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Review article

Nutrition in captive penguins: What is known and what can be improved?

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Abstract

Penguins are seabirds of the southern hemisphere, occupying a diverse range of environments, such as tropical, temperate, sub-Antarctic and high-Antarctic regions. There are 18 recognised species, two-thirds of which are considered threatened according to the International Union for Conservation of Nature (IUCN). This ranks penguins as some of the most endangered seabirds. In human care, a combination of needs extrapolated from reports on free-ranging penguins, domestic poultry, carnivorous mammals and other fish-eating vertebrates are used as references for diet formulation. There is heavy dependence on ingestion rates when discussing feeding requirements. Most penguins in zoos and aquariums have the opportunity to eat to the point of satiety, assuming that the proper environmental conditions will oscillate and regulate their normal cycles of activity and energy requirements. However, energy-dense fish species commonly used are likely to limit food intake, leading animals to cease consumption before ingesting the minimum amount of essential nutrients. Not all institutions maintain environmental seasonality in terms of photoperiod and temperature. The lack of these features might compromise the penguins' ability to auto-regulate consumption or keep adequate rhythms of moulting and reproduction. Even when environmental seasonality is provided, it is not uncommon to observe food intakes above what is required in captivity. To avoid overfeeding effects and guarantee healthy conditions in managed populations, diet formulation should consider energy requirements and seasonal physiological states, as well as adequate feeding rates and body condition scoring or weighing. This review aims to help optimise feeding protocols for captive penguins, differentiating energy requirements by species and developmental stages.

Knowledge gaps in penguin nutrition

Penguins are southern hemisphere seabirds, ranging from tropical, temperate, sub-Antarctic and high-Antarctic regions. They comprise 18 species that collectively rank among the most endangered seabirds, with two-thirds threatened according to the IUCN (Crawford et al. 2017). Penguins are highly adapted marine birds, presenting solid bones and a fusiform body with flippers (Smith et al. 2022). Species differ in size, feather ornaments and foraging habits, with diets ranging from fish to crustaceans and cephalopods (Henry 2020). Diets vary based on habitat, seasonal prey availability, standard distance travelled from nest sites and reproductive demands (Cavallo et al. 2020; Jafari et al. 2021; Proud et al. 2021). In the wild, penguins spend most of their time at sea where food is abundant, but must come on land for reproduction and moult, leading to fasting periods (Ward and Henry 2022).

Regarding natural food items, little is known about the nutritional value of Notothenioid fish species commonly consumed by wild Antarctic penguins (Tabassum et al. 2022). Yet, Antarctic krill *Euphausia superba*, the predominant prey for at least three penguin species, has shown marked variation in nutritional content, depending on the season, sex and life stage of the krill (Crissey et al. 2001; Plum et al. 2023; Polito et al. 2019; Watanabe et al. 2020). Most penguin species seem to adapt well to a fish diet in captivity, as long as adequate feeding regimes and supplementation are provided (AZA 2014; Crissey et al. 2001). A combination of needs extrapolated from domestic poultry, carnivorous mammals and other fish-eating vertebrates, besides partial knowledge of diets in natural habitats, is usually used as a reference for penguin diet formulation in zoos (AZA 2014; Crissey et al. 2001).

The digestive system of penguins is relatively simple and can be related to the anatomy of other carnivorous birds.

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They have a long, expandable and muscular oesophagus, which allows the consumption of large prey, and have no crop (Kline et al. 2020; Olsen et al. 2002). The lack of a crop indicates that the oesophagus has no storage function in these birds (Olsen et al. 2002). The stomach can be divided into two different chambers: the proventriculus (the glandular stomach) and the gizzard (Cho et al. 1998; Olsen et al. 2002). Besides the secretion of gastric juice, the anterior stomach also plays a role in storing food for chicks, including acid regulation mechanisms to avoid the complete digestion of food items meant for chicks (Olsen et al. 2002). Although not as mechanically active as observed in granivorous birds, the gizzard is often reported to contain small stones and grit in a few species of penguin (Beaune et al. 2009; Hocken 2005; Olsen and Mathiesen 1996). It is suggested that the stones might help break prey items, enhancing digestive processes and/or help control buoyancy (Taylor 1993; Wings 2007). While there is little data on the cecum in penguins, it is present, but small and vestigial (Olsen et al. 2002).

The anatomy and physiology of the gastrointestinal tract of penguin species are well described, but the distinctive environments of different species might influence its functionality. Small intestine length may differ up to threefold in similar-sized species such as Adelie and Magellanic penguins (Table 1). In seabirds, the mean retention time of digesta is significantly correlated with intestinal length rather than with body mass (Jackson 1992). Based on this information, a relatively short intestinal passage time is predicted in the Adelie penguin compared to other penguin species within the same size category. Although considerations of retention time are not used in practical aspects of diet formulation, it does imply a change in feeding rate and frequency as the difference in intestinal length/retention rate might be an evolutionary reflection of time spent foraging and number of foraging trips of that particular species in the wild (Hilton et al. 2000). With a shorter retention time, the need for multiple meals a day is far more relevant for Adelie than for other small penguin species. Taking into account these data would help define the ideal feeding regime—in terms of number of meals per day—which is often based only on the size of animals (AZA 2014).

There is heavy dependence on ingestion rates (kilograms of food per kilogram of body weight, expressed as a percentage) when discussing feeding requirements for captive penguins (AZA 2014; Crissey et al. 2001). In this scenario, the penguin manual developed by AZA (2014) suggests that small penguin species should be given the equivalent of 10 to 14% of their body weight in food, on a daily basis, and for bigger penguins, 2 to 3% (as fed weight basis). If those values are taken as a rule, available dietary energy could vary drastically depending on the fish species comprising the diet. Considering a small penguin of about 5 kg, an appropriate daily diet would range from 0.5 to 0.7 kg of fish (AZA 2014). However, fish species differ in energy content. If this animal is fed *Anchoviella lepidentostole*, its daily energy intake would range from 525 to 735 kcal provided by 0.5 to 0.7 kg of fish as fed weight basis (Giamas et al. 1985). In contrast, adopting a diet based on *Cynoscion steindachneri* would provide only 348 to 488 kcal in 0.5 to 0.7 kg (Oliveira 2003). Thus, it is recommended that feeding programmes are based on energy requirements, rather than intake alone. Proximal composition might vary within the same fish species according to season and sex (El Oudiani et al. 2019) or storage temperature (Romotowska et al. 2016). Mean values should be taken into account to choose appropriate fish (lean or fat species) to supply the required energy intake for each season and physiological state. Offering items on a seasonal basis—according to their catch season—is a promising option, as relatively fresh fish would be fed and proximal composition would fluctuate along the natural cycle (Crissey et al. 2001). Ideally, the company selling the fish to the zoo should provide a proximate nutrient composition for each batch—a standard practice for some companies. In theory, buying fish from such a company would be the best approach, as it would facilitate energy calculations based on nutrient composition and allocation of the amount of fish on an energy basis. However, if no such company is available, then zoos have to rely on other sources to estimate the energy content of fish, such as literature reviews or laboratory tests.

Although a variety of fish species could be used, mackerel *Scomber scombrus,* herring *Clupea pallasii* and capelin *Mallotus villosus* are often chosen for captive penguins and other marine

Table 1. Variation in the length of the small intestine for different penguin species

Species	BM (Kg)	Length of small intestine (cm)	Length of small intestine/BL
Little blue *Eudyptula minor*	1.1	148	3.7
Rockhopper *Eudyptes chrysocome*	2.5	488	8.9
African *Spheniscus demersus*	3.1	559	10.4
Macaroni *Eudyptes chrysolophus*	3.9	633	9.0
Magellanic *Spheniscus magellanicus*	4.5	873	12.5
Adélie *Pygoscelis adeliae*	4.9	297	5.2
King *Aptenodytes patagonicus*	13.2	686	7.0
Emperor *Aptenodytes forsteri*	27.6	618	5.3

Adapted from Olsen et al. 2002. BM = “body mass” of animals observed in the study; BL = “body length”.

animals (Bernard and Allen 2002; Bos et al. 2018; Crissey et al. 2001; Fernandez et al. 2021). Mazzaro et al. (2016) consider these species to represent food of high, moderate and low energy density, respectively. However, when compared to southern Atlantic fish species, the energy content of all these species is relatively high. Therefore, special attention should be given if these species are used, because high energy levels are likely to limit food intake, given that animals may stop consuming when meeting their energy demands (Ardente and Hill 2015; Classen 2017; Wu 2017). In this scenario, it is not uncommon for high-energy diets to be associated with malnourishment, if not well balanced (Cederholm et al. 2017), because individuals eating to satiety on an energy-dense diet might not ingest the minimum amount of essential nutrients. This effect is especially important when dealing with chicks or animals in rehabilitation programmes.

Values from wild populations should be considered with caution. Besides known periods of fasting and heavy exercise, the energy cost of foraging could reach up to 120 kcal kg^{-1} per trip for Adelie penguins, for example (Watanabe et al. 2020). Thus, when translating values of intake or energy demands based on wild populations, values should always be considered high, as in captivity little or no effort is needed for foraging. Furthermore, data on preferred food items vary hugely among species (Colominas-Ciuró et al. 2021). For example gentoo penguins usually exploit more cephalopods and fish in coastal and benthic habitats, while chinstraps forage more on krill and fish in pelagic waters (Carpenter-Kling et al. 2019; Colominas-Ciuró et al. 2021). Species that depend on pelagic prey are expected to have higher intakes in terms of lipid and energy per unit of prey mass, while those that forage on cephalopods are likely to be adapted to diets with lower lipid and energy content per unit of prey.

Regarding husbandry practices, controlled fasting periods could be positive for zoo populations, because caloric restrictions could induce a reduction in mitochondrial oxygen consumption and a decreased production of mitochondrial oxidative species (Gredilla et al. 2001). Considering the high metabolic cost of reproduction and moulting, fasting may help alleviate and protect penguins from excess oxidant generation, limiting oxidative stress (Alonso-Alvarez et al. 2004; Colominas-Ciuró et al. 2017; Ensminger et al. 2021). In other aquatic avian species, oxidative damage levels decreased by 95% during fasting (Geiger et al. 2012). Non-breeding birds at colonies display qualitatively similar seasonal mass change patterns to breeders, suggesting that breeding itself is not the main reason for fasting and body mass fluctuations (Emmerson et al. 2019). The specific mechanism through which fasting reduces oxidative stress in penguins is still unknown (Ensminger et al. 2021).

Although information on penguin nutrition is lacking, there are several studies that could help estimate energy intake. Thus, this review aims to help optimise feeding protocols for captive penguins, differentiating requirements among species and developmental stages. This information may help institutions maintain these species for conservation or rehabilitation purposes.

Energy requirements

Most penguins kept under human care have the opportunity to eat to the point of satiety, assuming that environmental conditions will oscillate and regulate their normal cycles of activity (AZA 2014). However, energy-dense fish species commonly adopted in captivity might result in overfeeding, in terms of energy demands, and are likely to limit the intake of certain nutrients. Thus, animals fed ad libitum might voluntarily cease consumption before ingesting the minimum amount of essential nutrients and still be overweight. Not all institutions maintain environmental seasonality in terms of photoperiod and temperature. In tropical zone zoos, for example, it is common for penguins to be kept indoors because in those regions animals would be exposed to high temperatures all year round and be particularly susceptible to avian malaria vectors (Grilo et al. 2016). Avian malaria is considered one of the most important causes of morbidity and mortality in captive Spheniscidae penguins (Ings and Denk 2022). Thus, the most straightforward strategy to prevent malarial infection is to maintain penguins in mosquito-free indoor facilities year-round (Graczyk et al. 1994).

The lack of seasonality in indoor enclosures might compromise the animals' ability to auto-regulate consumption or to keep adequate rhythms of moulting and reproduction (Golembeski et al. 2020). Besides seasonally driven hormonal changes, seasonality—in terms of food availability, at least—might be beneficial when integrated into management strategies (Golembeski et al. 2020; Mafunda et al. 2021). However, even when environmental seasonality is provided, feeding intake should be controlled to avoid consumption above what is required. In order to avoid overfeeding effects and guarantee healthy conditions in captive populations, diet formulation should consider energy requirements for the species and its physiological state, as well as adequate feeding rates. If aiming to keep regular cycles of change in body weight, body condition score methodologies and regular weighing might help define appropriate levels of energy content to be offered (Clements and Sanchez 2015).

When managing overweight specimens, knowing the energy content of fish species allows staff to successfully promote weight loss, without having to actually reduce feeding rates. As exemplified before, by shifting diets from *A. lepidentostole* to *C. steindachneri*, it is possible to reduce daily energy intake by up to 1.5 times, without altering the amount of fish offered as fed weight basis. Maintaining the quantity of food offered but correcting energy intake is a good strategy to start regulating diets. It allows maintenance of satiety—with regards to a full stomach—while decreasing energy intake. In terms of husbandry and welfare, this practice avoids aggressive behaviours towards others based on hunger (Catitti et al. 2022). However, the proximate composition of seafood varies by season, sex and age (Ahmed et al. 2022). Therefore, if the actual proximate composition is not known, literature values should be used as a guide rather than taken as fixed rules.

Several studies suggest energy requirements for different penguin species in the wild based on rates of oxygen consumption during respirometry, including energy expenditure during moult, breeding season and for growing chicks (Adams and Brown 1990). Moreno and Sanz (1996) have pointed out that metabolic rates could increase 4–4.7 times above the basal rate during breeding. During moult, an increase of up to 2.3 times the resting metabolic rate (RMR) is expected. Although there seem to be sex differences regarding oxidative damage during moult periods (Colominas-Ciuró et. 2019), no differences in energy expenditure were reported (Green et al. 2009; Groscolas et al. 2010). Overall, it is agreed that in wild populations, breeding is more stressful and challenging than moulting for most penguin species in terms of energy demand (Colominas-Ciuró et al. 2019; Palacios et al. 2018).

Considering the importance of accounting for energy requirements when formulating diets, the main literature regarding energy expenditure for penguin species was reviewed. Few or no data were found on metabolism for *Spheniscus magellanicus, S. mendiculus* and *Eudyptes schlegeli;* recent studies tend to extrapolate data from the most related species already described.

Evidently, larger species require more absolute energy per day than smaller species. However, energy requirements do not scale linearly with body mass, but (more or less) to metabolic body weight (kg$^{0.75}$). Therefore, per metabolic body weight, the energy requirements are relatively similar for birds at about 80 kcal kg$^{-0.75}$ day^{-1} (Kirkwood 1996). Care should be taken when interpreting

Table 2. Resting metabolic rate (RMR) determined from oxygen consumption measurements of resting, non-molting wild penguins

Species	Common name	Mean mass (kg)*	Mean resting metabolic rate (kcal.day^{-1})	Mean values per metabolic body weight (kcal.kg$^{-0.75}$.day^{-1})
Eudyptula minor minor	Little penguin	1	87	87
Eudyptes chrysocome	Rockhopper	2.5	168	84
Eudyptes pachyrhynchus	Fiordland penguin	2.6	143	70
Spheniscus demersus	African Penguim	2.88	127	58
Eudyptes chrysolophus	Macaroni penguin	3.8	227	83
Spheniscus humboldti	Humboldt penguin	3.87	196	71
Pygoscelis adeliae	Adélie penguin	4.2	308	105
Megadyptes antipodes	Yellow-eyed penguin	4.8	238	73
Pygoscelis papua	Gentoo penguim	6.3	384	97
Aptenodytes patagonicus	King penguin	12.3	555	84
Aptenodytes forsteri	Emperor penguin	25	1003	90

*Observed in the study. Adapted from Adams and Brown (1990).

the data in Table 2. Rather than considering them indicative of specific-species differences, they indicate that per metabolic body weight, the species are relatively similar; small differences may well be due to chance when the measurements were taken. Bigger species require less energy per kilogram of body weight compared to small species. In other words, the mass-specific (per kg) metabolic rate of small animals is higher than that of larger animals (Nagy 2001). Therefore, expressing energy requirements based on metabolic body weight (kg$^{0.75}$) is appropriate, as reflected in equations used to estimate energy requirements in animals (Kirkwood 1996). Adelie penguins stand out, presenting higher energetic demands when compared to every other penguin species evaluated. As stated before, the relatively short small intestine length in the Adelie penguin, together with its putatively higher metabolic demand, imply that the need for multiple meals a day might be particularly relevant for this species.

RMR values do not account for activities such as foraging and swimming. For estimating daily expenditures, it is suggested that those values be multiplied by 1.5 to 2 for periods ashore, outside moult and reproduction seasons (in general, Kirkwood 1996; for penguins, Green et al. 2009).

For moulting, energy expenditure increases from 1.07 to 2.27 times the RMR (Adams and Brown 1990), as demonstrated for a few species in Table 3. The energy used during moult is based on lipids previously stored (Enstipp et al. 2019). Thus, when planning nutrition protocols for captive penguins, increases in dietary energy content should be considered weeks, or even months, before moulting starts because animals will present low to no

Table 3. Estimates of energy expenditure during molt determined from rates of oxygen consumption in wild penguins

Species	Mean mass (kg)*	Mean energy expenditure during molt (Kcal.day^{-1})	Mean values per metabolic body weight (kcal.kg$^{0.75}$.day^{-1})	Increase in energy requirements (times RMR)
Little blue *Eudyptula minor*	1.4	143	111	1.27
Rockhopper *Eudyptes chrysocome*	2.95	252	112	1.33
Macaroni *Eudyptes chrysolophus*	4.81	363	112	1.34
Gentoo *Pygoscelis papua*	6.50	521	128	1.32
King *Aptenodytes patagonicus*	13.13	861	125	1.48

*Observed in the study. Adapted from Adams and Brown (1990). RMR resting metabolic rate

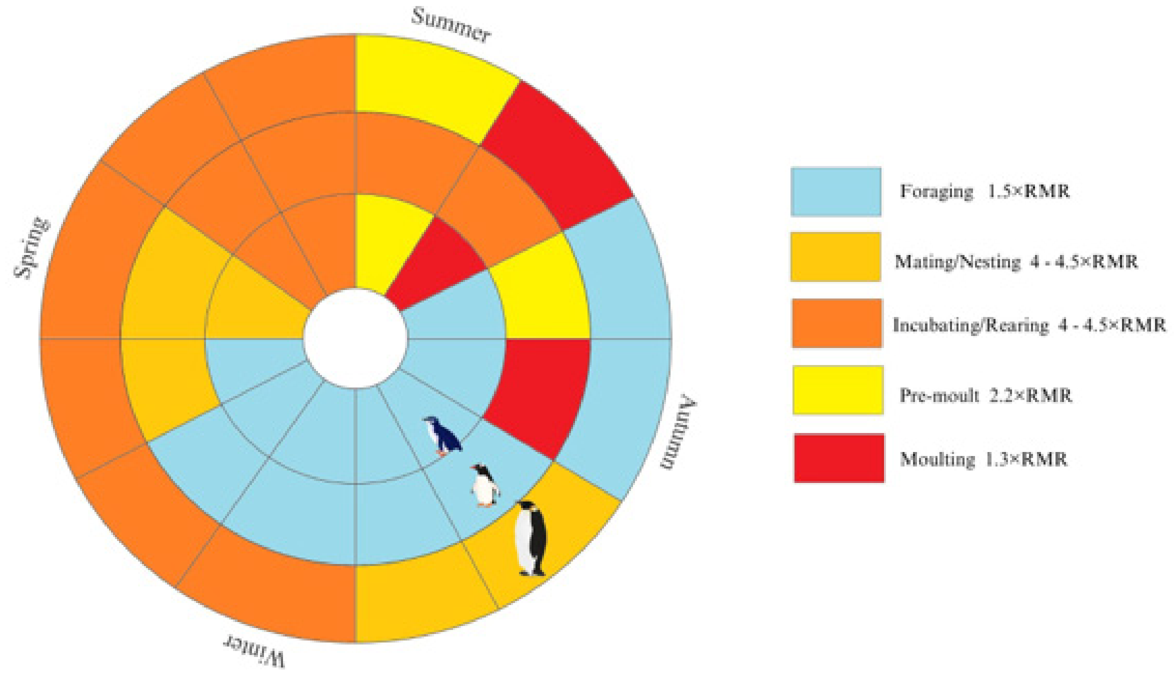

Figure 1. Adult penguin life cycles of three species of penguin with different size ranges in the wild: Emperor *Aptenodytes forsteri*, Gentoo *Pygoscelis papua*, and Little penguin *Eudyptula minor*, and the suggested adjustments in terms of energy intake. Adapted from Handley et al. (2021). * Pre-molting season are only considered in the captive environment for animals that do not engage in reproduction. Note that during molt, intake may well drop below the level indicated here.

appetite during moult season. Considering that the instinctive urge for food might impose feeding intakes above what is actually required, increases in daily rations should be controlled based on energy requirements. Those measures might help decrease bumblefoot incidence due to overweight, especially before the moulting season (Blair 2013).

Considering data on energy requirements for the different species, feeding protocols can be adjusted based, for example, on the seasonal physiology of wild penguins (Figure 1). For non-breeding individuals and in non-breeding seasons, mean energy demands would range from 1.5 to 2 times the RMR. During breeding seasons, animals that engage in reproductive behaviours should have energy intake adjusted to meet up to 4.5 times RMR during critical stages, such as parents feeding growing chicks. In managed care, for those animals that do not engage in reproductive behaviours, a 'pre-moult' season is included aiming to provide increased energy intake (up to 2.2 times the RMR) to create stores for the moulting season. During moulting, it is common for animals to decline food. If they do not, energy intake should be lowered to promote the usage of lipid and protein stored during the pre-moulting season. Considering that the main idea of this practice is to keep regular cycles of change in body weight, body condition score methodologies and regular weighing might help define appropriate levels of calorie restriction (Clements and Sanchez 2015).

Chicks

It is common for provision of chick diets to be based on analysis of gut contents of free-ranging specimens (Fernandez et al. 2019; Panasiuk et al. 2020). Recent data on chick-rearing have been made available by Henry (2020), who highlights that problems encountered when hand-rearing penguins often occur as a consequence of overheating or overfeeding. In agreement, Alden et al. (2021) have pointed out that rehabilitated chicks fledged at a higher body mass showed lower post-fledging survival when compared to underweight wild-fledging conspecifics. In the wild, penguin chicks usually fast near fledging, before leaving for the sea for the first time, as parents stop feeding them. This suggests that there is probably a positive correlation between fasting and hormonal signalling related to the first foraging behaviours (Slezacek et al. 2022).

Thus, when hand-feeding penguin chicks, caution is needed to attend to energetic and nutritional demands with a controlled feeding rate. Extreme attention to high-density diets is necessary because animals could stop consuming due to energy content, but before ingesting the minimum amount of essential nutrients. In this scenario, considering energy values when choosing feeding items is recommended.

Various hand-feeding formulas have been described and might include whole fish, krill, brewer's yeast, vitamin supplements and calcium carbonate, although full proximate composition reports

Table 4. Estimates of energy expenditure for growing chicks determined from rates of oxygen consumption wild for Macaroni *Eudptes chrysolophus* and Rockhopper *Eudyptes chrysocome* chicks

	Age (days)	Body weight (kg)	Energy requirement for maintenance (kcal/d)	Energy requirement for growth (kcal/d)*	Energy for maintenance (kcal.kg$^{0.75}$.d^{-1})	Energy for growth (kcal.kg$^{0.75}$.d^{-1})
Macaroni	0	0.106	32	68	172	364
	15	0.879	103	82	113	90
	30	1.653	164	204	113	140
	45	2.776	210	159	98	74
	60	2.569	212	11	104	5
Rockhopper	0	0.079	8	43	53	286
	15	0.518	53	59	87	97
	30	0.943	162	114	169	119
	45	1.68	187	89	127	60
	60	1.629	213	2	148	1

Adapted from Brown (1987). * Assuming a production efficiency of 75%.

were not included (Henry 2020; Stander and Klusener 2020). A few authors suggest removing the fish head, tail, fins and skin when producing a rearing formula; however when doing so, considerable amounts of mineral content are being removed from the diet because ashes are usually concentrated in fins and skin (Jaziri et al. 2022). Despite reducing mineral content, the use of clean fish meat consequently increases the proportions of protein, lipids and energy offered by these items. When supplementing calcium carbonate, caution is needed to avoid problems related to bone mineralisation; as a general rule, Ca:P ratios should be balanced to a proportion of 2:1 to 3:1 as per observed in both captive and wild penguin species (Gallo et al. 2019; Leineweber et al. 2023).

For chicks, Brown (1987) provides energy requirements for a few wild species during growth (Table 4). In the wild, chicks might have fasting periods, depending on the species—it is not natural for wild chicks to receive frequent, high-volume and energy-dense diets (Slezacek et al. 2022). Thus, the data gathered by Brown (1987) can be used to control ingestion rates. Cooper (1977) demonstrated that captive, hand-reared African penguin chicks might consume twice as much energy as that estimated in the field, despite having fewer challenges in terms of environmental stability. Although hand-reared penguin chicks have shown good survival rates (Barham et al. 2008; Klusener et al. 2018; Sherley et al. 2014), overfeeding should be avoided because it could promote negative effects on chicks' development or impose higher metabolic costs for eliminating excess nutrients (Maharjan et al. 2021).

Energy requirements of macaroni and rockhopper penguin chicks increase rapidly in the first week after hatching (Brown 1987). After seven weeks, energy allocated for growth decreases sharply, once chicks are fledged and ready to allocate energy to foraging and other behaviours. There is not much information on energy requirements for other penguin chick species and data regarding energy requirements for tropical species have not yet been determined. When extrapolating data, caution is needed since energy requirements might differ among tropical and arctic species.

Fish species

To avoid dependence on a particular food item, it is prudent to offer a variety of fish species in a controlled environment (AZA 2014). If a penguin becomes 'imprinted' on a specific food item and that item becomes unavailable, it may be difficult to coax acceptance of an alternative (AZA 2014; Crissey et al. 2001). In addition, offering a variety of foods will help ensure that the diet provides a complementary and complete nutrient profile, mineral and vitamin supplementation notwithstanding.

In terms of the sole use of energy-dense diets, it is not uncommon for captive avian carnivore species to become overweight or even obese (Mason 2005; Tully et al. 2009). In fact, there are reports of obesity in both wild and captive penguins (Clements and Sanchez 2015; Willener et al. 2016). Overweight avian specimens can experience a range of health problems, such as liver disease, heart disease, reproductive problems, pododermatitis and aggravated lameness related to musculoskeletal disease (Boatswain 2011; Erlacher-Reid et al. 2012; Mangus et al. 2021; Willener et al. 2016; Zaefarian et al. 2019). Therefore, as for most other animals, monitoring body weight and body condition is important for the management of zoo penguins (Clements and Sanchez 2015).

Working with restricted diets might be difficult in big flocks and group feeding practices. When required, restricted feeding should be associated with individual control sheets combined with individual hand feeding (Wallace 2014). However, husbandry guidelines suggest that hand-feeding can lead to poor

Table 5. Proximate analysis of common food items adopted for captive penguins. Moisture, crude protein, lipids, ash and carbohydrate contents are expressed in percentage (g.100g^{-1} wet weight). Energy is expressed in Kcal/kg in wet weight and was determined by the caloric coefficients for proteins and lipids (4 and 9 kcal/g, respectively).

Common name	Scientific name	Region	Water (%)	Protein (%)	Lipids (%)	Ash (%)	Energy kcal/100g	Source
			As fed					
Capelin	*Mallotus villosus*	North Atlantic and Pacific	68.2	16.1	13.7	2.1	187	Lawson et al. 1988
Herring	*Clupea harengus*	North Atlantic	68.6	18.4	11.1	1.5	174	Olagunju et al. 2012
Krill	*Euphausia superba*	Antarctic	96.2	2.2	0.5	0.5	13	Kim et al. 2014
Mackerel	*Scomberomorus scombrus*	North Atlantic	63.3	23.1	10.2	1.1	184	Ogundiran et al. 2014
Mackerel	*Scomberomorus japonicus*	Indo-Pacific	61.9	20.7	15.9	1.6	225	Agustinelli and Yeannes 2014
Smelt	*Hypomesus pretiosus*	Eastern Pacific	73.7	18.4	7.2	2.0	138	Payne et al. 1999
Squid	*Illex illecebrosus*	Atlantic Ocean	75.1	17	6.6	1.4	127	Lawson et al. 1988
Squid	*Loligo opalescens*	Eastern Pacific	79.3	15.3	1	1.8	70	Berntsen 1987
Atlantic Spanish mackerel	*Scomberomorus maculatus*	South Atlantic	75.8	21.9	1.4	1.3	101	Quadros and Bolini 2015
Sardine	*Sardinella brasiliensis*	South Atlantic	77.3	19.5	2.0	1.3	96	Oliveira et al. 2003
Smooth weakfish	*Cynoscion leiarchus*	South Atlantic	79.6	16.5	0.4	0.9	70	Carvalho and Tomita 2016
Broadband anchovy	*Anchoviella lepidentostole*	South Atlantic	75.2	17.7	5.1	2.6	116	Giamas et al. 2018
Southern kingcroaker	*Menticirrhus americanus*	South Atlantic	79.6	18.4	0.9	1.3	82	Carvalho and Tomita 2016
Smalltooth weakfish	*Cynoscion steindacheri*	South Atlantic	82.5	16.7	1.3	0.7	79	Oliveira et al. 2003

swimming and lethargy, so pool feeding might be a better choice (Goodenough et al. 2023). An intermediate solution would be to alternate between the methods, offering restricted amounts of food either way. Careful choice of fish species allows maintenance of food quantity while manipulating energy intake.

Most literature on captive penguin nutrition only refers to fish species available in the no rthern hemisphere and rarely includes data on proximate composition. In Table 5, values for protein, lipid and energy content of most fish species accepted by captive penguins are listed. Data on fish species available at low cost in the southern hemisphere were included for institutions based at these locations. Apart from the listed species, it seems that penguins might accept whitebait *Allosmerus elongatus,* sardines *Sardinella aurita* and *Sardinops caerulea,* anchovies *Engraulis mordax,* smalleye croaker *Nebris microps,* banded croaker *Paralonchurus brasiliensis* and striped weakfish *Cynoscion striatus.* However, values for proximate composition were not found.

Data on naturally preferred food items vary within penguin species (Carpenter-Kling et al. 2019; Colominas-Ciuró et al. 2021) and the proximate composition of seafood varies by season, sex and age (Ahmed et al. 2022). Therefore, values should be used as a base rather than a rule. Preferably, nutrient analysis of the particular batch acquired (which is often provided by fish sellers) should be considered. Northern fish species are usually high in lipids and energy content when compared to species from further south.

Although fish adopted for the diet of marine animals in the northern hemisphere tend to represent high-fat species when compared to tropical fish, selection is usually based on availability and cost. However, considering extreme regions for example, Arctic fish—found in the northern hemisphere—have high levels of lipids and consequently high energy values, while Antarctic fish—found in the southern hemisphere—tend to have lower lipid concentrations (Hagen et al. 2000; Sushchik et al. 2020). Therefore, there is no reason to keep ingestion rates as high as those observed in the wild when feeding captive individuals, especially if adopting diets with higher lipid and energy content. On the other hand, there is no need for tropical zone zoos to search for particularly high-fat species for feeding penguins.

Taking into account energy requirements within different penguin species and associating this with fish species will suggest different feed intake for each case. For example, for a 5 kg Humboldt penguin considering the feeding intake proposed by AZA (2014), 0.5 to 0.7 kg of fish would be sufficient. Considering energy requirements, the same animal would need 71 kcal kg$^{-0.75}$ day^{-1} for RMR, or 237 kcal day^{-1} for a 5 kg animal. Accounting for the additional energy required for daily exercise, energy requirement would increase by 1.5 to 2 times (i.e. a daily requirement from 355 to 474 kcal). In this example, for an animal feeding on *Engraulis ringens,* a common prey in the wild, a mean of 440 g of fish would be necessary to meet energy demands and the expected feeding intake suggested by AZA (2014). However, if fed herring *Clupea*

Table 6. Proximate analysis of common food items explored by wild penguins. Moisture, crude protein, lipids, ash, and carbohydrate contents are expressed in percentage (g.100g^{-1} wet weight). Energy is expressed in kcal/kg (wet weight) and was determined by the caloric coefficients for proteins and lipids, respectively, 4 and 9 kcal/g.

Fish species	Water (%) As fed	Protein (%)	Lipids (%)	Ash (%)	Energy kcal/100g	Source
Champsocephalus gunnari	66	9.2	10.16	11.92	128	Iboyi et al. 2021
Electrona antarctica	69.6	12.2	15.2	15.8	186	Lenky et al. 2012
Electrona carlsbergi	73.9	13.9	7.6	15.1	124	Lenky et al. 2012
Engraulis anchoita	77.6	16.2	4.2	1.2	103	Czerner et al. 2015
Hemerocoetes spp.	53.3	30.3	4.2	-	159	Meynier et al. 2008
Engraulis rigens	76.5	19.9	1.5	1.9	93	Albrecht-Ruiz and Salas-Maldonado 2015
Etrumeus teres	75.0	22.2	0.2	1.5	91	Küçükgülmez et al. 2010
Merluccius gayi	82.4	15.8	0.5	1.2	67	Castillo Manrique 2021
Myctophidae	78.0	16.5	4.9	0.5	110	Fernandez et al. 2014
Notothenia rossii	78.3	16.1	3.9	1.1	99	Oehlenschläge and Rehbein 1982
Odontesthes regia	76.2	19.7	2.4	1.5	100	Barriga et al. 2003
Pleuragramma antarcticum	82.1	8.3	7.2	13.1	98	Lenky et al. 2012
Pseudophycis bachus	69	18	4	-	108	Meynier et al. 2008
Trachurus murphyi	68.2	17.9	11.2	3.4	17	Vlieg and Bailey 1989
Illex illecebrosus	75.1	17	6.6	1.4	12	Lawson et al. 1988
Loligo opalescens	79.3	15.3	1	1.8	70	Berntsen 1987
Euphausia superba	96.2	2.2	0.5	0.5	13	Kim et al. 2014

harengus the same animal would require only 270 g of fish to fulfil its daily need for energy (Table 4); almost half of the minimum fish intake indicated by AZA guidelines.

Results may differ between penguin species. The Adelie penguin also weighs 5 kg and 105 kcal kg$^{-0.75}$ day^{-1} for RMR is expected or 351 kcal day^{-1} for a 5 kg animal. Accounting for energy for exercise, a need for 526 to 702 kcal per day is anticipated. Even though the feeding intake proposed by AZA (2014) is the same for different penguins weighing 5 kg, if energy requirements are considered, a 5 kg Adelie penguin would need up to twice the amount of *Clupea harengus* to fulfil its daily needs considering its possibly higher metabolic rate. Any feeding management should use calculated estimates and also monitor the effect of the calculated diet by weighing and regularly applying body condition scoring (Clements and Sanchez 2015).

In Table 6, values of the proximate composition of natural food items for different penguin species are listed. Ash content seems to be higher in wild diets (Table 6). Besides fish, most of the species in the wild forage for krill and other crustaceans and a range of cephalopods (Dakwa et al. 2021; White 2020). These usually contain higher proportions of minerals, which might indicate a need for supplementation.

Supplementation

Vitamin and mineral supplementation aims to replace nutrients lost during food storage, for example water-soluble vitamins such as vitamin B1 that are broken down by thiaminase present in fish muscle. Supplementation also aims to provide nutrients not offered in the diet, such as when generalists are fed exclusively on fish (Bos et al. 2018; Krogdahl et al. 2022). There are no specific data on the requirements of vitamins and minerals for penguins. When supplements are offered, general recommendations for domestic avian and carnivore species are adopted (AZA 2014).

Several commercial supplements for fish-eating animals, including specific formulations for penguins, are available. However, not all institutions have easy access to these products. In some regions, commercial supplements for wildlife are only available upon importation. Thus a common solution for these institutions is to formulate their own supplements.

Nutrient and vitamin content of fish fed in captivity varies. Supplementation of fat-soluble vitamins (A, D, E and K) must be especially conditioned to the fish species provided. Besides penguins storing those vitamins in their body reserves, fatty fish usually contain reasonable amounts of these vitamins (Bos et al.

2018; Colchao et al. 2020). Yet, vitamin E supplementation is usually associated with antioxidant effects on fat and is recommended for penguins (Wallace 2014). Cases of deficiency and high plasma levels of these vitamins have been reported (Keymer 1980; Naylor et al. 2018; Ueda et al. 2019a, b). However, it is not clear how low or high vitamin dosages may affect penguins (Stidworthy and Denk 2018).

When formulating a supplement, it is necessary to keep in mind that requirement values presented in the literature represent total concentrations provided in the diet. The food item provided already supplies levels of vitamins and minerals and the supplement should only complement nutrients lost during storage or according to specific recommendations. Often, vitamin requirements in the literature are expressed in mg IU^{-1} per kg of dry matter (DM). Considering that dry matter content varies among fish species, the range of vitamins supplied should meet the current diet adopted by the institution. Thus, when formulating supplements, institutions should take into consideration the common fish species used on a daily basis.

Consider for example, that dietary vitamin A requirements for avian species range between 1,700 and 5,600 IU kg^{-1} of diet on a DM basis (Crissey et al. 2001). A group of penguins fed 1 kg of mackerel *Scomber japonicus* with 31.8% DM would need a minimum of only 540 IU of vitamin A. If the same group was fed 1 kg of *Cynoscion steindachneri,* the minimum supplementation of vitamin A would change to 297 IU, as the values of dry matter are lower for this particular fish species (17.5%). Although the values presented are perhaps not different enough to trigger a clinical response, it is clear that changing the fish changes the supplementation required. Considering that vitamin A is liposoluble, daily overdosage over several years would probably result in health problems, as increasing blood levels are often associated with diet (Ueda et al. 2019a, b). If by mistake vitamin requirements were calculated based on fed weight rather than DM, 1,700 IU would be offered to this same group, regardless of fish species, resulting in a critical overdose. Thus, custom-made supplements should always be formulated by nutritionists and based on the feeding regime of the institution.

Final thoughts

Although there is valuable information on penguin nutrition gathered from husbandry practice manuals, knowledge and information regarding proximal analysis of fish species and specific nutrient requirements are still scarce. Considering that animal nutrition is a key factor for achieving optimal levels of health, growth, reproduction, survival and longevity of wild species under human care, this review aims to help optimise feeding protocols for captive penguins, differentiating requirements by species and developmental stage, hoping that the information provided helps institutions maintaining these species for conservation or rehabilitation purposes.

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