, Virginia), using petroleum ether (Randall, 1974). Mineral content was estimated after overnight combustion of 4-5 g samples in a muffle furnace at 500°C. Protein content was calculated by subtracting water, fat, and mineral from total body mass; this procedure provides similar results as chemical determination of N content (Adamczewski et al., 1995). All analyses were duplicated and when differences between replicates exceeded 15% of the mean, a third analysis was performed. In all calculations, means were used.

Statistical analyses

We developed models to predict the 4 major body components of live and dead red foxes (water, fat, protein, and mineral) using stepwise multiple regression analyses (SAS Inst. Inc., 1989). We used, as independent variables, all morphometric and electric measurements, and masses taken on live and dead foxes, which yielded 8 multiple regression models. As measurements of BIA might not be widely available, we also computed models without considering it among the independent variables. We selected, as final models, the multiple regressions with highest adjusted r^2, provided that residues were homogenous,

linear (visual examination of the plot), and normally distributed (Shapiro-Wilk test). Multicolinearity was tested using the variance inflation factor (VIF: Proc Reg, SAS Institute Inc, 1989). All final models included only those variables that contributed significantly ($p < 0.1$) to a r^2 increase of ≥1%. Complete information was not available for all specimens and consequently, sample sizes varied for different components. We treated IWD separately due to a small sample size and compared predicted and measured water body with a simple linear regression.

Results

Total body mass of sampled red foxes averaged 3676 ± 714 g (*SD*; Table 1). Fat content varied from 36 to 1362 g (average: 253 ± 282); in percentage, body fat ranged from 1.1 to 28.4%. Water (2336 ± 387), protein (884 ± 187) and mineral (179 ± 34) contents exhibited less variation among individuals.

All final models were highly significant ($p < 0.0001$) for live (Table 2) as well as for dead (Table 3) animals. For measurements taken on live foxes, the final model for water mass included TBM, BL, resistance, and WC ($r^2 = 0.95$). SS, WC, and BL served to predict absolute mass of fat ($r^2 = 0.89$). Protein mass was predicted with a three-variable regression model which included TBM, TC, and SS ($r^2 = 0.92$). PLL, STS, WC, and reactance were retained in the model predicting mineral mass ($r^2 = 0.81$). Without access to BIA measurements, r^2 of selected models dropped by ≈ 3%.

For dead foxes, the final model included TBM, KFI, and TC to predict water mass ($r^2 = 0.94$); KFI, ThC, SP, and SCV to estimate fat mass ($r^2 = 0.93$); TBM, HFM, TC, and FMF to predict protein mass ($r^2 = 0.94$) and SBM, KFM, and CC for mineral mass ($r^2 = 0.82$). As a supplementary independent variable in multiple regression, sex never significantly improved the fit for any model.

We found a close relationship between body water as determined by freeze-drying and IWD estimates ($r^2 = 0.92$; n = 8; Fig. 2); however all estimates were biased downward by ≈ 45%.

Discussion

The models that we developed make it possible to rapidly estimate absolute mass of each major body component using morphometric and electrical measurements taken on live or dead red foxes. All the coefficients of determination obtained were relatively high, and the distribution of the residuals was normal, homogenous, and linear. Our models permit safe interpolation for most situations as our animals covered a wide range of physical condition i.e. 1.1 to 28.4% body fat.

Even if regression models do not necessarily imply a cause-effect relationship between dependent and independent variables, the inclusion of most variables in our models seems logical. For instance, there was at least one index of the animal's size in all equations, i.e. TBM, BL, PLL, SBM, WC, ThC, or CC. The model predicting water mass of live foxes included the resistance, a variable directly related to water content. In the model predicting body water for dead foxes, KFI replaced BIA measurements, which probably reflects the negative relationship between body fat and water in body composition (Farley and Robbins, 1994), including our samples ($r^2 = 0.82$; $n = 29$). Our estimates of body water with IWD were strongly biased for unexplained reasons. Other researchers also obtained unexplained biased estimates with IWD, e.g. Gauthier and Thomas (1990), Sheng and Huggins (1971). Given the cumbersome administrative and security constraints associated with the use of IWD and our disappointing results, we do not recommend this procedure for estimating body water (or fat) as a routine procedure.

The two regression models predicting body fat included either KFI and/or three skinfold sites on the back. Prestrud and Nilssen (1992) demonstrated that the fat on the rump and back was the last subcutaneous fat to be depleted and the first to be deposited in the arctic fox, a pattern seemingly similar in the red fox. On the other hand, KFI was found to be related to total body fat in many mammal species (Finger et al., 1981; Torbit et al., 1988).

The two regressions predicting body protein included body mass as the major explanatory variable, similarly to models predicting body water. This is not surprising given that protein generally represents the second body component in mass. Both models also included a variable related to fatness (SS and FMF), likely reflecting the balance existing between protein, water, and fat in the body of mammals.

For live foxes, the equation predicting mineral mass included PLL, an index of the skeleton size. This is plausible as the skeleton contains most of the minerals (Adamczewski et al., 1995). The coefficients of determination for models predicting mineral masses were lower than the others. This may depend on an increased difficulty for predicting the mass of a minor body component, i.e. ≈ 5%. The lower precision of mineral predictions has limited consequences because this body component plays a minor role in the bioenergetics of mammals.

Our models are versatile enough to correctly predict the body composition of both lean and fat red foxes of both sexes and can be used for comparing body composition on a yearly and regional basis. They are inexpensive, rapid to use, and non-destructive. However, some measurements, in particular circumferences, require careful readings.

Acknowledgments

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Table 1. Descriptive statistics (mean and *SD*) of live and post-mortem measurements taken on red foxes collected in southcentral Québec and used for regression models predicting ingesta-free body composition of red foxes.

Variable	Acronym	Mean	*SD*	Range (min.-max.)	*n*
Water mass (g)		2336	387.0	1675-3147	29
Fat mass (g)		252.6	281.5	36.1-1362	29
Protein mass (g)		884.3	187.3	525.8-1170	29
Ashable mineral mass (g)		179.2	33.6	120.9-261.9	29
Resistance (ohm)		466.0	31.6	407-529	26
Reactance (ohm)		60.6	8.3	43-77	26
Body length (cm)	BL	61.8	4.3	53.5-70.0	27
Chest circumference (cm)	CC	27.7	1.1	22.4-33.0	27
Femur marrow fat (%)	FMF	44.6	17.7	20.3-87.5	29
Heart fat mass (g)	HFM	1.84	2.01	0.0-9.1	29
Kidney fat index	KFI	22.6	20.7	3.8-95.6	29
Kidney fat mass (g)	KFM	5.71	5.86	0.9-26.1	29
Posterior limb length (cm)	PLL	44.2	3.5	37.4-50.5	27
Skinned body mass (g)	SBM	3158	630.1	2029-4304	29
Skinfold on cervical vertebrae (mm)	SCV	3.5	0.9	2.2-6.0	27
Skinfold in the back at the level of pelvis (mm)	SP	4.5	1.5	3.0-9.3	27
Skinfold 1 cm behind scapulae (mm)	SS	3.7	1.1	2.7-7.7	27
Skinfold on thorax side (mm)	STS	3.3	0.9	2.0-6.0	27
Thigh circumference (cm)	TC	17.4	3.3	11.2-22.5	27
Thorax circumference (cm)	ThC	29.6	3.1	24.0-36.9	27
Total body mass (g)	TBM	3676	714	2400-4800	29
Waist circumference (cm)	WC	21.2	3.4	15.7-31.1	27

Table 2. Multiple regression models for predicting total ingesta-free body content (g) in water, fat, proteins and minerals of live red foxes.

Dependant variable	Independant variable	Partial r^2	r^2	Prob>F	Parameter estimate	*SE*
Water	TBM	0.8154	0.8154	0.0001	0.41	0.07
$n = 26$	BL	0.0820	0.8974	0.0003	37.07	8.02
	resistance	0.0369	0.9343	0.0019	-2.43	0.66
	WC	0.0214	0.9557	0.0045	-33.03	10.38
	intercept				358.01	531.02
Water	TBM	0.8157	0.8157	0.0001	0.52	0.078
(without BIA readings)	WC	0.0653	0.881	0.0013	-43.67	12.62
$n = 27$	BL	0.0398	0.9208	0.0024	31.39	9.23
	intercept				-596.24	449.17
Fat	SS	0.8490	0.8490	0.0001	150.39	31.94
$n = 27$	WC	0.0205	0.8695	0.0640	42.01	12.45
	BL	0.0311	0.9006	0.0133	-15.88	5.92
	intercept				-212.85	281.05
Protein	TBM	0.8434	0.8434	0.0001	0.21	0.03
$n = 27$	TC	0.0516	0.8949	0.0022	22.96	5.75
	SS	0.0309	0.9258	0.0051	-41.37	13.36
	intercept				-128.59	61.85
Mineral	PLL	0.6674	0.6674	0.0001	7.98	1.01
$n = 26$	STS	0.0544	0.7218	0.045	-15.08	3.76
	WC	0.0862	0.808	0.0047	4.01	1.12
	reactance	0.0319	0.8399	0.0537	-0.76	0.37
	intercept				-163.82	42.39
Mineral	PLL	0.6773	0.6773	0.0001	4.97	1.40
(without BIA readings)	TBM	0.0499	0.7273	0.0468	0.02	0.007
$n = 27$	SCV	0.0856	0.8128	0.0036	-12.1	3.73
	intercept				-84.55	47.66

n = number of animals used in the regression

Table 3. Multiple regression models for predicting total ingesta-free body content (g) in water, fat, proteins and minerals of dead foxes.

Dependant variable	Independant variable	Partial r^2	r^2	Prob>F	Parameter estimate	*SE*
Water	TBM	0.8157	0.8157	0.0001	0.74	0.05
$n = 27$	KFI	0.0819	0.8976	0.0002	-6.83	1.02
	TC	0.0451	0.9427	0.0003	-45.96	10.8
	intercept				595.84	111.46
Fat	KFI	0.7165	0.7165	0.0001	8.27	0.89
$n = 27$	ThC	0.1741	0.8906	0.0001	31.65	6.41
	SP	0.0308	0.9213	0.0064	58.7	14.87
	SCV	0.0232	0.9446	0.0061	-59.89	19.72
	intercept				-934.1	163.49
Protein	TBM	0.8434	0.8434	0.0001	0.21	0.03
$n = 27$	HFM	0.0596	0.903	0.0008	-37.53	8.71
	TC	0.0322	0.9353	0.0025	14.01	5.57
	FMF	0.0109	0.9462	0.0463	2.42	1.15
	intercept				-187.4	58.6
Mineral	SBM	0.5959	0.5959	0.0001	0.09	0.01
$n = 27$	KFM	0.1806	0.7765	0.0002	-2.76	0.56
	CC	0.0656	0.8421	0.0051	-9.51	3.08
	intercept				159.39	47.38

n = number of animals used in the regression

Figure 1. Morphologic measurements taken on live red foxes. Acronyms are defined in Table 1.

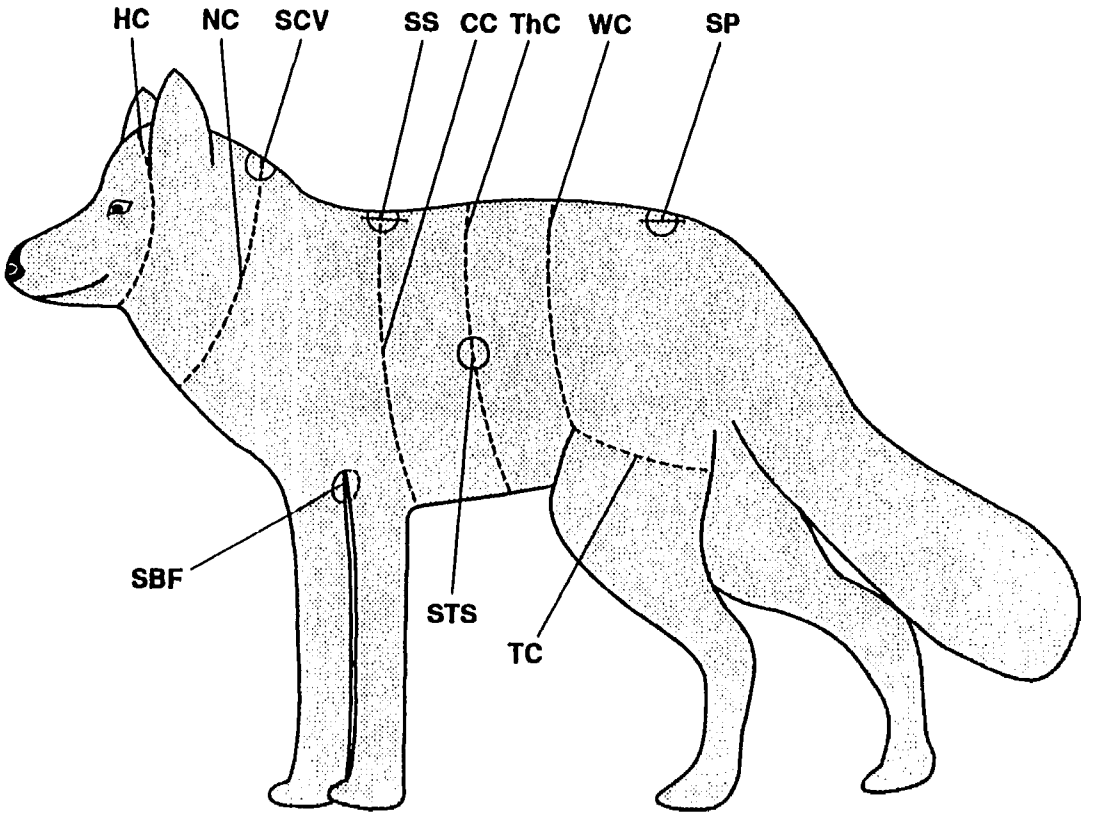
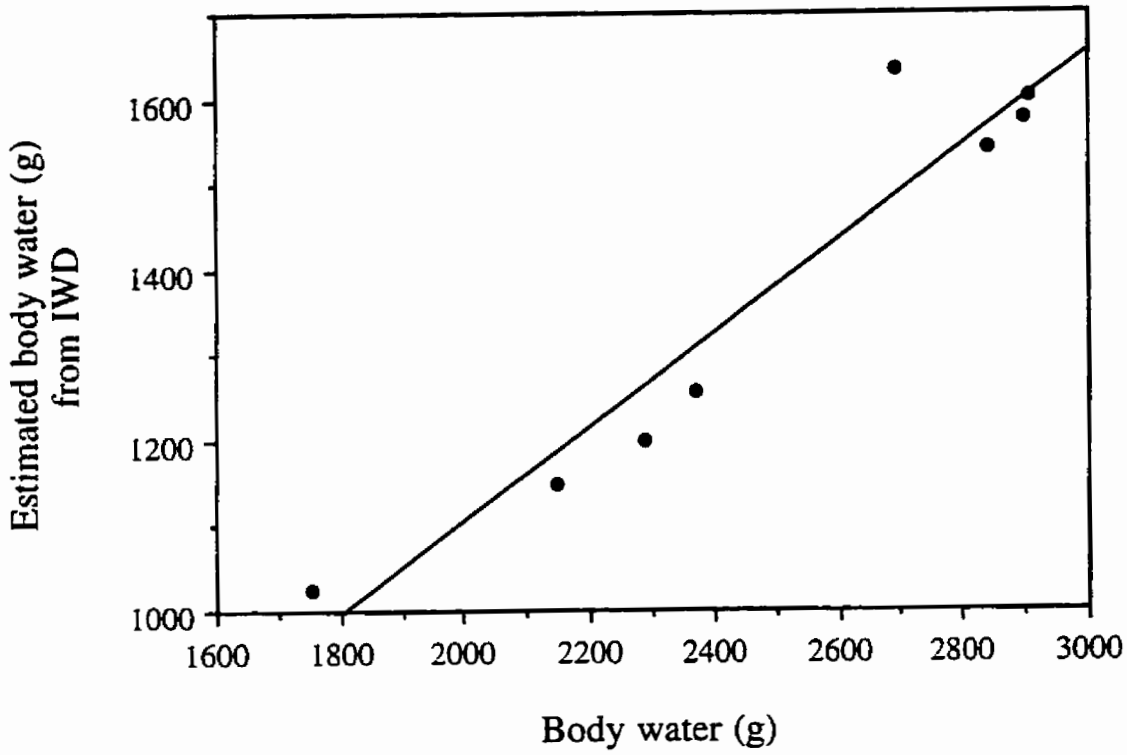

HC
NC
SCV
SS
CC
ThC
WC
SP
SBF
STS
TC

Figure 2. Linear relationship between body water of 8 red foxes as determined by freeze-drying and estimated body water with isotope (tritium) dilution. The regression equation is $y = 8.598+0.548x$ ($r^2 = 0.92$, $n = 8$).


Estimated body water (g)
from IWD
1000
1200
1400
1600
1600
1800
2000
2200
2400
2600
2800
3000
Body water (g)

Chapitre II

Annual variations in body composition, reproduction hormones and blood parameters of red foxes (*Vulpes vulpes*)

Cet article étant destiné à la revue *Journal of Mammalogy* pour fins de publication, le format utilisé répond aux exigences de la revue.

Résumé

Nous avons vérifié s'il existait des variations annuelles de la composition corporelle chez des renards roux, gardés en captivité à l'extérieur et maintenus sur un régime alimentaire constant. Nous avons prédit mensuellement la composition corporelle (eau, gras, protéines, minéraux) chez 12 renards gardés au Jardin zoologique du Québec, à l'aide de régressions multiples utilisant des mesures pondérales, morphométriques et électriques (février 1995 à janvier 1996). Nous avons également quantifié les variations mensuelles de la FSH, de la progestérone, de la testostérone, du phosphore et de l'albumine sanguins. Malgré une légère augmentation de la masse totale des renards au cours de l'étude, les réserves adipeuses ont diminué de 50% durant l'été (mai à octobre). Au contraire, le contenu en protéines, en eau et en minéraux était plus élevé durant cette saison. La concentration de la FSH était maximale entre décembre et mars pour les femelles et entre septembre et janvier pour les mâles. Chez les femelles, la concentration en progestérone plafonnait en avril et chez les mâles, la concentration en testostérone était maximale entre janvier et mars. Nous discutons des fonctions possibles d'un cycle annuel des composantes corporelles chez le renard roux.

Abstract

We tested the hypothesis that there exists a seasonal variation in the body composition of red foxes maintained outdoors in captivity under a constant diet. We monitored the monthly variations of body components (water, fat, protein, mineral) of 12 wild foxes kept at the Jardin zoologique du Québec (February 1995 to January 1996). We estimated the mass of body components using regression models that relied on body mass, linear measurements and electrical resistance. We also monitored plasma FSH, testosterone and progesterone together with serum phosphorus and albumin. Total body mass increased slightly during the study probably due to captivity and to a constant high quality diet. Fat reserves exhibited a marked annual cycle, decreasing by 50% in summer (May to October). In contrast, protein, water and mineral contents peaked at this time. FSH reached high levels in December-March and in September-January for females and males respectively, while progesterone peaked in April for females and testosterone in January-March for males. We discuss possible functions of an annual cycle of body components in red fox.

Introduction

Understanding the dynamics of body composition of living animals has implications for assessing physical condition and habitat quality as well as identifying critical times or events in the animal's life cycle (Farley and Robbins, 1994). In ecological studies of mammals, the body components usually considered are: water, fat, proteins and minerals. The mass and the relative proportion of those components may vary seasonnally, according to sex, to age, and to environmental conditions whereas mineral content is relatively stable in adults. Although proteins may be partially responsible for the variations in body composition (Torbit et al., 1985; Buskirk and Harlow, 1989; Huot, 1989; Poulle et al., 1995), most of the change usually involves fats, which are primarily used as an energy source (Allen, 1976), and body water, which is inversely correlated with fat content, on a relative basis (e.g. Poulle et al., 1995). Because total body mass is not necessarily a good index of body condition, it is essential to follow all components (e.g. Poulle et al., 1995).

In vertebrates, lipids stored in adipose tissue may act as an energy reserve, support and padding around some sense and internal organs, as well as an insulating layer to conserve heat (Pond, 1978). Stored lipids are usually catabolized during periods of food shortage or when energy requirements are increased such as during reproduction or migration (Prestrud and Nilssen, 1992). Nevertheless, stored fat also imposes disadvantages to an animal. Additional mass increases energy expenditure and slows movements during physical activity, a major constraint for carnivores that depend on speed and agility to catch prey (Prestrud and Nilssen, 1992). Consequently, deposition of fat must have an adaptive significance because fat should not be accumulated for longer periods than needed (Pond, 1981).

In northern environments, it is well known that cervids accumulate fat reserves in late summer and autumn when food is abundant and use these reserves during winter as an energy source, when forage quality and availability are lower (Mautz, 1978; Kistner et al., 1980; Worden and Pekins, 1995). In reindeer (*Rangifer tarandus*), pregnant females spare fat for early lactation as parturition preceeds green-up (Tyler, 1987). Lactation (Allaye Chan-Mclead et al., 1994) and summer range condition affects dam body composition and calf growth in caribou, and the probability of conception during the next autumn (Dauphiné, 1976; Crête and Huot, 1993). This might also be the case for moose (*Alces alces*; Crête and Courtois, 1997). However, variations in body composition of mammalian carnivores remain relatively unstudied. Buskirk and Harlow (1989) observed that body fat of american martens

(*Martes americana*) stayed stable and low during a two-month period in winter. Prestrud (1982) and Prestrud and Nilssen (1992) found that arctic foxes (*Alopex lagopus*) caught during winter had a greater fat content than those caught during spring and summer whereas body protein remained stable during the two seasons. In southeastern Québec, Poulle et al. (1995) noted that coyotes (*Canis latrans*) were 28% heavier during autumn-winter than during summer: body fat and protein declined by 44 and 17% respectively, from late winter to summer. These coyotes exhibited slow pup growth (Tremblay et al., 1997), low fecundity (Poulle et al., 1995) and included a high proportion of wildberries in their diet during the second half of the summer (Samson and Crête, 1997; Tremblay et al., 1997). In red foxes, Lindström (1983) observed a relationship between fecundity and vole abundance. Prestrud and Nilssen (1992) found that female arctic foxes that had reproduced the previous spring were leaner in winter than the other foxes. They concluded that fat stores might contribute to reproductive success because being in good condition through winter may be important for successful mating, gestation, lactation, and pup rearing.

Several factors can explain such variations in body composition, particularly those of fat content. Firstly, declining fat reserves in summer could be caused by food shortage, especially when protein mass decreases too. Fat is usually the main body component to be catabolized but in a situation of negative energy balance, proteins are also used (Reimers et al., 1982; Torbit et al., 1985; Buskirk and Harlow, 1989; Huot, 1989; Virgil and Messier, 1992). Secondly, seasonal variations in body composition could persist independently of food availability. The present study aims at verify the last hypothesis, by keeping animals in captivity on a constant diet and preventing reproduction. As nutrition, body composition and fecundity could be interrelated in carnivores, we also monitored reproductive hormones and two blood components (phosphorus and albumin) susceptible to reflect physical condition and nutritive status (LeResche et al., 1974; Bistner and Ford, 1995).

Methods

Sample collection and conditions of captivity

Red foxes (6 males and 6 females) were captured by trappers and government personnel within a 250 km radius of Québec City during November and December 1994. They were caught with padded foot traps (Victor Coil No. 3, Animal Trap Co., Lititz, Pennsylvania) and snares equipped with a safety catch. Foxes were then immobilized with a catch pole and

carried to the Jardin zoologique du Québec. As juvenile foxes reach adult body mass in November-December of their first year (Wakely and Mallory, 1988), we did not determine the age of our specimens. We began the measurements on February 1995, in order to leave an adaptation period of 6 to 11 weeks for our study animals.

Foxes were kept outside in 2 rows of juxtaposed cages. Each fox had access to an enclosure (2 x 3 m), an adjacent covered cage (2 x 2 m), and an insulated shelter (1 x 1 m). Foxes had visual and olfactory contacts with neighbours. Each animal received daily ≈ 125 g (dry mass) of a commercial canine food (Hill's-Science maintenance diet: carbohydrates = 53.1%, protein = 25.3%, fat = 15.6%, mineral = 4.6% of dry mass). This quantity was established with tables furnished by the company. Dry matter digestibility averaged 80.2% (SE = 2.5; n = 6) as estimated with chromium oxyde (Faulkner et al., 1992; Barboza et al., 1994), which provided daily 2460 kJ to each fox (Paradis, unpubl.). Food consumption did not vary significantly between August and December 1995 (Paradis, unpubl.). Generally, foxes consumed all their food although they showed individual variation of appetite. Uneaten food was removed daily before offering a new ration. Water was available *ad libitum*.

Experimental session

Every 4 weeks during one year (February 1, 1995 to January 10, 1996), we took all foxes inside and anesthetized them with a mixture of Rogarsetic® 26.7 $mg \cdot kg^{-1}$ (Rogar STB, London, Ontario) and Rompun® 8.9 $mg \cdot kg^{-1}$ (Bayer Inc., Etobicoke, Ontario) for measurements. Two samples of ≈ 3 ml of blood were drawn from the jugular vein: one for assaying reproduction hormones in an heparin vaccum tube for plasma collection and one for determining phosphorus and albumin concentrations in a plain vacuum tube for serum collection. Blood samples were centrifuged (International Centrifuge, model CM, Boston, Massachusetts) at 1500 RPM for 10 min., supernatants were collected and frozen for further analyses. During the anticipated reproduction period (February 1 to April 26), we collected blood samples weekly for females (biweekly in April) and biweekly for males.

Testosterone concentrations were measured in males according to Price (1994). Samples (200 µl) were extracted with diethyl ether, with a mean extraction efficiency of 70%. The minimum detectable concentration was equivalent to 38 $pg \cdot ml^{-1}$. All samples were run in a single assay, with an intra-assay coefficient of variation (CV) of 7%. Progesterone concentrations were determined in females according to Lafrance and Goff (1985), as

modified by Ben Jebara et al. (1994). The minimum detectable concentration was 40 pg·ml^{-1}, and all samples were run in a single assay with a *CV* of 8%. FSH concentrations were measured in plasma from males and females with a modification of the assay developed by Colon et al., 1993. The assay employed anti-human FSH (M94; McNeilly et al., 1976) at a final dilution of 1:40 000, iodinated bovine FSH (USDA-bFSH-I1) as tracer, and ovine FSH (NIAMDD-oFSH-RP1) as reference standard. The minimum detectable concentration was 0.5 ng·ml^{-1}, and all samples were run in a single assay with a *CV* of 9%. Analyses of blood constituents were done with a Kodak Ektachem DT 60 II for phosphorus and with an Ektachem DTSC II Module (Clinical Diagnostics, Johnson-Johnson) for albumin.

We took monthly measurements on each fox in order to estimate their total mass of water, protein, fat and mineral, using Lefebvre et al. (1997) regression models. Animals were weighed (total body mass, TBM; Sunbeam, Chubutu, Missouri, graduation: ± 100 g) and measured with a tape (graduation: ± 5 mm): body length (BL) as the distance between the anterior edge of the muzzle to the base of the first tail vertebra, posterior limb length (PLL) from the iliac crest to the last claw of the extended limb, waist circumference (WC) in front of posterior limbs, and thigh circumference (TC) on the proximal part of the thigh. When measuring circumferences, we exerted a tension equivalent to a mass of ≈ 500 g on the tape, measured with a spring scale. We also measured skinfolds with a caliper (Slimguide®, Creative Health Products, Plymouth, Michigan, graduation: ± 0.5 mm) at the following sites: on the dorsal surface 1 cm behind scapulae (SS) and on thorax side (STS) i.e towards the distal part of the xiphoid cartilage. For each sites, we took three measurements that were averaged. We measured resistance and reactance in the scale 0-1000 and 0-500 ohms, respectively, with a bioelectrical impedance analyzer (Model 101A instrument, RJL Systems, Detroit, Michigan).

Statistical analyses

A nested analysis of variance served to test for monthly or sex-related variations of TBM, body components, reproductive hormones and blood parameters (GLM procedure, SAS Inst. Inc. 1989). We tested the effect of the 2 main factors and their interaction. We ensured that residues were homogeneous, linear (visual examination of the plot), and normally distributed (Shapiro-Wilk test). An inverse transformation allowed to normalize the residues for hormone concentrations, but we found no transformation to achieve this goal for albumin. We excluded one female from the analysis because of unhealthy condition during several months.

Results

Total body mass increased slightly ($p < 0.0002$) during the study (Fig. 1) and both males and females followed the same pattern ($p = 0.108$). Body mass varied within a narrow range, though male weighted more than females ($p < 0.0001$). The sum of the masses of the 4 components (water, protein, fat, mineral) estimated with the regression models, developed by Lefebvre et al. (1997), was compared with TBM of each fox at time of autopsy; the 2 variables differed by only 0-5% for monthly averages. On a relative basis, regression models performed equally well for both sexes ($p = 0.478$).

Body fat mass did not differ between males and females ($p = 0.11$), but it showed a marked annual cycle ($p < 0.0001$), culminating at 800-900 g in winter and dropping by half in July and August (Fig. 2). Annual variation followed the same pattern in males and females ($p = 0.369$). On a relative basis, females had more fat than males ($p < 0.0002$). Total body mass of protein, water and mineral differed according to sex and months ($p < 0.0001$), without interaction between the two factors ($p \geq 0.264$). The 3 body components followed a trend opposed to that of fat, peaking in summer (May to October, which corresponds to the period without snow) and being lower in winter (November to April; Fig. 3, 4 and 5). The water:protein ratio varied slightly but significantly ($p < 0.0001$) throughout the year, being lower between October to February (2.46-2.53) than for the rest of the year (2.58-2.70); this ratio differed significantly between sexes ($p = 0.022$).

Reproductive hormones exhibited significant ($p < 0.0001$) annual variations. For FSH, there was a phase difference between males and females ($p < 0.0001$). In females, FSH remained elevated between December and March, and progesterone increased for about one month, the highest concentration being in mid-April (Fig. 6 and 7). In males, FSH increased in September and remained elevated for 4 months whereas testosterone peaked in late January (Fig. 7 and 8). We observed another peak of testosterone in May.

Blood phosphorus levels differed between males and females ($p < 0.0005$) but followed a similar annual pattern ($p = 0.320$), comparable to those of protein, water and mineral. Albumin concentration did not vary between sexes, but monthly differences were detected ($p < 0.0001$) without any clear pattern (Fig. 10).

Discussion

As our hypothesis predicted, we observed annual variations in body composition of red foxes even if they were well fed throughout the year. Our captive foxes gained only 250 g in one year, which most likely resulted from a high quality diet and from low activity. However, this apparent stability hid major changes in body composition. During mid-summer, fat stores decreased by half whereas proteins, water and minerals were highest at this time.

As proposed by Prestrud and Nilssen (1992) for arctic foxes, fat deposition by red fox before winter could represent an adaptation to cope with food shortages and cold temperatures, as well as the increased energy demand of reproduction that occurs during winter. In fact, because prey availability is likely reduced in winter, fat reserves are essential to survive during food shortages that are more frequent and longer in winter than during summer. Furthermore, cold temperature imposes an energetic stress to red foxes, a relatively small mammal whose winter critical lower temperature is -13°C (Litvaitis and Mautz, 1976); in Québec, temperature commonly drops below this threshold. Moreover, locomotion in the snow most likely varies exponentially with sinking depth in canids as in cervids (Mattfield, 1974; Parker, 1984). Larger body reserves in winter than in summer might have then been selected to cope with stochastic climatic variables which could affect hunting success. The breeding season might also necessitate large body reserves for males to compete with rivals whereas females might need sufficient fat stores for successful reproduction as in cervids (e.g. Crête et al., 1993). However, it seems that fat reserves in canids are not used gradually as in ungulates throughout the winter (e.g. Tyler, 1987). In arctic foxes, neither the rump fat thickness nor the total body mass declined significantly between November and March for 7 years (Prestud and Nilssen, 1992). Similarly, mean fat mass of coyotes from southeastern Québec did not vary significantly from November to March, suggesting that it is not the first function of wintering fat reserves of coyotes to enhance survival during a prolonged period of food scarcity (Poulle et al., 1995). By opposition, Lindström (1983) observed a significant decrease in subcutaneous and visceral fat for Swedish red foxes during winter and concluded that animals were in negative energy balance. On figure 2, we noted an unexpected low point in February 95 that can be explained by the fact that at the outset of the experiment, few foxes did not accept to eat the commercial canine food.

Although receiving a constant ration, our captive foxes lost half of their body fat in summer. With arctic foxes, Prestrud and Nilssen (1992) also observed a decrease in body fat during spring, in spite of apparently greater availability of food. Variations in body fat could be adjusted to a level called the set-point. McFarland (1971) defined set-point as "an input variable, or a command, established as a standard of comparison for a feedback control system". For instance, male red deer (*Cervus elaphus*) lost weight even if they were in captivity, fed *ad libitum* but without the opportunity to perform their full reproductive activities (Baxter et al., 1974). Mrosovsky and Sherry (1980) proposed that one way to avoid conflicts between feeding and other activities such as hibernation, incubation, molting or territorial defense, is to lower the programmed weight or set-point for body fat. The same pattern was observed with male polecats (*Mustela putorius*) and with canvasbacks (*Aythya valisineria*; Korhonen and Harri, 1986; Perry et al., 1986). This suggests the presence of endogeneously controlled changes in reserves.

From our results we cannot conclude that annual variations are only due to endogeneous mechanism because we did not control neither the photoperiod nor the temperature but we can conclude that in absence of changes in food, there exists variations in body composition. A combination of an endogeneous mechanism, photoperiod and temperature could induce accretion of body reserves in autumn and reduction of these reserves during summer months.

Ouellet et al. (1997) observed that Southampton Island caribou were lighter and had less fat in autumn than Coats Island caribou, but Southampton Island caribou were both heavier and fatter in spring. They suggested that the body condition set-points vary with environmental conditions which affect winter energy budgets. Caribou from Coats Island, where they suffered poor winter nutrition, accumulated less body fat when they were introduced to the forage-rich Southampton Island (Ouellet, 1992). As Huot (1988) suggested, it seems that the accumulation of fat reserves depends not only on the quality of the environment, but also on the animal's expected requirements for the coming season.

The set-point for body weight, called the ponderostat, has been widely investigated in humans. Hervey (1969) hypothesized that body mass, is constant over the adult life span because it, or a variable closely correlated to body mass, such as body fat content, is regulated (Cabanac and Richard, 1996). Steen et al. (1988) observed a lower resting metabolic rate for wrestlers having provoked repeated cycles of their body mass than for wrestlers with stable weight. St-Pierre et al. (1996) observed that the metabolic rate of a skier that crossed Greenland decreased after his trip, where he lost much body reserves. In

addition, the skier's appetite remained elevated after he returned to his normal weight, which was interpreted as an adaptation for preventing subsequent energy deficit.

Set-point is a useful way to characterize the level about which the regulation of fat stores occurs (Mrovosky and Powley, 1977). These last authors suggest that a lipostat rather than a ponderostat can exist. For example, in hibernators, changes in body fat are responsible for most of the weight changes, so a falling set-point for body fat may be a more accurate description (Jameson and Mead, 1964; Mrovosky and Sherry, 1980). In reindeer, Ryg (1983) provided evidence of a set-point for body fatness. Keesey and Powley (1986) proposed that if defenses for maintaining fat were rigid, perfect, and powerful, then fat could not serve its function as a reserve. Set-points are resetable in biological systems. Seasonal changes in food availability, and in breeding activities that compete with foraging, make reserves particularly important at certain times in the life cycle (Mrosovsky, 1990).

Body proteins of our foxes increased by 10-15% between April and July-August. Body water, which is closely related to proteins (Husband, 1976) and minerals, followed the same trend. The accretion of proteins in summer could be related to completion of growth in young adults and to higher needs for structural and metabolic proteins. Red foxes complete their skeletal development by the age of 9 months (Wakely and Mallory, 1988). For this reason, we did not determine their age, assuming they had reached their full size at the beginning of the experiment. However, completion of musculature development might be delayed until the second summer of life in red foxes. Moult could also favor protein accretion in summer. Our foxes moulted in July-August, when proteins culminated. Proteins make up the principal component of hair (Robbins, 1983), which creates a strong demand during growth of winter fur. In white-tailed deer and muskoxen, winter coat represents respectively 1.4 and 4.5% of the ingesta-free body mass (Robbins et al., 1974; Adamczewski et al., 1995).

The reproductive hormones monitored (progesterone, testosterone, FSH) fluctuated in accordance with the normal reproductive cycle of red foxes. The peak concentration of serum progesterone observed in our females in April and of testosterone in our males in January-March coincides with that observed in European red foxes for progesterone and in silver foxes for testosterone (Mondain-Monval et al., 1977; Maurel and Boissin, 1982; Osadchuk, 1993). Maximum concentrations of all hormones were delayed by two months in our red foxes compared to blue foxes (*Alopex lagopus* : Mondain-Monval et al., 1993). The

visual and olfactive contacts that our animals had was sufficient to provoke normal secretion of testosterone in males, which can be affected by the proximity of potential mates (Osadchuk, 1992). As this author observed for the silver fox, we noted a testosterone surge in mid-summer. Osadchuk (1993) interpreted this surge as a pulsative release of the hormone from the testicles rather than be correlated with spermatogenesis and sexual activity. We did not made direct observations of oestrus timing, but our results suggest that it happened in early March 1995.

Blood phosphorus concentration followed the same pattern as total body water, proteins and minerals. The ratio phosphorus:minerals stayed constant throughout the year but concentration of both presented annual fluctuations. Albumin did not show a particular annual pattern. However, as albumin carries fatty acids, its decline in spring and its increase in autumn might testify physiological processes. As Huot (1988) noted, blood constituents are better for identifying deficiency rather than for comparing physical condition of non-deficient animals. However, baseline data on these parameters must be available for healthy animals.

Our results illustrate that total body mass is not a good index of the dynamics of body composition. Moreover, fat reserves alone cannot be used as an index of body condition of red fox during summer, however decreasing body proteins during this period could indicate poor physical condition. In carnivores as in cervids, the annual accretion and utilisation of body components further complicate our understanding of the mechanisms relating attainment of puberty, fecundity, body reserves and foraging condition. Monitoring of all body compartments is essential to fully understand the bioenergetics of mammals.

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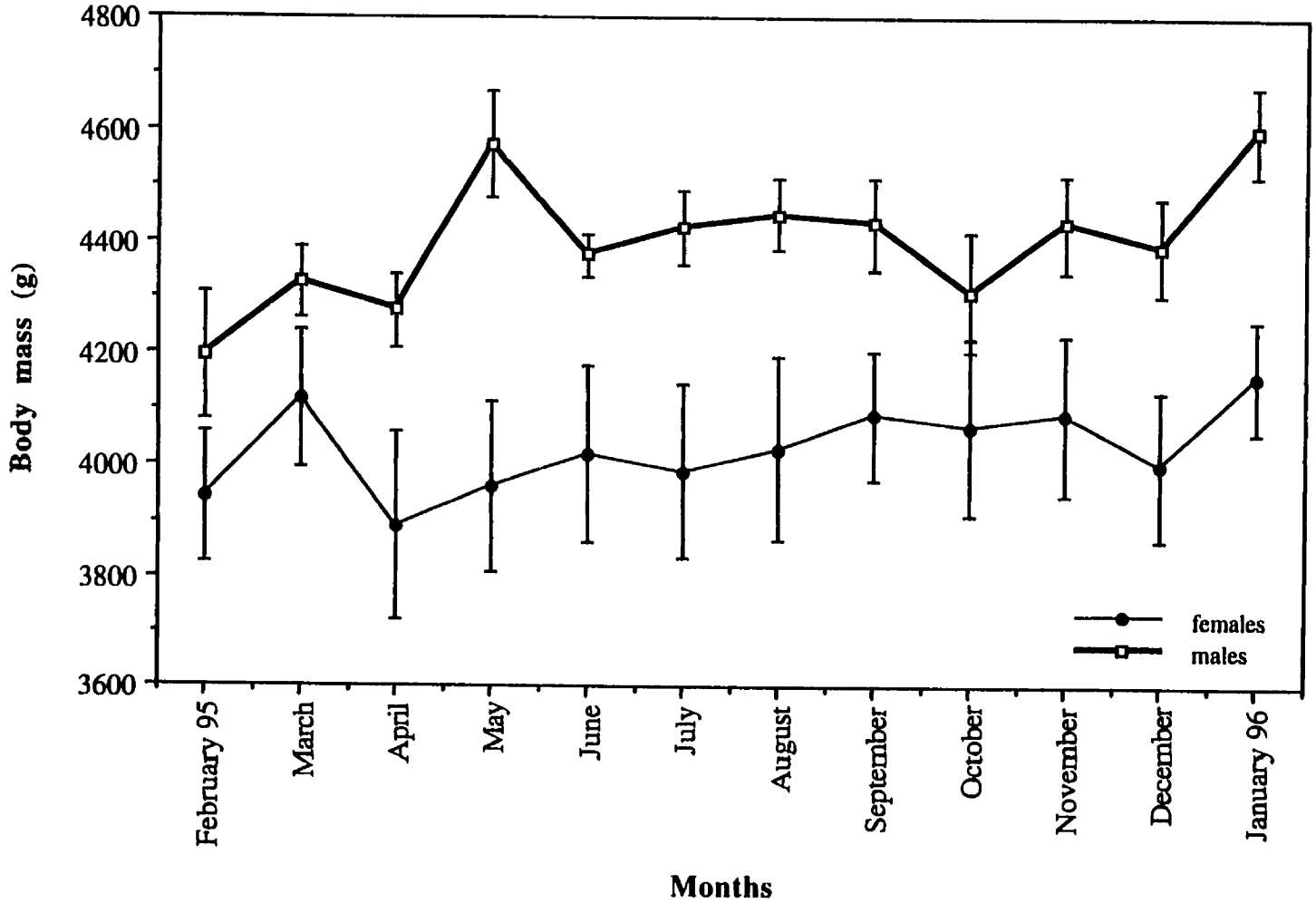


Figure 1. Mean (± SE) monthly body mass of wild red foxes kept in captivity.

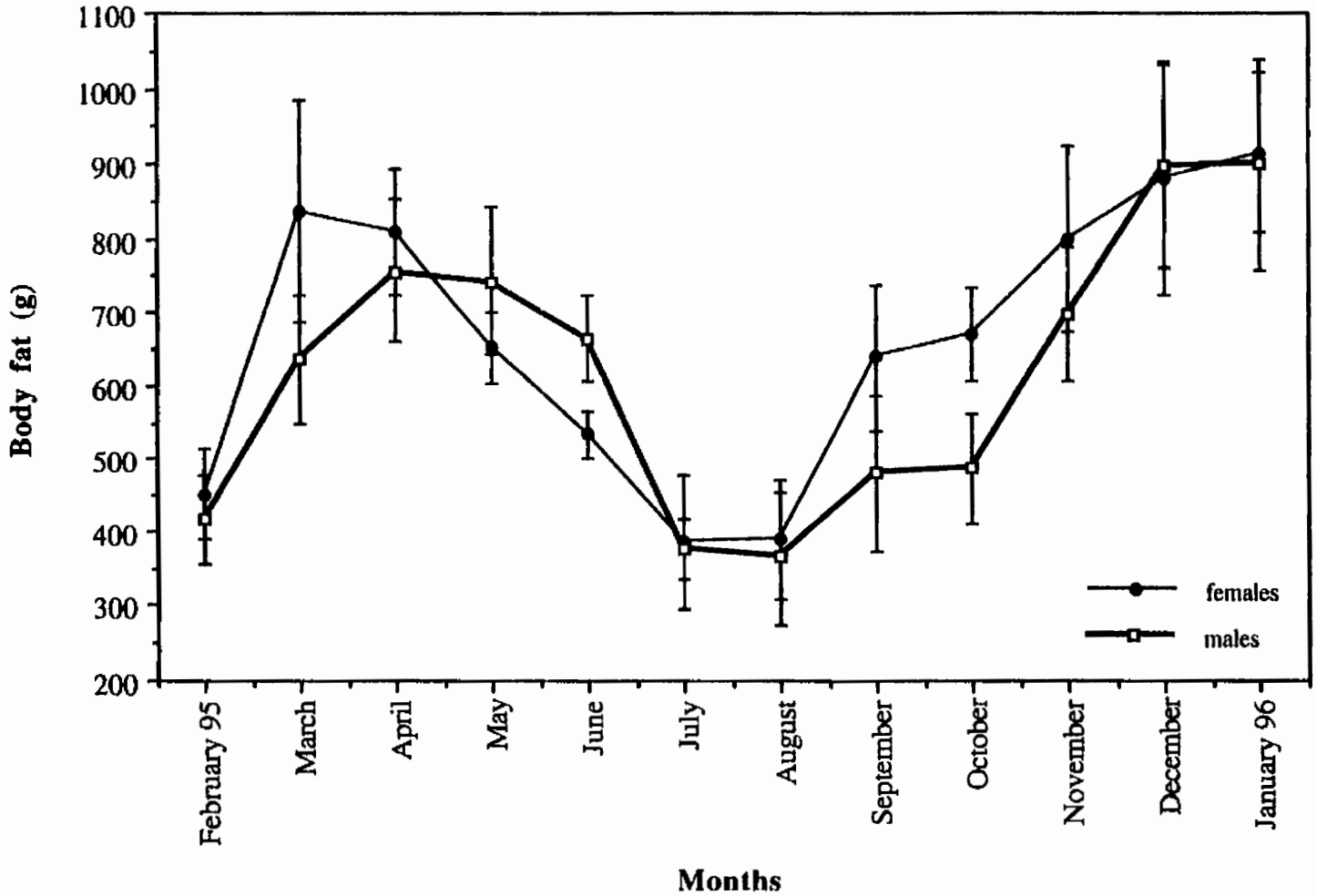


Figure 2. Estimate of mean (± SE) monthly body fat of wild red foxes kept in captivity.

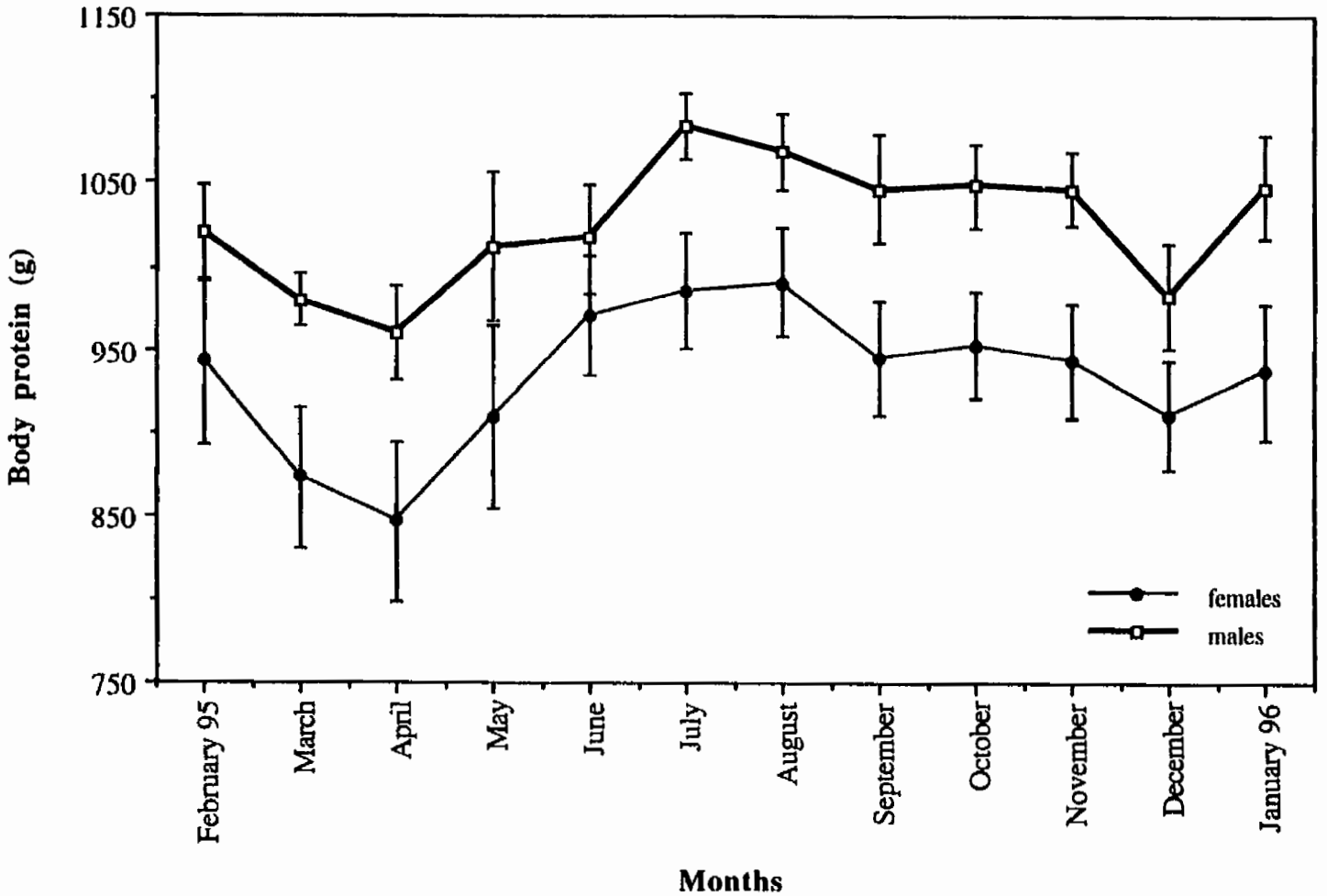


Figure 3. Estimate of mean (± SE) monthly body protein of wild red foxes kept in captivity.

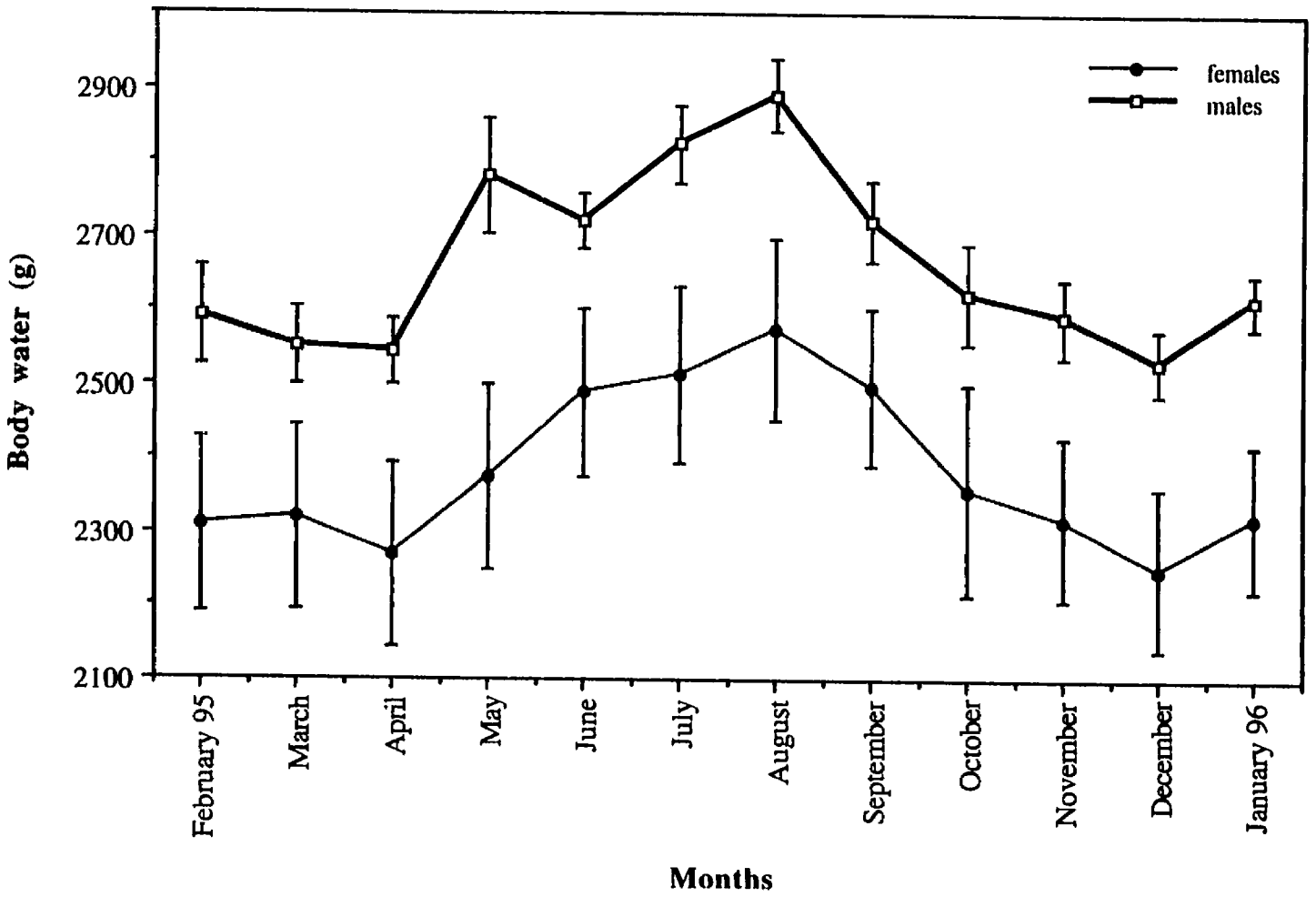


Figure 4. Estimate of mean (± SE) monthly body water of wild red foxes kept in captivity.

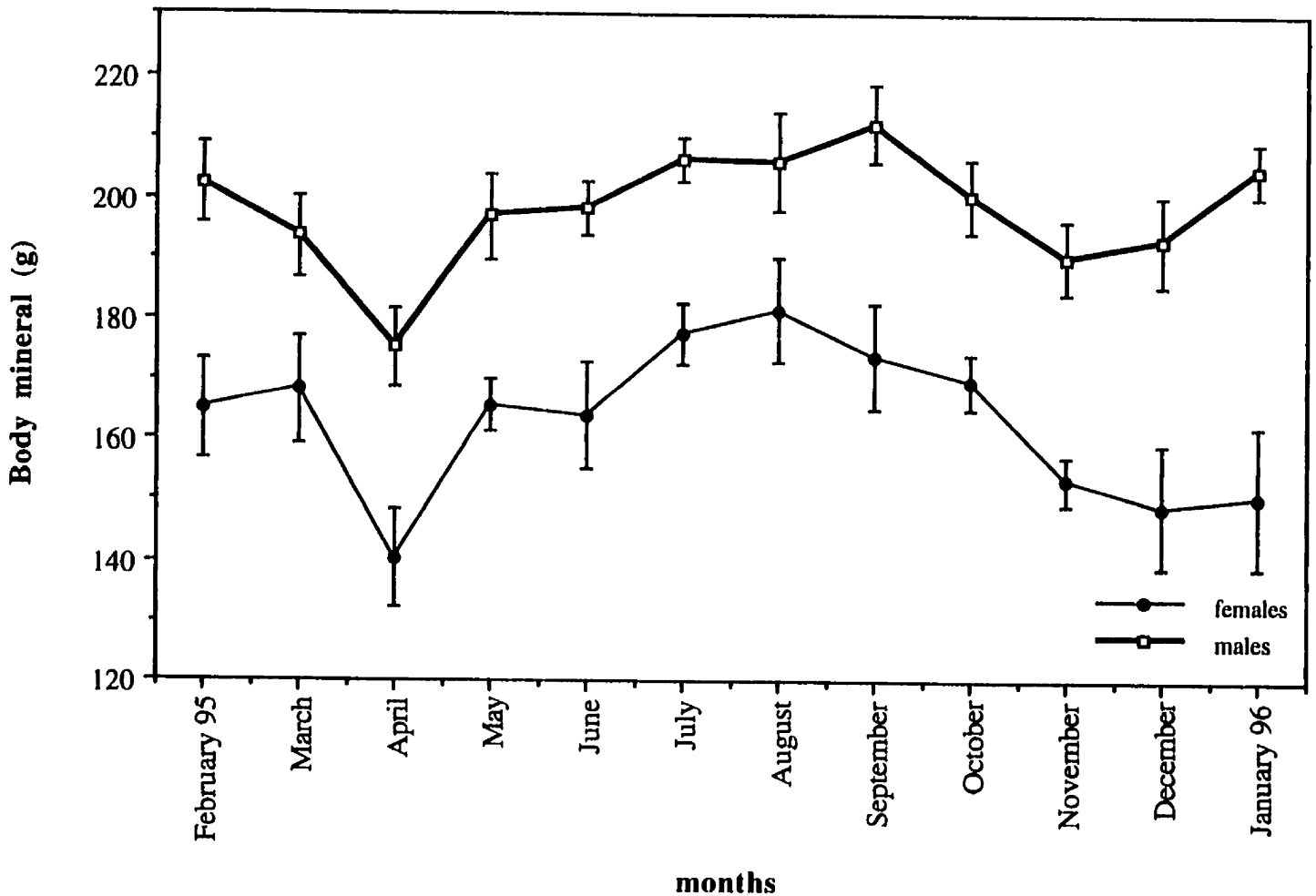


Figure 5. Estimate of mean (± SE) monthly body mineral of wild red foxes kept in captivity.

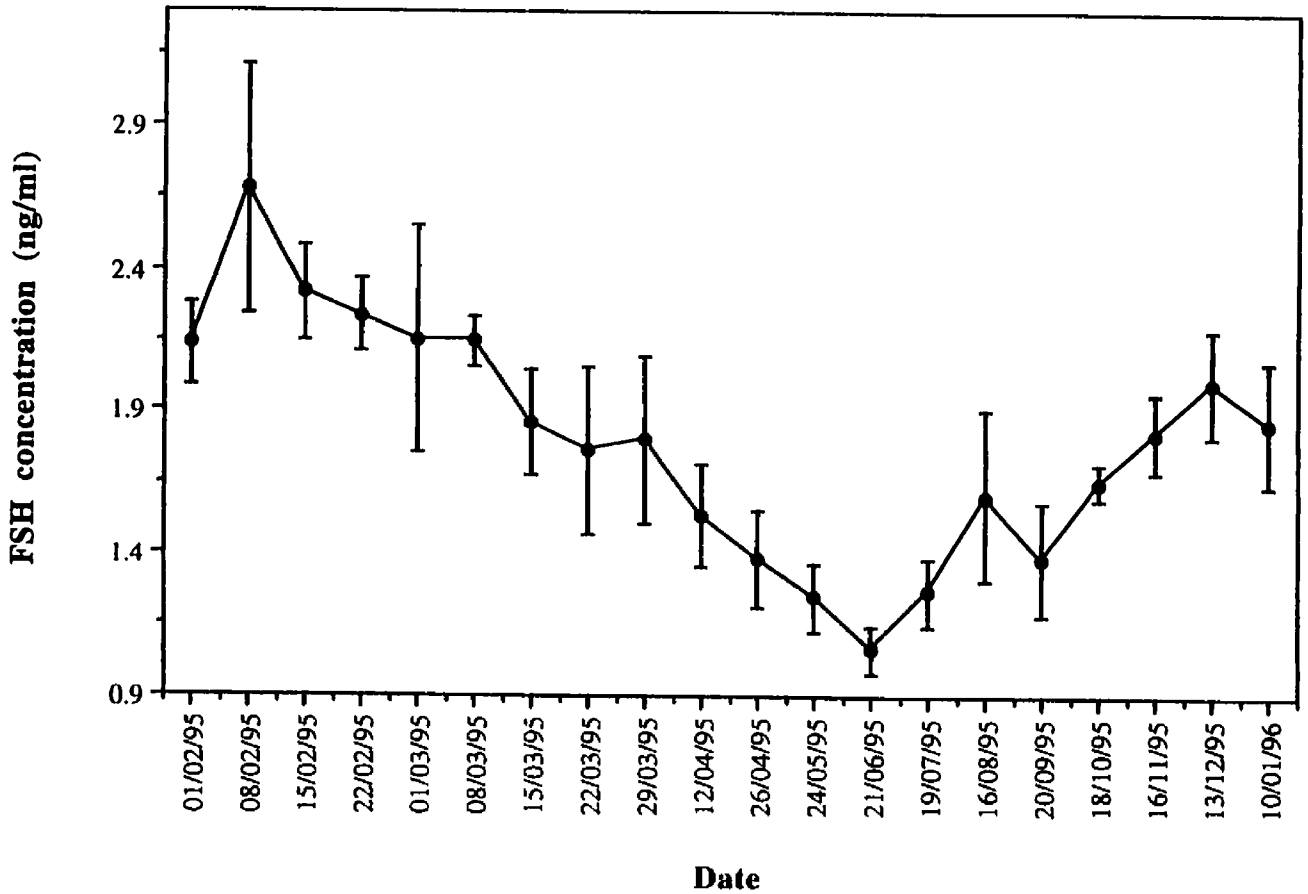


Figure 6. Annual variation of the mean (± SE) concentration of FSH in the blood of female red foxes kept in captivity.

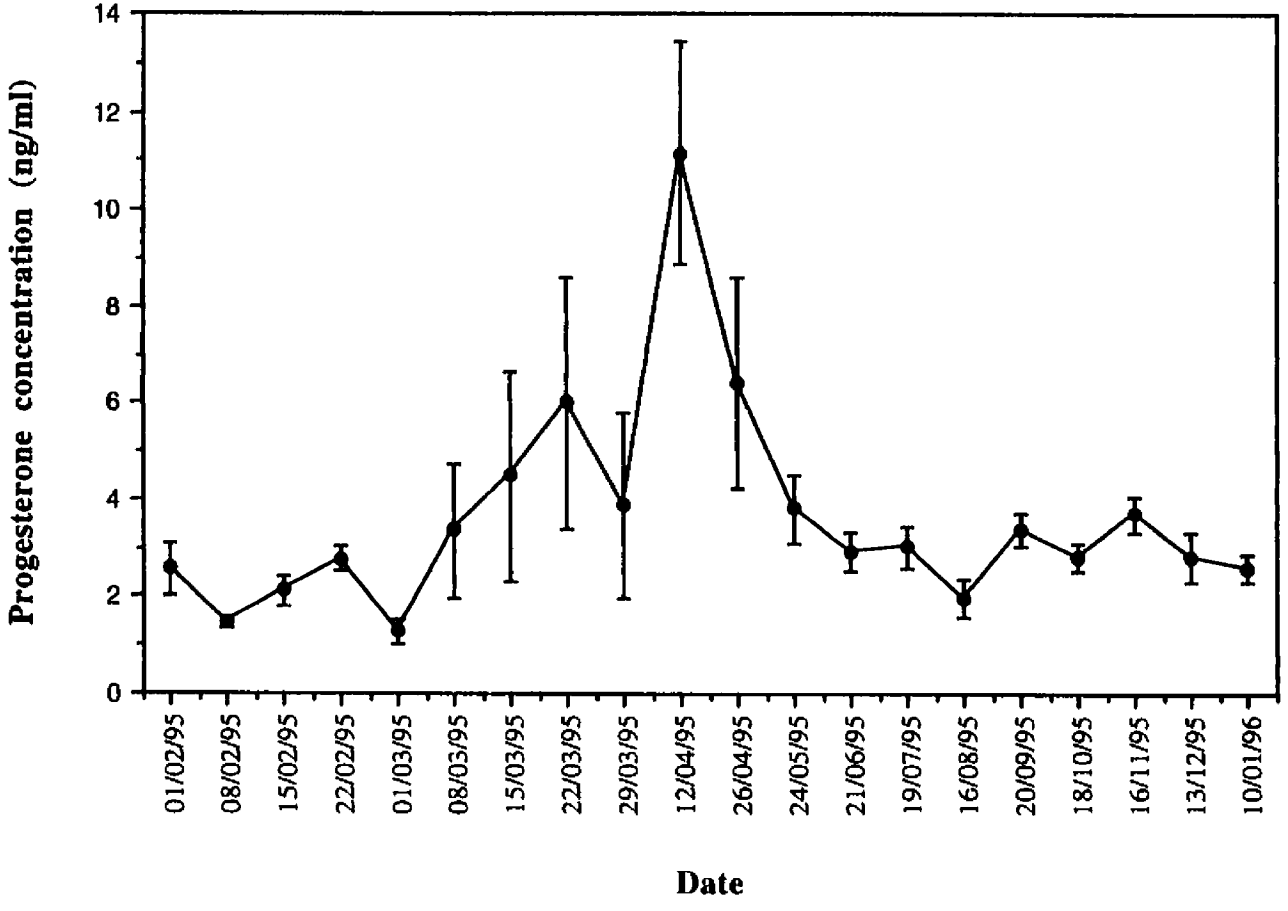


Figure 7. Annual variation of the mean (± SE) concentration of progesterone in the blood of female red foxes kept in captivity.

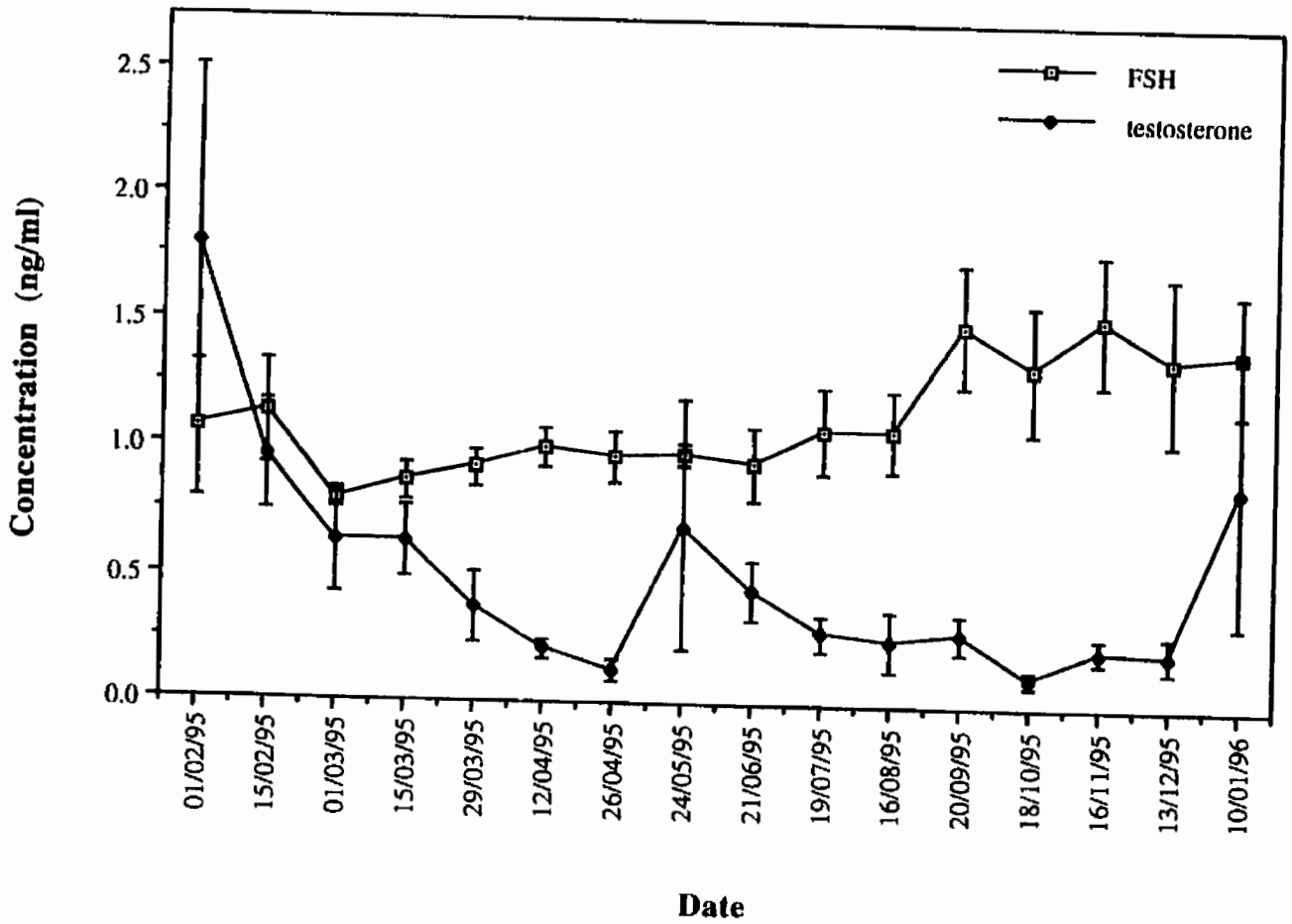


Figure 8. Annual variation of the mean (± SE) concentration of FSH and testosterone in the blood of male red foxes kept in captivity.

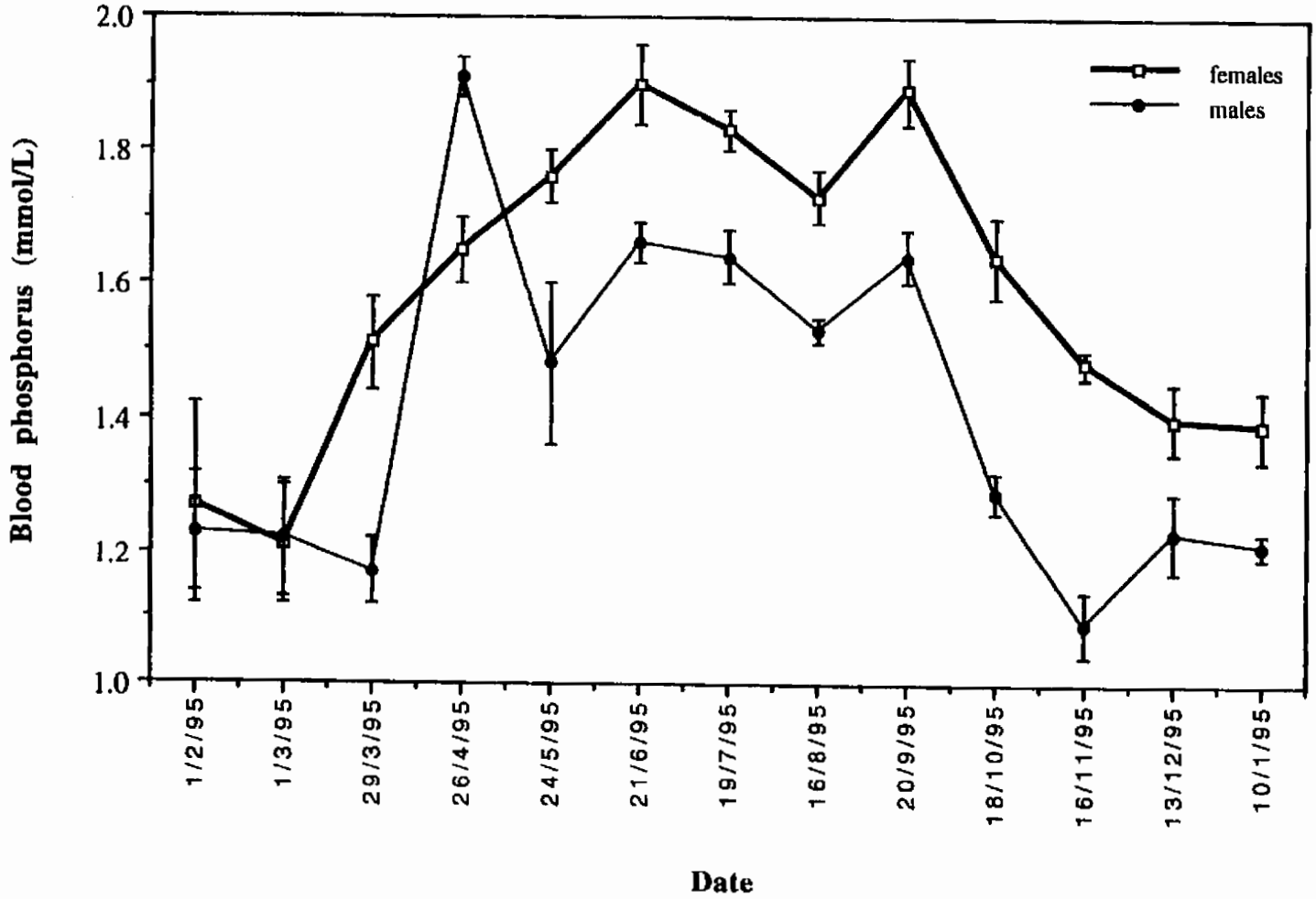


Figure 9. Annual variation of the mean (± SE) concentration of phosphorus in the blood of red foxes kept in captivity.

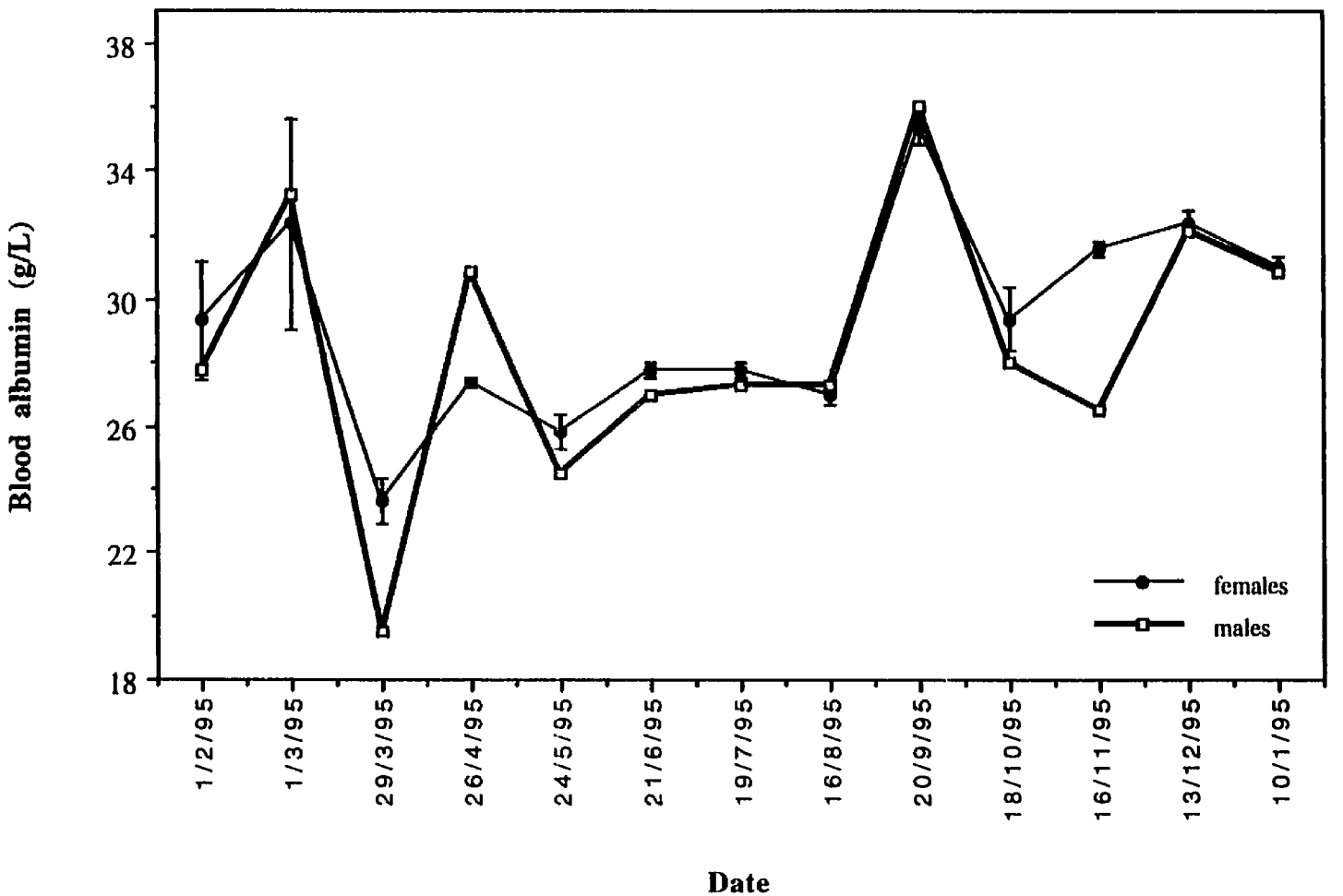


Figure 10. Annual variation of the mean (± SE) concentration of albumin in the blood of red foxes kept in captivity.

CONCLUSION GÉNÉRALE

À notre connaissance, aucune autre étude n'a utilisé des modèles de régression multiple pour quantifier les variations annuelles de la composition corporelle chez des animaux vivants. En effet, la plupart des modèles utilisent des carcasses d'animaux (Buskirk et Harlow 1989; Prestrud et Nilssen 1992; Poulle *et al.* 1995). Pourtant, ces modèles s'avèrent être des outils fort utiles, voire nécessaires, pour comprendre la dynamique des composantes corporelles à long terme. De plus, ils nous permettent d'éliminer les variations intra-individuelles qui limitent l'interprétation des résultats. Les indices que nous avons développés dans le chapitre un permettent d'estimer rapidement la masse absolue de l'eau, du gras, des protéines et des minéraux chez des renards des deux sexes sous diverses conditions, et ils peuvent être utilisés pour comparer la composition corporelle sur une base annuelle ou régionale. Nos modèles sont simples et peu coûteux à utiliser. De plus, ils requièrent au maximum quatre variables et ne nécessitent pas l'euthanasie des animaux. Cependant, les mesures de circonférences nécessitent une attention particulière, et c'est pourquoi il est préférable qu'elles soient prises par le même manipulateur. Les mesures retenues pour estimer la composition corporelle de renards vivants se résument à la masse totale, à la longueur du corps et de la patte arrière, à la circonférence de la taille et de la cuisse, à une pinçée entre les omoplates et sur le côté du thorax et, finalement, à une lecture de la résistance et de la réactance prise à l'aide d'un adipomètre électrique.

Les résultats du chapitre deux démontrent bien l'existence de variations annuelles de la composition corporelle chez le renard roux. Les fluctuations des réserves adipeuses en sont certainement le meilleur exemple puisqu'elles ont doublé, de l'été à l'automne, pour atteindre des valeurs maximales durant l'hiver. À l'inverse, la teneur en protéines, en eau et en minéraux était minimale durant la saison hivernale. D'après nos données, la masse totale n'est pas un bon indice pour prédire la composition corporelle en tout temps de l'année. En effet, la masse est demeurée à peu près stable tout au long de l'étude malgré des fluctuations d'importance variable des composantes corporelles. Pour prédire la composition corporelle estivale, les réserves de gras ne constitueraient pas un bon indice puisqu'elles sont minimales durant cette période. De plus, une diminution de la teneur en protéines pendant l'été pourrait être un signe de carence puisqu'à ce moment de l'année, la teneur en protéines était la plus élevée. D'ailleurs, ce dernier résultat peut nous aider à mieux comprendre ce qui se passe chez les coyotes de l'Est du Québec (*Canis latrans*) qui ont perdu, entre la fin de l'hiver et

l'été, 44% de leur masse lipidique et 17% de leur masse protéique (Poulle *et al.* 1995). Le déclin des réserves lipidiques serait associé, du moins en partie, au cycle normal du gras. Cependant, en ce qui concerne le déclin des protéines, il semble que les coyotes auraient subi une carence alimentaire. Comme les auteurs l'ont suggéré, il se pourrait que le printemps et l'été aient été des périodes de rareté de nourriture pour ces animaux ou qu'un changement dans le régime alimentaire soit survenu. À cet effet, Michel Crête poursuivra l'étude avec les renards roux, mais cette fois en changeant l'alimentation des animaux. La moitié des renards recevra un régime alimentaire principalement composé de fruits pour vérifier l'effet d'un changement dans l'alimentation sur la composition corporelle. L'autre moitié du groupe, qui recevra le même régime alimentaire que lors de la présente étude, servira de témoin. Nous pourrons ainsi vérifier si les variations annuelles des composantes corporelles sont en fait dues à un effet combiné de fluctuations annuelles endogènes et de changements dans le régime alimentaire.

La variable qui régulerait en partie les réserves lipidiques est appelé la consigne (set-point; Mrovosky et Powley 1977). Mrosovsky et Sherry (1980) ont proposé que la diminution du niveau de cette consigne permettrait d'éviter les conflits entre l'alimentation et les autres activités comme l'hibernation, l'incubation, la mue ou la défense d'un territoire ou d'un harem. Selon Huot (1988), il semble que l'accumulation des réserves lipidiques dépendrait à la fois de la qualité de l'environnement et des besoins anticipés de l'animal pour la saison à venir. Étant donné que nous n'avons contrôlé ni la photopériode ni la température, nous ne pouvons pas conclure que les variations annuelles des composantes corporelles soient endogènes. Une combinaison de ces trois variables pourrait cependant réguler l'accumulation des réserves lipidiques à l'automne et la réduction de celles-ci durant l'été. Les changements saisonnniers dans la disponibilité de la nourriture et les activités reproductrices, qui entrent en conflit avec l'alimentation durant certaines périodes de la vie d'un animal, rendraient les réserves lipidiques essentielles (Mrosovsky 1990).

En ce qui concerne les constituants sanguins, nous n'avons pas été en mesure d'expliquer les variations importantes du phosphore et de l'albumine. Même si le phosphore semble étroitement lié à la teneur en eau, en protéines et en minéraux, il nous semble difficile d'en conclure quoi que ce soit. L'albumine étant un transporteur d'acides gras, il aurait peut-être été intéressant de tracer un profil lipidique en quantifiant les acides gras libres et les triglycérides sanguins. Malgré le fait que le sang contienne une multitude d'informations sur l'état nutritif et physiologique des animaux (Huot 1988), il s'avère difficile d'expliquer les

fluctuations de certaines de ces composantes car les sources de variation sont nombreuses. Huot (1988) a fait ressortir pour les ongulés ces sources de variation qui seraient liées soit à l'état des individus examinés (ex. stress, sexe, âge, saison, l'état reproducteur, effet de tranquilisants) ou aux échantillons (ex. veine utilisée, déshydratation, hémolyse, méthode d'analyse, méthodes de préservation du sang). Même si les données recueillies peuvent nous servir de point de comparaison lors d'études ultérieures au cours desquelles la composition et la quantité de nourriture fournie aux renards seraient manipulées, les indices sanguins semblent surtout efficaces pour identifier des carences plutôt que pour comparer la condition physique relative d'animaux non carencés (Huot 1988).

Pour ce genre d'étude, l'utilisation d'animaux gardés en captivité est nécessaire, le contrôle du régime alimentaire étant à la base de l'expérimentation. De plus, il est primordial d'empêcher la reproduction pour réduire au minimum les variables pouvant avoir un impact sur les variations annuelles. Cependant, les études en captivité peuvent rendre difficile l'interprétation des résultats, par exemple dans le cas des fluctuations de la teneur en protéines. Compte tenu des limites d'interprétation, l'expérimentation en conditions contrôlées s'avère être parfois essentielle pour comprendre un phénomène.

RÉFÉRENCES

Adamczewski, J.Z., Flood, P.F. et Gunn, A. 1995. Body composition of muskoxen (*Ovibos moschatus*) and its estimation from condition index and mass measurements. Can. J. Zool. 73: 2021-2034.

Adamczewski, J.Z., Gates, C.C., Hudson, R.J. et Price, M.A. 1987. Seasonal changes in body composition of mature female caribou and calves (*Rangifer tarandus groenlandicus*) on an arctic island with limited winter ressources. Can. J. Zool. 65: 1149-1157.

Allaye Chan-McLeod, A.C., White, R.G. et Holleman, D.F. 1994. Effects of protein and energy intake, body composition, and season on nutrient partitioning and milk production in caribou and reindeer. Can. J. Zool. 72: 938-947.

Allen, W.V. 1976. Biochemical aspect of lipid storage and utilization in animals. Am. Zool. 16: 631-647.

Barboza, P.S., Allen, M.E., Rodden, M. et Pojeta, K. 1994. Feed intake and digestion in maned wolf (*Chrysocyon brachyurus*): consequence for dietary management. Zoo Bibl. 13: 375-381.

Ben Jebara, M.K., Carrière, P.D. et Price, C.A. 1994. Decreased pulsatile LH secretion in heifers superovulated with eCG or FSH. Theriogenology 42: 685-694.

Blaxter, K.L., Kay, R.N.B., Sharman, G.A.M., Cunningham, J.M.M. et Hamilton, W.J. 1974. Farming the red deer. Department of Agriculture and Fisheries for Scotland. Her Majesty's Stationery Office, Edinburgh.

Bistner, S.I et Ford, R.R. 1995. Kirk and Bistner. Handbook of veterinary procedures and emergency treatments (6ème édition). Saunders, Philadelphia.

Buskirk, S.W. et Harlow, H.J. 1989. Body-fat dynamics of the American marten (*Martes americanus*) in winter. J. Mammal. 70: 191-193.

Cabanac, M. 1989. Palatability of Food and the Ponderostat. The Psychobiology of Human Eating Disorders: Preclinical and Clinical Perspectives 575: 340-352.

Cabanac, M. et Richard D. 1996. The Nature of the Ponderostat: Hervey's Hypothesis Revived. Appetite 26: 45-54.

Cahill, G.F. 1970. Starvation in man. N. Engl. J. Med. 282: 668-675.

Castro, G., Wunder, J.P. et Knopf, F.L. 1990. Total body electrical conductivity (TOBEC) to estimate total body fat of free-living birds. Condor 92: 496-499.

Colon, J., Kimball, M., Hansen, B. et Concannon, P.W. 1993. Effects of contraceptive doses of the progestagen megestrol acetate on luteinizing hormone and follicle-stimulating hormone in female dogs. J. Reprod Fert., Suppl. 47: 519-521.

Crête, M. et Courtois, R. 1997. Limiting factors might obscure population regulation of moose (Cervidae: *Alces alces*) in unproductive boreal forests. J. Zool. 242: (sous presse).

Crête, M. et Huot, J. 1993. Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserve of dams. Can. J. Zool. 71: 2291-2296.

Crête, M. et Lemieux, R. 1994. Dynamique de population des coyotes colonisant la péninsule gaspésienne. Rep. 94-2429-07, Ministère de l'Environnement et de la Faune, Québec.

Crête, M., Huot, J., Nault, R. et Patenaude, R. 1993. Reproduction, growth and body condition of Rivière George caribou in captivity. Arctic 46: 189-196.

Dauphiné, T.C. 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 4. Growth, reproduction and energy reserves. Can. Wildl. Serv. Rep. Ser. No. 38.

Farley, S.D. et Robbins, C.T. 1994. Development of two methods to estimate body composition of bears. Can. J. Zool. 72: 220-226.

Faulkner, W.L., Egan, L.A. et Anderson, D.M. 1992. Apparent and true digestibility of dry matter, crude protein and amino acids in diets for mature silver foxes. Norwegian J. Agric. Sci. Suppl. 9: 268-274.

Finger, S.E., Brisbin Jr., I.L., Smith, M.H. et Urbston, D.F. 1981. Kidney fat as a predictor of body condition in white-tailed deer. J. Wildl. Manage. 45: 964-968.

Fiorroto, M.A., Cochran, W.J., Funk, R.C., Sheng, H.P et Klish, W.J. 1987. Total body electrical conductivity measurements: effects of body composition and geometry. Am. J. Physiol. 252: R794-R800.

Gauthier, M. et Thomas, D.W. 1990. Evaluation of the accuracy of ^{22}Na and tritiated water for the estimation of food consumption and fat reserves in passerine birds. Can. J. Zool. 68: 1590-1594.

Hall, C.B., Lukaski, H.C. et Marchello, M.J. 1989. Estimation of rat body composition using tetrapolar bioelectrical impedance analysis. Nutr. Rep. Int. 39: 627-633.

Hammill, M.O. 1983. The arctic fox, *Alopex lagopus*, as a marine mammal: physical condition and population age structure. Université McGill, Montréal, thèse de M.Sc.

Hervey, G.R. 1969. Regulation of energy balance. Nature 223: 629-631.

Huot, J. 1988. Review of methods for evaluating the physical condition of wild ungulates in northern environments. Centre d'études nordiques, Université Laval, Québec. Nordicana No. 50.

Huot, J. 1989. Body composition of the George River caribou (*Rangifer tarandus caribou*) in fall and late winter. Can. J. Zool. 67: 103-107.

Huot, J. et Picard, G. 1988. A simplified method for assessment of caribou body composition. J. Wildl. Manage. 52: 606-609.

Huot, J., Poulle, M.-L. et Crête, M. 1995. Evaluation of several indices for assessement of coyote (*Canis latrans*) body composition. Can. J. Zool. 73: 1620-1624.

Husband, T.P. 1976. Energy metabolism and body composition of the fox squirrel. J. Wild. Manage. 40: 255-263.

Jameson, E.W. et Mead, R.A. 1964. Seasonal changes in body fat, water and basic weight in *Citellus lateralis*, *Eutamias speciosus* and *E. amoenus*. J. Mammal. 45: 359-365.

Keesey, R.E. et Powley, T.L. 1986. The regulation of body weight. Ann. Rev. Psychol. 37: 109-133.

Korhonen, H. et Harri, M. 1986. Seasonal changes in energy economy of farmed polecat as evaluated by body weight, food intake and behavioural strategy. Physiol. Behav. 37: 777-783.

Kistner, T.P., Trainer, C.E. et Hartmann, N.A. 1980. A field technique for evaluating physical condition deer. Wildl. Soc. Bull. 8: 11-17.

Kushner, R.F. 1992. Bioelectrical impedance analysis: a review of principles and applications. J. Am. Coll. Nutr. 11: 199-209.

Lafrance, M. et Goff, A.K. 1985. Effect of pregnancy on oxytocin-induced release of prostaglandin F2a in heifers. Biol. Reprod. No. 33: 1113-1119.

Lefebvre, C., Crête, M., Huot, J. et Patenaude, R. 1997. Prediction of live and post-mortem body composition of red foxes (*Vulpes vulpes*). J. Wildl. Dis. (soumis).

LeResche, R.R., Seal, U.S., Karns, P.D. et Franzmann, A.W. 1974. A review of blood chemistry of moose and others cervidae with emphasis on nutritional assessment. Nat. Can. 101: 263-290.

Lindström, E. 1983. Condition and growth of Red foxes (*Vulpes vulpes*) in relation to food supply. J. Zool. Lond. 199: 117-122.

Litvaitis, J.A. et Mautz, W.W. 1976. Energy utilization of three diets fed to a captive red fox. J. Wildl. Manage. 40: 365-368.

Lukaski, H.C. 1987. Methods for the assessment of human body composition: traditional and new. Am. J. Clin. Nutr. 46: 537-556.

Mattfeld, G.F. 1974. The energetics of winter foraging by white-tailed deer: a perspective on winter concentration. Ph.D. Thesis, State Univ. New York, Syracuse.

Maurel, D. et Boissin, J. 1982. Métabolisme périphérique de la testotérone en relation avec le cycle annuel de la testostérone et de la 5a-dihydrotestostérone plasmatiques chez le Blaireau européen (*Meles meles* L.) et le Renard roux (*Vulpes vulpes* L.). Can. J. Zool. 60: 406-416.

Mautz, W.W. 1978. Nutrition and carrying capacity. Big game of North America: Ecology and Management 1st Ed. Wildl. Mon. Inst. Stackpole books, Harr. Pa. pp. 321-348

Mautz, W.W., Kanter, J. et Pekins, P.J. 1992. Seasonal metabolic rhythms of captive female white-tailed deer: a reexamination. J. Wildl. Manage. 56: 656-661.

McArdle, W.D., Katch, F.I. et Katch, V.L. 1996. Exercise physiology: Energy, nutrition, and human performance. (4ème édition). William and Wilkins, Maryland.

McFarland, D.J. 1971. Feedback mechanisms in animal behaviour. Academic Press, London/New York.

McNeilly, J.R., McNeilly, A.S., Walton, J.S et Cunningham, F.J. 1976. Development and application of a heterologous radioimmunoassay for ovine follicle-stimulating hormone. J. Endocr. 70: 69-79.

Miller, M. E. 1962. Guide to the dissection of the dog. (3ème édition). Ithaca, N. Y, droits d'auteur accordés à Mary Miller.

Mitchell, B., McCowan, D. et Nicholson, A.I. 1976. Annual cycles of body weight and condition in Scottish Red Deer, *Cervus elaphus*. J. Zool. 180: 107-127.

Mondain-Monval, M., Dutourne, B., Bonnin-Laffargue, M., Canivenc, R. et Scholler, R. 1977. Ovarian activity during the anoestrus and the reproductive season of the red fox (*Vulpes vulpes* L.). J. Steroid Biochem. 8: 761-769.

Mondain-Monval, M. Bonnin, M., Scholler, R. et Canivenc, R. 1980. Androgens in peripherical blood of the red fox (*Vulpes vulpes* L.) during the reproductive season and anoestrus. J. Steroid Bioch. 11: 1315-1322.

Mondain-Monval, M., Farstad, W., Smith, A.J., Roger, M. et Lahlon, N. 1993. Relationship between gonadotrophins, inhibin and sex steroid secretion during periovulatory period and the luteal phase in the blue fox (*Alopex lagopus*). J. Reprod. Fert. Suppl. 47: 47-56.

Morton, M.L. et Tung, H.-C.L. 1971. The relationship of total body lipid to fat depot weight and body weight in the belding ground squirrel. J. Mammal. 52: 839-842.

Moore, G.C. et Millar, J.S. 1984. Comparative study of colonizing and longer established eastern coyote population. J. Wildl. Manage 48: 691-699.

Mrosovsky, N. et Powley, T.L. 1977. Set Points for Body Weight and Fat. Behav. Biol. 20: 205-223.

Mrosovsky, N. et Sherry, D.F. 1980. Animal Anorexias. Science 207: 837-842.

Mrosovsky, N. 1990. Rheostasis. The Physiology of Change. Oxford University Press, Inc., New York.

Osadchuk, L.V. 1992. Genetic and endocrine aspects in the regulation of the reproductive function in silver fox. Norwegian. J. Agric. Sci. Suppl. No. 9: 161-166.

Osadchuk, L.V. 1993. Sexual steroid hormones in the reproductive cycle of silver fox. Norwegian. J. Agric. Sci. 7: 189-201.

Ouellet, J.-P. 1992. Ecology of an introduced caribou of population of Southhampton Island, N. W. T., Canada. Université de l'Alberta, thèse de Ph. D.

Ouellet, J.-P. 1997. A comparison of body condition and reproduction of caribou on two predator-free arctic islands. Can. J. Zool. 75: 11-17.

Pace, N., Kline, L., Schachman, H.K. et Harfenist, M. 1947. Studies on body composition. IV. Use of radioactive hydrogen for measurement in vivo of total body water. J. Biol. Chem. 168: 459-469.

Parker, K.L., Robbins, C.T. et Hanley, T.A. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. 48: 474-488.

Perry, M.C, Kuenzel W.J., Williams, B.K. et Serafin, J.A. 1986. Influence of nutrients on feed intake and condition of captive canvasbacks in winter. J. Wildl. Manage. 50: 427-434.

Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. National Park Service Scientific Monograph Series. No. 11.

Pethig, R. 1979. Dielectric and electronic properties of biological materials. John Wiley and Sons, Chichester, England.

Pond, C.M. 1978. Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. Ann. Rev. Ecol. Syst. 9: 519-570.

Pond, C.M, 1981. Storage. Physiological ecology. Townsend, C.R. et Calow, P (éditeurs). Blackwell Scientific Publications, Oxford. pp. 190-219.

Pond, C.M., Mattacks, C.A. et Ramsay, M.A. 1994. The anatomy and chemical composition of adipose tissue in wild wolverines (*Gulo gulo*) in northern Canada. J. Zool. Lond. 232: 603-616.

Poulle, M.-L., Crête, M. et Huot, J. 1995. Seasonal variation in body composition of eastern coyotes. Can. J. Zool. 73: 1625-1633.

Prestrud, P. 1982. Seasonal variation in basal metabolic rate and fat deposition in the arctic fox in Svalbard. Université de Oslo, Norvège, thèse de M.Sc.

Prestrud, P. et Nilssen, K. 1992. Fat deposition and seasonal variation in body composition of arctic foxes in Svalbard. J. Wildl. Manage. 56: 221-233.

Price, C.A. 1994. Evidence that testosterone and inhibin do not interact in the control of FSH in rams. Theriogenology 41: 471-482.

Pritchard, G.T. et Robbins, C.T. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Can. J. Zool. 68: 1645-1651.

Randall, E.L. 1974. Improved method for fat and oil analysis by a new process of extraction. J. Assoc. Off. Anal. Chem. 57: 1165-1168.

Reimers, E., Ringberg, T. et Sorumgard, R. 1982. Body composition of Svalbard reindeer. Can. J. Zool. 60: 1812-1821.

Ricklefs, R.E., Konarzewski, M. et Daan, S. 1996. The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. Am. Nat. 147: 1047-1071.

Riney, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to New Zealand. N. Z. J. Sci. Technol. 36: 429-463.

Robbins, C.T. 1983. Wildlife feeding and nutrition. Academic Press, San Diego.

Robbins, C.T., Moen, A.N. et Reid, J.T. 1974. Body composition of white-tailed deer. J. Anim. Sci. 38: 871-876.

Roby, D.D. 1991. A comparison of two noninvasive techniques to measure total body lipid in live birds. The Auk 108: 509-518.

Rosenthal, R.D. 1986. Characteristics of non-destructive near infrared instruments for grain and food products. Proc. Mtg. Japan Food Science Inst. 1986: 1-23.

Ryg, M. 1983. Relationships between hormone-induced and compensatory weight changes in reindeer (*Rangifer tarandus tarandus*). Comp. Biochem. Physiol. 74: 33-35.

Schwartz, C.C., Regelin, W.L. et Franzmann, A.W. 1984. Seasonal dynamics of food intake in moose. Alces 20: 223-244.

Samson, C. et Crête, M. 1997. Summer food habits and population density of coyotes, *Canis latrans*, in boreal forest of south eastern Québec. Can. Field-Nat. 111 (sous presse).

SAS Institute Inc. 1989. SAS user's guide: statistics, version 5. SAS Institute Inc., Cary, N.C.

Sheng, H.-P. et Huggins, R.A. 1971. Direct and indirect measurement of total body water in the growing beagle. Proc. Soc. Exptl. Biol. Med. 137: 1093, 1971.

Sheng, H.-P. et Huggins, R.A. 1979. A review of body composition studies with emphasis on total body water and fat. Am. J. Clin. Nutr. 32: 630-647.

Steen, S.N., Opplinger, R.A. et Brownell, K.D. 1988. Metabolic Effects of Repeated Weight Loss and Regain in Adolescent wrestlers. J. Am. Med. Ass. 260: 47-50.

St-Pierre, S., Roy, B. et Tremblay, A. 1996. A case study on energy balance during an expedition through Greenland. Int. J. Obesity 20: 493-495.

Thomas, D.C. 1982. The relationship between fertility and fat reserves of Peary Caribou. Can. J. Zool. 60: 597-602.

Thomas, V.G. 1990. Control of reproduction in animal species with high and low body fat reserves. Prog. Reprod. Biol. Med. 14: 27-41.

Todd, A.W. et Keith, L.B. 1983. Coyote demography during a snowshoe hare decline in Alberta. J. Wildl. Manage. 47: 394-404.

Torbit, S.C., Carpenter, L.H., Swift, D.M. et Alldredge, A.W. 1985. Differential loss of fat and protein by mule deer during winter. J. Wildl. Manage. 49: 80-85.

Torbit, S.C., Carpenter, L.H., Bartmann, R.M., Alldredge, A.W. et White, G.C. 1988. Calibration of carcass fat indices in wintering mule deer. J. Wildl. Manage. 52: 582-588.

Tremblay, J.-P., Crête, M. et Huot, J. 1997. Summer forage behavior of eastern coyotes: evidence for source and sink dynamics. Écoscience: (soumis).

Tyler, N.J.C. 1987. Body composition and energy balance of pregnant and non-pregnant Svalbard reindeer during winter. Symp. Zool. Soc. Lond. No. 57: 203-229.

Van Loan, M.L. et Mayclin, P. 1987. A new TOBEC instrument and procedure for the assessment of body composition: use of Fourier coefficients to predict lean body mass and total body water. Am. J. Clin. Nutr. 45: 131-137.

Verme, L.J. et Ozoga, J.J. 1980. Effects of diet on growth and lipogenis in deer fawns. J. Wildl. Manage. 44: 315-324.

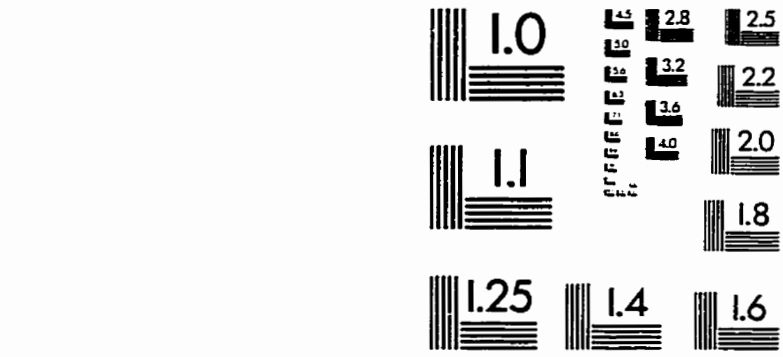
Virgil, J.A. et Messier, F. 1992. Seasonal variation in body composition and morphology of adults muskrats in central Sakatchewan, Canada. J. Zool. Lond. 228: 461-477.

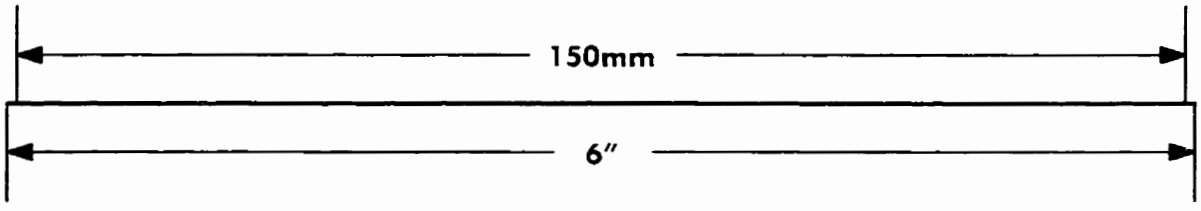
Wakely, L.G. et Mallory, F.F. 1988. Hierarchical development, agonistic behaviours, and growth rates in captive arctic fox. Can. J. Zool. 66: 1672-1678.

Walsberg, G.E. 1988. Evaluation of a nondestructive method for determining fat stores in small birds and mammals. Physiol. Zool. 61: 153-159.

Worden, K.A. et Pekins, P.J. 1995. Seasonal change in feed intake, body compostion, and metabolic rate of white-tailed deer. Can. J. Zool. 73: 452-457.

IMAGE EVALUATION TEST TARGET (QA-3)





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