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Lactation in the Dog: Milk Composition and Intake by Puppies

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ABSTRACT The composition and intake of milk by mother-reared puppies was studied to compare protein and energy intakes of puppies with estimated requirements. Milk samples were obtained from five beagle bitches over the period of 7–37 days postpartum. Dog milk contained on average 22.7% dry matter, 9.47% fat, 7.53% protein, 3.81% sugar and 146 kcal gross energy per 100 g. Protein comprised 31% of milk energy. Nonprotein nitrogen averaged 0.054%, equivalent to 4.4% of total nitrogen. Milk intakes of puppies in the five litters were estimated from water kinetics following administration of deuterium oxide (D₂O). D₂O dilution indicated that body water comprised 72–73% of puppy body weight, and fractional turnover rate of body water averaged 0.15–0.17% per day in weeks 3 and 4 postpartum. Milk intakes were calculated as 160 ± 5.4 g (mean ± SEM) at 19 days and 175 ± 5.3 g at 26 days, equivalent to 17.0 and 14.6% of body weight, respectively. Daily milk yields of the bitches averaged 964 g at 19 days and 1054 g at 26 days. Dry matter intakes of the puppies were equivalent to 3.9 and 3.3% of body weight at 19 and 26 days, respectively. Gross energy intakes averaged 223–224 kcal/kg^{0.75} per day, and protein intakes averaged 0.33–0.36 g per gram body weight gain at these ages. Estimates of the energy requirements of young puppies by the National Research Council appear to be too high. *J. Nutr.* 114: 803–812, 1984.

INDEXING KEY WORDS dogs • lactation • milk composition • milk yield • water kinetics

Milk composition and yield vary greatly among diverse mammalian species (1–3). Estimation of the nutrient requirements of both mother and suckling young requires quantitative information on lactation performance. Dogs are known to produce a rather concentrated milk containing 21–26% total solids, 8–12% fat and 7–10% protein (4–7), although lower levels of fat and protein have recently been reported (8). Little information is available on milk yields in dogs. Several litters of various breeds have been studied by weighing puppies before and after suckling (6, 7). A German shepherd was estimated to produce 1.7 kg milk per day at the lactation peak at 3 weeks postpartum, whereas bitches of smaller breeds produced less milk but were only studied in the first 9 days postpartum (6). Suckling puppies 4 weeks of

age or less are reported to consume the equivalent of 10–14% of body weight per day (7, 9). The effects of maternal nutrition (9, 10), maternal size (2), breed (6), and litter size and mass on lactation performance in dogs need clarification.

The following study was undertaken to measure milk composition and milk yield at peak lactation in well-nourished dogs of the beagle breed. This study is part of a larger project in which lactation performance is compared among several species, and nutrient intakes of suckling young are related to body size, growth rates and estimated requirements (3, 11). Milk production was

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measured from the dilution and turnover of deuterium oxide (D_2O) administered to puppies. Hydrogen isotopes have been shown to yield valid estimates of milk production if corrections are made for changes in body water pool size and for isotope recycling via maternal milk (11-15). Peak lactation was assumed to occur in week 3 or 4 postpartum since puppies do not initiate feeding on semisolid food until the emergence of deciduous dentition at 21 to 35 days postpartum (16-18). Milk alone will support normal growth up to 4 weeks postpartum; thereafter, withholding of supplemental food may result in a reduced growth rate (19).

MATERIALS AND METHODS

Experimental animals. Five bitches were studied at the long-established beagle research colony at Cornell University (20). The bitches were 1.5-3.7 years of age, had postpartum weights of 9.3-15.2 kg (mean = 12.7 kg) and were producing their first or second litters. One week prior to the expected parturition date each dog was removed from the main colony to an isolated whelping room. They were individually housed in 1.2- × 1.1-m cages (horizontal dimensions) with 0.7- × 0.7-m heated whelping boards, and were fed a commercial dry dog food (Wayne Dry Dog Food, Allied Mills, Inc., Chicago, IL) containing about 26% crude protein, 9% fat, 4% crude fiber and 2.75 kcal metabolizable energy (ME) per gram.² Water was provided ad libitum in elevated stainless-steel bowls that were too high for the puppies to drink from. At birth litter size ranged from 5 to 10 puppies; 5 to 7 puppies per litter survived beyond 1 week postpartum. The puppies were first offered supplemental feed [dry dog food (Wayne Dry Dog Food) soaked in evaporated milk and water] at 29-30 days postpartum. Puppies were weighed to the nearest gram at least three times per week over the course of the study.

Milk sampling and analysis. Milk samples were collected at weekly intervals from 7-37 days postpartum. Additional samples were also taken during weeks 2 and 5 postpartum. Bitches were removed from their litters for 2-3 hours prior to milking. Oxy-

tocin (5 IU) was administered by intramuscular injection, and one or two teats evacuated as completely as possible by gentle manual expression. An average of 21 ml (\pm 6.3 SD) was obtained in 10-15 minutes. Samples were frozen in sealed vials until analyzed.

Milk samples were thawed quickly, homogenized in a Potter-Elvehjem tissue grinder and subsampled. The weekly samples were assayed in duplicate for major constituents. Total solids were determined by oven drying, total nitrogen (TN) and nonprotein nitrogen (NPN) by a Kjeldahl procedure, fat by the Roese-Gottlieb method (21) and sugar by the phenol-sulfuric acid colorimetric method, as previously described (21). Sample size did not permit NPN determination on eight samples. In such cases an additional sample collected from the same bitch within 2 to 3 days was substituted. Both TN and NPN were measured on these additional samples. Protein was calculated as $6.38 \times (TPN - NPN)$. Gross energy was estimated from an equation developed by Perrin (22), as previously presented (21).

Milk intake estimation procedure. Milk intake was estimated from water kinetics of 25 puppies in the five litters. D_2O (99.8% purity) was administered by stomach tube to puppies at 15-16 days and 22-23 days postpartum at a rate of 2.3 g/kg body weight. One young in each litter was not given D_2O so that correction could be made for isotope recycling. Two hours were allowed for isotope equilibration prior to collection of about 2 ml of blood by jugular puncture; in young puppies hydrogen isotopes equilibrate in 1.5 hours (23). Each puppy was bled at 2- to 3-day intervals such that four samples were collected during each weekly study period for determination of water turnover. The second isotope administration immediately followed the final bleeding of the preceding period such that residual isotope levels could be measured. Blood water was isolated by heat distillation and assayed for deuterium concentration by infrared spectrophotometry (24) using matched barium fluoride cells (0.11-mm path length) in a double beam

²Nutritional information supplied by manufacturer.

grating infrared spectrophotometer (Model 521, Perkin-Elmer Corp., Norwalk, CT).

Assayed deuterium levels were corrected for body weight changes in computations of fractional turnover rate (k) and body water fraction (F) (11). Isotope recycling via maternal ingestion of the excreta of suckling young, followed by transfer of isotope in milk water from mother to young (12), necessitated an additional correction. The accumulation of deuterium in an uninjected, control puppy in each litter was monitored. On the assumption that these levels are representative of recycled isotope in littermates, the deuterium levels in control puppies were subtracted from the deuterium levels of their littermates prior to regression of corrected log D_2O concentration against time after administration. Daily water loss, water gain and water intake were computed as previously described (21). The proportions of milk constituents catabolized to produce metabolic water were estimated by iterative calculations detailed elsewhere (11). Statistical analyses were performed using programs of the Statistical Package for the Social Sciences (SPSS) on a Honeywell computer at the Smithsonian Institution. Mean values are presented as mean \pm SEM unless otherwise indicated.

RESULTS

Milk composition. Over the period of 7 to 37 days postpartum (table 1) there were no significant differences in total solids, fat, protein or gross energy content among sampling times [$P > 0.05$, analysis of vari-

ance (ANOVA)]. Sugar content did differ among sampling times ($P < 0.05$, ANOVA), the mean value rising from 3.47% at 7 to 9 days postpartum to 4.13% at 29 to 30 days postpartum. The mean values for all sampling times were: 22.7 \pm 0.41% total solids, 9.47 \pm 0.386% fat, 7.53 \pm 0.123% protein, 3.81 \pm 0.079% sugar and 146 \pm 3.6 kcal gross energy per 100 g. If converted to a dry matter basis dog milk was found to contain 41.4 \pm 0.87% fat, 33.4 \pm 0.60% protein, 17.0 \pm 0.049% sugar and 641 \pm 3.9 kcal/100 g dry matter. Fat, protein and sugar provided 58.7 \pm 0.86%, 30.5 \pm 0.66% and 10.5 \pm 0.33% of total gross energy, respectively. There were no significant differences in milk composition among the five bitches, whether compared on a whole-milk, dry matter or gross energy basis ($P > 0.05$, ANOVA). NPN ranged from 0.045 to 0.068% (mean = 0.054 \pm 0.0012%), equivalent to 3.4–5.2% of total nitrogen. NPN did not differ significantly among bitches or sampling times ($P > 0.05$, ANOVA).

Water and milk intakes. Water and milk intakes were calculated for the midpoints of each study period, i.e., for 19 and 26 days postpartum (table 2). Growth rates and estimated body weights at these ages derive from regressions of puppy weight on postnatal age. These regressions were highly linear (mean $r^2 = 0.990$). Regressions of the logarithm of corrected deuterium concentration on time after isotope administration were also highly linear (mean $r^2 = 0.996$). Deuterium content in body water of uninjected control puppies reached levels equivalent to 11.5 \pm 0.45% and 10.6 \pm 0.30% of the levels in injected littermates by the final

TABLE 1
Composition of dog milk^{1,2}

Constituent ³	Time of milk sampling, days postpartum					Total
	7-9	15-16	22-23	29-30	36-37	
Total solids, %	23.5 \pm 1.31 ^a	22.9 \pm 1.41 ^a	22.1 \pm 0.51 ^a	22.3 \pm 0.64 ^a	22.6 \pm 0.72 ^a	22.7 \pm 0.41
Fat, %	10.90 \pm 1.370 ^a	9.67 \pm 1.171 ^a	8.73 \pm 0.230 ^a	8.89 \pm 0.410 ^a	9.16 \pm 0.482 ^a	9.47 \pm 0.386
Protein, %	7.17 \pm 0.092 ^a	7.59 \pm 0.275 ^a	7.72 \pm 0.390 ^a	7.49 \pm 0.303 ^a	7.70 \pm 0.281 ^a	7.53 \pm 0.123
Sugar, %	3.47 \pm 0.087 ^a	3.61 \pm 0.111 ^{ab}	4.04 \pm 0.176 ^{bc}	4.13 \pm 0.149 ^c	3.81 \pm 0.186 ^{abc}	3.81 \pm 0.079
Gross energy, kcal/100 g	155 \pm 12.3 ^a	147 \pm 11.9 ^a	141 \pm 3.4 ^a	142 \pm 4.5 ^a	144 \pm 5.0 ^a	146 \pm 3.6

¹Mean \pm SEM; $n = 5$ for each time period; $n = 25$ for total. ²Means with the same superscript in a row do not differ by more than the shortest significant range at the 0.05 significance level (Duncan's multiple-range test). ³Percentage values represent gram per 100 g.

blood sampling in the first and second study periods, respectively. Correction for isotope recycling was therefore warranted.

Fractional turnover rate of body water (k) declined from 0.168 ± 0.0036 per day for the first study period to 0.152 ± 0.0034 per day for the second ($P < 0.001$, paired t -test). By contrast body water fraction (F) did not differ significantly ($P > 0.05$, paired t -test) between the two periods (table 2). Calculated water losses, water gains and water intakes at 19 and 26 days postpartum are presented in table 2. Water intake was equivalent to 15.1 and 13.9% of body weight at 19 and 26 days, respectively.

Water intake derives from both preformed milk water and metabolic water from the catabolism of milk solids. Body composition data presented by Sheng and Huggins (25) indicate weight gain comprises 12% protein and 13% fat in the period of 16–33 days postpartum. On the basis of these values, combined with milk composition, growth rate and water intake data, one can calculate that the amounts of fat and protein catabolized are equivalent to 69 and 72% of ingested fat and 63 and 67% of ingested protein at 19 and 26 days, respectively. It was assumed that 100% of ingested sugar was catabolized. Ingestion of 100 g milk will then yield 77.3 g preformed and 11.7 g metabolic water at 19 days and 77.3 g preformed and 11.7 g metabolic water at 26 days. Milk intake was estimated as water intake $\times 1.129$ at 19 days and water intake $\times 1.124$ at 26 days (table 3). Individual milk intakes of puppies ranged from 126 to 239 g/day at 19 days and from 134 to 229 g/day at 26 days.

TABLE 2

Body water turnover in suckling puppies		
Measure	Time after parturition, day	
	19	26
Body wt, g	942 \pm 25.4	1199 \pm 33.3
Wt gain, g/day	36.8 \pm 1.28	36.8 \pm 1.28
Fractional turnover, (k)	0.168 \pm 0.0036	0.152 \pm 0.0034
Wt fraction, ¹ (F)	0.726 \pm 0.0068	0.716 \pm 0.0084
Water loss, g/day	115 \pm 4.2	130 \pm 4.1
Water gain, g/day	26.6 \pm 0.80	26.1 \pm 0.68
Water intake, g/day	142 \pm 4.8	156 \pm 4.7

¹Grams body water per gram body weight.

Milk intakes of puppies were compared among litters and between the two post-natal ages by two-way ANOVA. Whether expressed as a daily amount, as a percentage of body weight per day, or per gram body weight gain, milk intake was significantly influenced by both litter and age effects (table 3). Although the absolute amount of milk consumed per day at 26 days (175 ± 5.3 g) was greater ($P < 0.01$) than that at 19 days (160 ± 5.4 g), this amount represented a smaller percentage of body weight (14.6% at 26 days vs. 17.0% at 19 days, $P < 0.001$). Since the same estimate of growth rate was used for both age categories, milk intake per gram body weight gain was of course greater at 26 days (table 3). The mean milk intakes in four litters were relatively similar (147–156 g/day at 19 days; 159–178 g/day at 26 days), but the puppies in the litter of bitch BR 82 consumed appreciably more milk on average (203 g/day at 19 days and 221 g/day at 26 days). Puppies in the larger litters tended to be smaller and grow at a reduced rate but did not appear to ingest substantially less milk than the puppies in smaller litters at these ages (table 3).

Total milk output of lactating bitches (milk intake per puppy \times litter size) was estimated as 964 ± 57.6 g/day ($n = 5$) at 19 days and 1054 ± 57.7 g/day at 26 days (table 3). These estimates are not significantly different ($P > 0.05$, paired t -test). These yields correspond to 7.6% of maternal weight or $143 \text{ g/kg}^{0.75}$ at 19 days and 8.3% or $157 \text{ g/kg}^{0.75}$ at 26 days.

Nutrient intakes. By combining mean milk composition (table 1) and mean milk intake (table 3) data, the intake of various constituents can be calculated. At 19 days suckling puppies ingested 36.3 g dry matter (3.86% of body weight), 15.2 g fat, 12.0 g protein, 6.1 g sugar and 234 kcal ($224 \text{ kcal/kg}^{0.75}$). At 26 days intakes were 39.7 g dry matter (3.31% of body weight), 16.6 g fat, 13.2 g protein, 6.7 g sugar and 256 kcal ($223 \text{ kcal/kg}^{0.75}$). For each gram of body weight gain, puppies ingested 0.33 g protein and 6.4 kcal at 19 days and 0.36 g protein and 7.0 kcal at 26 days.

DISCUSSION

Milk composition. Milk collected from beagle bitches contained on average 22.7%

TABLE 3
Milk intakes of suckling puppies¹

Bitch designation	Litter size	Milk intake of puppies			Milk output of bitch
		Daily intake	As % wt	Per gram wt gain	
		g	%	g	
<i>19 days postpartum</i>					
BR 82	5	203	18.7	4.51	1015
BR 50	5	152	14.8	4.02	760
CA 46	6	154	16.7	4.13	924
CD 18	7	156	17.3	4.54	1092
CA 45	7	147	17.3	4.55	1029
All litters		160 ± 5.4	17.0 ± 0.30	4.37 ± 0.074	964 ± 57.6
<i>26 days postpartum</i>					
BR 82	5	221	15.7	4.91	1105
BR 50	5	166	12.8	4.39	830
CA 46	6	178	15.1	4.80	1068
CD 18	7	165	14.4	4.82	1155
CA 45	7	159	14.8	4.92	1113
All litters		175 ± 5.3	14.6 ± 0.22	4.79 ± 0.071	1054 ± 57.7
<i>Analysis of variance</i>					
Litter effect					
<i>F</i> (4,44)		<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> < 0.001	—
Age effect					
<i>F</i> (1,44)		<i>P</i> < 0.01	<i>P</i> < 0.001	<i>P</i> < 0.001	—

¹Milk intakes are litter means. Values after ± are SEM.

total solids, 9.5% fat, 7.5% protein and 3.8% sugar. Mean values from prior studies on dog milk are tabulated for comparison (table 4). This list includes 19th century results of questionable analytical accuracy as well as studies involving only a few samples from one or two dogs. Samples collected very early or late in lactation have been excluded as not representative of established lactation. Despite variation in sampling and analytical procedures, most reports fall within the ranges of 21–26% total solids, 8–12% fat, 7–10% protein and 3–4% sugar (table 4). The results reported herein are consistent with these values. By contrast the recent data of Lønnerdal and colleagues (8) indicate much lower fat (4.8%) and protein (5.2%) levels in beagle milk collected 11–40 days postpartum. This discrepancy may stem from inappropriate application of rapid spectrophotometric methods. Color development in the sulfuric acid–phosphoric acid–vanillin reaction employed in the

determination of fat depends on the degree of unsaturation of the lipids (34). Binding of Coomassie brilliant blue G250 dye to protein is likewise a function of the amino acid composition of the protein (35, 36). These methods are valid only if standardized to the particular mix of lipid and protein constituents found in dog milk. It appears that this was not done.

The variation among the remaining studies may be a function of sampling or analytical bias or may represent real differences among dogs. Dog breeds vary tremendously in body size and conformation, but no correlation to the gross composition of milk could be determined by Rüsse (6) who studied breeds ranging in size from dachshunds to Saint Bernards. Beagle milk collected by Luick and colleagues (5) contained more total solids, fat and protein, but less sugar (table 4) than was found in the present study. By contrast the recent data of Mundt and colleagues (7) are very similar to

TABLE 4

Published data on the composition of dog milk at midlactation

Source	Females milked	Days after birth	No. of samples	Total solids	Fat	Protein	Sugar
				%	%	%	%
Ssubotin 1866 (26)	3	12-38 [?]	12 ¹	20.8	8.8	8.8 ²	2.7
Tolmatscheff 1867 (27)	1	35	2	—	11.8	8.2 ²	3.2
Abderhalden 1898 (28)	2	5-11	9 ¹	—	11.5	7.0 ²	3.3
Abderhalden 1899 (29)	1	10-14	3	—	11.6	7.3 ²	3.1
Dijkstra 1910 (30)	1	6-20	2	—	6.5	6.8 ³	2.6
Grimmer 1915 (31)	1	5-26	22 ¹	20.8	8.5	7.2 ⁴	—
Daggs 1931 (10)	3	21-35	8 ¹	23.9	12.4	8.0 ³	3.2
Deniges 1935 (32)	2	?	2	24.2	10.6	9.3 ³	2.7
Anderson et al. 1940 (4)	1	18-30	2-4 ¹	22.6	8.3	7.5 ⁵	3.7
Luick et al. 1960 (5)	3	15-36	30	26.0	12.3	9.8 ⁵	3.3
Rüsse 1961 (6)	7	5-35	32-63 ¹	22.0	11.1	6.9 ⁵	3.3
Lauer et al. 1969 (33)	2	30	2	26.4	12.3	8.2 ⁵	2.9
Mundt et al. 1981 (7)	7	7-28	18-28 ¹	22.0	9.7	7.3 ⁵	3.6
Lønnerdal et al. 1981 (8)	16	11-40	62-71 ¹	—	4.8	5.2 ⁶	4.5
Present study	5	7-37	25	22.7	9.5	7.5 ⁴	3.8

¹Early and/or late lactation samples excluded. ²Protein determined by precipitation and weighing. ³Assay method not specified. ⁴Protein calculated as protein nitrogen (Kjeldahl) \times 6.38. ⁵Protein calculated as total nitrogen (Kjeldahl) \times 6.38. ⁶Protein measured by dye-binding procedure.

the present results although four breeds as well as mongrels were included. Breed differences in the composition of dog milk must be minor if they exist at all.

An elevation in total solids and protein at both the beginning and the end of lactation has been noted in prior reports (4, 6, 31). In the present study there were no substantial changes in milk composition from 7 to 37 days postpartum, a week after supplemental feeding of puppies commenced. Marked compositional changes are apparently associated with mammary involution at about 39-49 days (4, 6). Weaning is of course influenced by feeding and management practices, and perhaps by breed as well (6). Lønnerdal et al. (8) have reported a rise in fat and protein contents of beagle milk from 0 to 40 days, and a subsequent decline in fat content. These trends are at odds with other findings and could reflect sensitivity of the spectrophotometric assay procedures to qualitative as well as quantitative changes in milk constituents. Canine caseins and whey proteins certainly differ in amino acid composition (37) such that varying proportions during lactation (6) will affect protein content as measured by dye-binding.

The NPN content of dog milk averaged 0.054%. The data of Grimmer (31) and Rüsse (6) indicate mean NPN values of 0.068 and 0.112%, respectively. In the present study NPN accounted for only 4.4% of total nitrogen, as compared to 5.7 (31) and 9.3% (6). Protein estimates based on total nitrogen (e.g., see refs. 4, 5, 7, 33) will overestimate true protein by an amount equal to $\text{NPN} \times 6.38$, i.e., by about 0.3 to 0.7 percentage points.

In 100 g milk, 1.88 ± 0.062 g of solids was not accounted for by the summation of fat, protein and sugar. Part of the residual is due to ash and part to NPN constituents. If published data on the ash content of dog milk in the period of 5 to 35 days postpartum (4, 7, 10, 28, 30-33) are considered collectively, a mean ash content of 1.15% can be calculated ($n = 57$). Assuming the NPN constituents of dog milk to be similar in proportion to those of cow's milk (38), $\text{NPN} \times 5.34 = 0.29\%$ gives an approximation of the combined weight of NPN constituents (11). The remaining 0.44 g ($= 1.88 - 1.15 - 0.29$) represents minor organic and inorganic compounds not included in the various analytical fractions (38) as well as

analytical error. On this basis it would appear that any such error was small.

Water and milk intakes. Suckling beagle puppies were estimated to consume 142 g water, equivalent to 160 g milk, at 19 days postpartum, and 156 g water, equivalent to 175 g milk, at 26 days postpartum (table 2). These values are only as accurate as the estimates of body water fraction (F) and water turnover rate (k) on which the calculations are based. Isotope dilution procedures have been reported by Sheng and Huggins (23, 25) to overestimate body water content in growing beagles when compared to values obtained by direct dessication. Dilution of tritiated water indicated body water percentages of 75–92% at 8–21 days (23), whereas direct dessication values were 65–74% at the same sampling times (25). These results have been contested with allegations that the analytical procedures must have been in error (39). Neither the mean values obtained in the present study (72–73%) nor the values reported by Romsos and colleagues (9) for 4-week-old puppies administered tritiated water (74–76%) appear to be greatly in excess of expected values. Widdowson (40) reported that 3-week-old puppies contain 68% water. It appears that isotope dilution may overestimate body water in puppies by a few percentage points but not to the degree reported by Sheng and Huggins (23).

The decline in water turnover rate from 0.168 in the first week of study to 0.152 in the second may reflect in part that puppies were not allowed supplemental water or feed prior to 29 to 30 days postpartum. Maternal regurgitation of feed to puppies was not observed; disgorging of food has been reported as early as 21–24 days postpartum by Martins (41). Any ingestion of water from sources other than mother's milk would lead to overestimation of milk intake. Fractional turnover rates of 0.168 and 0.152 correspond to body water half-lives of 4.1 and 4.6 days. Four-week-old beagle puppies suckling bitches fed canned, semipurified diets of high or low carbohydrate content had somewhat longer half-lives of 5.0 and 6.8 days, respectively (9). These data were not corrected for either isotope recycling or changing size of the body water pool, however. Baverstock and Green (12) calculate

that at least 47% of the isotope lost by dingo puppies is ingested by the mother; some of this is recycled to the young in milk. Isotope recycling was not measured directly in the present study although accumulation of D_2O in uninjected control puppies indicated that it did occur.

The milk intakes determined herein are much higher than the 81 ± 13 ml/day and 59 ± 13 ml/day reported by Romsos et al. (9) for beagle puppies suckling bitches fed two semipurified diets. Aside from the methodological problems mentioned above, these puppies exhibited abnormally low growth rates, gaining on average only 13 and 11 g/day in the two groups. Normal growth rates for beagle puppies are 35–40 g/day (17, 19, 42, 43). Records for the Cornell dog colony for 1975–1976 indicate average growth rates of 34.9 ± 0.99 g/day for puppies in litters of five ($n = 25$ puppies), 29.9 ± 1.23 g/day for puppies in litters of six ($n = 30$) and 27.2 ± 1.08 g/day for puppies in litters of seven ($n = 35$). The growth rates observed in the present study (36.8 ± 1.28 g/day) for puppies suckling bitches fed a commercial dry dog food are somewhat above the colony norms, but within the normal range for beagle puppies. The semipurified diets used by Romsos et al. (9) apparently did not support normal milk yields.

The milk intake of 26-day-old puppies was equivalent to 14.6% body weight, a decline from the 17.0% of body weight consumed at 19 days. Mundt and colleagues (7) reported that milk intakes of puppies in three litters of various breeds averaged 10.0–13.5% of body weight in the first 4 weeks postpartum. These data derive from weights taken before and after puppies were allowed to suckle. The experimental regimen of separation and periodic, controlled access of young to mother may cause a reduction in secretion rates, may interfere with normal maternal nursing behavior, or may result in the accumulation of amounts of milk that young are unable to consume in relatively short suckling bouts (3). Hence weight differential procedures tend to underestimate milk consumption rates. Mundt et al. (7) note that puppies consumed more than 95% of daily milk intake in four or five of the six suckling bouts permitted

per day; i.e., one or two suckling bouts per day were relatively unsuccessful. These puppies reportedly consumed 1.7–3.0 g milk per gram body weight gain in weeks 3 and 4 (7). By contrast puppies in the present study were calculated to consume 4.4 g milk per gram gain during week 3 and 4.8 g milk per gram gain during week 4. On this basis it appears that the weight differential procedure underestimated milk intake by about one-third.

Peak milk yields of beagle bitches appear to be about 1 kg/day in week 4 postpartum. Milk yield is undoubtedly influenced by body size (2, 3). Using a weight differential procedure, Rüsse (6) estimated that at 6 days postpartum a German shepherd produced 915 g as compared to 102 g and 184 g for two dachshunds. Only the German shepherd was studied throughout lactation; peak yield (about 1.7 kg/day) was observed at 22–27 days (6). Assuming a body weight of 30 kg, milk production of this dog was about 130 g/kg^{0.75} as compared to 157 g/kg^{0.75} for beagle bitches at 26 days postpartum in the present study. Bias associated with the weight differential method may explain some or all of this 20% difference.

Nutrient intakes in relation to estimated requirements. The Subcommittee on Dog Nutrition of the National Research Council (NRC) (44), following Payne (45), listed the daily ME requirement of 3- and 6-week-old puppies as 274 kcal/kg^{0.75}. In the present study puppies ingested only 244 kcal gross energy per kilogram^{0.75} at 26 days. If conversion factors of 4.0 kcal ME per gram protein or sugar and 9.0 kcal ME per gram fat are adopted, dog milk can be calculated to contain 131 kcal ME/100 g. The ME intakes would then be 219 kcal/kg^{0.75} at 19 days and 200 kcal/kg^{0.75} at 26 days. It appears that the National Research Council (44) overestimated the metabolizable energy needs of young puppies by 25–35%.

Recently Mundt et al. (7) estimated the daily maintenance requirements of puppies as 72 kcal gross energy per kilogram^{0.75} from a regression of gross energy intake of suckling puppies on growth rate. As the milk intakes of the puppies were probably underestimated by a substantial amount (see above), this estimate cannot be considered reliable.

Weaned puppies have been estimated by the Subcommittee on Dog Nutrition, NRC (44) to require 22% protein in the dry matter of a diet containing 3.5–4.0 kcal ME per gram dry matter. Dog milk contains about 131 kcal ME/100 g or 5.77 kcal ME per gram dry matter, a value about 50% above the NRC diet. If dog milk is to meet NRC requirements it should contain $1.5 \times 22 = 33\%$ protein on a dry matter basis. The protein content of dog milk was indeed found to be 33.4% of dry matter.

Puppies ingested 0.33 g protein per gram body weight gain at 19 days and 0.36 g protein per gram body weight gain at 26 days. Payne (45) assumed weight gain in puppies to contain 17% protein, whereas carcass analyses by Sheng and Huggins (25) indicate protein content to remain at about 10–12% of body weight from birth to 6 weeks postpartum. At peak lactation puppies apparently incorporate only one-third to one-half of ingested protein into tissue.

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