

Excess digestive capacity in predators reflects a life of feast and famine

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A central challenge for predators is achieving positive energy balance when prey are spatially and temporally heterogeneous. Ecological heterogeneity produces evolutionary trade-offs in the physiological design of predators; this is because the ability to capitalize on pulses of food abundance requires high capacity for food-processing, yet maintaining such capacity imposes energetic costs that are taxing during periods of food scarcity^{1,2}. Recent advances in physiology show that when variation in foraging opportunities is predictable, animals may adjust energetic trade-offs by rapidly modulating their digestive system to track variation in foraging opportunities¹. However, it is increasingly recognized that foraging opportunities for animals are unpredictable³, which should favour animals that maintain a capacity for food-processing that exceeds average levels of consumption (loads)^{2,4}. Despite this basic principle of quantitative evolutionary design, estimates of digestive load:capacity ratios in wild animals are virtually non-existent¹. Here we provide an extensive assessment of load:capacity ratios for the digestive systems of predators in the wild, compiling 639 estimates across 38 species of fish. We found that piscine predators typically maintain the physiological capacity to feed at daily rates 2–3 times higher than what they experience on average. A numerical simulation of the trade-off between food-processing capacity and metabolic cost suggests that the observed level of physiological opportunism is profitable only if predator–prey encounters, and thus predator energy budgets, are far more variable in nature than currently assumed.

Predation opportunities for animals in the wild are distributed heterogeneously in space and time owing to a variety of interactions between predator behaviour⁵ (for example, how they allocate time to foraging, avoiding predators, and finding mates), prey behaviour⁶, and heterogeneity in the physical attributes of habitats where predator–prey interactions occur^{7,8}. As a result, encounter rates between predators and prey in their natural habitats are exceedingly difficult to estimate⁶ and may be far more heterogeneous than assumed. To cope with such ecological heterogeneity, predators employ behavioural and physiological tactics that allow them to store energy when food is plentiful, and utilize such reserves when food is scarce. For predators that store energy internally (for example, as fat reserves or somatic growth), physiological constraints on food-processing may limit rates of energy storage⁹ and compensatory growth¹⁰ and thus the potential to capitalize on pulses of food. To thrive in an environment where foraging opportunities vary widely but unpredictably, predators should maintain physiological opportunism and exhibit maximum capacities for food-processing that considerably exceed the average capacity required.

Acquiring energy from prey is a serial process that spans foraging (attacking, handling, and ingesting prey) to assimilation (digesting food and absorbing nutrients)¹¹. In a homogeneous world, the most economic pathway would exhibit symmorphosis, where the maximal processing rate at each stage is equal to the average input rate (load) from the prior stage¹². However, if the load at any stage varies in time, performance at that stage should exhibit excess capacity, such that the

maximal rate exceeds the mean and the system can accommodate spikes in load⁴. Surprisingly, the role of excess capacity along the food-to-fuel pathway is poorly understood. It is known that parts of the foregut (for example, the oesophagus, stomach, or other comparable structures) can act as food storage reservoirs, enabling predators to ingest prey faster than they can process it^{13,14}. This excess capacity for feeding accommodates short-term variation in prey encounters¹⁴ but it does not facilitate sustained increases in energy gain, which predators would require in order to build energy reserves or achieve compensatory growth. To sustain increased consumption rates, predators require excess capacity for assimilation (that is, digestion and absorption). Current knowledge of excess capacity in the digestive system is primarily limited to measurements at the cellular level², and estimates of load:capacity ratios for integrated rates of assimilation are virtually non-existent for wild animals. Measurements of excess assimilation capacity are important for both physiologists, who seek to evaluate symmorphosis (or lack of it) across the energy intake chain, and ecologists, who lack reliable data to characterize the variation in foraging opportunities experienced by predators in the wild. Here we quantitatively assess how daily variation in foraging opportunity should affect the profitability of excess assimilative capacity, and use our results to interpret observed load:capacity ratios from animals in the wild.

Predators require excess assimilative capacity to capitalize on large pulses of prey abundance as reflected in the positive tail of the distribution of predator foraging opportunities^{8,14}. However, increasing assimilative capacity also increases the energetic costs of physiological maintenance and locomotion¹. We developed a simple numerical simulation to characterize this trade-off and explore its response to the underlying distribution describing daily variation in foraging opportunity. We simulated variation in daily foraging opportunities using a gamma distribution with a fixed arbitrary value for the mean, but different coefficients of variation (c.v., defined as (s.d./mean) × 100) to simulate different levels of variability in the environment (see Methods, Supplementary Fig. 1). A type I functional response¹⁵ modelled how assimilative capacity (C_{\max} , the maximum amount of food that can be consumed in one day) determines the daily food consumption, C , that a predator derives from a daily foraging opportunity, x :

$$C(x) = \begin{cases} x & \text{if } x < C_{\max} \\ C_{\max} & \text{if } x \geq C_{\max} \end{cases} \quad (1)$$

The expected consumption rate ($J d^{-1}$) for an individual with a specified C_{\max} and gamma-distributed variation in daily foraging opportunity is:

$$E(C_{\max}) = \int_0^{\infty} C(x)g(x|k,\theta)dx \quad (2)$$

where $C(x)$ is the type I functional response of equation (1), and $g(x)$ is the gamma distribution with shape and scale parameters (k and θ) varied to produce specified levels of mean and c.v.

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The load:capacity ratio for assimilation is given by equation (3) below, and its inverse is synonymous with excess capacity, Z :

$$E(C_{\max})/C_{\max} = 1/Z \quad (3)$$

The net energetic profit (N) is the energy remaining after gains from consumption are paid to maintenance and activity costs, M :

$$N = E(C_{\max}) - M \quad (4)$$

The energetic costs associated with increased assimilative capacity are poorly described and are likely to vary among taxa. We model M as a constant fraction, r , of C_{\max} (see Methods):

$$M = rC_{\max}, \text{ where } 0 < r < 1 \quad (5)$$

thus

$$N = E(C_{\max}) - rC_{\max} \quad (6)$$

In our analysis, we used numerical simulation to calculate the load:capacity ratio that maximized the net profit function (equation (6)), given the c.v. in daily foraging opportunity and the cost of the gut. The optimal load:capacity ratio for assimilation decreased with increasing variation in foraging opportunity, but did not exhibit substantial levels of excess capacity until the c.v. was very high, indicating strong right-skew in the distribution of foraging opportunities (Fig. 1 and Supplementary Fig. 1). For example, the optimal load:capacity ratio reached ~ 0.4 when the c.v. in foraging opportunity ranged from 70% to 150%, depending on the costs of maintaining excess capacity (Fig. 1e). This suggests that, in order for integrated rates of assimilation to exhibit levels of excess capacity seen in many other biological structures² (for example, load:capacity ratios < 0.5), predator–prey encounters would need to be extremely heterogeneous in time.

To assess the variation in foraging opportunities that predators experience in nature, we compared our model scenarios to assimilative load:capacity ratios estimated for piscine predators in the wild. We compiled 639 estimates of mean daily consumption rate in fishes. The estimates were calculated from bioenergetics models that integrate across field measurements of growth and express consumption relative to maximum physiological rates. This bioenergetics framework^{16,17} (described in Supplementary Information) has been parameterized for different species through laboratory studies that measure the effects of water temperature and body mass on both metabolism and C_{\max} , the daily consumption rate observed under *ad libitum* feeding. C_{\max} is determined by assimilative capacity¹⁸, and corresponds well to the consumption rates of wild fish in conditions where food is unlimited¹⁹. The model uses field data on predator growth achieved over a defined time period, diet composition and quality, and water temperature to estimate the proportion of C_{\max} (which we call p) that balances an energy budget where growth is surplus energy after energetic gains from consumption are paid to metabolism, excretion and specific dynamic action. Thus, p represents the load:capacity ratio for assimilation. We searched research databases for all papers citing this bioenergetics model and compiled all estimates of p recorded in the wild (Supplementary Table 1). We grouped p estimates by population (unique combinations of species and publication, $n = 66$). The mean length of time over which p was estimated was 208 days (s.d., 143 days).

Across 66 populations from 38 species, the median p was 43% (s.d., 16%), indicating a load:capacity ratio for assimilation of 0.43. The distribution of p was right-skewed and similar in shape whether grouped by population or not (Fig. 2). Populations from marine ($n = 11$), lake ($n = 49$) and stream ($n = 6$) environments did not exhibit significantly different load:capacity ratios (Kruskal–Wallis test: $P = 0.10$, d.f. = 2) and less than 5% of populations exhibited load:capacity ratios greater than 0.8. Among the $>60\%$ of populations that

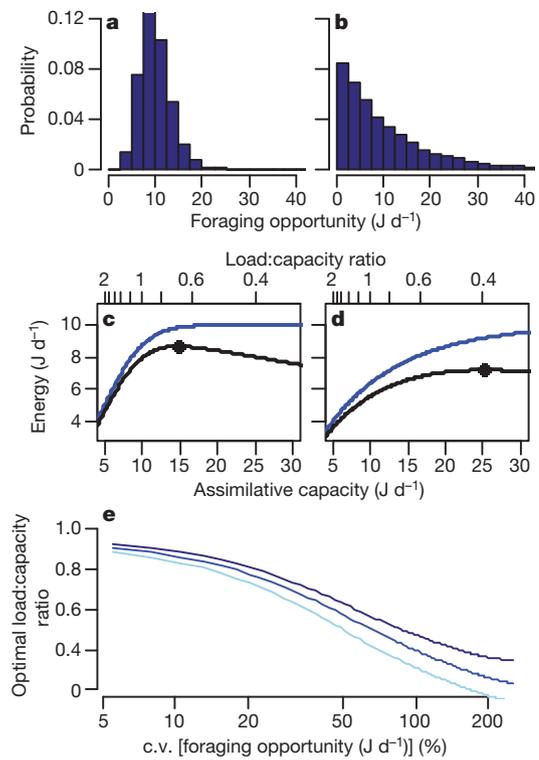


Figure 1 | Results from a simulation model exploring the energetic profitability of excess capacity for assimilation as a function of the daily variation in foraging opportunity. We define assimilation as digestion and absorption. **a, b**, Gamma distributions characterizing two scenarios of ecological heterogeneity that both yield an average of 10 energy units per day in foraging opportunity. **a**, Variance in daily foraging opportunity is equal to the mean, as from a Poisson distribution (c.v. = 32%, $\theta = 1$, $k = 10$). See main text for nomenclature. **b**, Foraging opportunities are highly right-skewed and show 10 times more variance than a Poisson distribution with similar mean (c.v. = 100%, $\theta = 10$, $k = 1$). **c, d**, Cost–benefit analysis of excess assimilative capacity under the two scenarios of ecological heterogeneity; **c** and **d** correspond respectively to distributions displayed in **a** and **b**. Lines represent gross and net energetic gains (blue and black, respectively) resulting from different levels of assimilative capacity (that is, maximum daily consumption rate). The upper x-axis measures excess capacity in terms of the load:capacity ratio (the mean daily consumption rate relative to the maximum rate). Filled circle represents the energetically optimal digestive capacity. Results shown are from the medium cost scenario (see Supplementary Information for a full description). **e**, Model results showing the energetically optimal load:capacity ratio as a function of the c.v. in daily foraging opportunity. Curves depict different cost scenarios (light blue, low; blue, medium; dark blue, high; see Supplementary Information for full description).

exhibited load: capacity ratios less than 0.5, all functional guilds of predators were represented, including planktivores, benthivores and piscivores.

Digestive machinery is expensive^{1,20}, so why do piscine predators maintain the physiological capacity to feed at daily rates that are 2–3 times higher than what they achieve on average? Our numerical simulation demonstrates that such low ratios of assimilative load: capacity become energetically profitable when the distribution of daily foraging opportunities is highly heterogeneous (that is, right-skewed; Fig. 1, Supplementary Fig. 1). This suggests that episodes of gorging and fasting are common in fishes, and occur not only in ambush predators that pursue large prey²¹, but also in predators that feed on insects and zooplankton. These results question common assumptions regarding the variance in foraging opportunities experienced by predators in the wild.

Foraging models frequently simulate variation in a predator’s feeding opportunities by drawing prey encounters from the Poisson

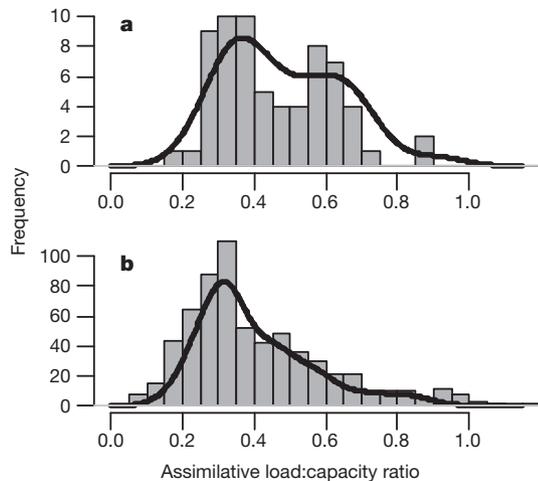


Figure 2 | Histograms showing bioenergetics estimates of integrated consumption rates in wild piscine predators, expressed as the assimilative load:capacity ratio. This ratio is defined as average daily consumption rate divided by the physiological maximum. **a**, Estimates grouped by unique combinations of species and publication ($n = 66$). **b**, All estimates ($n = 639$). Lines show a non-parametric density estimate of each distribution (see Methods).

distribution^{21,22}, which exhibits equal mean and variance (λ). Under most configurations of the Poisson (for example, if $\lambda \geq 3$), values greater than twice the mean have extremely low probabilities (0–3% of occurrences). Thus, foraging models frequently simulate a world in which predators would almost never take advantage of the excess assimilative capacity that we have shown in fishes (that is, median capacity is 2.3 times expected load). This suggests that the feeding opportunities of piscine predators, and perhaps many others, are more heterogeneous than has been appreciated in ecology.

In the past decade, three meta-analyses have concluded that lizards²³, fish²⁴, birds and mammals²⁵ rarely exhibit negative energy budgets at daily timescales, based on observations that predators rarely have completely empty stomachs^{23,24}, or that their integrated rates of energy gain exceed losses at seasonal to annual timescales²⁵. In our analysis, we found that piscine predators probably experience foraging opportunities that are distributed extremely patchily in time, such that the median population would actually spend 18–53% of days feeding at levels that are lower than a typical maintenance ration ($\sim 20\%$ of C_{\max} ; ref. 17). This suggests that fishes routinely run negative energy budgets and warns that prior syntheses of empirical data may have underestimated variability in the daily energy balance of not only fishes, but other taxa as well. Future work should consider how patterns of capacity through the food–fuel pathway are associated with different strategies of energy regulation. For example, many small birds and mammals hoard food during resource pulses or employ torpor to avoid energy deficits²⁶. These mechanisms may stabilize consumption rates and energy budgets enough to make maintaining excess capacity for assimilating food unnecessary, but would probably require increased capacity for handling food.

We have assumed that the assimilative capacity observed in fishes has evolved to optimize energy budgets under trade-offs between the capacity and metabolic cost of the gut. There is widespread evidence that the energetic profitability of the gut has strong fitness consequences^{1,20} and that its morphology and function evolve in response to energetic demands²⁷. Further, the fishes in our analyses exhibit indeterminate somatic growth that is indeed limited by energy acquisition²⁸. Therefore it is reasonable to use an energy maximization model to interpret the function of physiological capacity. The temporal pattern of foraging opportunities may vary among generations such that the optimal level of digestive capacity is not static in time. Our general conclusions are robust to such evolutionary disequilibrium because we found high levels

of excess digestive capacity across numerous taxa inhabiting diverse environments. The most parsimonious explanation of these findings is that piscine predators have evolved excess assimilative capacity to profit in a world where binging and fasting are regular occurrences.

Phenotypic flexibility can improve performance if energy budgets vary predictably¹. For example, female mammals increase digestive capacity during pregnancy, and birds adjust digestive capacity during migration as they alternate between fuelling and flight¹. Although seasonal changes in food abundance may be predictable, pulses of food are frequently both unpredictable and ephemeral²⁹, causing the performance of consumers to be measured by the guts they possess in the moment and not the ones they can construct days or weeks later (except certain sit-and-wait predators that are capable of rapid intestinal regulation²⁰). Similarly to the fishes in our analysis, birds may maintain excess capacity for consumption despite their ability to modify gut size over relatively short timescales³⁰. Flexibility in gut size has been suggested³⁰ to facilitate adaptive responses to long-term but not short-term variation in resource abundance. Our meta-analysis and model strongly suggest that predator–prey encounters are patchier than most ecologists assume, that fish run negative energy budgets more frequently than assumed, and that eco-physiology should consider the combined roles of excess capacity and phenotypic flexibility when considering how organisms cope with a world far more heterogeneous than the laboratory or treadmill. The insights derived from our analysis have important implications for models of predator–prey dynamics, community structure and the stability of food webs, which can be sensitive to heterogeneity in predator–prey interactions⁶.

METHODS SUMMARY

To characterize the assimilative load:capacity ratios of piscine predators, we compiled data from bioenergetics analyses that express integrated consumption rates relative to the physiological maximum. These models^{16,17} use field measurements of growth at monthly to annual timescales to reconstruct consumption rates, based on the energy budget:

$$G = C - (R + W + SDA) \quad (7)$$

where G is growth, C is food consumption, R is active metabolism, W is waste (faeces and urine) and SDA is specific dynamic action (the cost of digestion). Empirically derived, species-specific functions model the effects of water temperature and body mass on respiration and the maximum daily consumption rate (C_{\max}). Additional functions model waste and SDA as taxes on consumption. To incorporate thermal and allometric constraints on C , the parameter p scales the actual consumption rate relative to the maximum consumption rate according to $p = C/C_{\max}$. Thus, equation (7) becomes:

$$G = pC_{\max} - (R + W + SDA) \quad (8)$$

On the basis of observed growth, diet composition, predator and prey energy densities, and the temperature regime experienced by a fish for the time interval over which growth is estimated, the model solves for the value of p that produces the value of G observed in the field. Because C_{\max} is determined by rates of food-processing¹⁸, p represents the load:capacity ratio for assimilation—the process that includes both the break down of food macromolecules and the transportation of nutrients across the gut wall.

For our meta-analysis of p estimates, we searched Web of Science and Google Scholar for all publications ($n = 345$) citing the bioenergetics framework outlined above^{16,17}. We compiled data from all publications (42 journal articles and 4 theses) that studied predators *in situ* and reported the parameter p . The metadata and source publications are provided in Supplementary Table 1.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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METHODS

The fish bioenergetics model (FBEM). This model^{16,17} is used to estimate assimilative load:capacity ratios. It uses an energy balance approach to bioenergetics that provides an adaptable modelling framework, which has been applied to a wide variety of species and ecosystems. The model balances an energy budget where inputs must equal outputs, specifically:

$$C = G + R + W + SDA \quad (9)$$

Here C is food consumption, G is growth, R is active metabolism, W is waste (faeces and urine), and SDA is specific dynamic action (the cost of digestion). The FBEM provides functions that model the effects of water temperature and body mass on respiration and the maximum daily consumption rate (C_{\max}). These functions are parameterized for individual species through controlled laboratory experiments. To formulate the respiration functions, oxygen consumption is measured in experiments that manipulate body size and water temperature. In addition, an activity multiplier is calculated to relate basal and active metabolism. To formulate the C_{\max} functions, daily consumption rates are measured in *ad libitum* feeding experiments that manipulate temperature and body size. Additional functions model waste and SDA as taxes on consumption. A full description of these functions is available in the Bioenergetics 3.0 software manual¹⁷.

Researchers typically use the FBEM to estimate consumption rates based on the observed growth rates of fishes in the field. This is done by rearranging the original terms in the energy budget so that growth represents surplus energy after gains from consumption are paid to energetic costs:

$$G = C - (R + W + SDA) \quad (10)$$

Growth is measured directly over some relatively long time interval (for example, monthly to annual growth increments) and the model is used to estimate the consumption rate C required to satisfy equation (10) to produce the observed growth increment. To incorporate thermal and allometric constraints on C , the parameter p scales the actual consumption rate relative to the maximum consumption rate according to $p = C/C_{\max}$. Thus, equation (10) becomes:

$$G = pC_{\max} - (R + W + SDA) \quad (11)$$

On the basis of observed growth, diet composition, predator and prey energy densities, and the temperature regime experienced by a fish for the time interval over which growth is estimated, the model solves for the value of p that produces the value of G observed in the field. The model is implemented at a daily time step and linearly interpolates between observations of temperature, diet composition and energy density. Because growth of fishes is indeterminate, the value of p is a sensitive but informative integrated parameter that reflects the realized consumption rate relative to the physiological maximum rate that an individual fish is capable of, based on its metabolic parameters, its body size, its energy density and the energy density of its prey, and water temperature. Because C_{\max} is determined by rates of food-processing¹⁸, p represents the load:capacity ratio for assimilation—the process that includes both the break-down of food macromolecules and the transportation of nutrients across the gut wall. Consumption estimates from the FBEM have been independently corroborated by intensive field-based methods^{31,32}.

For our meta-analysis of p estimates, we searched Web of Science and Google Scholar for all publications ($n = 345$) citing the bioenergetics framework outlined above^{16,17}. We compiled data from all publications that studied predators *in situ* and reported the parameter p (42 journal articles and 4 theses). The meta-data and source publications are provided in Supplementary Table 1. To characterize distributions of p estimates (Fig. 2), we fitted kernel density estimates to the data in R^{33} . We used a Gaussian smoothing kernel and selected the bandwidth following standard methods³⁴.

Modelling trade-offs associated with digestive capacity. Here we give details of our numerical model in which we simulate these trade-offs. We used the gamma distribution to simulate variation in daily foraging opportunity because it can generate a diversity of biologically realistic shapes, ranging from narrow and

Gaussian to extremely right-skewed, representing an environment where prey encounters are extremely patchy. The gamma distribution has two parameters, namely k and θ , which relate to the mean and variance of the distribution as follows:

$$\begin{aligned} \bar{x} &= k\theta \\ \sigma^2 &= k\theta^2 \end{aligned} \quad (12)$$

Rearranging equation (12) yields:

$$\begin{aligned} k &= \bar{x}^2/\sigma^2 \\ \theta &= \sigma^2/\bar{x} \end{aligned} \quad (13)$$

In order to examine the effect of variability in foraging opportunity on the energetic profitability of excess assimilative capacity, we varied θ and k to generate gamma distributions with an equal mean, but different levels of variation. This simulates ecosystems that have an equal amount of prey available to predators, but different levels of variation in the temporal patterning of daily predator–prey encounters.

To provide biologically interpretable results, we used the coefficient of variation (c.v., defined as (s.d./mean) \times 100) to describe variation in the gamma distribution. Unlike other metrics of variation (for example, the variance to mean ratio) the relationship between the c.v. and the shape of the gamma distribution scales isometrically with the mean of the distribution (for example, if the c.v. is held constant, changing the mean does not affect the skew of the distribution). Therefore, we could explore all ecologically relevant shapes of the gamma distribution by changing the c.v. of the distribution (range, 0.1–500%) while keeping the mean fixed at an arbitrary value. Supplementary Fig. 1 shows a subset of the gamma distributions that were generated in our simulations to illustrate the diversity of shapes that we considered.

The relationship between the maintenance cost and assimilative capacity of the gut (R_{gut} and C_{\max}) is poorly documented. For the sake of parsimony, and because empirical data suggest that assimilative capacity in fish is related to the surface area of the gut³⁵, we modelled a linear relationship between C_{\max} and R_{gut} , such that a proportional change in C_{\max} produces the same proportional change in R_{gut} (for example, doubling C_{\max} would double R_{gut}). The relationship between C_{\max} and total metabolic cost, M , depends on the ratios of $R_{\text{gut}}:M$ and $M:C_{\max}$. Under the assumed linear relationship, the slope (r) of M as a function of C_{\max} is:

$$r = R_{\text{gut}}/R_{\text{tot}} \times R_{\text{tot}}/C_{\max} \quad (14)$$

We assumed that one-third of total daily respiration goes to maintaining digestive capacity, as this is the approximate proportion of total cardiac output delivered to an empty gut³⁶. The empirically derived functions in the FBEM¹⁷ suggest energetic losses due to respiration typically represent one-third to one-ninth of C_{\max} in fishes. Given these estimations, r ranges from 0.04 to 0.11. Because the y -intercept of a linear cost function (here, the cost of metabolism not associated with the gut) does not affect the optimal value for profit maximization, we modelled total metabolic cost, M , as a constant fraction, r , of C_{\max} , and included three cost scenarios: low ($r = 4\%$), medium ($r = 8\%$) and high ($r = 12\%$). We did not consider specific dynamic action or excretion in our cost analysis, because we assumed these were taxes on consumption that do not represent physiological maintenance.

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