

RATES OF FOOD CONSUMPTION IN FREE-LIVING MAGELLANIC PENGUINS *SPHENISCUS MAGELLANICUS*

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SUMMARY

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We measured feeding rates in an abundant colonial seabird, the Magellanic Penguin *Spheniscus magellanicus*, and found them to be highly variable and up to three times those predicted by conventional estimates. Captive birds that eat more have higher gastrointestinal throughput rates and, thus, likely lower digestive efficiencies. Density-dependent rates of ingestion coupled with decreasing digestive efficiency means that penguins will tend to have a greater impact on prey stocks when fish densities are high. That relationship may contribute to the stability of predator–prey balance in marine systems and should be considered in fishing policies as well as in estimates of top predator consumption rates.

Key words: Magellanic Penguin, *Spheniscus magellanicus*, feeding habits, consumption, digestion

INTRODUCTION

Effective fishing policies must allow for a sustainable yield while maintaining ecosystem integrity (Worm & Myers 2004). Key consumption variables used in models are typically determined in laboratory studies, with results scaled up to the situation in the wild (Boyd 2002). To examine the validity of this approach, we determined feeding rates of wild Magellanic Penguins *Spheniscus magellanicus*, an abundant seabird exploiting the high productivity of the Patagonian Shelf. Feeding rates were then assessed in the light of data derived from penguins fed in captivity to determine throughput rates. Here, we combine measurements on the digestive physiology of seabirds with our data on the feeding behaviour of wild penguins and discuss the implications that our findings have with respect to the effect of marine predators on fisheries and the putative stability of predator–prey relationships.

METHODS

Studies of wild birds

Seven Magellanic Penguins brooding small chicks at Cabo Virgenes, Santa Cruz, Argentina, were equipped with beak-angle sensors based on a magnet/Hall sensor system (Wilson *et al.* 2002) to record beak angle at 10 Hz and depth at 1 Hz. Those birds, and 10 others equipped with time–depth recorders only, were surveyed until they had completed one foraging trip. Five of the birds equipped with beak-angle sensors underwent stomach lavage (Wilson 1984) within 10 minutes of returning to the nest. Prey were sorted on site, and lengths and masses taken directly.

Data on diving and feeding behaviour were analysed using Multitrace-Beak (Jensen Software Systems, Laboe, Germany),

which defines the primary parameters describing each dive (e.g. depths, durations) and all prey ingested (Wilson *et al.* 2002). Definitive prey capture, rather than unsuccessful snaps at prey, could be ascertained by a right-hand skewed pattern in beak angle over time, with several minor peaks corresponding to gulping movements (Wilson *et al.* 2002). The mass of the prey ingested is linearly related to the integration of the area under the beak-angle-over-time curve (Wilson *et al.* 2002). The determined mode in the frequency distribution of the integrals of prey ingested was set to tally with the determined modal mass of prey ingested by each of the equipped birds to derive a relationship between integral units and grams. Because the penguins were all feeding on the same prey, the inter-individual variance was extremely low; mean modal values for prey masses from all birds were therefore used to derive a standard value for two individuals whose stomach samples could not be obtained. Those values were then used to calculate the rate of prey acquisition in the two cases.

Captive studies

Eleven King Penguins *Aptenodytes patagonicus* were fed varying amounts of food, and the corresponding faeces were collected to examine the relationship between meal mass and faecal mass and the rate of faeces production as a function of meal mass. Birds ingested single meals of Pilchard *Sardinops ocellatus* (wet mass: 1000 g, 950 g, 670 g or 350 g; n = 3 for each category, except 1000 g, for which n = 2).

To confirm the positive relationship between intake and gastrointestinal passage rates, two Humboldt Penguins *Spheniscus humboldti* were fed varying amounts of Sprat *Sprattus sprattus* (50–280 g/meal) over 54 daily trials, and defecation rate noted by watching the birds continuously and collecting and weighing

faeces immediately upon production. Cumulative masses of faeces produced were plotted against time to derive linear regressions of rates of faeces produced according to original meal mass. These derived rates were then plotted against original meal mass.

RESULTS

Activity patterns

Wild Magellanic Penguins spent a mean of 13.8 hours at sea (standard deviation: 7.1; $n = 18$). Time underwater was related to the time spent at sea by $T_{\text{under}} = 0.58 T_{\text{at sea}}$ ($R^2 = 0.67$, $F = 31.5$, $P < 0.001$), so that penguins spent a mean of 8.0 hours underwater. Birds spent between 0.1 hour and 4.8 hours travelling between the colony and the foraging area, exemplified by short, shallow (<2 m) dives. During active foraging periods, prey—which was composed, more than 95% by number, of Sprat *Sprattus fuegensis*—could be ingested at rates of up to 20 individuals per dive. Overall, prey consumption rates were roughly constant (Fig. 1), with values that varied according to the individual (between 1.86 g and 4.87 g per minute at sea).

Faeces mass

Total faeces mass increased exponentially as a function of meal mass among 11 King Penguins (Fig. 2), and the rate of faeces

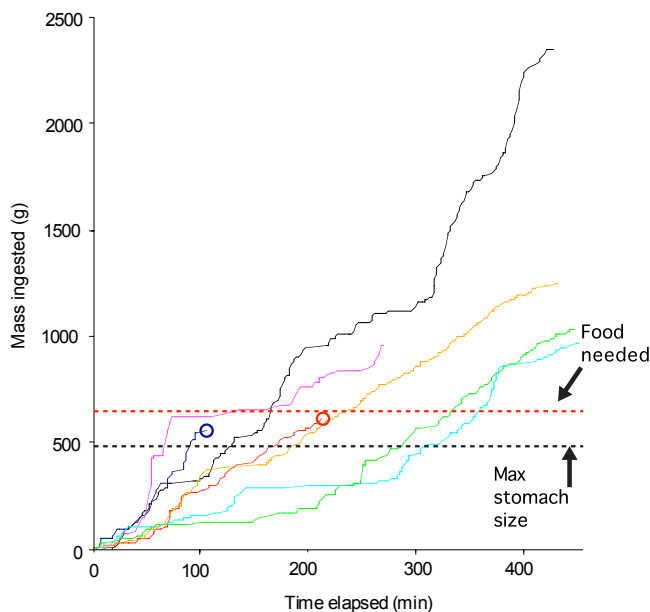


Fig. 1. Cumulative mass (in grams) ingested by free-living Magellanic Penguins *Spheniscus magellanicus* foraging over the Patagonian Shelf as a function of time at sea. Note that the zero point for the graph corresponds with the moment that the birds first consume more than one prey per dive, so that time at sea does not include travel time between the colony and the foraging location. (Return travel—characterised by short, shallow dives with a parabolic dive profile—to the colony is also omitted.) Lines that terminate in circles show traces derived from individuals in which the ingestion-measuring system fell off prematurely. The black, dashed horizontal line shows the approximate maximum mass of food that can be contained in a Magellanic Penguin stomach while provisioning small chicks and demonstrates the rapidity with which digestion must take place. The red dashed line shows the putative amount consumed by a Magellanic Penguin foraging for two small chicks according to conventional calculations (see text).

production increased significantly with meal mass in two individual Humboldt Penguins ($P < 0.01$).

Estimating energy intake of Magellanic Penguins

Diving Magellanic Penguins expend about 50.7 J/s during swimming and 23.6 J/s during resting at the sea surface between dives (Wilson *et al.* 2004a). Thus, birds spending 58% of their time at sea underwater will expend a mean of 39.3 J/s at sea. If, for every 13.8 hours at sea, a Magellanic Penguin spends a further 13.8 hours resting on land brooding chicks, where energy expenditure is 18.3 J/s [scaled up for a four-kilogram *Spheniscus* penguin (Nagy *et al.* 1984)] and spends a further 30 minutes commuting between the nest and the sea, where metabolic rate is 65.6 J/s (Wilson *et al.* 2001), the overall energy expenditure for a complete cycle is *c.* 2.12 MJ. If the energy content of the prey is assumed to be 5.93 kJ/g wet weight and penguin assimilation efficiency is taken to be 77% (see references in Wilson *et al.* 2004a), a Magellanic Penguin will have to ingest 464 g of prey to cover its own energetic needs per cycle. In addition, a further *c.* 200 g would be needed for a small, two-chick brood (Heath & Randall 1985), for a total of about 664 g prey ingested.

DISCUSSION

Our data show that, although Magellanic Penguins sometimes ingest as little as 664 g of prey, at other times, the birds exceed that quantity by a factor of more than 3.5 to ingest up to 60% of their body mass over eight hours. These findings point to large differences between captive and wild animals, because only in rare instances have captive marine endotherms demonstrated a capacity to ingest up to 28.4% of body mass over a few hours (Kvist & Lindstrom 2003, Rosen & Trites 2004). Such a high ingestion rate necessitates a corresponding rise in processing rate, and the rise in processing rate should be reflected in the defecation rate. In fact, defecation rates measured in wild Magellanic Penguins rise by a factor of about 8 almost immediately the birds start feeding (Wilson *et al.* 2004b).

Digestive efficiency is positively related to gut retention time, both between different species of seabirds (Hilton *et al.* 2000), and within individual bird species fed different food types (Afik & Karasov 1995). Changes in extraction efficiencies of selected

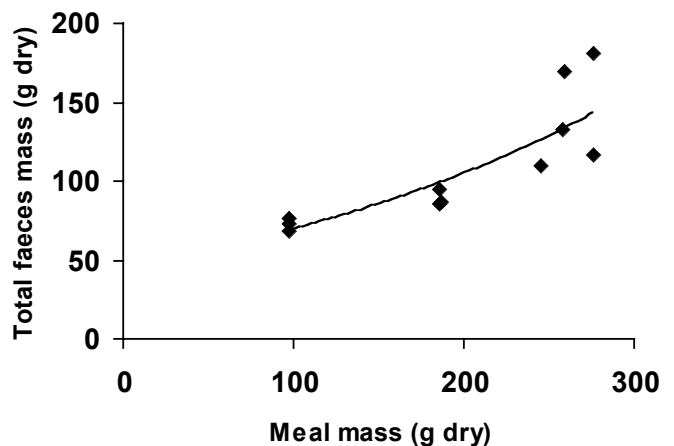


Fig. 2. The relationship between total faeces mass (y , in dry grams) and meal mass (x , in dry grams) for 11 King Penguins *Aptenodytes patagonicus* ($y = 46.72e^{0.0041x}$, $R^2 = 0.79$, $P < 0.001$).

nutrients, particularly lipids, occur within hours and are attributed to reduced contact time between enzymes and digesta, and reduced time for transport of substances across the luminal membranes of mucosal cells (Afik & Karasov 1995). Lipids, which constitute a significant and highly variable fraction of marine predators' energy intake, are passively absorbed by diffusion. Their absorption is thus more likely to be influenced by short retention times than is the absorption of actively transported nutrients such as amino acids. The decreased absorption efficiency associated with rapid clearance of food from the gut means that net energy gain with increasing ingestion rates will be nonlinear. The resulting implications are that birds should produce a greater mass of faeces per unit food ingested at higher ingestion rates and should show a greater rate of faeces production. Those suppositions are confirmed by our data for captive King and Humboldt Penguins.

If potential overeating in predators proves to be a general phenomenon, the implications for predator pressure on marine prey stocks are profound, because food consumption by predators will track short-term fluctuations in prey abundance and yet have little short-term effect on the welfare of predator populations. It amounts to density-dependent prey regulation balanced by predator digestive physiology, operating on a time scale of days rather than the generations discussed in some classic studies (Matsuda & Abrams 2004). It could also explain why, historically, seabird colonies thrived under conditions of what must have been variable prey abundance (Jackson *et al.* 2001), although presumably upper limits on seabird populations could still be regulated during particularly prey-scarce years (Furness & Birkhead 1984, Jahncke *et al.* 2004). In contrast, human-determined fishing practises that lack quotas regulated day-to-day according to prey abundance must clearly be more detrimental to fish stocks, which may help to explain observed overfishing (Myers & Worm 2003). In the interests of general ecosystem management (Velarde *et al.* 2004), we suggest that a high priority must now be assigned to measuring ingestion rates in a variety of free-living marine animals so as to go beyond the conventional models based solely on performance in captive individuals. Studies of this kind should allow us to identify how marine predators deal with variation in prey abundance, both in terms of behaviour and digestive physiology, and should ultimately lead to better ecosystem understanding.

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