

NUTRITION OF THE NORTH AMERICAN PORCUPINE, *Erethizon dorsatum*

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EXECUTIVE SUMMARY

The North American porcupine, *Erethizon dorsatum*, is native to much of North America and is found in temperate habitats ranging from desert-shrub to tundra. *Erethizon* is the only porcupine genus found above the sub-arctic tree line (Roze, 1989). Because of the various habitats, adult weights range from 6-31 lbs. (2.7-14 kg).

Considered a generalist herbivore, porcupines consume tree bark, leaves, conifer needles, buds from conifers and deciduous trees, fruit and ground vegetation. Porcupines are nocturnal and active year round. The diet varies in composition and nutrient quality seasonally. The porcupine is a monogastric herbivore, hindgut fermenter. Microbial fermentation occurs in the cecum (Balows and Jennison, 1949; Odenyo, et al., 1999), which is approximately 6% of total body weight and is similar in size to the stomach (Johnson and McBee, 1967). Based on Kleiber's (1947) equation for basal metabolic rate (BMR), $70 \times \text{body weight (kg)}^{-0.75}$, and maintenance energy requirement (MER) value of 1.5, a 15 lb. (6.8 kg) porcupine would require 443 kcal/day. Felicetti, et al. (2000) and Fournier and Thomas (1997) reported maintenance nitrogen requirements (MNR) of 346mg. N/kg^{0.75}/day and 389.4mg. N/kg^{0.75}/day, respectively.

A comprehensive reference on feeding ecology includes Roze (1989). A good reference for digestive physiology is Vispo and Hume (1995). Felicetti, et al. (2000) and Fournier and Thomas (1997) have performed comprehensive analyses on nutrients, particularly protein.

SUMMARY OF CAPTIVE DIET

The challenges associated with a captive diet for North American porcupines include:

1. Providing adequate levels of crude protein, without offering excess which may contribute to overweight.
2. Determining if browse, and associated secondary plant compounds, are required to maintain proper nutrient balances (e.g. protein).
3. Providing appropriate levels of fiber for optimum protein absorption
4. Providing optimum vitamin and mineral levels, particularly vitamin D

At this time, a diet composed of a commercial rodent chow, an herbivore browser and/or high fiber biscuit as the base, with additional vegetables, browse and small amount of fruit should provide adequate nutrition in captivity. Diets high in protein or fat, and commercial diets manufactured for primates that are high in vitamin D₃ should be avoided or at least minimized.

FEEDING ECOLOGY

The natural diet of *Erethizon* varies seasonally. In spring and summer, the porcupine is adaptive in its diet, consuming various ground plants and leaves, depending on the geographical location. Grasses, leaves, flowers, herbs and raspberry canes are consumed (Dodge, 1967; Betancourt, et al., 1986; Roze, 1989). In the autumn and winter however, the diet is restricted to nuts, phloem and cambium of coniferous and deciduous trees and coniferous foliage. These plant parts, especially in the crown of trees, contain the highest amounts of fats and carbohydrates available during the winter, so they provide the best nutrition (Harder, 1979).

Roze (1985) indicated individual porcupines limited their winter diet to one - three tree species, even though on a population level, up to ten tree species were consumed in a given habitat. The conclusion the author gave was that either this strategy limited intraspecific competition and allowed more animals to exploit a given habitat, and/or it increased digestive efficiency of intestinal microorganisms.

In the northeastern U.S. study sites, the tree species fed upon in the winter were coniferous and deciduous, particularly hemlock, sugar maple and beech (Roze, 1984; Shapiro, 1949; Curtis and Kozicky, 1944; Griesemer, et al., 1998). Farther west, diets were limited to coniferous species, specifically fir and pine species, depending on what was available in areas of Alberta, Canada, the Rocky Mountain region and Pacific Northwest. See Appendix 2a for specific species listed by geographical region.

There is no indication that the basal metabolic rate (BMR) of porcupines decreases in winter as a way to offset the effects of food deprivation. Roze (1989) indicated that porcupines were only able to survive the winter if they had built up fat reserves during the summer and fall to maintain them until spring. A study looking at death rates of porcupines in winter indicated there was a high incidence of starvation (Sweitzer and Berger, 1993). Body mass losses of >30% were common. Weight loss was highest in December-January, when fat reserves were spent, and spring forage was not yet available.

Porcupines have some behavioral adaptations to conserve energy during the winter: they decrease their home range size to a fraction of the summer range (Smith, 1979; Craig and Keller, 1986; Brander, 1973; Tenneson and Oring, 1985), and they spend a considerable amount of time in dens or crowns of trees to reduce heat loss. There are also reports of porcupine foraging in open areas while risking predator attacks, in an attempt to find enough food to sustain them until spring (Sweitzer 1996).

During the spring, overall weight increases of 25 - 40% between April and October were observed by Roze (1989), although it should be noted that this occurred in pregnant females, which normally increase body weight from the growing fetus.

DIGESTIVE PHYSIOLOGY

The closest domestic hystricomorph relative of the porcupine is the guinea pig (Rowlands and Weir, 1974). Anatomically they have similar characteristics, including the digestive system. However, there are some important inherent differences regarding nutrition and diet, the most important being that, unlike porcupines, guinea pigs cannot synthesize Vitamin C, making it an essential nutrient (NRC, 1995). Additionally, the diet of guinea pigs consists mainly of grasses and forbs, as opposed to the woody material fed upon by porcupines.

The American beaver (*Castor canadensis*), while not a domestic species, has been successfully kept in captivity for many years, and is more closely associated with the porcupine, regarding diet. Digestively, they are similar in that they are both hindgut fermenters, but differ in that the fermentation chamber of the beaver consists of the cecum and proximal colon, whereas fermentation occurs only on the cecum of the porcupine (Vispo and Hume, 1995). Other differences between the two species are listed in Table 1.

Table 1: Difference between beaver and porcupine digestive tract. Vispo and Hume (1995)

Beaver	Porcupine
cardiogastric gland on lesser curvature of stomach	cardiogastric gland not present
small intestine 74% of digestive tract	small intestine 41% of digestive tract
fermentation chamber consists of cecum and proximal colon	fermentation chamber consists of cecum only
distal colon 9% of total tract length	distal colon 38% of tract length
coprophagic	not coprophagic
no accumulation of Na ⁺ in cecum	accumulation of Na ⁺ in cecum

Wet weight measurements of the porcupine digestive tract are: Stomach = 15-19%, small intestine = 26-34%, cecum = 32-36% proximal colon = 7-11%, distal colon = 10-12% (Vispo and Hume, 1995).

The porcupine is a hindgut fermenter. Alexander (1993) indicated that foregut fermenters were better adapted to poor quality food, and that hindgut fermentation was optimal only on higher quality forage. This is not the case with porcupines, which consume a diet very low in protein, and high in fibrous material. They have several adaptations that allow them to utilize hindgut fermentation morphology to exploit a diet poor in nutritional quality.

Adaptations include:

1. large cecum for fermentation
2. separation chamber in cecum
3. resorption of sodium
4. mastication of particles into very small pieces
5. large distal colon
6. reduced metabolic fecal nitrogen (MFN) excretion

The individual points are explained below:

1. The cecum is the site of fermentation in the porcupine and it aids digestion and produces fermentation products, namely, volatile fatty acids (Johnson and McBee, 1967). In the porcupine, the largest proportion of dry matter digesta was in the cecum and was of the smallest size category (<45 μ m), which included bacteria (Vispo and Hume, 1995). This differed from the beaver, which had the greatest proportion of dry matter digesta in the largest particle size class (>500 μ m), although the smallest particles (<45 μ m) were concentrated in the cecum. Selective retention of fluid and fine particles in the cecum maintains a higher concentration of bacteria and leads to more complete digestion of dry matter (Bjorndahl, et al., 1990).

The volatile fatty acids (VFA's) are absorbed directly from the cecum and proximal colon of the porcupine. Approximately 83% of VFA's are absorbed from the cecum. Of the amount that left the cecum, approximately two-thirds were absorbed from the small intestine (Johnson and McBee, 1967). Acetic acid was the predominant VFA in the cecum (74.2%), followed by butyric and propionic acids (13.8% and 12.0%, respectively). The authors didn't detect lactic or succinic acids. Vispo and Hume (1995) found branched-chain VFA's of *i*-butyrate, *i*-valerate and *n*-valerate in the cardiac region of the stomach. The authors indicated there was faster absorption of butyrate and propionate than acetate. Fermentation in the cecum provided 18-19% of the porcupine's energy needs, in the form of VFA's (Vispo and Hume, 1995).

2. A study by Hume, et al. (1993) demonstrated that a separation chamber in the cecum of voles, to separate large particles from fluids and small dry matter particles, allowed them to consume a more fibrous diet than sciurids, which did not have that adaptation. Porcupines also have a colonic separator mechanism, which allows them to retain particles longer for more efficient microbial and mechanical breakdown. Felicetti, et al. (2000) reported that porcupines digested highly lignified fiber more efficiently and had a mean retention time (MRT) longer than similarly sized hindgut fermenters (38.43 \pm 0.56 hours vs. 21 hours). Staaland et. al. (1995) indicated the separation of fluid from large particles may be important for mineral metabolism.

3. In addition to fermentation, high levels of sodium accumulate in the porcupine digestive tract, particularly in the cecum, which provides an effective sodium conservation mechanism, not found in the beaver. The cecum contained 76% of the total sodium concentration in the hindgut.

Table 2: Mineral content in porcupine digestive tract in early spring. Vispo and Hume (1995). Values in g/kg DM.

	Na ⁺	K ⁺	Ca ⁺⁺	P ⁺⁺
Stomach	2.6-3.4	4.7-8.	10.7-2.5	1.8-2.6
Cecum	14.8-21.6	12.6-22.2	1.6-2.2	5.5-7.5
Proximal colon	6.2-8.4	13.8-17.8	1.5-3.3	5.2-6.0

In Table 2 there is a significant decline in sodium from the cecum to the proximal colon, indicating a great amount of absorption. However, the high concentration of the other minerals in the colon indicated there was little absorption of potassium, calcium and phosphorus. In all hindgut fermenters, high levels of Na⁺, K⁺ and P⁺⁺ are maintained throughout the cecum and colon, and are absorbed in the distal colon (Staaland, et al., 1995), which is true for the porcupine, as well. High levels of minerals in the cecum are important for fermentation. In most species, sodium concentrations remained approximately the same or increased through the small intestine, which is not the case with porcupines. Roze (1989) suggested that the higher concentration of sodium in the cecum might give evidence that porcupines have a sodium storage mechanism analogous to that found in the rumen fluid of moose at Isle Royale, as reported by Belovsky and Jordan (1981). This mechanism could be an adaptation to sodium-depleted environments, particularly in the winter, or as a way to offset the deleterious effects of excess potassium in the spring diet.

4. The porcupine's ability to masticate food into small particles may contribute to digestion, by increasing the surface area and further exposing particles to fermentation (Felicetti, et al., 2000).

5. Vispo and Hume (1995) suggested that the large distal colon in the porcupine was beneficial in water and possibly electrolyte resorption. This would be an ideal adaptation for a diet low in minerals, such as sodium, in order to maintain the necessary physiologic balance.

6. Metabolic fecal nitrogen (MFN) in herbivores ranges from 1-9 g. N/ kg dry matter intake (DMI) (Robbins, 1993), and is generally on the high end in animals consuming forage and high fiber. The MFN for porcupines is on the low end of normal (2.8g. N/ kg. DMI) (Felicetti, et al., 2000), but is consistent with that of leaf-eating marsupials consuming diets high in tannins (2.3 – 5.9g. N/kg. DMI) (Robbins, 1993). The ability to reduce MFN lowers the amount of protein required to meet metabolic needs, so is a benefit for animals on a low-protein diet.

One unique difference in the digestive tract of porcupines, not found in most other rodents, is the presence of a sixth lobe of the liver. A major function of the liver is detoxification. Porcupines also lack a gall bladder, although adults do possess a bile duct (Dodge, 1982). The adaptive importance of these modifications is unknown.

DIETARY PROTEIN, FAT AND FIBER

The winter diet is very low in protein and high in indigestible fiber. Feeding on the most nutritious plants or plant parts may ultimately determine survival until the more nutritious spring vegetation emerges. Gill and Cordes (1972) analyzed the crude protein and fiber content of Limber pine (*Pinus flexilis*), Lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*) and White spruce (*Picea glauca*) in their study site. Limber pine, which was the preferred food item, had the highest crude protein (CP) level (3.2%) and lowest fiber content (9.7%). Lodgepole pine, the least preferred species, had the lowest CP level (1.9%) and highest fiber content (24.3%). Limber pine also had a higher percentage of crude fat than the other species (12.7%). The conclusion was that porcupines exploited species with the highest protein and fat, and lowest fiber content available.

Stricklan, et al. (1995) compared nutrients of Gambel Oak (*Quercus gambelii*), white fir (*Abies concolor*) and Douglas fir (*Pseudotsuga menziesii*) in Utah. Gambel oak was preferred over the conifer species, even though the tannin level, which binds protein, was higher in oak. The conclusion was that even though the fiber content in oak was higher, it had a higher protein level

(5.0% CP) compared to Douglas fir (3.9% CP) so was a more nutritious choice.

In a study in Minnesota, conifers were preferred over the Northern red oak (*Quercus rubra*). Tenneson and Oring (1985) reported white pine (*Pinus strobus*) was prevalent in the two utilized study sites, and 58-85% of the porcupines fed on this species, whereas the Northern red oak was the prevalent species in the unused areas of the study sites. Red oak acorns have two – three times the amount of tannins as white oaks (Short and Epps, 1976), so it is reasonable to assume other plants parts are also higher in tannins, which may offset the benefits of higher protein and fat.

Table 3: Crude Protein, Crude Fat and Crude Fiber contents of food items. Gill and Cordes, 1972¹; Smith, 1957²; Stricklan, et al.,1995³; Roze, 1989⁴; Masslich, et al.,1988⁵.

Values based on dry weight.

SPECIES	% CP	% Crude Fat	% Crude Fiber
Chokecherry (<i>Prunus virginiana</i>) ²	9.9	2.4	29.1
Douglas fir (<i>Pseudotsuga menziesii</i>) ¹	2.9	3.1	11.8
Douglas fir (<i>Pseudotsuga menziesii</i>) ³	3.9	n/a	n/a
Gambel oak (<i>Quercus gambelii</i>) ²	5.4	3.2	34.0
Hemlock (<i>Tsuga</i> spp.) ⁴	8.0	n/a	n/a
Juniper (<i>Juniperus</i> spp.) ²	6.2	14.1	24.9
Limber pine (<i>Pinus flexilis</i>) ¹	3.2	12.7	9.7
Lodgepole pine (<i>Pinus contorta</i>) ¹	1.9	7.7	24.3
Quaking aspen (<i>Populus tremuloides</i>) ⁵	6.0	n/a	n/a
White fir (<i>Abies concolor</i>) ³	4.2	n/a	n/a
White spruce (<i>Picea glauca</i>) ¹	3.0	2.0	21.3

Protein levels and tannin concentrations of plant species changed seasonally. The porcupine diet changed in relation to plant chemistry. On an as fed basis, tannin levels of oak leaves went from <1% in spring, to 6% in summer (Roze, 1989). A tannin level of 6% in foliage is intolerable to porcupines, and is not consumed at this time of year. Plant parts also varied in protein levels. Leaves and buds of several species were readily consumed, which had high protein levels. Petioles (leaf stalks) and twigs consistently had low protein concentrations and were discarded by porcupines. By summer, sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*) and white ash (*Fraxinus americana*) dropped out of the diet as mature leaves became less palatable, and possibly more lignified. Table 4 lists the protein levels of selected and discarded plant parts of the porcupine's diet in the Catskill Mountains of New York. With the exception of raspberry plants, all of the plant parts consumed contained $\geq 13\%$ crude protein (CP), and the parts discarded contained $\leq 8.5\%$ CP. Table 5 compares the tannin levels of plant parts that are either consumed or avoided by porcupines. Raspberry leaves and canes are low in tannins (Roze, 1989) which would make a greater proportion of the plant's proteins digestible.

Table 4: Protein levels of spring and summer food items. Roze 1989¹, Doucet and Fryxell, 1993.²

Plant parts eaten	CP % (DM)*	Plant parts discarded	CP % (DM)*
Ash leaf blades ¹	16.1	Ash terminal twigs ¹	7.0
Aspen leaves (summer) ¹	15.0	Linden petioles (leaf stalks) ¹	3.5
Linden leaf blades (summer) ¹	13.1	Linden twig tips ¹	4.6
Quaking aspen catkins ¹	20.0	Quaking aspen twigs ¹	7.0
Sugar maple buds ¹	22.0	Sugar maple twig tips ¹	8.5
Raspberry leaves, cane ²	8.8		
Water lily ²	15.3		

* values are on dry matter (DM) basis.

Table 5: Tannin concentrations of plant parts. Roze, 1989¹; Ofcarcik and Burns, 1971².

Plant parts eaten	Tannin % (as fed)	Plant parts avoided	Tannin % (as fed)
Beech emergent leaves (spring) ¹	<1	Beech leaves (summer) ¹	≥2
Gambel oak acorns (fall and winter) ²	0.5-2.5%		
Oak leaves (spring) ¹	<1	Oak leaves (summer) ¹	6
Red oak acorns (fall and winter) ²	6-10%		
Sugar maple buds (spring) ¹	<2	Sugar maple leaves (summer) ¹	6.5
White ash emergent leaves (spring) ¹	<1		

MINERALS

The spring diet is high in protein and allows for large weight gains, but the plants are also high in potassium and prompt porcupines to seek out additional sodium sources. The intense salt-seeking behavior has two peak periods for the porcupine. The first occurs in April-May, the second in August-September (Roze, 1989). The explanation for increased seasonal intakes of sodium may be related to three factors:

1. Need to balance the skewed dietary potassium: sodium ratio
2. Reproductive hormones in pregnant and lactating females
3. Urinary and/or fecal sodium loss

1. The explanation for the peak in April-May revolves around the increased potassium levels of buds and leaves in the spring. The whole-body potassium: sodium ratio in rodents, including fox squirrel (*Sciurus niger*) and old-field mouse (*Peromyscus polionotus*) range from 1:1 to 3:1 (Robbins, 1993, pg. 34). It's reasonable to assume the porcupine has a comparable physiological requirement. The potassium: sodium ratios of plants can be ≥500:1 (Roze, 1989). The excess potassium from the diet must be excreted in the urine and feces, otherwise muscle and nerve function will be disrupted, and death can occur. Roze (1989) reported significant increases of potassium excretion in the feces between May and July, and also in September, while the fecal sodium excretion rate was fairly constant year round. When potassium is excreted in the urine, sodium can be lost as well. To reduce sodium loss and maintain the proper blood ratio, sodium must be replenished in the diet. Roze (1989) indicated the increased sodium intake was a function of improving the overall balance between potassium and sodium, rather than as a need for an absolute amount of sodium.

A study on woodchucks (*Marmota monax*) and fox squirrel (*Sciurus niger*) showed increased salt consumption in the spring, similar to that seen with porcupines. Weeks and Kirkpatrick (1978) set up a station with different salts (Na⁺, K⁺, Ca⁺⁺ and Mg⁺⁺) to determine preferences by the two

rodents. Both species preferentially sought out sodium. The authors concluded that the drive to find dietary sodium was a function of the high K: Na ratio of the spring diet. This was consistent with conditions of sodium-depleted soil and a high influx of potassium in the diet, from spring vegetation. Weeks and Kirkpatrick (1976) reported a potassium range of winter plants to be 10,000-12,000 ppm, and $\geq 25,000$ ppm in spring vegetation. Christian (1989) reported an average potassium level of 5000 ppm in winter vegetation and 35,000 ppm in spring plants. The squirrels in the study also had an autumn salt drive, similar to that of porcupines. Weeks and Kirkpatrick (1978) proposed that this peak for salt consumption was associated with the dietary change to acorns, which had a high K: Na ratio. They indicated K: Na ratios of $\geq 18:1$ caused sodium loss and initiated the drive for additional dietary sodium to regain balance.

Interestingly, porcupines didn't exhibit a salt drive in the autumn when they started consuming acorns and beechnuts, but sought out sodium when they remained on the apple diet (when nuts weren't plentiful). This may have been as a result of acidity in the apples (Roze, 1989). Apples are considerably more acidic than leaves from linden trees (pH of 3.1-4.1 and 6.0-6.8, respectively). The acidity interferes with sodium resorption in the kidneys, and increases urinary sodium loss (Roze, 1989). Porcupines preferentially consumed apples that had the highest pH, both on an individual apple basis and by variety. The main difference between apples consumed and rejected was the acid content (Roze, 1989). From his analysis, the rejected apples (regardless of variety) were significantly more acidic than the consumed apples. The porcupines predominantly fed upon the red delicious variety. The author analyzed the acidity of apples in the Catskill Mountains. The pH of the apples tested was: granny smith = 3.1, McIntosh = 3.35, yellow delicious = 3.9, red delicious = 4.1. Porcupines selected apples with a pH of approximately 4.07. The average pH of rejected apples was 2.95. Total sugars, crude protein and potassium-sodium ratios of selected and rejected apples were comparable.

Apples (*Malus sylvestris*) are readily consumed by porcupines year round, if available, but they become a major component of the summer diet, as observed in 30-50% of feeding bouts (Roze, 1989). Apples provide a highly digestible source of carbohydrates, which is associated with pre-winter weight gain. The meaty fruit (exocarp) is consumed and the core (endocarp) and seeds are discarded, presumably because of the cyanide content. Porcupines avoid eating apple leaves and bark year round (Roze, 1989).

The form of sodium the porcupines sought out was in the more alkaline salts, such as sodium bicarbonate rather than sodium chloride, and in its most concentrated form, 0.45N, which is equivalent to the salinity of seawater (Roze, 1989). This was related to the second salt drive peak in late summer, which coincides with the end of the apple consumption period (July - August).

When Northern red oak (*Quercus rubra*) acorns and beech (*Fagus grandifolia*) nuts were available in the autumn, apple consumption stopped and sodium-feeding was not observed (Roze, 1989). When acorns and beechnuts were not readily available, apples continued to be used as a food source (Roze, 1989). When apples were consumed in the autumn, aspen and linden leaves were also a major food item, presumably because of the protein content (CP in apples = 0.7%, in leaves = approx. 15%). The leaves were consumed less frequently when nuts were available.

2. Roze (1989) indicated there was a skewed sex ratio towards females in the salt consumption drive. In the Catskill Mountains of New York, 78% of the porcupines that utilized a salt house were female. Infants were not observed consuming salt, and were presumably receiving adequate amounts from the mother's milk.

One explanation for the high proportion of females consuming dietary sodium was a hormonal response related to pregnancy and lactation. Estrogen, ACTH, prolactin and oxytocin, when in the proper ratios, will induce a sodium hunger in the females to ensure the fetuses and nursing young meet their metabolic needs. Additionally, lactating females lose sodium through the milk. Denton (1982) indicated female rabbits in Australia had a 10-fold increase in sodium consumption during

pregnancy and a 30-fold increase during peak lactation.

3. Spring vegetation also has a much higher water content than the winter diet, which may allow for electrolyte loss through the urine and/or feces. Sodium and potassium would both be lost through these routes. Weeks and Kirkpatrick (1976) indicated that the high concentration of potassium in the body may interfere with normal movement of sodium into the cells, and so would be excreted in the urine, rather than resorbed into the blood.

Porcupines utilize many sources to obtain concentrated amounts of sodium.

1. Water plants, such as yellow pond lily (*Nymphaea mexicana*); aquatic liverworts (*Riccia fluitans*) and arrowhead leaf (*Sagittaria spp.*) contain high levels of sodium. The yellow pond lily has 9375 ppm Na⁺, compared to an average of 9 ppm Na⁺ for terrestrial vegetation (Roze, 1989).

2. Invertebrates – beetles, ant fragments and larvae, including fall cankerworm (*Alsophila pometaria*), fall webworm (*Hyphantria cunea*), linden looper (*Erannis tiliaria*) and American daggerworm (*Acronicta americana*), have been found in the stomach contents of porcupines (Roze, 1989). They may be consumed incidentally with vegetation. Invertebrates contain relatively high amounts of sodium. A study on prairie dogs (*Cynomys spp.*), indicated they consumed insects, which may have alleviated a sodium deficiency (Belovsky and Jordan, 1981).

3. Animal bones - porcupines gnaw on deer bones (Roze, 1989). Bone contains calcium, phosphorus and sodium, as well as protein. On a DM basis, deer antlers contained 52-56% ash, 45% protein and 1% fat (Hyvarinen, et al., 1977). It is unclear as to whether porcupines gnaw on bones for calcium, magnesium, sodium or protein. In general, plant material contains adequate amounts of calcium, although nuts are very low in it. Squirrels, which consume a large proportion of nuts in their diet, utilize bone and fungi for calcium sources (Havera, 1978). Roze (1989) determined that porcupines excreted excess calcium in the urine, and concluded the spring diet wasn't deficient in that mineral, although the conclusion was based on the urine sample of one catheterized female. Approximately 70% of the body's store of magnesium is in bone (Robbins, 1993). High levels of potassium may interfere with magnesium absorption, and bone would be a good source of that mineral when porcupines are consuming lush, spring forage. Additionally, porcupines coming out of a protein deficient winter may be seeking out foods with high protein levels, of which bone would be a good source.

4. Outer bark of trees - not to be confused with consumption of the cambium layer of bark during winter. The outer bark, consumed in the spring, has relatively high levels of sodium, with an average of 546 ppm in deciduous hardwoods, compared to 57.9 ppm in leaves (Seastedt and Crossley, 1981).

5. Soil of river banks and sand bars. Murie (1926) observed porcupines licking and chewing on sandy soils in Alaska.

TANNINS

Tannins are secondary plant compounds that act as a defense mechanism to herbivory. They can act by reducing the palatability of a plant; by interfering with protein absorption of food consumed, or by toxicity and death from acute concentrations. Tannins can also reduce the intestinal microflora's ability to break down plant proteins for nitrogen absorption through leaf protein-tannin complexes (Feeny, 1970). It has been suggested that increased amounts of crude protein in the diet would mitigate the effects of tannins (Fleck and Tomback, 1996). The theory is that tannin protein-binding components would bind to available protein and reach a saturation point, so any additional unbound protein would be available for nutrient absorption. This study was done on birds however, there may be practical applications for porcupines which would warrant investigation.

A study on rats by Glick and Joslyn (1970a) indicated a diet with 4% tannic acid was not lethal, but an 8% concentration had a 90% fatality rate. Branched-chain condensed tannins, such as quebracho, found in maple, adversely affects digestion more than hydrolyzable tannins, such as tannic acid (Koenig, 1991). Although a lethal tannin level has not been established for porcupines, Roze (1989) indicated a 6% tannin concentration was intolerable to them, which may be related to insufficient protein availability at that level. Glick and Joslyn (1970b) reported in

another study, that rats fed a low protein diet with 5% tannic acid suffered from anemia.

Food choices may be related to the animal's ability to mitigate the effects of tannins. Robbins (1993, pg. 254) stated that approximately 79% of deciduous woody perennials and up to 87% of evergreen woody perennials contain tannins. It is therefore reasonable to assume that porcupines have at least one adaptation for reducing the negative dietary effects of secondary plant compounds, specifically tannins. Three potential adaptations are:

- 1) salivary tannin-binding proteins
- 2) gastro-intestinal mechanism or specialization to detoxify tannins
- 3) mastication modifications and specialized cecal bacteria.

1. Robbins, et al. (1991) studied tannin-binding salivary proteins in several herbivores. They hypothesized that the salivary proteins would minimize nitrogen loss in the feces, and minimize tannin absorption and toxic effects by forming tannin-binding complexes that could be excreted. This could be an adaptation in hindgut fermenters to maximize fiber digestion.

The North American beaver (*Castor canadensis*) has a winter diet similar to that of porcupines. In a study by Hagerman and Robbins (1993) it was determined that beaver had salivary tannin-binding proteins that were specific only to *Sorghum* and willow tannins, which are linear, condensed tannins, as opposed to branched-chain condensed tannins, such as quebracho, and hydrolyzable tannins (gallo- and ellagi-tannins). This was consistent with the beaver diet choices of aspen, birch, willow and alder, all of which are either tannin-free, or have low levels of linear, condensed tannins. Porcupines consume aspen, birch and willow. However, they also consume large amounts of sugar maple bark in the winter and buds in the spring. Maple contains branched-chain condensed or hydrolyzable tannins, particularly ellagitannins, although the amount and type depends on the species (Bate-Smith, 1977). Hagerman and Robbins (1993) stated that beaver do consume some quebracho tannins, but the cost associated with them is balanced by the high protein and/or energy content of the forbs. It has not been determined whether porcupines have salivary tannin-binding proteins, and if they would be considered specialists/selective browsers, like beaver and moose, or generalist/non-selective tannin scavengers like mule deer, in tannin-binding affinity. Roze (1989) indicated porcupine individuals consumed one - three tree species in the winter, although a population within a given area consumed up to ten different tree species. It is reasonable to assume however, that salivary tannin-binding proteins would benefit the porcupine.

2. A mechanism to detoxify tannins in acorns was demonstrated in Eastern grey squirrels (*Sciurus carolinensis*) (Smallwood and Peters, 1986). Grey squirrels consume acorns of both red and white oak subgenera. The most noteworthy nutritional differences between acorns of these groups are the fat and tannin contents. Gambel oak is considered a white oak. The red oak group, which includes the Northern red oak, has four times the amount of fat and a considerably higher tannin concentration than the white oaks. The tannin concentration level of 6-10%, found in the red oaks, is above the tolerable limit for porcupines (Roze, 1989) and lethal limit for laboratory rats (Glick and Joslyn, 1970a). Smallwood and Peters (1986) indicated the tannin concentration of the red oak acorns was not toxic to grey squirrels, nor did it affect the squirrels' ability to digest protein. The authors indicated the squirrels had evolved a mechanism to detoxify tannins in their diet. This selective mechanism allows the squirrels to benefit from the substantially higher energy content of the black and red oak acorns, which they can live on throughout the winter, without deleterious effects from the tannins. Porcupines also consume red oak acorns, and could possibly have a mechanism to detoxify tannins.

Table 6: Comparison of Nutrients and Tannin concentrations of red and white oak acorns. Short and Epps (1976). Values based on dry matter (DM)

	Red/black oak acorn Subgenus <i>Erythrobalanus</i>	White oak acorn Subgenus <i>Lepidobalanus</i>
Crude fat %	17.9	4.3
Crude fiber %	18.4	18.7
Crude protein %	5.9	5.9
Cell contents %	65.2	53.0
Cell wall components %	34.8	47.0
Calcium %	0.24	0.15
Phosphorus %	0.10	0.09
Tannin %	6-10	0.5-2.5

3. A third mechanism for dealing with tannins in the diet, relates to the common ringtail possum (*Pseudocheirus peregrinus*). This species is an arboreal folivore in Australia, which feeds predominantly on tannin-rich eucalyptus leaves. Like the porcupine, it is a hindgut fermenter, and must find a way around tannins so they can absorb protein from the diet. Ringtail possums don't appear to have tannin-binding salivary proteins. However, one mechanism that they use is to chew the plant parts into very small pieces, thereby increasing surface area for digestive bacteria to adhere to. Additionally, specialization of the cecum and specialized cecal bacteria may allow dissociation of tannin-protein complexes (McArthur and Sanson, 1991).

The specific mechanisms that porcupines use to counteract the effects of tannins have not, as of yet, been determined. This is an area that should be investigated, as it relates to captive care, and dietary needs.

CAPTIVE CARE

The captive care section is broken down by physiological stages of nutrition:

1. Adult maintenance
2. Gestation/Lactation
3. Neonates to Weanlings
4. Hand-rearing infants
5. Geriatrics

ADULT MAINTENANCE

Johnson and McBee (1967) recommended a caloric intake of 435 kcal/day for a 10 kg. (22 lb.) porcupine and 262.5 kcal/day for a 5 kg. (11 lb.) porcupine. This is comparable to the basal metabolic rate (BMR) equation by McNab (1988) of $57.2 \times \text{body weight (kg)}^{.716} \times 1.5$ (for maintenance). Additionally, Johnson and McBee (1967) stated that the fermentation rate in the cecum decreased after 12 hours of feeding and resulted in reduced acetic acid production, so they recommended feeding porcupines twice daily.

PROTEIN

The maintenance nitrogen requirement (MNR) range for porcupines is 346 -389.4mg. N/kg^{.75}/d. (Felicetti et al., 2000; Fournier and Thomas, 1997). The MNR range for eutherian mammals is 582 ± 235 mg. N/kg^{.75}/d. (Robbins, 1993). The value for porcupines is considerably less than average for other eutherians, but falls within the mean for marsupials (356 ± 136 mg. N/kg^{.75}/d) and desert rodents, such as the antelope ground squirrel (*Ammospermophilus* spp.) and rock hyrax (*Procapra capensis*) (283 and 311mg N/kg^{.75}/d, respectively) which consume low protein diets (Robbins, 1993).

Fournier and Thomas (1997) conducted food trials on porcupines using three diets containing

different levels of crude protein and fiber. One diet was rodent chow, the other two were a combination of fruit, nuts, oats and molasses. The rodent chow diet contained the highest level of crude protein (29%) and fiber (11%). The mixed diets contained 10% CP, 4% fiber and 5% CP, 5% fiber, respectively. The dry matter digestibility (DMD) of the three diets was 81-98%. Food trials conducted by Felicetti et al, (2000), where several natural food items, alfalfa and rodent chow were offered individually, gave a DMD of 45-91% (browse, alfalfa and acorns) and 83-96% (rodent chow and apples). Fournier and Thomas (1997) determined that the high fiber diet (11%) had a lower apparent digestibility (80%), compared to that of the 5% fiber diet (95-97%). Additionally, the porcupines on the high protein/high fiber diet consumed $\geq 60\%$ more food than those on the low protein/low fiber diet. The authors indicated the animals maintained constant body weight on the five day trial period. However, porcupines are able to replace body water with fat, while maintaining the same weight (Alkon et al., 1986), so continuation on a high protein/moderately high fiber/high caloric diet may result in an increase of percent body fat in captivity.

So the question is raised: why can't porcupines increase their food intake to meet their protein requirements in the wild, when they can clearly consume considerably more than their metabolic needs in captivity? Roze (1989) indicated porcupines were not able to increase their protein intake during the winter, when consuming high levels of indigestible fiber. This was due to the long transit time of food through the cecum, which limited the amount of DMI porcupines could consume. Felicetti, et al. (2000) gave a mean retention time (MRT) of 38.43 ± 0.56 hr., which is longer than that of other hindgut fermenters of comparable size. Increased MRT is beneficial with high fiber diets because it enhances the time available for intestinal cellulolytic microbes to break down cellulose (Felicetti, et al., 2000). Fournier and Thomas (1997) indicated that animals on the 11% fiber diet were able to consume considerably more DMI than animals on the 5% fiber diet, so the stomach capacity is available. However, Felicetti, et al. (2000) gave neutral detergent fiber (NDF), the indigestible content of fiber, levels of 16-60% in apples and natural browse species, which is considerably higher than 11%. Increased fiber decreases food intake and nutrient digestibility, so in the wild, the animals may not be able to consume enough bulk to receive absolute protein requirements. In this scenario, allowing more time for digestive microbes and mechanical action for fiber breakdown, through a long MRT, would increase nutrient absorption.

Fournier and Thomas (1997) indicated porcupines in their study achieved a positive nitrogen balance on a tannin-free diet with 10% crude protein (CP), and based on the low MFN, may be able to reach MNR at 6.25% CP (1% N). They also indicated that animals on the 5% CP / 5% fiber diet were protein-deficient. Felicetti, et al. (2000) stated animals in their study were in positive nitrogen balance on a 3% CP diet. Food trials in both studies were limited to five days in length, so the long term effects of extremely low protein diets was not determined.

For an animal that has adapted to a low protein diet, and regularly consume tannins, which inhibit protein absorption, it may be beneficial to investigate whether or not porcupines develop protein toxicity from captive diets that provide considerably more protein than 10%. Church and Pond (1988) reported depressed weight gain in pigs that were offered increasing amounts of protein (from 16-48%). Reduced feed intake and a dull, coarse hair coat were signs attributed to excess protein. In protein toxicity, blood ammonia levels rise and may inhibit citric acid cycle function. The authors reported a blood ammonia level of 1-4 mg/dl associated with toxic signs in pigs.

The effects tannins have on porcupine nutrition has not yet been investigated well enough to determine its role in the captive diet. Felicetti et al. (2000) used the bovine serum albumin (BSA) assay to determine the tannin binding capacity of several browse species. The conclusion was that tannins did decrease digestibility, although this method may not have taken into account adaptations by porcupines to counteract the effect of tannins, such as salivary tannin-binding proteins. From a captive management perspective, it would be prudent to investigate whether tannins are required in the porcupine diet to reduce protein absorption and possible toxicity, or if protein levels need to be increased when tannins, in the form of browse, are included in the diet.

FIBER

Felicetti, et al. (2000) analyzed the neutral detergent fiber (NDF) content of several natural food items, including apples, acorns and tree parts; and a commercial rodent diet (Harlan Teklad™ 8604 rodent chow). NDF refers to the cellulose, hemicellulose and lignin component of fiber in the food item. Apples had the lowest NDF of 16%; ponderosa pine cambium had the highest (60%). Even though the NDF content in browse was high, the porcupines were able to digest it better than other similarly-sized hindgut fermenters. The NDF digestibility ranged from 46% in lodgepole pine needles, to 97% in apples, with an NDF of 60% in the rodent chow.

Fournier and Thomas (1997) experimented with three diets which had different concentrations of protein and fiber. Their results indicated porcupines had the highest apparent digestibility (95%) on the diet with 10% crude protein and 4% crude fiber. As the fiber content increased to 11%, digestibility dropped to 81% and weight loss occurred, even though the animals consumed more energy. It should be noted that on the 11% fiber diet, the protein level was also the highest (29%).

VITAMIN D

Vitamin D is found in two forms – D₃ (cholecalciferol), which is synthesized in the skin after exposure to UV light; and D₂ (ergocalciferol) which is present in plants and invertebrates. Birds, reptiles, New World primates and a few other mammals can only utilize the vitamin D₃ form (Robbins, 1993). Most other mammals can utilize either D₂ or D₃, so are able to absorb it from plant foods or from exposure to sunlight. Many plants have the precursor to ergocalciferol (D₂), which may be an important source of the vitamin for herbivorous crepuscular and nocturnal species. The main function of Vitamin D is in calcium absorption.

There are a few mammal species that have adaptations which cause them to be particularly sensitive to vitamin D₃ supplementation. Naked mole rats (*Heterocephalus glaber*), a subterranean rodent, when supplemented with dietary vitamin D in captivity, have reportedly died from calcification of the kidneys (nephrocalcinosis) (Robbins, 1993, pg. 90). Vitamin D toxicity raises the blood calcium levels, which is then deposited in the organs and soft tissue, and causes calcification of those body parts (McDowell, 2000, pg. 140-141).

The agouti (*Dasyprocta* spp.), a South American crepuscular rodent, also has a low vitamin D requirement, and can utilize any form of the vitamin. Kenny, et al. (1993) reported fatalities of spotted pacas (*Cuniculus paca*) and orange-rumped agoutis (*Dasyprocta aguti*) at three zoos, which were attributed to vitamin D₃ toxicity. The animals were housed in the same enclosure as various primate species, including marmosets, and regularly consumed pieces of primate chow that had fallen to the ground. The commercial primate diets were fortified with vitamin D₃ at the rate of 7333-22,564 IU/kg diet. The amount in the food was a toxic dose for the agoutis and pacas. The animals died from calcification of the soft tissues and heart, and renal failure.

The vitamin D requirement for rats and guinea pigs is 1000 IU/kg dry diet (NRC 1995). At this time, there have been no studies on the vitamin D requirement for porcupines. So the question is raised: do porcupines meet their vitamin D requirement from plant material in the natural diet, or do they have an adaptation, as a nocturnal species, that lowers their vitamin D requirement? Until studies are performed giving data on vitamin content in browse, it is recommended to provide 1000 IU/kg dry diet to porcupines.

MINERALS

Blood serum chemistries and electrolyte values for North American porcupine (*Erethizon dorsatum*) and prehensile-tailed porcupines (*Coendou prehensilis* and *C. melanurus*) are compared to those of the domestic rat (*Rattus domesticus*) and guinea pig (*Cavia porcellus*) in Table 7.

Table 7: Comparison of mineral levels in blood serum of porcupines and domestic rodents. Moreau, et. al., 2003¹; Hillyer and Quesenberry, 1997², I.S.I.S., 2002³

	<i>Erethizon</i> ³ <i>dorsatum</i>	<i>Coendou</i> ¹ <i>prehensilis</i>	<i>Coendou</i> ¹ <i>melanurus</i>	Domestic rat ²	Guinea pig ²
Calcium, mg/dl	10.4	9.6	7.7	10.7-13.7	8.2-12.0
Phosphorus, mg/dl	5.1	4.9	3.69	6.2-11.7	3.0-7.6
Potassium, mEq/L*	4.5	5.2 ± 0.9 (M) 4.27 ± 0.7 (F)	5.2 ± 1.3	5.2-7.8	3.8-7.9
Sodium, mEq/L*	138	140 ± 15	139 ± 5	141-150	120-152

mEq: milliequivalent = 10⁻³

Although the mineral values from the stomach of a porcupine will not be an exact determination of their nutrient requirements, it does provide some pertinent information regarding the composition of nutrients wild porcupines consume. In comparison to the recommended nutrient requirements for domestic rats and guinea pigs (NRC, 1995), the stomach contents of porcupines, as reported by Vispo and Hume (1995) indicate their nutrient levels more closely match those of the guinea pig. See Table 8 for specific comparisons.

Table 8: Comparison of porcupine stomach contents and domestic rodent mineral nutrient requirements. Vispo and Hume, 1995¹, NRC, 1995².

Mineral	Porcupine stomach ¹	Rat requirement ²	Guinea pig req. ²
Calcium, g / kg DMI	1.6 ± 0.9	5.0	8.0
Phosphorus, g / kg DMI	2.2 ± 0.4	3.0	4.0
Potassium, g / kg DMI	6.4 ± 1.7	3.6	5.0
Sodium, g / kg DMI	3.0 ± 0.4	0.5	0.5
Copper, mg / kg DMI	7 ± 2	5.0	6.0
Iron, mg / kg DMI	72 ± 27	35	50
Magnesium, g / kg DMI	0.6 ± 0.3	0.5	1.0
Manganese, mg / kg DMI	103 ± 55	10	40
Zinc, mg / kg DMI	22 ± 16	12	20

It is interesting to note that from Table 8 the mineral levels in the stomach contents of the porcupine were within the normal range of the guinea pig requirements, with the exception of sodium, calcium and manganese. The higher sodium levels may have been related to a sodium conservation mechanism, as previously stated. It is unclear as to why calcium levels would be much lower than for the other species, especially in comparison to the phosphorus level. The data above indicates the porcupines had a Ca: P ratio of 0.7:1, whereas it is generally accepted that a dietary ratio of 1:1 or 2:1 is required to maintain a physiologic balance (NRC, 1995). The recommended Ca: P ratio for rats and guinea pigs is 1.7:1 and 2:1, respectively. The calcium level in the porcupine was also comparatively lower than was found in the beaver (11.1 ± 5.0 g./kg. DMI) (Vispo and Hume, 1995). The authors attributed the higher value in beavers to a diet higher in calcium. The high manganese level in the porcupine was also higher than that found in the old-field mouse (*Peromyscus polionotus*) which was 3.5-17.6 mg/kg DMI (Robbins, 1993, pg. 34). Manganese plays a role in carbohydrate and lipid metabolism. Excess manganese has been reported to adversely affect calcium and phosphorus absorption (Church and Pond, 1988, pg. 201).

DENTITION

Adult dentition: (I 1/1, C 0/0, P 1/1, M 3/3) x 2 = 20. The incisors grow continuously and are stained orange, from iron salts, which act as a hardening agent. (Roze and Ilse, 2003). Estimation of age by tooth wear and cementum growth rings is explained in Earle and Krumm (1980).

BODY SCORING

Body weight is not a good indicator of a porcupine's body composition. Alkon, et al. (1986) indicated animals that were on significantly different caloric diets weighed approximately the same, but had very different percentages of body fat. Porcupines have the ability to store a large amount of body fat as an adaptation to extremely poor nutrient winter diets (Roze, 1989). In the summer, *Hystrix* spp. is able to replace lost body fat with water, as an adaptation to desert conditions. Whether or not *Erethizon* has the same ability to store body water has not been determined.

Alkon et al. (1986) indicated measuring total body water (TBW), as explained in Nagy (1975) was the best way to determine percent body water, which is inversely proportional to percent body fat. The total body water (TBW) for porcupines ranged from 50.1 - 72.2%, indicating there was potential storage for large amounts of fat. Animals were fed a diet containing 16.5% CP. In Fournier and Thomas (1997), porcupines consuming diets with high levels of protein (29%) also consumed more calories. In captivity, crude protein levels >10% may lead to excess body fat, even when the animals maintain a given weight. TBW may not be a practical method for monitoring body fat levels in zoos.

FECAL SCORING

At this time, there are no documented reports of fecal scoring for porcupines. The normal stool consists of hard pellets. However, during the spring, porcupines reportedly have soft feces, that could be considered diarrheic. One theory is that it results from increased potassium and water loss from spring vegetation (Weeks and Kirkpatrick, 1976). In captivity, where porcupines are on a fairly consistent diet year round, this phenomenon may not occur.

Another potential cause of loose stool may be related to changing food items and introducing forage with which the porcupine is not familiar. Roze (1989) indicated porcupines tend to feed from very few species of trees in a given region, even though other porcupines in the population consume other species. The author indicated this may be related to the adaptability of intestinal microbial populations to digest fiber and secondary plant compounds in different species.

The presence of soft feces in porcupines, should not be considered normal, and may be related to sudden dietary changes, stress and/or parasites and disease. New foods should be introduced slowly and in small percentages of the overall diet to allow for adequate development of microbial populations. Stress-related digestive problems might clear up without intervention, although it may be advisable to decrease food intake somewhat during particularly stressful periods associated with transportation and introduction into new exhibits. Fecal analysis can be performed using standard veterinary techniques (Sloss, et al., 1994). A variety of endo- and ectoparasites have been identified in the porcupine including tapeworms, roundworms, protozoa, mites, ticks and lice (Curtis and Kozicky, 1944; Dubey, et al., 1992; Payne and O'Meara, 1958). These may or may not be associated with clinical signs of disease.

GESTATION AND LACTATION

The porcupine has low reproductive costs, but high energy allocations to offspring, compared to other rodents. The porcupine has one precocial offspring (porcupette) in April or May, after a long gestation period of 209-217 days (Shadle, 1948). Embryonic development is usually in the right uterine horn, presumably because the large cecum interferes with proper development in the left horn (Dodge, 1982). Birth weights have been reported to range from 414 - 476g. (15-17 oz.) (Shadle, 1948; Farrell and Christian, 1987; Shadle and Ploss, 1943) which is a comparatively low mother: infant weight ratio. Gosling (1980) reported a birth weight to maternal weight ratio of 2.2% for the Himalayan porcupine (*Hystrix hudsoni*) that has single and twin births, and compared it to

the 18.8% ratio found in the nutria (*Myocastor coypus*), which has an average litter size of five. Farrell and Christian (1987) indicated that the birth weight for a single porcupette is comparable to the total litter weight ratio for other rodents. The long gestation period of approximately seven months may be associated with the poor quality diet during the winter, when the porcupines are pregnant. Robbins (1993, pg. 201) indicated that slowing the fetal growth rate by lengthening the gestation period is common with folivorous mammals when dietary protein or other nutrients are a limiting factor.

Farrell and Christian (1987) reported that lactating porcupines in their study consumed 17% more food and 16-20% more water than non-lactating females. The authors also observed a depression in food intake immediately after parturition, lasting a few days, and another depression at the time of weaning. Robbins (1993, pg. 203) indicated that in general, the energy expenditure for lactating mammals ranged from 65-215% above that of non-lactating females.

NEONATES TO WEANLINGS

Porcupines are precocial and weigh approximately one pound (454g.) at birth. The eyes are open and they are able to amble about with an unsteady gait within five to six hours after birth. They are born with a dense coat of dark brown, soft, transparent quills that harden within hours. The incisors are present and well-formed. Shadle and Ploss (1943) and Farrell and Christian (1987) both reported porcupettes exhibiting the tail-striking defense within hours of birth. Shadle and Ploss (1943) reported teeth chatter on the fifth day, and porcupettes drank water on day 22. Farrell and Christian (1987) gave a lactation period of 68-78 days. In the Shadle and Ploss (1943) study, porcupettes actively nursed for 52 days, but continued to periodically suckle until 14-15 weeks of age. The porcupettes started eating solid foods on the ninth day, and ate poplar bark on day 13. Shadle (1950) observed nursing bouts until three to five months of age. Gosling (1980) gave a lactation period of 16-20 weeks for *Hystrix*, although captive infants started consuming solid foods at 18 days of age. Reports of hand-raised porcupettes in zoos gave weaning ages of approximately 15 weeks, and one report of 11 days, although solid food consumption started as early as birth (Mathias, 1994). Weanling weight is approximately 44% of the adult weight (Farrell and Christian, 1987). Kleiman (1974, pg. 194) indicated that suckling after the weaning period commonly occurred and may be a social bonding behavior rather than a nutritional need.

Vispo and Hume (1995) compared the size of the near-term porcupine fetus digestive system to that of an adult. The stomach of the fetus was proportionally larger (23% vs. 17%) and the distal colon smaller (22% vs. 38%) than the adult. The cecum was proportionally the same size in the fetus and adult. The small intestine comprised 61% of the digestive tract, compared to 41% in the adult. The total mass of the fetus digestive system was 7% of the body weight, compared to 28% of the adult's body weight.

Table 9: Growth rates of captive infant porcupines. Shadle and Ploss, 1943.

Age	Weight
Birth	1 lb, 1 oz.
1 month	2 lb., 12 oz.
2 months	3 lbs., 7 oz.
3 months	5 lbs., 5 oz.
4 months	6 lbs., 3 oz.
5 months	8 lbs., 3 oz.
6 months	10 lbs., 2 oz.
7 months	11 lbs., 7 oz.
8 months	12 lbs., 3 oz.

DENTITION

The following description is from Dodge (1982) and Roze and Ilse (2003).

Birth – 3 weeks = 4 incisors (I) and 4 deciduous premolars (PM) erupted

1 - 4 months = PM₁, molars (M₁, M₂) erupted

5 - 11 months = M₃ erupted, little wear on cheek teeth

12 -13 months = Eruption of permanent PM₁ beginning

14 - 21 months = Excessive wear on PM, M₃ has some wear

22 - 26 months = Permanent PM₁ fully erupted, no wear

26+ months = lose deciduous premolars, permanent premolars present, M₁ and M₂ have irregular wear.

HAND-REARING INFANTS

Occasionally it is necessary to hand-rear an infant porcupine. Unlike many rodents, porcupines are able to start consuming solid foods shortly after birth (Shadle and Ploss, 1943; Gosling, 1980; Mathias, 1994). However, they do need the nutrient composition that is provided from the milk formula for several weeks.

The first milk that is common for mammals is the colostrum. It is well known that ungulates require colostrum and the associated passive maternal antibodies shortly after birth in order to survive. It is unclear whether porcupines receive immunoglobulins (Ig) in the milk or *in utero*. Guinea pigs receive all of their maternal antibodies *in utero*, whereas rats and mice receive them *in utero* and in the colostrum (Robbins, 1993, pg.203). Whereas IgG can only be absorbed in the intestine of ruminants in the first 24-48 hours of birth, Robbins (1993, pg.204) indicated rats and mice could absorb the immunoglobulin until 16-20 days of age.

The maternal milk composition for porcupines, as reported by Jenness and Sloan (1970), on an as fed basis, is as follows: 28.8% solids, 12.4% protein, 13.2% fat, 1.8% carbohydrates and provides 1.76 kcal/ml of formula. Like many of the rodent species, porcupines have a very low percentage of carbohydrates in the maternal milk.

It is possible to make a substitute milk formula using commercial milk replacers intended for domestic species. PetAg™ has manufactured a line of milk replacers (Zoologic™) in the United States, which can be shipped internationally as well. The products can be mixed well together to make a diet comparable to the mother's milk. One product, Milk-Matrix 33/40 is similar to the puppy formula, Esbilac™. In 1993, PetAg™ changed the fat ingredient in Esbilac™ from coconut oil to butterfat. Anecdotal information from wildlife rehabilitators indicated increased mixing problems as well as some digestive problems in squirrels on the new formula. PetAg™ then developed the Zoologic line using the previous recipes, including plant-based fats.

Grober™ makes a line of milk replacers in Canada that may be acceptable substitutes for the PetAg™ formulas, however, the specific recipe for porcupines won't be the same as the one included in this paper. Grober™ does have a puppy milk replacer; although the protein and fat content is lower than that of PetAg's™ (27% vs. 33% protein, 30% vs. 40% fat, respectively). Grober™ also does not, at this time, have a milk replacer that is comparable to multi-milk (Zoologic™ Milk Matrix 30/55). The Multi-Milk™ replacer has a very small percentage of carbohydrates, which is an imperative component of the recipe to keep the milk sugar level as close to the maternal milk formula as possible. Providing excessive amounts of sugars, or possibly the wrong type (e.g., lactose) may cause digestive upset and diarrhea (Robbins, 1993, pg. 213).

Nutrient composition of milk replacer formulas (dry matter basis) PetAg, 1992

	Energy (Kcal/100g.)	Protein %	Fat %	Carb. %	Fiber %	Moisture %	Ash %
Milk-Matrix 30/55™	625.0	31.7	55.0	2.7	0	3.6	7.0
Milk-Matrix 33/40™	578.0	34.0	42.9	15.6	0	2.1	6.3

One recommended substitute milk formula for porcupines (Marcum, 1997):

1 part Esbilac™ or Zoologic™ Milk Matrix 33/40
1 part Multi-Milk™, or Zoologic™ Milk Matrix 30/55
2 parts water

Nutrient composition for the above formula, on an as fed basis, is as follows: 73.3% moisture, 8.9% protein, 13.4% fat, 2.1% carbohydrates and provide 1.65 kcal/ml of formula (Marcum, 1997).

At this time, with the milk replacers that are available, it is not possible to create an artificial milk formula that matches the maternal milk exactly in nutrient composition. The above formula has a protein content that is approximately 30% lower and carbohydrate content 15% higher than the maternal milk. Although it has not been documented in the porcupine, carbohydrates appear to be the limiting factor in milk formulas for many rodents which are sensitive to lactose. The result, from a formula high in carbohydrates, is diarrhea (Edwards, 1993; Clark and Olfert, 1986). For that reason, it is preferable to maintain a carbohydrate concentration as close to the maternal milk composition as possible, with fat and protein having second and third priority. Decreased protein in the diet may contribute to reduced growth rates in hand-raised porcupettes (Mathias, 1994), but is, at this time, a trade-off for controlling diarrhea and enteritis that can result in death. Since porcupettes are able to eat solid foods at a very young age, consumption of vegetables and hay will provide additional protein to the diet. Small pieces of fruit (apples, carrots) and vegetables (broccoli, yam, sweet potato) can be offered in between formula feedings, as well as hay, ad. lib. Small tree branches, such as poplar, beech and sugar maple can be provided at two weeks of age for eating and climbing. The weaning process can be completed by 16 weeks of age, although porcupettes may refuse the milk formula before that age. For additional, general information on rodent infant care, see Edwards (1993).

When starting an infant on a substitute milk formula, it is important to introduce the diet gradually to prevent digestive upset and diarrhea. It is recommended to dilute the milk formula with water for the first few feedings, starting at a 3:1 ratio of water to mixed formula and working towards the full-strength formula over a period of 48 hours (Marcum, 1997). The addition of Lact-aid™ may be beneficial to help digest milk sugars (Kirk, 1993, pg. 2-3).

To determine the volume of formula and caloric needs of the porcupette, several calculations must be made to ensure adequate nutrition.

1. The stomach capacity of most mammals is approximately 5-7% of the body weight (Edwards, 1993). This value can be used for the porcupine.
2. The basal metabolic rate (BMR) must be determined.
Kleiber's (1947) formula: $70 \times \text{body wt (kg.)}^{.75}$
3. Calculate maintenance energy requirement (MER) for growth. The value is 3.
Formula: $\text{BMR} \times 3$
4. Divide the MER by the kcal/ml in the formula to determine the volume to be fed in a 24-hour period. In the recipe above, the kcal/ml is 1.65.
5. Divide the kcal/ml by the stomach capacity to determine the number of feedings per 24-hour period.

Example: a 1 pound (454 g.) porcupine.

1. $454\text{g.} \times 0.05 = 22.7\text{g.}$ (converts to 22.7mls. for liquid). (stomach capacity)
2. $70 \times 0.454\text{kg}^{.75} = 38.7 \text{ kcal/day}$ (BMR)
3. $38.7 \times 3 = 116 \text{ kcal/day}$ (MER for neonate)
4. $\frac{116 \text{ kcal/day}}{1.65 \text{ kcal/ml}} = 70.4 \text{ ml of formula per day}$

5. $\frac{70.4 \text{ ml formula per day}}{22.7 \text{ ml}} = 3.1$ feedings (round down to 3 feedings** per 24 hour period)

** feedings should be split into approx. equal time periods (i.e. 3 feedings = every 8 hrs.)

FEEDING TECHNIQUE

Porcupettes can be wrapped in a towel, papoose-style and fed while sitting or lying in a prone position so their head is higher than the stomach, to aid in swallowing (Mathias, 1994). A pet nurser bottle or 10-35 ml.(or cc.) luer-tip syringe, depending on the volume offered at each feeding, can be used to administer the formula. A Catac™ nipple can be attached to the end of the syringe tip for easier suckling. The milk formula should be warmed to body temperature (approx. 100°F). The substitute formula provided above is very thick (yogurt consistency) when cold, but is more liquid when warmed. Unused portions of the formula must be refrigerated between uses. New formula should be prepared every 1-2 days. The addition of Lact-aid™ products may require the formula be prepared several hours in advance of feeding.

GERIATRICS

Unlike incisors, porcupine cheek teeth are not replaced throughout the animal's life, but are worn down with age. Geriatric animals can have their cheek teeth worn down to the gum line (Roze, 1989). Exposure of the pulp cavity can result in dental problems including decay and pain, which may affect the porcupine's ability to eat properly. In the wild, 12 year old porcupines are considered geriatric. They are generally smaller than three to four year old adults, presumably from reduced feed intake, which may be related to worn cheek teeth (Earle and Kramm, 1980). The average life span of a porcupine in the wild is approximately eight years, although there have been reports of animals 25-30 years of age (Roze and Ilse, 2003). Dental care plays an important role in maintaining the health of animals. Providing browse and other chewable items may help to maintain the teeth. Animals that have decreased food intake and/or appear to eat on one side of the mouth should be examined for dental problems.

PORCUPINE DIET SURVEY RESULTS

12 zoos in the United States completed a survey on porcupine husbandry, including nutrition. Following are the results regarding diet.

All 12 zoos fed some type of commercial diet:

- 4 fed rodent chow as the only commercial diet item
- 3 fed a combination of rodent chow and primate chow/biscuit
- 1 fed rodent chow and dry dog food
- 1 fed primate chow and alfalfa pellets (rabbit diet)
- 3 fed primate chow only

The specific commercial diets included the following:

Non-specified rodent chow	6 zoos
High fiber pellets	1 zoo
Leaf-eater primate biscuit	3 zoos
High fiber herbivore pellets	1 zoo
Alfalfa pellets (rabbit diet)	1 zoo
Monkey chow biscuit	4 zoos
Zupreem primate diet	1 zoo
Dry dog food (maintenance formula)	1 zoo
Mazuri rodent chow	2 zoos

Six zoos provided more than one commercial diet item in their food list. Combinations included:

- Leafeater and herbivore diet
- Alfalfa pellets and monkey chow
- Rodent chow and monkey chow
- Zupreem primate, monkey chow, leafeater biscuit and rodent chow
- Rodent chow and leafeater biscuit
- Mazuri rodent chow and dry dog food

Eight facilities fed fresh fruit. Three diets mentioned fruit in a general term. Six diets included apples; one diet included each of the following, cantaloupe, melon and pear. Apple was the most common fruit offered. Eleven diets included fresh vegetables. Three diets gave unspecified vegetables. The other items provided are listed in order of frequency: carrots = 6, lettuce = 4, corn = 4, yam = 3, spinach = 2, sweet potato = 2, celery = 1, greens (unspecified) = 1, broccoli = 1. Most zoos fed multiple types of vegetables. Carrots, corn and lettuce were the most common items offered. Six zoos offered browse, as an occasional treat, or seasonally, based on availability. One zoo indicated species of browse offered included bamboo and mulberry. The other zoos didn't provide specific information on browse species.

Miscellaneous items offered were:

Bread, peanuts and hard nuts were offered at one zoo. "Variable root" was offered at another facility.

Table 10: Nutrient composition of commercial diets used in Diet Survey. All products are manufactured by Mazuri™, with the exception of Zupreem™ Primate diet.

	Rodent pellets	Browser biscuit	Primate High fiber sticks	Primate Leafeater	Zupreem Primate	Primate Maint.
Crude protein	24	12.4	18.5	23	≥ 20	16.6
Crude fat	6.5	2.9	5.6	5	≥ 5	4.5
Crude fiber	3.8	24.2	13.9	12.4	≥ 2.5	9.5
NDF*	11.9	43.3	29.6	24.7	n/a	23.5
ADF*	4.6	30.3	18.9	16.0	n/a	13.3
Calcium	0.95	0.98	1.25	1.03	n/a	1.3
Phosphorus	0.65	0.55	0.70	0.67	n/a	1.23
Potassium	1.10	0.99	0.84	1.06	n/a	0.75
Sodium	0.28	0.24	0.55	0.27	n/a	0.40
Vit. A (IU/kg)	0.015	9750	0.02	20,000	n/a	0.02
Vit. D (IU/kg)	0.0017	1950	0.0035	3000	n/a	0.0035
Kcal/g.	3.27	2.67	2.60	2.75	n/a	2.71

* NDF = neutral detergent fiber (cellulose, hemicellulose and lignin). ADF = acid detergent fiber (cellulose and lignin).

Table 11: Browse and native foods included in captive porcupine diet. Felicetti, et al. 2000.

SPECIES	CP % dry wt.	NDF %	Energy (kcal/g)
Douglas fir bark/cambium (<i>Pseudotsuga menziesii</i>)	2.75	43.20	5.38
English oak acorns (<i>Quercus robur</i>)	3.56	23.30	5.24
Lodgepole pine needles (<i>Pinus contorta</i>)	7.06	47.30	4.56
Ponderosa pine bark/cambium (<i>Pinus ponderosa</i>)	3.50	60.20	6.31
Red oak acorns (<i>Quercus rubra</i>)	6.80	16.95	5.38
Willow leaves (<i>Salix lasiandra</i>)	16.88	43.61	4.44

DIET RECOMMENDATIONS

Based on the research that has been presented in this paper, a few general nutrient recommendations have been made for developing a captive porcupine diet. See Table 12 for details.

Table 12: Proposed dietary nutrient levels for captive porcupine diet. Fournier and Thomas, 1997; Felicetti, et al., 2000; Vispo and Hume, 1995; Alkon, et al., 1986; NRC, 1995.

	Recommendation
Crude Protein, % dry wt.	6.25-10% DMI **
Nitrogen	346-389 mg / kg ^{.75} /day
Fat	2-4%
Crude fiber	9-12%
NDF	< 60% total DMI
Calcium	2-5 g / kg DMI
Phosphorus	2-5 g / kg DMI
Ca:P ratio	1:1 - 2:1
Sodium	0.5 g / kg DMI
Potassium	3.6 - 8.0 g / kg DMI
Potassium : Sodium ratio	≤ 10 : 1
Vitamin D	≤ 1000 IU / kg DMI / day
Apparent digestibility	≥ 80%
Kcal / day (maintenance)	70 x bw (kg) ^{.75} x 1.5
Kcal / day (late gestation / lactation)	increase maint. by 17%
Kcal / day (for hand-raised infants)	70 x bw (kg) ^{.75} x 3
Kcal / day (for weaned infants, juveniles)	70 x bw (kg) ^{.75} x 2 - 2.5

** CP recommendation is for non-tannin protein sources. If tannins are provided in the diet, in the form of browse, the CP requirement may be higher.

From a comparison of commercial diets in Table 10, and recommendations in Table 12, it is apparent that most of the commercial diets currently offered to porcupines in zoo and wildlife facilities may provide some nutritional imbalances. All of the diets have crude protein levels greater than the recommended 10%. With the exception of the rodent pellets and Zupreem™ primate, the diets have crude fiber contents of 9-12%, which is comparable to the 11% in the high fiber trial of Fournier and Thomas (1997). However, animals on 11% fiber, coupled with high protein in that study and in Alkon et al. (1986) consumed excess calories, which could lead to overweight if maintained long term. The other nutrient of concern is vitamin D. The leafeater diet contains vitamin D₃ at the rate of 3000 IU/kg diet. The recommended level for rodents is one-third that amount. Nocturnal animals, such as the porcupine, may have an even lower requirement. Since deaths have occurred from vitamin D₃ toxicity in other crepuscular and nocturnal rodents (Kenny, et al., 1993), until further studies are conducted, this nutrient should not exceed the dietary recommendation of 1000 IU/kg DM for guinea pigs (NRC, 1995).

The nutrient composition of primate high fiber sticks and herbivore browser maintenance biscuit more closely match the needs of the porcupine. As with the other diets, the protein level is higher than recommended, but can be lowered by adding browse to the daily diet, which will reduce protein absorption. The addition of vegetables and small amount of fruit will also reduce the percent of crude protein in the diet. The fat content of the browser biscuit falls within the range given by Alkon, et al. (1986) of 2-4% fat. Since porcupines are able to store a high level of body fat without increasing body weight, it is preferable to keep the fat content of the diet as low as possible. Rodent pellets are acceptable, especially in vitamin and mineral content. The drawback is that they tend to be high in protein and low in fiber. Other brands of rodent chow, including Harlan Teklad™ 2014 and 2016S and Kaytee™ Forti-diet have CP of 14, 16 and 21%, respectively; fat content of 3.5 - 4.5% and fiber content of 3.9 - 7.0%, which may be more suitable choices, particularly if they are mixed with the browser or high fiber diets. The browser biscuit and high fiber sticks are high in NDF and ADF, which may be important in maintaining a healthy

cellulolytic microbial gut population in the porcupine. The main concern with the browser biscuit is the high fat-soluble vitamin content. Vitamin A requirements haven't been established for porcupines, but in domestic rodents it ranges from 500-23,000 IU/kg DM (Robbins, 1993, pg. 82). The level in the browser biscuit is considerably higher than that of the rodent pellet and high fiber stick. Additionally, vitamin A occurs in fruits and vegetables, so porcupines will be obtaining the vitamin from other food sources. Since this vitamin is fat-soluble, it will accumulate in the body, and could potentially reach toxic levels (Robbins, 1993). To this date, there have not been documented reports of vitamin A toxicity in porcupines. However, if the browser biscuit is used as a major food item in the porcupine diet, it may be advisable to include either the rodent pellets or high fiber sticks, and to limit produce items high in vitamin A. The browser biscuit is also high in vitamin D₃ --- almost twice that recommended for guinea pigs. Again, it would be advisable to mix the browser biscuit with one of the other acceptable commercial diets to reduce the overall vitamin D₃ intake.

Summary of diet recommendations:

A diet containing one or more of the following commercial diets (50-60% of DMI):

Herbivore browser maintenance biscuit
 Primate High fiber sticks
 Primate maintenance diet
 Rodent chow (mix with one of the above diets)

Produce:

Fresh vegetables: 20%
 Broccoli, sweet potato, yam, pumpkin, greens, carrots

Fruit*: 10%

Apple, melon, pear, berries, bananas
 *Avoid citrus fruits, as they can lower the pH of the gut and potentially cause digestive upsets.

Browse: 10-20%

Used for nutrition, enrichment and proper dental care. A variety of natural browse species have been included in this paper. See appendix 2a for examples.

Appendix 1: Spring and summer plants as reported in Dodge, 1982; Roze, 1989; Griesemer, et al., 1998.

Tree parts

American elm (*Ulmus americana*) foliage
 aspen (*Populus* spp.) foliage and catkins
 beech (*Fagus grandifolia*) foliage
 birch (*Betula* spp.) foliage
 linden (*Tilia americana*) foliage
 oak (*Quercus* spp.) buds, foliage
 sugar maple (*Acer saccharum*) buds
 white ash (*Fraxinus americana*) foliage

Ground vegetation, water plants

alfalfa (*Medicago* spp.)
 apples (*Pyrus malus*)
 aquatic liverworts (*Riccia* spp.)
 arrowhead (*Sagittaria* spp.)
 bindweed (*Convolvulus* spp.)
 buckbrush (*Ceanothus fendleri*)
 clover (*Trifolium* spp.)
 dandelion (*Taraxacum* spp.)
 goosefoot (*Chenopodium* spp.)
 grapes (*Vitis* spp.)
 grasses (*Gramineae*)
 milkweed (*Asclepias* spp.)
 pondweeds (*Potamogeton* spp.)
 raspberry (*Rubus* spp.) leaves
 sedges (*Carex* spp.)
 thistle (*Cirsium* spp.)
 violets (*Viola* spp.)
 water lilies (*Nymphaea* spp.)

Appendix 2a: Tree species used as food items based on geographical region.

References: 1=Speer and Dilworth (1978). 2= Roze (1984). 3= Shapiro (1949). 4= Curtis and Kozicky (1944). 5= Griesemer, et al. (1998). 6= Brander (1973). 7= Tenneson and Oring (1985). 8= Harder (1979). 9= Snyder and Linhart (1997). 10= Stricklan et al. (1995). 11= Curtis and Wilson (1953). 12= Craig and Keller (1986). 13= Taylor (1935). 14= Reynolds (1957). 15= Gabrielson (1928).

Tree Species	NB ¹	CM ²	AM ³	ME ⁴	MA ⁵	MI ⁶	MN ⁷	AC ⁸	CO ⁹	UT ¹⁰	ID ¹¹	IDD ¹²	AZ ¹³	AZD ¹⁴	OR ¹⁵
American elm		S		W			W								
American linden		S		S			S								
Balsam fir	W		W				W								
Beech		W S	W	S											
Bigtooth aspen		S			S		W								
Birch spp.	W			S											
Chokecherry												W			
Douglas fir								W		W		W	W		
Gambel oak					S					W					
Hemlock		W	W	W	W S	W									
Limber pine								W							
Lodgepole pine								W							W
Northern red oak				W	W S		W								
Northern white cedar		W		W											
Ocotillo														W	
Pinion													W		
Ponderosa pine									W		W				
Quaking aspen		S		S	S		W					S			
Red spruce			W	W											
River hawthorn												W S			
Spruce spp.	W														W
Striped maple		W	W												
Sugar maple		W S	W	W S	S	W	W								
Sugar pine															W
White ash		S		W	W										
White cedar	W			W											
White fir										W					
White pine	W			W			W								
White spruce				W			W	W							
Yellow birch		S	W	W											
Yellow pine		S											W		W

NB= New Brunswick, NY. CM= Catskill Mtns., NY. AM= Adirondack Mtns., NY. ME= Maine. MA = Massachusetts. MI = Michigan. MN= Minnesota. AC = Alberta, Canada. CO= Colorado. UT= Utah. ID= Idaho. IDD= Idaho desert. AZ= Arizona. AZD= Arizona desert. OR= Oregon

** W, S denote whether the species is consumed in winter or spring/summer

Appendix 2b: Species names of trees listed in appendix 2a.

American elm (<i>Ulmus americana</i>)	Pinion (<i>Pinus edulis</i>)
American linden (<i>Tilia americana</i>)	Ponderosa pine (<i>Pinus ponderosa</i>)
Balsam fir (<i>Abies balsamea</i>)	Quaking aspen (<i>Populus tremuloides</i>)
Beech (<i>Fagus grandifolia</i>)	Red spruce (<i>Picea rubens</i>)
Bigtooth aspen (<i>Populus grandidentata</i>)	River hawthorn (<i>Crataegus rivularis</i>)
Birch spp. (<i>Betula</i> spp.)	Striped maple (<i>Acer pensylvanicum</i>)
Chokecherry (<i>Prunus virginiana</i>)	Sugar maple (<i>Acer saccharum</i>)
Douglas fir (<i>Pseudotsuga menziesii</i>)	Sugar pine (<i>Pinus lamertiana</i>)
Eastern hemlock (<i>Tsuga canadensis</i>)	White ash (<i>Fraxinus americana</i>)
Gambel oak (<i>Quercus gambelii</i>)	White cedar (<i>Thuja occidentalis</i>)
Limber pine (<i>Pinus flexilis</i>)	White fir (<i>Abies concolor</i>)
Lodgepole pine (<i>Pinus contorta latifolia</i>)	White pine (<i>Pinus strobus</i>)
Northern red oak (<i>Quercus rubra</i>)	White spruce (<i>Picea glauca</i>)
Northern white cedar (<i>Thuja occidentalis</i>)	Yellow birch (<i>Betula alleghaniensis</i>)
Ocotillo (<i>Fouquieria splendens</i>)	Yellow pine (<i>Pinus ponderosa</i>)

Appendix 3: Product and Manufacturer List

Catac Products, Ltd. Catac House 1, Newnham Str., Bedford MK40 3JR, England.
(Can order in the U.S. from UPCO, PO Box 969, St. Joseph, MO. 64502. 1-800-254-8726).

Grober Animal Nutrition. Cambridge, Ontario, Canada. 519-622-2500. Drummondville, Quebec, Canada. 819-475-6317. www.grober.com

Harlan Teklad: P.O.Box 29176, Indianapolis, Indiana 46229-0176. USA (317) 894-7521.
www.teklad.com

Kaytee™ Forti-diet for rats and mice. 1-800-529-8331. www.kaytee.com

Lact-aid: McNeil Nutritionals, Ft. Washington, PA, USA. 1-800-522-8243. www.lactaid.com

Mazuri: 1-800-227-8941. <http://mazuri.purinamills.com/main.html>

Pet-Ag: 255 Keyes Ave., Hampshire, IL. 60140, USA. 1-800-323-6878. www.petag.com

Zupreem: PO Box 2094, Mission KS 66202, USA. 1-800-345-4767. www.zupreem.com

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