

Nutrient-specific compensatory feeding in a mammalian carnivore, the mink, *Neovison vison*

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Abstract

Balancing of macronutrient intake has only recently been demonstrated in predators. In particular, the ability to regulate carbohydrate intake is little studied in obligate carnivores, as carbohydrate is present at very low concentrations in prey animal tissue. In the present study, we determined whether American mink (*Neovison vison*) would compensate for dietary nutritional imbalances by foraging for complementary macronutrients (protein, lipid and carbohydrate) when subsequently given a dietary choice. We used three food pairings, within which two macronutrients differed relative to each other (high *v.* low concentration), while the third was kept at a constant level. The mink were first restricted to a single nutritionally imbalanced food for 7 d and then given a free choice to feed from the same food or a nutritionally complementary food for three consecutive days. When restricted to nutritionally imbalanced foods, the mink were willing to overingest protein only to a certain level ('ceiling'). When subsequently given a choice, the mink compensated for the period of nutritional imbalance by selecting the nutritionally complementary food in the food choice pairing. Notably, this rebalancing occurred for all the three macronutrients, including carbohydrate, which is particularly interesting as carbohydrate is not a major macronutrient for obligate carnivores in nature. However, there was also a ceiling to carbohydrate intake, as has been demonstrated previously in domestic cats. The results of the present study show that mink regulate their intake of all the three macronutrients within limits imposed by ceilings on protein and carbohydrate intake and that they will compensate for a period of nutritional imbalance by subsequently selecting nutritionally complementary foods.

Key words: Carnivore nutrition: Diet self-selection: Geometric Framework: Macronutrient balancing: Mustelidae: Predators: Protein *v.* non-protein energy

Nutrient balancing in herbivorous and omnivorous animals is well known^(1–9), but the evidence that predators balance their intake of specific nutrients is much more recent^(10–16). The previously widespread assumption that predators do not exhibit nutrient balancing has partly been predicated on a narrower range of nutrient compositions in prey than in the food sources of herbivores and omnivores and partly on the premise that predators are typically food limited^(17,18).

In nature, available prey may vary markedly not only in abundance but also in nutrient composition across species

and seasons^(19,20), and some mammalian predators have been reported to feed selectively among their prey to maximise their energy intake^(21,22). Similarly, two marsupial predators have been found to selectively consume the body parts of their prey containing the highest density of lipid⁽²³⁾. However, comparison of carnivore energy requirements with prey availability suggests that prey are often present in surplus and carnivores are therefore not energy limited across the seasons^(24,25). This indicates that carnivores do not always have to forage to maximise their energy intake, but often

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have the chance to balance their intake of other food components from various prey species or prey body parts.

In addition to experimental evidence that piscivorous fish balance their intake of all the three macronutrients^(26,27), it has recently been shown that both the domestic cat (*Felis catus*) and dog (*Canis lupus familiaris*) regulate the macronutrient balance of their diet when given the opportunity to self-select among complementary foods^(13,16). It has previously been shown that captive American mink (*Neovision vison*) regulate their intake of protein and lipid to an intake target⁽¹²⁾, but whether they have the capacity to also regulate their intake of carbohydrate and to compensate for previous nutritional imbalances has not been studied.

Wild mink primarily prey on small vertebrates^(28–32). The nutrient content in small vertebrates mainly consists of protein and lipid, with carbohydrate being present at very low concentrations^(32,33). Thus, lipid and protein are the macronutrients that obligate carnivores would be expected to regulate. Indeed, evidence from cats indicates a low tolerance for dietary carbohydrate, such that when restricted to carbohydrate-rich foods they undereat protein and lipid to avoid a carbohydrate surplus⁽¹³⁾. Nevertheless, the physiological pathways for utilising carbohydrate are functional in both mink and cats⁽³²⁾, and carbohydrate is included at relatively high amounts in both standard farmed mink diets and commercial cat foods to reduce economic cost^(12,13,34). Furthermore, occasional insect prey may contain significant amounts of carbohydrate⁽³⁵⁾.

In the present study, we used the Geometric Framework for Nutrition⁽³⁶⁾ to measure the regulatory responses of mink to variation in the dietary contents of protein, lipid and carbohydrate. In the first phase of the experiment, we determined how mink resolve the trade-off between overingesting some macronutrients and underingesting others when restricted to nutritionally imbalanced diets. In the second phase, we provided the mink with a choice of complementary foods and determined whether they would feed selectively to redress the imbalances accrued during the previous phase. The results of the present study show that mink respond to nutritional imbalances involving all the three macronutrients and forage selectively for deficient nutrients when given a choice.

Experimental methods

Animals and housing

The present experiment was carried out in the mink farm at Research Centre Foulum near Viborg in Denmark from 5th to 18th August 2010. The mink had been farmed for more than eighty generations. From a stock population of about 2000 mink of the colour type standard brown, 120 males aged 98–109 d were selected for the experiment. The mink were housed individually in standard wired mesh cages (30 × 45 cm wide and 90 cm high) in an open farm shed. Temperature and lighting fluctuated with external conditions. The mink had free access to drinking-water and a closed nest furred with straw. They were reared on a standard farm diet until the start of the experiment. Each mink was weighed to

the nearest 10 g the day before the start of the experiment. All procedures were approved by the Danish Animal Experiments Inspectorate.

Experimental foods and feeding procedure

A total of six foods varying in protein, lipid and carbohydrate contents were prepared by varying the mixing ratios of ingredients normally used for preparing unpelleted farmed mink diets (Table 1). In three food pairings, the content of one of the three macronutrients was kept constant in both foods, while the content of the other two macronutrients varied relative to each other (Table 1). The nutrient ratios of the foods were selected to achieve an appropriate spread around the regulated intake point previously indicated for mink and the composition of a standard farm food⁽¹²⁾ while keeping energy content per unit dry mass as constant as possible across the foods. Furthermore, carbohydrate content had to be kept at fairly low levels to ensure that the foods were palatable to the mink. As the ingredients differed in water content and level of water binding, different amounts of water were used for food preparation to obtain foods of similar texture (Table 1).

Foods were stored at -18°C for up to 1 month and defrosted at 5°C for 12–18 h before use. Uneaten remains were collected and replaced with fresh food every morning. As in standard farming conditions, unpelleted foods were placed on top of the mink cage, allowing the mink to feed through the cage mesh. The water content of foods was titrated such that they were readily ingested and yet not so friable that they fell through the mesh. At each of the three choice feedings, we randomly chose which of the two foods was to be placed on either side of each cage. A felt mat placed under the cages allowed liquids but not food remains to pass through. This gave the mink another chance to eat the spilled food and permitted easy recollection and weighing of any uneaten spillage, which was minimal. Faeces were rarely left on the felt mat and were separated from the spilled food before collection.

Experimental design

In the initial stage of the experiment, the mink were allocated to one of the three dietary treatment groups (n 40 mink per group) where they were provided access to both foods in one of the three food pairings (Table 1). This ensured that the mink had access to both foods in the food pair before the same pair of foods was again provided during the choice feeding period. Furthermore, it ensured that the mink had the chance to balance their macronutrient intake before the following no-choice feeding period. After 3 d of access to both foods, each group of mink was split into two subgroups (n 20) where the mink in each subgroup were provided only one of the two foods in the food pair for 7 d. During the no-choice feeding period, one mink receiving the 48:42:10 food died due to an internal infection and was excluded from the analysis. To determine whether the mink would compensate for nutritional imbalances during the no-choice feeding period when given the opportunity to select their diet, both foods in the food pairs were again

Table 1. Ingredients, dry masses, digestible nutrient contents and metabolisable energy contents of the six foods used in the experiment*

	Metabolisable energy distribution (%P:%L:%C)					
	P v. L		P v. C		L v. C	
	42:46:12	26:62:12	48:42:10	36:42:22	35:55:10	35:45:20
Ingredients (g/kg fresh food)						
Fish by-product	446.4	383.9	393.9	295.7	363.0	304.9
Industrial fish	103.3	88.8	160.5	120.4	155.5	130.6
Fishmeal	46.9	39.7	42.2	31.7	36.0	31.9
Poultry by-product	80.6	69.4	168.8	126.8	155.5	130.6
Hb meal	24.2	20.8	16.9	12.7	15.2	12.8
Heat-treated wheat	40.9	60.5	27.7	70.6	36.0	67.1
Heat-treated barley	40.9	60.5	27.7	70.6	36.0	67.1
Maize gluten	24.2	20.8	16.9	12.7	15.2	12.8
Potato protein	24.2	20.8	16.9	12.7	12.9	10.9
Soya bean oil	38.1	95.7	14.3	23.8	45.4	28.1
Lard	19.2	47.9	7.1	11.9	22.7	14.0
Vitamin and mineral mixture†	0.2	0.2	0.2	0.2	0.2	0.2
Water	110.9	90.8	106.9	210.2	106.5	188.9
Dry mass (g/kg fresh food)	378.1	434.4	340.9	348.5	362.9	357.6
Nutrient contents (g/kg dry food)						
Digestible P	414.9	300.7	453.3	338.9	374.2	338.2
Digestible L	216.2	340.4	188.1	187.6	278.1	204.9
Digestible C	127.5	148.7	101.2	221.2	113.7	207.8
Energy contents (MJ/kg dry food)						
Digestible P	7.8	5.7	8.5	6.4	7.0	6.4
Digestible L	8.6	13.5	7.5	7.5	11.1	8.1
Digestible C	2.2	2.6	1.8	3.9	2.0	3.7
Total metabolisable energy	18.6	21.8	17.8	17.7	20.1	18.2

*P, percentage protein; %L, percentage lipid; %C, percentage carbohydrate.

†The contents and distributions of metabolisable energy and digestible nutrients were estimated using AgroSoft WinOpti 2010 from the values of the ingredients provided by the suppliers. Different amounts of water were used for food preparation to obtain foods of a similar texture.

‡Contained per kg: 1050000 mg vitamin A; 8750 mg vitamin D₃; 32965 mg vitamin E; 29998 mg α -tocopherol; 12500 mg vitamin B₁; 4000 mg vitamin B₂; 4200 mg vitamin B₆; 20 mg vitamin B₁₂; 17199 mg pantothenic acid; 8000 mg niacin; 75 mg biotin; 346 mg folic acid; 60003 mg choline; 24999 mg C₄H₂FeO₄; 1025 mg CuSO₄; 6237 mg MnO; 12563 mg ZnO; 120 mg Ca(IO₃)₂; 200 mg Na₂Se; 120 mg CoSO₄.

provided over a subsequent period of 3 d. The amount of all foods consumed was measured over each 24 h during the no-choice feeding period and the following 3 d of choice.

Intake measurements

Before feeding, foods were pre-weighed in a metal foil box in amounts exceeding *ad libitum* food intake, and the remaining food was recollected in the same metal foil box the following morning. Recollected food was stored at -18°C until drying at 40°C for 12 h followed by drying for another 36 h at 110°C and weighed to the nearest 1 g. Additionally fifteen to twenty samples of each food were weighed and dried to establish the dry mass contents of fresh foods. Dry mass intake was calculated as the difference between dry mass provided and dry mass recollected. Specific intakes of protein, lipid and carbohydrate were calculated by multiplying dry food mass intakes with the proportion of each digestible nutrient in the dry food (Table 1). Digestible nutrient and metabolisable energy contents of the foods were estimated using AgroSoft WinOpti 2010, based on the ingredient contents of the foods and values provided by the suppliers.

Statistical analyses

Effects of the no-choice food on intake during the no-choice pre-treatment period were analysed across dietary treatments using ANCOVA tests with initial mink body weight as the covariate after testing for effects of body weight on dry mass intake using linear regression. The dietary treatments were compared individually using Tukey–Kramer tests. Effects of the no-choice food on intake of the two foods in each food pair during the following choice feeding period were analysed using multivariate ANOVA tests with intake from each of the two foods as the dependent variable and no-choice diet as the independent variable. Intake from the two choice foods was analysed within the no-choice pre-treatment groups using paired *t* tests. In all statistical tests, differences were considered to be significant if $P < 0.05$. All statistical analyses were carried out in JMP 7.0 (SAS Institute).

Results

Regulation under no-choice

Dry mass intake during the no-choice feeding period was significantly affected by mink body weight across dietary

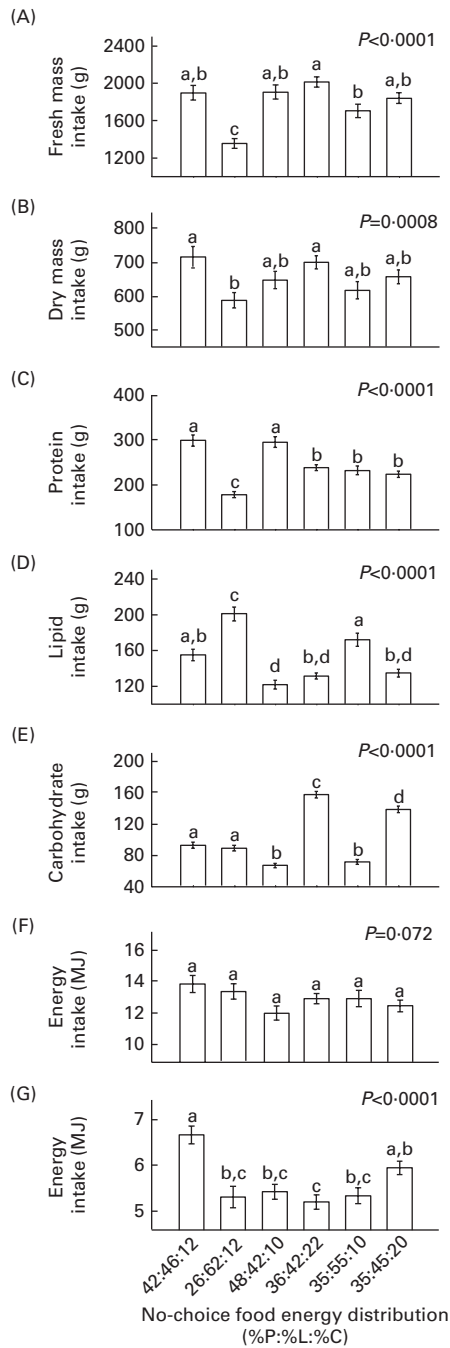


Fig. 1. Intake of (A) fresh mass, (B) dry mass, (C) digestible protein, (D) digestible lipid, (E) digestible carbohydrate and (F) metabolisable energy during the no-choice feeding period and of (G) metabolisable energy during the choice feeding period. Values are means, with standard errors represented by vertical bars. The *P* values are from ANCOVA tests across dietary treatments with mink mass as the covariate. ^{a,b,c,d} Mean values with unlike letters were significantly different ($P < 0.05$; Tukey–Kramer tests). %P, percentage protein; %L, percentage lipid; %C, percentage carbohydrate.

treatments ($R^2 0.11$, $P = 0.0002$), which justifies controlling for mink weight when comparing feeding responses. During the period of restriction to single foods, the intake of total fresh mass (Fig. 1(A)), dry mass (Fig. 1(B)), protein (Fig. 1(C)), lipid (Fig. 1(D)) and carbohydrate (Fig. 1(E)) differed significantly across dietary treatments ($P < 0.001$), while differences

in the intake of metabolisable energy were close to statistical significance ($P = 0.072$; Fig. 1(F)).

On plotting protein *v.* non-protein macronutrient (lipid plus carbohydrate) intake on a mass basis, the diet-specific intake points were found to exhibit no apparent pattern across dietary treatments (Fig. 2(A)). However, on plotting the intake of metabolisable energy from protein *v.* non-protein macronutrients, a clearer pattern was observed (Fig. 2(B)). First of all, the protein *v.* non-protein energy intake in mink restricted to three of the single foods (35:55:10, 35:45:20 or 36:42:22) converged to the same point in nutrient space (Fig. 2(B)). When plotting the regulated intake point over 7 d of feeding in a previous study in mink⁽¹²⁾, it was found to coincide with the protein *v.* non-protein energy intake in mink restricted to these three diets (Fig. 2(B)).

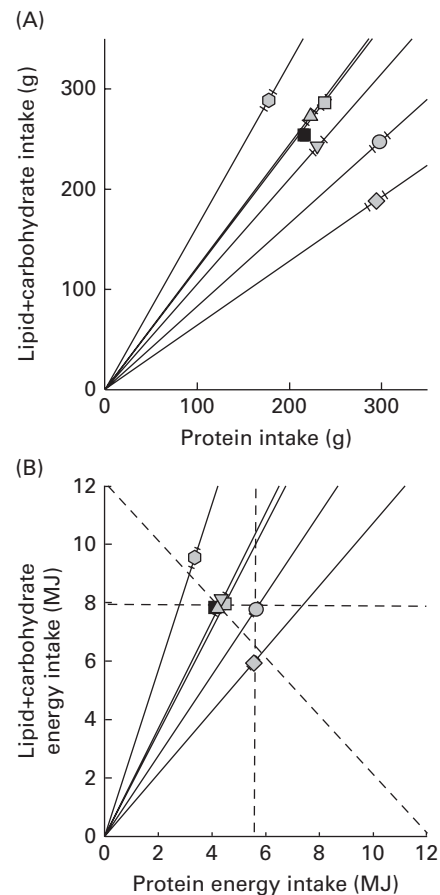


Fig. 2. Intake of (A) digestible protein *v.* non-protein macronutrients (lipid plus carbohydrate) and (B) metabolisable energy from protein *v.* non-protein macronutrients during the 7 d no-choice feeding period in mink restricted to one of the six diets. As the protein *v.* non-protein energy content is equal in the 35:55:10 food (∇) and the 35:45:20 food (Δ), there are only five slopes in (B). The intake target is indicated by the regulated intake point (\blacksquare) over the first 7 d of feeding for mink given choice in Mayntz *et al.*⁽¹²⁾, excluding the choice group that was nutritionally restrained from attaining this intake. Broken lines indicate equal ingestion of metabolisable energy from protein (vertical), non-protein macronutrients (horizontal), or protein plus non-protein macronutrients (slope of -1). Values are means, with standard errors represented by bars following the slopes. \circ , 42:46:12 Food; \diamond , 26:62:12 food; \square , 48:42:10 food; \triangle , 36:42:22 food. Food composition is given as percentage protein:percentage lipid:percentage carbohydrate based on energy contents.

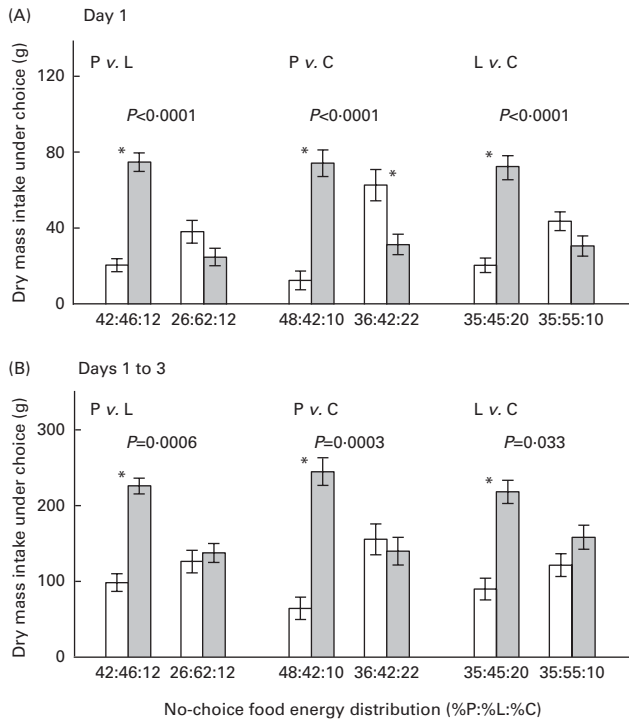


Fig. 3. Intake from each of the two foods in the three food pairings during (A) the 1st day and (B) all the 3 d of choice feeding in mink after 7 d of restriction to single no-choice foods. Within each food pair, white bars represent consumption from the food presented as no-choice food to the left and grey bars represent consumption from the food presented as no-choice food to the right on the figure. Values are means, with standard errors represented by vertical bars. The *P* values indicate significant differences in food selection between the mink provided with either of the two no-choice foods before choice feeding within each food pair using multivariate ANOVA tests. * Significant difference in selection between the two choice foods within mink that had been restricted to the same no-choice food ($P < 0.05$; paired *t* test). %P, percentage protein; %L, percentage lipid; %C, percentage carbohydrate.

When restricted to the high-lipid food (26:62:12), the mink overingested non-protein energy to a point where the surplus was slightly greater than the deficit of protein energy ingested relative to the regulated intake point (Fig. 2(B)). In contrast, mink restricted to the food with a moderate excess of protein (42:46:12) were able to achieve their presumed target intake for non-protein energy while overingesting protein (Fig. 2(B)). Mink that were restricted to the food with the highest excess of protein (48:42:10), however, ingested an amount of protein similar to that ingested by mink restricted to the 42:46:12 food at the consequence of attaining a considerably lower intake of non-protein energy (Fig. 2(B)).

Regulation under choice

When given a choice between two foods after restriction to a single food, energy intake was found to differ significantly across dietary treatments ($P < 0.0001$; Fig. 1(G)). This reflects that food selection was significantly affected by the macro-nutrient composition of the previous no-choice diet, both during the 1st day ($P < 0.0001$; Fig. 3(A)) and during all the 3 d ($P < 0.05$; Fig. 3(B)) of choice feeding. Within each of the three food pairings, we found asymmetric preference patterns during the choice feeding period. Mink provided one

of the two foods during the no-choice feeding period (42:46:12, 48:42:10 or 35:45:20) consumed significantly larger ($P < 0.0005$) amounts of the nutritionally complementary food during the choice feeding period, whereas mink that had been restricted to the other food during the no-choice feeding period (26:62:12, 36:42:22 or 35:55:10) did not consume significantly different amounts ($P > 0.2$) of the two foods (Fig. 3(B)). Mink that had been restricted to one of the two foods in each food pair thus showed a strong subsequent preference for the nutritionally complementary food, whereas mink that had been restricted to the other food in the food pair did not.

Within the two food pairings in which protein levels varied, mink that had been restricted to a high-protein, but low-lipid or low-carbohydrate food (42:46:12 or 48:42:10) consumed significantly larger amounts of the complementary food containing more lipid or carbohydrate but less protein (26:62:12 and 36:42:22, respectively) throughout the choice feeding period ($P < 0.0001$; Fig. 3(B)). The intake trajectory of these mink thus closely followed the maximum limitation of lipid (Fig. 4(A)) or carbohydrate (Fig. 4(B)) within the nutritional span of the two choice foods. Similarly, mink that had been restricted to a high-carbohydrate, but low-lipid food (35:45:20) consumed significantly larger amounts of the complementary high-lipid, low-carbohydrate food (35:55:10) during the choice feeding period ($P = 0.0003$; Fig. 3(B)). The intake trajectory thus closely followed the nutrient composition of the 35:55:10 food, although diverging during the 2nd day of choice feeding (Fig. 4(C)).

Mink that had been restricted to high-lipid foods (26:62:12 or 35:55:10), in contrast, did not consume significantly different amounts of the two foods provided during the choice feeding period ($P > 0.2$; Fig. 3), and the intake trajectories of these mink therefore passed midway between the nutrient compositions of their choice foods (Fig. 4(A) and (C)). Mink that had been restricted to the high-carbohydrate, but low-protein food (36:42:22) significantly selected the complementary high-protein, low-carbohydrate food (48:42:10) during the 1st day of choice feeding ($P = 0.027$; Fig. 3(A)), but did not maintain this preference throughout the choice feeding period ($P = 0.68$; Fig. 3(B)). The intake trajectory of these mink therefore followed the nutrient composition of the 48:42:10 food during the 1st day of choice feeding only, and overall nutrient intake during the choice feeding period was intermediate between the nutrient compositions of the choice foods (Fig. 4(B)).

Discussion

Predatory animals have traditionally been believed to be prey limited. In addition, prey has generally been assumed to be a nutritionally balanced food source and predators would therefore not require mechanisms to balance the intake of specific nutrients^(17,18,37). More recently, a number of predators have been shown to balance their nutrient intake^(11–16). Compensatory feeding for specific nutrients after ingestion of nutritionally imbalanced food has been demonstrated in invertebrate predators⁽¹⁰⁾ and has recently been demonstrated during sequential assays of single foods in cats⁽¹³⁾. The results of the present study show that mink will select food that compensates for the nutritional imbalances imposed during a

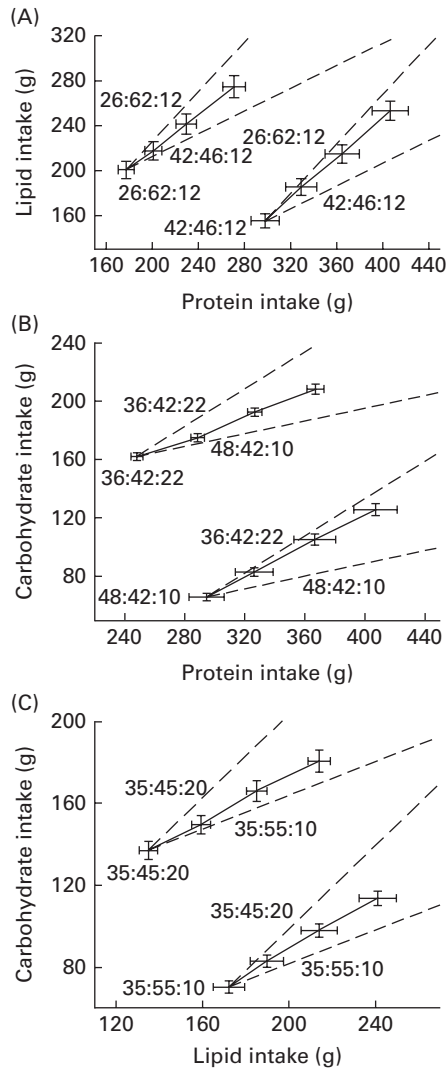


Fig. 4. Intake trajectories (solid lines) connecting the cumulative intake of specific digestible macronutrients from the end of the 7 d no-choice feeding period and during each of the three subsequent days of choice feeding. Values are means, with standard errors represented by horizontal and vertical bars. The slopes of the dashed lines show the nutrient ratios of the two provided choice foods. The area spanned by these lines indicates the overall nutritional intake composition that was available to the mink during the choice feeding period. (A) Protein *v.* lipid intake (fixed carbohydrate). (B) Protein *v.* carbohydrate intake (fixed lipid). (C) Lipid *v.* carbohydrate intake (fixed protein). Food composition is given as percentage protein:percentage lipid:percentage carbohydrate based on energy contents.

period of restriction to a nutritionally imbalanced food. Such intake regulation reflects balancing of requirements for amino acids from protein with requirements for energy primarily from non-protein macronutrients⁽³⁸⁾. Interestingly, compensatory feeding also involved carbohydrate, which is generally not considered to be an important macronutrient in the diet of obligate carnivores⁽³²⁾.

Regulation under no-choice

In the present study, the mink clearly did not regulate their intake of fresh or dry mass (Fig. 1(A) and (B)) or any individual macronutrient (Fig. 1(C)–(E)) to a constant intake level across

dietary treatments when restricted to a single food, while energy intake did not differ significantly across dietary treatments (Fig. 1(F)). Similar energy intake across dietary treatments indicates that the mink regulated their total energy intake to a specific level, but it does not discount the alternative hypothesis that they balanced excesses and deficits of macronutrient-specific energy sources⁽³⁹⁾. As we varied both carbohydrate and lipid contents in addition to protein content in the foods, pronounced differences were observed when comparing the mass and the energy relationships of the non-protein *v.* the protein component across dietary treatments (Fig. 2(A) and (B)). Therefore, using different combinations of carbohydrate *v.* lipid as the non-protein energy source across the foods allows us to establish that the mink did not regulate their intake on the basis of protein *v.* non-protein mass ingested (Fig. 2(A)), and instead strongly suggests that they balanced their intake of protein *v.* non-protein energy (Fig. 2(B)).

Protein *v.* non-protein energy intake in mink restricted to the 42:46:12 food with a moderate excess of protein did not align on a negative diagonal like the intake in mink restricted to the other foods (Fig. 2(B)). Instead, it aligned with the non-protein energy coordinate of the proposed intake target (Fig. 2(B)). Protein intake in mink restricted to the food with the most extreme surplus of protein (48:42:10), however, aligned with the protein intake in mink restricted to the 42:46:12 food, suggesting a limit to the protein ingestion capacity at this intake level. A similar limit to protein intake is typically observed in omnivorous animals^(1,3,5,7,9), whereas some predators have been found willing to overingest large amounts of protein to increase their overall energy intake^(14,15). However, these predators did not overingest protein extensively over the short term, but only when foods were consistently protein rich over a longer term, and a longer-term experiment would therefore be necessary to conclusively determine whether mink continue maintaining a limited protein intake if foods are consistently protein rich. Such phenotypic adaptation could occur as a gradual metabolic adjustment to cope with excessive amounts of amino acids and the load of ammonia and urea thus generated⁽⁴⁰⁾.

Regulation under choice

The asymmetric pattern of food preference depending on the no-choice diet within each food pair strongly indicates that the mink foraged to rebalance their intake of specific macronutrients (Fig. 3), rather than due to a preference for a more novel taste. It has been reported that many animals, including cats and dogs⁽⁴¹⁾, show a preference for novel foods when in a state of nutritional imbalance. As we ensured that the mink had access to both foods in their food pair before the no-choice feeding period, the likelihood of them preferring the nutritionally complementary food based on novelty was reduced. Nevertheless, there is the possibility that sensory-specific satiety may have contributed to the pattern of food selection^(42,43). Selection of the complementary food may thus in part have been driven by the fact that this food represented a change from the food available in the previous no-choice feeding period. Sensory-specific satiety, however, does not

appear to represent true nutrient-specific regulation based on nutritional feedback mechanisms^(36,44), and the role of this mechanism in nutrient balancing is therefore unclear.

In addition to balancing their intake of protein and lipid⁽¹²⁾, the mink regulated their intake of carbohydrate in the present study. Indeed, the growth of mink kits during lactation is faster when their mothers are provided a diet containing equal amounts of energy from carbohydrate and protein (protein: carbohydrate 34:33) relative to a diet high in protein (protein: carbohydrate 65:3)⁽⁴⁵⁾. Mink that were restricted to a high-protein diet in the present study (42:46:12 or 48:42:10) correspondingly showed a strong preference for the complementary high-lipid or high-carbohydrate food (26:62:12 and 36:42:22, respectively) when given a choice (Fig. 3), indicating that there are costs associated with attaining higher amounts of metabolic energy from protein than required. However, when restricted to a high-carbohydrate diet (35:45:20 or 36:42:22), the mink selectively ingested the complementary high-lipid food (35:55:10) and initially the complementary high-protein food (48:42:10), indicating rebalancing of nutrients and a ceiling to carbohydrate intake similar to that found in cats⁽¹³⁾.

The results of the present study indicate a strong preference for lipid to support the majority of the energetic requirements in mink. This is further supported by the fact that the mink did not show any significant preference for the high-carbohydrate food after restriction to a high-lipid food in the present study (Fig. 3). Most probably, Fink *et al.*⁽⁴⁵⁾ would therefore have found a similar or higher increase in kit growth if they had substituted carbohydrate with lipid in their experiment. The finding that mink avoid high intake of protein is interesting because the natural prey of mink, small vertebrates, are protein-rich food sources⁽³²⁾. At the same time, mink, similar to cats, have a physiological requirement for protein as metabolic energy and therefore must have a proportion of their energy contributed by protein⁽³²⁾. The results of the present study indicate that protein intake in excess of this requirement, however, is a deterrent to mink and presumably costly. If the nutrient compositions of small vertebrate prey reported by Eisert⁽³²⁾ are representative, mink in nature may therefore often be limited by the amount of non-protein energy that they can attain, especially in the form of lipid.

The choice of a high-lipid diet is similar to the case observed in dogs⁽¹⁶⁾, whereas cats select a diet higher in protein⁽¹³⁾. Laboratory cats, however, select a carbohydrate content similar to that in standard mink food^(12,13), although feral cats consume a diet containing very little carbohydrate⁽⁴⁶⁾. As the natural prey of mink is also rich in protein but contains limited amounts of carbohydrate⁽³²⁾, mink in nature would likely be ecologically constrained from attaining a composition of protein and carbohydrate the same as that selected in the present study. Whether this choice in mink and cats could be an adaptive response to domestication and associated rearing diets and whether wild-caught mink and cats would show similar preferences remain to be investigated. When comparing digestion in farmed and feral American mink, farmed mink were found to exhibit a tendency towards higher digestibility of both carbohydrate and

lipid and more efficient retention of nitrogen⁽⁴⁷⁾, and in arctic foxes (*Alopex lagopus*), carbohydrate digestion was found to be significantly higher in farmed individuals than in wild individuals⁽⁴⁸⁾. The results of the present study support the hypothesis that farmed or domesticated carnivores have adapted (phenotypically and/or genetically) to attain a more omnivorous gastrointestinal function and nitrogen metabolism in response to domesticated foods with high carbohydrate and low protein contents relative to their natural diets^(12,48). Genetic adaptations to a carbohydrate-rich diet might theoretically have evolved at a rapid rate during artificial selection of better-performing animals by the farmers.

Conclusions

The results of the present study show that American farmed mink balance their intake of protein *v.* non-protein energy when restricted to imbalanced diets and that they will compensate for a period of nutritional imbalance by subsequently selecting a nutritionally complementary diet. This demonstration of compensatory feeding for specific nutrients in a mammalian carnivore adds to the recent evidence that predators forage to balance their intake of specific nutrients rather than merely to meet their energetic requirements. Furthermore, the results show that carbohydrate intake is regulated in addition to lipid and protein intake.

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