Comparative Plasma and Urine Chemistry of Fasting White-tailed Prairie Dogs (Cynomys leucurus) and American Martens (Martes americana): Representative Fat- and Lean-bodied Animals

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Abstract
American martens and white-tailed prairie dogs are mammals of similar body mass, exposed to periods of food deprivation, but of vastly different body fat content. While both species demonstrated a protein conservation phase during a short-term fast, martens had a greater reliance on protein as depicted by greater loss of body weight, higher daily urine volume, and glomerular clearance rates, as well as higher daily urinary urea excretion. Protein use was calculated to be 3.15 and 1.23 g/d for martens and prairie dogs, respectively. Martens did not hydrolyze a greater amount of urea as they were hypothesized to do in order to conserve water. Urinary beta-hydroxybutyrate (BHBA) excretion decreased during the fast in both species but prairie dogs had higher plasma levels of BHBA, which suggests that regulation of protein catabolism may be in part from ketone bodies. By using fat and protein in a ratio of about 2:1, martens may maintain sufficient hydration, extend their fat stores, and retain muscle integrity during short-term fasts.

Introduction

Animals living in temperate or polar climates are exposed to periods of potential negative energy balance and must draw on fat and protein to meet energy requirements. Adipose tissue containing triglycerides traditionally

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has been viewed as the primary storage fuel because of its high energy density and ability to be stored in a dehydrated form (Allen 1976). However, it has been shown that weight loss during starvation results not only from fat catabolism but from considerable breakdown of lean tissue (Benoit, Martin, and Walter 1965). In addition, it is now believed that protein (like triglycerides in adipose tissue) may be stored in visceral as well as skeletal sites (Kendall, Ward, and Bacchus 1973; Le Maho et al. 1981; Torbit et al. 1985). As a result, seasonal fat stores do not appear to be the overriding determinant of winter survival by all temperate mammals. Lean animals, therefore, may not have the strict limitations on fasting endurance previously thought. The question addressed in this study is whether lean-bodied mammals are adapted to cope with short-term starvation in a manner basically similar to that of fat mammals. Two species of comparable size but different body mass were chosen for study: American martens (*Martes americana*) and white-tailed prairie dogs (*Cynomys leucurus*). In earlier work we have reported the marten to be a lean-bodied mustelid (only 5.6% of its body mass is fat in the fall) that shows no significant decline in fat content over winter (Buskirk and Harlow 1989). However, during extreme inclement weather, martens can be without food and forced to rely on body reserves for several days (Buskirk, Harlow, and Forrest 1988). The white-tailed prairie dog was chosen to represent a fat mammal of comparable size (also about 1 kg). Although white-tailed prairie dogs are unlike martens in being herbivorous rodents, they possess critical similarities to martens that make them a reasonable subject for comparison. White-tailed prairie dogs, like martens, spend much of their winter below ground in well-insulated nests and experience periods of food scarcity or deprivation (Tileston and Lechleitner 1966). However, unlike martens, white-tailed prairie dogs have a fat content in the fall of about 27% of their body mass (H. J. Harlow, unpublished data), which is reduced during the winter in field populations (D. Biggins, personal communication).

How then do martens compare with white-tailed prairie dogs in coping with periods of food deprivation without the benefit of large fat reserves? To answer this question it is necessary to investigate the biochemical changes that occur during three phases of fasting. Phase 1 occurs during the first several hours or days of a fast and is characterized by the retention of blood glucose levels through the catabolism of glycogen and protein reserves. Phase 2 is identified by an elevation of blood ketone bodies from triglyceride breakdown and a reduction in protein catabolism with a concomitant drop in blood glucose. The depletion of fat reserves marks the onset of phase 3 fast as protein is, once again, catabolized as the major substrate and blood glucose levels elevate (see Le Maho et al. 1981).
The metabolite profile and duration of these phases should be different for martens and prairie dogs as a result of the type and amount of stored tissue in each species. It is important to note that lean laboratory rats, which are not considered to be tolerant fasters, do not show a protein-conserving phase 2, but continue in a phase 1 (or phase 3) fast with high protein catabolism (Li and Goldberg 1976). A question advanced in this study is whether martens behave like lean laboratory rats or use their limited fat stores to sustain a phase 2 protein-conserving stage similar in profile but not in amplitude to that of fat prairie dogs. It is believed that using a combination of fat and protein during a fast may enhance water balance, conserve muscle protein, and prolong the use of fat stores, whereas utilizing only a single substrate until depletion, as observed in lean laboratory rats, would not provide these benefits. For example, protein has a greater bound water content than fat, which is important for the maintenance of body hydration during fasting (Bintz and Mackin 1980). However, urinary loss accompanies the excretion of nitrogenous urea. This loss may be reduced by the passive movement of urea from the blood (Nelson et al. 1975; Bintz and Thorgerson 1981; Harlow 1987) and hydrolysis of this urea to CO₂ and ammonia by intestinal urealitic microbes (Silen et al. 1955; Nelson et al. 1975).

An investigation of selected blood and urine constituents as well as urea hydrolysis was, therefore, made to determine which strategy is used by these animals: (1) continued catabolism of protein for water production throughout the fast or (2) conservation of protein and heavy reliance on fat catabolism. It was our hypothesis that animals do not simply metabolize fat completely before shifting to protein substrate. Instead, they simultaneously catabolize both substrates in different ratios to serve different functions, depending on the type of stored nutrients.

**Material and Methods**

White-tailed prairie dogs and martens were trapped in southeastern Wyoming at elevations of 2,100 and 3,050 m, respectively. Prairie dogs were housed in 0.18 × 0.25 × 0.18-m stainless steel metabolic cages and martens in 0.5 × 0.64-m stainless steel metabolic cages for at least 2 wk before the study commencing in February. Animals were maintained on a natural photoperiod.

Martens received ad lib. Purina Cat Chow and water while prairie dogs received ad lib. Purina Lab Blox and water. Both species maintained weight during prefasting captivity. A stainless steel funnel matching the dimensions of the bottom of the cage directed all of the voided urine to a bottle con-
taining a layer of mineral oil. In order to insure freshness of the urine (to minimize oxidation and bacterial decay of metabolites) each funnel was fitted with electrodes that, when bridged by a drop of urine, activated a remote alarm when a fresh sample was available. Urine samples were generally retrieved and frozen at \(-70^\circ\text{C}\) within 10 min of being voided. Blood samples were obtained (in lithium heparin–treated containers) by cardiac puncture on animals anesthetized with ketamine hydrochloride (0.02 mg/kg body weight). A portion of the blood was measured for hematocrit and then deproteinized with perchloric acid–Tris–KCl treatment in accordance with the Wildenhoff (1970) assay procedure for beta-hydroxybutyrate (BHBA). The remaining blood was centrifuged for plasma and frozen at \(-70^\circ\text{C}\).

Due to the martens’ lean condition, a period of 5 d without food and water was believed to be at the upper end of a safe fast. The health of all animals was closely monitored during the fast. Particular attention was paid to the activity level and general appearance of each individual. Five martens (four males, one female) were anesthetized, weighed, and a blood sample taken. Food and water were removed and after 5 d, these animals were again anesthetized, weighed, and a blood sample taken. Fresh urine samples were taken night and day. The volumes were measured, and an aliquot frozen for future analysis. Eight white-tailed prairie dogs (four males, four females) were fasted for 5 d. Blood samples were taken before fasting and at 3 d and 5 d after removal of food and water. Fresh urine samples were obtained throughout the day and night for volume measurement and frozen for later analysis.

Deproteinized blood and urine samples were assayed for BHBA by monitoring the reduction of NAD in the presence of beta-hydroxybutyric dehydrogenase at a wavelength of 320 \(\mu\text{m}\) as outlined by Wildenhoff (1970). Plasma and urine samples were assayed for urea by the Berthelot reaction (Searcy 1969), creatinine by Sigma kits using the Jaffe reaction (Tietz 1976, pp. 996–998), and plasma glucose by the glucose oxidase method. Daily urinary loss of creatinine, urea, and BHBA were calculated from 24-h urine volumes and concentrations. Urea/creatinine ratios were calculated by dividing urea by creatinine concentrations expressed as percent by weight (mg%) rather than in millimoles. Because the molecular weight of urea and creatinine differ, a ratio based on millimoles will be different from ones based on percent by volume. The latter units were selected to conform with those presented in the majority of studies reporting this ratio. Glomerular filtration rate (GFR) was expressed as creatinine clearance calculated from blood and urinary creatinine concentrations and from urine volume. Creatinine clearance was used to estimate GFR by the equation \(C = \frac{U}{P} \times V\),
where \( C = \) filtration rate (mL/min), \( U = \) urinary creatinine (\( \mu \)M), \( P = \) plasma creatinine (\( \mu \)M), and \( V = \) urine production (mL/min).

For determining the extent of urea hydrolysis by martens, 5 \( \mu \)Ci (18.5 Bq) of \((^{14}\text{C})\) urea \((8.92 \times 10^{-5} \text{ mM})\) diluted in sterile physiological saline was injected intraperitoneally into each individual placed into a flow-through respirometer chamber where expired air was passed through two organic CO\(_2\) traps containing a 2:1 volume ratio of ethylene glycol monomethylether and ethanolamine (Jaffay and Alvarez 1961) and through a third CO\(_2\) trap exiting into an \( \text{O}_2\) analyzer (fig. 1). Hourly samples were taken for the first 12 h followed by samples at 6-h intervals for the remaining 24-h sampling period. Each sample procedure consisted of drawing 600 \( \mu \)L of organic trap from each flask and placing it into separate scintillation vials containing a POPOP-PPO liquid scintillation fluor with Triton X-100. The samples were then monitored for \( ^{14}\text{C} \) activity on a Beckman model LS 900 liquid scintillation counter and the values added to give total activity of expired radioisotope. Oxygen consumption of individuals was determined by indirect calorimetry using positive flow through the respirometer and a Sybron-Taylor model 570A \( \text{O}_2\) analyzer. From these measurements, urea hydrolysis was expressed as the activity (cpm) of \(^{14}\text{CO}_2\) expired per unit volume (mL) of \( \text{O}_2\) consumed.

**Results**

There were no significant differences between sexes in either species for any of the parameters investigated. Mean loss of body mass by martens was 24% at the end of 5 d without food and water, as contrasted to only 7% by

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**Fig. 1.** Diagram of apparatus used to monitor urea hydrolysis as determined by the release of \(^{14}\text{CO}_2\).
the prairie dogs (fig. 2). Urine output significantly decreased during the fast for both species, but martens produced a significantly greater daily volume of urine at the end of the fast than did prairie dogs (fig. 3). Urinary urea eliminated per day significantly declined in both species during the fast, but the martens voided significantly greater amounts of urinary urea than prairie dogs at the end of the fast period (fig. 4). Urinary creatinine excretion per day was the same for martens and prairie dogs, in both of which it declined as the fast progressed (fig. 5). The combined alterations of urinary urea and creatinine resulted in a decreased urea/creatinine ratio for the marten. However, martens still had significantly higher ratios than prairie dogs at the end of the fast (fig. 6). While the martens' urinary BHBA concentration was lower at the end of the fast because of the difference in urine volume, the daily excretion of BHBA was not different between species at that time (fig. 7). During the prefast state, martens had a lower plasma creatinine and higher urea concentration, which led to a higher urea/creatinine ratio. However, this ratio dramatically dropped in martens at the end of the fast to a point where it no longer differed significantly from the ratio in prairie dogs (table 1). The GFR, as determined from creatinine clearance, was higher in martens than prairie dogs before the fast (5.06 vs. 2.46 mL/min). While these rates decreased in both species at the end of the fast, martens still had a significantly higher GFR than prairie dogs (2.07 vs. 0.825 mL/min). Plasma glucose values were the same for both species.

![Bar chart showing body mass (g) of five martens and eight white-tailed prairie dogs before and after 5 days deprivation of food and water. Vertical bars represent ±SEM.](image-url)
during a fed state, but martens had significantly lower values at the end of the fast (table 1). Hematocrits did not significantly change in either species as a result of deprivation of food and water.

When martens were injected intraperitoneally with $^{14}$C-urea and the $^{14}$CO$_2$ was collected, the activity of $^{14}$C released over the test period was 8.27 cpm/mL O$_2$ ($\pm$ 1.67 SEM) compared with 9.8 cpm/mL O$_2$ ($\pm$ 3.71 SEM) in prairie dogs (Harlow 1987).

Discussion

The major winter activities of temperate and arctic animals are to secure food, water, and shelter. The relative importance of these needs may differ between animals that store large fat reserves and those that balance energy budgets over short time periods. White-tailed prairie dogs are representative of those animals that seasonally store fat reserves and rely upon them during periods of deprivation. Martens, on the other hand, store little fat, but still must cope with periods without food while restricted within subnivean rest-
Fig. 4. Mean daily urinary urea production (mM/d) from five martens (circles, solid line) and eight white-tailed prairie dogs (triangles, dashed line) before and during 5 d deprivation of food and water. Vertical bars represent ±SEM.

ing sites during inclement weather. What is evident from this study is that both species are adapted to short-term fasts in spite of their differences in fat stores.

When fasting, an animal may first rely heavily on glycogen stores (phase 1), then adipose triglyceride reserves (phase 2), followed by use of protein as a fuel (phase 3). However, these phases are typified by utilization of not one substrate alone, but a combination of all three. For the most part, glycogen reserves are depleted within the first day of a fast (Cahill and Owen 1967). Any further glucose production must, therefore, result from gluconeogenesis. If, however, high protein catabolism were to continue, muscle protein would eventually be challenged, thereby jeopardizing locomotor ability. A mechanism by which protein could be conserved would, therefore, be a beneficial trait to animals such as the marten and prairie dog.

Phase 2 during a fast has been reported either not to exist in lean laboratory rats (Goodman et al. 1980) or to be so brief that it is difficult to assess (Le Maho et al. 1981). Martens contain no more fat reserves than lean rats, but, unlike rats, martens do enter a distinct phase 2 fast. The magnitude of this protein conservation phase, however, is not as extensive in martens as in prairie dogs. We conclude this from several lines of evidence. First, the loss
of body weight was greater for martens than prairie dogs (24% vs. 7%). This could be a result of a higher resting metabolism in martens, which is typical of long-lean mustelids. However, extrapolating this into tissue loss would account for only a portion of the differential weight reduction. In addition, prairie dogs did not enter torpor, and, although martens were more alert and aggressive when encountered, they were relatively inactive during the fast. Therefore, the greater weight loss of martens may also be a result of catabolizing more protein, which is lower in mass-specific energy and higher in bound water (Bintz et al. 1979) than fat. As a result, martens would require a greater mass of protein tissue to provide a comparable energy yield. Second, the daily urinary urea losses were significantly greater for martens. The percent protein contribution to total energy by fat animals such as obese humans (Goschke, Stahl, and Tholen 1975), seals (Pernia, Hill, and Ortiz 1980; Nordoy and Blix 1985), and domestic geese (Le Maho et al. 1981) is between 3% and 7%. In our study the daily energy contributed by protein was calculated from urinary urea and total energy expenditure. Only 10% of the total daily energy was derived from protein catabolism in obese prairie dogs, whereas more than 22% of daily energy came from protein in lean martens during fasting. This difference in protein catabolism is supported...
Fig. 6. Mean urinary urea/creatinine ratios (mg%/mg%) from five martens (circles, solid line) and eight white-tailed prairie dogs (triangles, dashed line) before and during 5 d deprivation of food and water. Vertical bars represent ±SEM.

by urea/creatinine ratios. While the urinary urea/creatinine ratio was greater for martens at the end of the fast, the plasma urea/creatinine ratio at that time was about the same. Plasma urea/creatinine ratios are traditionally used as indicators of total protein catabolism, assuming a relatively constant GFR. However, fasting can cause a reduction in GFR (Gelman et al. 1972). Indeed, both species demonstrated a decline in creatinine clearance, but at the end of the fast the GFR of martens was greater than that of the prairie dog, but with a concomitantly higher urinary urea/creatinine ratio. This implies there was a larger amount of urea filtered and eliminated by martens, which reduced the plasma urea concentration. Consequently, these data suggest martens have a higher protein catabolism at the end of the fast in spite of the absence of an elevated plasma urea/creatinine ratio.

As a third factor, there was an elevation in plasma BHBA in both species during the fast. However, at the end of 5 d without food, the concentration of ketone bodies was significantly greater in the plasma of prairie dogs. This suggests both a greater metabolism of fat by prairie dogs and a concomitant ketone body sparing of protein breakdown. Therefore, while protein catabolism was being depressed during the fast by these species, the depression was more marked in prairie dogs. However, martens do not function like
lean laboratory rats, which do not exhibit a phase 2 fast at all. Instead, martens appear to have a phase 2 characterized by mild protein conservation and codependence on fat reserves. By using a combination of fat and protein during a fast, we calculate fat stores to be maintained approximately 3 d longer by martens. Another advantage of this may be a slower but continuous breakdown of protein, which would maintain skeletal muscle integrity and mobility longer than if only protein were used as a substrate. This is in contrast to an abrupt and potentially destructive catabolism of protein with an accompanying urea load, as observed in fasting laboratory rats. The question that now arises is what determines this ratio of fat to protein catabolized. Three factors potentially affect this process: (1) the need for protein catabolism to provide 3- and 4-carbon citric-acid-cycle intermediates necessary for fat catabolism, (2) the role of fat via ketone bodies in regulating protein catabolism, and (3) the interrelationship of fat and protein catabolism for water to maintain body hydration.

In regard to the first point, Yacoe (1983) speculates that, in order to catabolize a specific amount of fat, there must be a constant proportion of protein breakdown to produce 3- and 4-carbon intermediates to the citric acid cycle to sustain the fat catabolism (Lee and Davis 1979). However, in
**TABLE 1**

_**Urea, P, BHBA, glucose concentration, and urea/creatinine ratio in plasma of five martens and eight white-tailed prairie dogs before and after 5 d deprivation of food and water**

| Metabolite               | Prefast       | After 5 d Fast |
|--------------------------|---------------|---------------|
|                          | Marten        | Prairie Dog   | Marten        | Prairie Dog   |
| BHBA (μM)                | 497.0         | 529.0         | 781.0         | 1,128.0       |
|                          | (19.0)        | (72.0)        | (98.0)        | (75.0)        |
| Plasma creatinine (μM)   | 39.5          | 60.4          | 55.5          | 68.0          |
|                          | (4.0)         | (5.6)         | (4.0)         | (5.1)         |
| Urea (mM)                | 16.2          | 12.1          | 7.4           | 10.3          |
|                          | (1.3)         | (.9)          | (1.4)         | (.8)          |
| Urea/creatinine (mg%/mg%)| 241.0         | 98.0          | 70.0          | 83.0          |
|                          | (58.0)        | (7.0)         | (11.0)        | (10.0)        |
| Glucose (mM)             | 109.0         | 123.0         | 67.0          | 126.0         |
|                          | (13.0)        | (8.0)         | (7.0)         | (9.0)         |

Note. Values in parentheses are SEMs.

Our study, the ratio of fat to protein was approximately 1.5:1 for lean martens and 4:1 for fat prairie dogs, which does not support Yacoe's (1983) hypothesis.

On the other hand, the fat-to-protein ratio may be determined by the amount of ketone bodies. It is thought that ketone bodies, specifically BHBA, are instrumental in sparing protein during phase 2 of a fast (see Williamson and Whitelaw [1978] for a review). This is believed to be the result of BHBA's acting as a substitute fuel to glucose and depressing glucose uptake by cells. In this study, the plasma BHBA levels for both species were reverse images of those for changes in body mass and nitrogen excretion (table 1; figs. 2, 4). This may suggest a key role for BHBA in sparing protein breakdown (Le Maho et al. 1981). We hypothesized that, in order to maximize the sparing by ketone bodies of protein catabolism in phase 2, urinary BHBA excretion would decline because of a greater reabsorption of BHBA by the kidneys with a concomitant increase in plasma levels. Both species demonstrated a decline in urinary BHBA loss, which suggests that ketone bodies are being reabsorbed by the kidneys of both species during the fast. Since neither
species became highly ketonemic, it appears that both are utilizing this substrate in metabolic pathways. However, the fact that martens did have significantly lower plasma ketone body levels and higher protein catabolism than prairie dogs at the end of the fast suggests that ketone bodies may not be sparing protein catabolism in this species to the same extent as in the prairie dog. Additionally, martens had a lower plasma glucose concentration at the end of the fast than prairie dogs in spite of higher protein catabolism. It may be that the lower ketone body concentrations in martens have a reduced role in retarding cellular absorption of glucose compared to that in prairie dogs. This would result in a greater glucose uptake and lower blood glucose level with a concomitantly high protein catabolism. A lower depression by ketone bodies of cellular glucose uptake would favor the use of ketone bodies as a metabolic substrate from protein. Consequently, an enhanced use of protein in concert with fat catabolism would provide energy to sustain the higher metabolic rate typical of martens.

A mechanism acting independently or in concert with ketone body regulation of protein catabolism may be in response to the need for water and maintenance of tissue hydration during fasting. Lipid catabolism is a major source of metabolic water. However, as pointed out by Bintz and associates (Bintz and Riedesel 1967; Bintz et al. 1979; Bintz and Mackin 1980), fat is stored in a dehydrated form, and there is a large insensible respiratory water loss causing a negative water balance from catabolism of adipose tissue alone (Chew 1965). But, free water represents about 75% of the mass of muscle tissue, in contrast to its relative absence in stored lipid (Allen 1976). Therefore, during fasting and water deprivation, catabolism of tissues with high protein can allow a positive water balance (Bintz et al. 1979). But, protein contains less energy than the same amount of fat. Therefore, an animal may derive the greatest part of its calories from oxidation of fat during fasting and catabolize just sufficient proteinaceous tissue to maintain water balance. Bintz et al. (1979) has advanced the hypothesis that the degree of tissue hydration may serve as a stimulus for selective tissue catabolism during a fast. Under these conditions, prairie dogs or martens could adjust their water balance by catabolizing a specific ratio of fat to protein. For example, Richardson's ground squirrels (Spermophilus richardsonii) can maintain water balance during euthermic fasting only by catabolizing adipose tissue and skeletal muscle in a ratio of about 1.9:1 (Bintz et al. 1979). The ratio of fat to protein in our study was estimated from standard calorimetric considerations. Daily caloric requirements of fasting martens and prairie dogs were estimated from resting O₂ consumption values assuming a relatively constant energy demand while the animals were confined within the metabolic cages. Average daily protein expenditure was calculated
from urinary nitrogen and its caloric equivalence subtracted from daily energy expenditure. The energy difference was divided by the caloric equivalence of fat to provide an estimate of daily fat utilization. The ratio of fat to protein catabolism is 1.56:1 for martens and 3.85:1 for prairie dogs. This ratio for martens in our study is close to the 1.9:1 calculated by Bintz et al. (1979) to be sufficient to maintain hydration in squirrels. Prairie dogs, on the other hand, catabolize far less protein and may have difficulty staying in water balance during fasting. Renal concentrating capacity did not appear to be greater for white-tailed prairie dogs, as exemplified by similar urine osmolalities and urea concentrations during the fast. While many factors influence water loss, Bintz et al. (1979) speculates that water balance may be enhanced during such a condition through reducing respiratory water loss associated with metabolic depression and living in a highly humid burrow. Indeed, Harlow and Menkens (1986) found that water deprivation enhanced the onset of torpor in black-tailed prairie dogs (Cynomys ludovicianus). Therefore, while the marten conserves protein during a fast, it still retains a fat-to-protein ratio that may aid in maintaining water balance. The prairie dog, on the other hand, with its large fat reserves may rely more on fat catabolism and a capacity for metabolic depression.

However, there is a limitation to protein catabolism for the production of energy and water—the concomitant need for water in the elimination of nitrogenous waste via a diluted urine. This problem could be reduced by the hydrolysis of urea accomplished through the movement of urea from the blood into the lumen of the small and large bowel, which contain urealitic microbes that hydrolyze urea to ammonia and CO₂ (Pernia et al. 1980; Harlow 1987). The ammonia is absorbed back into the blood and carried to the liver where it can be reamminated into amino acids (Nelson et al. 1975). The potential advantage of such a mechanism would be to conserve water by having less urea to be eliminated in the urine (Harlow 1987). It was our hypothesis that because martens catabolized a greater quantity of protein, both while fed and while fasted, they would have a greater capacity for urea hydrolysis, perhaps through a larger or more diverse fauna of intestinal urealitic microbes. However, in this study, the hydrolysis of injected ¹⁴C urea to ¹⁴CO₂ by martens was not significantly greater than that reported for white-tailed prairie dogs (Harlow 1987). A factor that confounds interpretation is that the urea-recycling portion of the study was conducted on fed martens; we did not compare the two species while fasted. In previous studies, we found that short-term fasting results in a decrease in urea hydrolysis by fat but not by lean animals (Harlow 1987). It could be that, during fasting, the higher protein catabolism in lean martens provides a continuous urea substrate and maintains a greater biomass of urealitic mi-
croflora in the gut and therefore higher urea hydrolysis. The consequence of such a mechanism would, indeed, allow for a greater use of protein as a source of energy and water.

In this study we have found that, while martens are considerably leaner than white-tailed prairie dogs, they appear to be adapted to withstand durations of food and water deprivation potentially encountered in their environment. Martens, being long-lean mustelids, have a greater resting metabolic rate and energy expenditure than white-tailed prairie dogs. Therefore, even though they enter a protein-conserving phase during a comparable fast, they require more protein as a source of fuel and water than do white-tailed prairie dogs. A definite adaptive advantage would be realized if martens had labile reserves of protein. Visceral and skeletal muscle protein have been referred to as corporal reserves in many vertebrate species (Kendall et al. 1973; Le Maho et al. 1981; Torbit et al. 1985). It may, therefore, be anticipated that muscle protein plays a significant role in the overall body metabolism of lean animals (Millward and Waterlow 1978) such as martens. Future studies on the possible existence of seasonal storage of protein as a corporal energy source may reveal an alternate strategy for winter survival by lean-bodied animals.

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