Long term variability in the diet and reproductive performance of penguins at Bird Island, South Georgia

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**Abstract**

Inter-annual variability in diet during crèche (December to February) over 22 years (1989 to 2010) was examined for gentoo penguins *Pygoscelis papua* breeding at Bird Island, South Georgia (54 º0’S, 38º2’W). Overall, diets comprised 51 % crustaceans and 49 % fish by mass. Crustaceans were present in 89 % of samples and were the main prey (> 50 % by mass) in 10 years of the study. Antarctic krill *Euphausia superba* were present in 85 % of all diet samples. Fish were present in 79 % of samples and were the main prey in 12 years, with *Champsocephalus gunnari* and *Lepidonotothen larseni* the most frequently recorded species, in 51 % and 33 % of samples respectively. The energy or mass of krill in the diet was the most reliable predictor of breeding success (the number of chicks fledged per breeding pair); the correlation between model-predicted and observed values was 0.58. We compared annual patterns of gentoo penguin diet variability with those of macaroni penguins *Eudyptes chrysolophus* breeding at the same location. Our results suggest that the availability of krill is a key source of diet variability for both species, but their diets indicate that gentoo penguins are generalist predators (feeding on pelagic and bentho-pelagic prey), while macaroni penguins are krill specialists (feeding on pelagic prey). Differences in the response to variability in key prey species is an important factor separating the ecological niches of these two sympatric krill predators.

**Introduction**

Understanding the interactions between predators and their prey is key to understanding ecosystem structure and functioning. By monitoring the diets of key predators over a number of years we can examine the relative availability of different prey items, as well as the particular characteristics of their foraging behaviour. Changes in predator diets can be used as an indicator of ecosystem change (Cairns 1987; Agnew 1997; Reid and Croxall 2001; Hanson et al. 2002; Dwyer et al. 2010) and combining diet data with measures of reproductive performance can give insights into predator responses to prey availability and ecosystem status (Cairns 1987; Boyd and Murray 2001; Piatt et al. 2007; Waluda et al. 2012).

The gentoo penguin *Pygoscelis papua* (Forster, 1781) has a circumpolar distribution between 46 and 65º S. Around 26 % (98,000 pairs) of the global population are resident at South Georgia in the southern Atlantic Ocean (Lynch 2012)**.** At Bird Island, at the north-western tip of the South Georgia archipelago (54º 00’S; 38º 02’W; Figure 1), the population consists of approximately 3,000 breeding pairs inhabiting five main rookery sites. The demography and diet of this population has been regularly monitored since the 1970s. Diet samples obtained during the chick-rearing periods of 1977, 1980, 1985 and 1986 comprised between 39 % and 80 % Antarctic krill *Euphausia superba*, and between 20 % and 61 % fish (Croxall and Prince 1980, Croxall et al. 1988a, Croxall et al. 1997). Crustaceans are the main prey during winter, with diet samples comprising 87 % crustaceans, mostly *E. superba* (Williams 1991). The fish component of the diet is generally dominated by channicthyids, particularly the commercially important mackerel icefish *Champsocephalus gunnari* (Croxall et al. 1997; Croxall et al. 1999; Hill et al. 2005; Reid et al. 2005a), with other families such as nototheniids and myctophids regularly reported (Croxall and Prince 1987; Croxall et al. 1988b; Croxall et al. 1997). Also present at Bird Island are three breeding colonies of macaroni penguins *Eudyptes chrysolophus,* numbering around 50,000 pairs in total (Trathan et al. 2012). The diets of macaroni penguins comprise krill, fish and amphipods; diet data from 1989 to 2010 are summarised by Waluda et al. (2012).

Diet data are routinely collected for both gentoo and macaroni penguins breeding at Bird Island, South Georgia using standardised methods (CCAMLR 2014) as part of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Programme (CEMP) (Agnew 1997). The principal objective of CEMP is to detect changes in the Southern Ocean ecosystem and to distinguish the potential impacts of commercial fishing from other drivers of change.

Here, we describe the diets of gentoo penguins during crèche for the 22-year period 1989 to 2010. We examine individual and inter-annual variability in diet composition and prey dominance and assess the influence of diet on reproductive performance using the number of chicks fledged per nesting pair as a measure of breeding success. Additionally, we compare annual variability in the diets of gentoo penguins with those of macaroni penguins breeding sympatrically at Bird Island (see Waluda et al. 2012).

**Material and methods**

*Diet sampling*

Diet samples were obtained from adult gentoo penguins breeding at the Square Pond colony, Bird Island, South Georgia (Figure 1). Samples were obtained during the crèche period (between December and February) 1989 to 2010 following the stomach lavage methods described in Wilson (1984) and Williams (1991). Each year, samples were obtained over a four-week period with approximately 10 birds sampled each week as they returned to the colony to feed their offspring. The breeding phenology of gentoo penguins at Bird Island is variable from year to year (Williams 1990), with the date of the first diet sample varying between 21 December (1992/93 season) and 28 January (1990/91 and 2009/10) (Table 1). Each year, the same methodologies for field sampling (CCAMLR 2014) were used, in order to ensure field workers followed consistent and repeatable sampling protocols. The meal mass sampled was considered to be representative of the amount brought back to the colony, and the contents representative of prey species fed to the chicks. For operational reasons, diet sampling for gentoo penguins ceased in 2010.

Each diet sample was drained through two sieves (3.35 and 250 µm) and weighed to calculate wet meal mass per penguin. Non-food items (e.g. small stones) were noted but excluded from the overall sample mass. Each sample was sorted into the crustacean, fish and cephalopod components and the constituent parts weighed. Crustaceans were further identified to species level where possible. Fish otoliths were separated and counted from all diet samples and used to identify fish species and back-calculate standard length and mass using regression equations (Reid and Arnould 1996; Hill et al. 2005). Cephalopods were identified from beaks by comparison with a reference collection held at the British Antarctic Survey, with regression equations used to relate the lower rostral length to the original mantle length where possible (Clarke 1986; Rodhouse et al. 1990). The total number of prey species identified in each year was recorded.

*Breeding success*

Gentoo penguins typically produce two eggs and attempt two raise two chicks during a breeding season (Williams 1990). Therefore, the number of chicks fledged per nesting pair was used as a simple index of reproductive performance for the population of gentoo penguins breeding at Square Pond, Bird Island. Nests were counted one week after the peak laying date (when 75 % of nests have eggs) and the number of chicks were counted when all birds had entered the crèche stage (CCAMLR 2014).

*Energy content of meals*

The energy content of each meal was calculated from the wet mass of each prey component and published data on calories per unit mass of prey (kilojoules per gram; kJ/g), assuming a constant mass-energy conversion for each prey type. Energy values from the same area and season (Scotia Sea during austral spring) were used whenever possible, but equivalent values from other areas and other seasons were used where necessary (Table 2). The energy content of Antarctic krill was calculated using a mean value for males and females (Clarke 1980). A single energy value was used for each of: euphausiids other than Antarctic krill, based on *Thysanoessa macura* (Torres et al. 1994); amphipods, based on *Themisto gaudichaudii* (Ciancio et al. 2007); and cephalopods, based on a mean value for muscular squid (Clarke et al. 1985) (Table 2). The energy content of fish was calculated based on the species composition for each year, using the energy values for key species given in Table 2. In years in which fish flesh was present but could not be identified to species level (i.e. years in which no otolith data were available; only 1989 and 1990) a mean value of 5.12 kJ/g (derived from the mean of all fish species listed in Table 2) was used to calculate the energy content of fish.

*Analyses*

*1. Gentoo penguin diets during crèche 1989-2010*

Using the long-term datasets presented above we examine: (a) individual diet composition, describing the frequency of occurrence, diversity and dominance of prey types and species, (b) meal mass and energy derived from individual meals, (c) variability in annual diet composition (1989 to 2010) and (d) variability in prey dominance in individual samples and between years.

*2. Relationship between diet and breeding success*

To examine possible relationships between diet and reproductive performance (number of chicks fledged per nesting pair) we used two candidate model forms. These were:

A standard linear model: $y=ax+b$ (1)

And a two-parameter, non-linear least squares model: $y=b(1-e^{-ax})$ (2)

Where *a*, and *b* are model parameters. In each case the dependent variable, *y*, was breeding success and we used each model form with a range of independent variables, *x*, representing the importance of different combinations of prey types in the diet

The variables included were the meal mass (wet mass in grams) or energy content (kJ g-1) of each prey group and all groups combined. Residual plots and partial residual plots were examined to assess model fits. We used the corrected Akaike Information Criterion (AICc) to compare the 24 resultant models. Data were analysed using the statistical package R (version 2.13, R Development Core Team 2011).

*3. Comparison of gentoo and macaroni penguin diets*

To compare patterns of annual variability in the diet preferences of the two species of penguin breeding at Bird Island we compared the annual meal mass and meal energy and the proportion of key prey types occurring in the diet of gentoo penguins (Square Pond colony) with the equivalent values for macaroni penguins also breeding at Bird Island (Goldcrest Point colony; see Waluda et al. 2012). Data were analysed using simple correlation analysis (Pearson’s R) for the period 1989 to 2010.

**Results**

*1a. Individual diet variability*

A total of 824 diet samples were obtained from gentoo penguins between 1989 and 2010. Meals comprised crustaceans, fish and cephalopods (Table 1). Of these, 135 samples (16 %) contained small stones (mean mass of stones per stomach sample = 0.73 ± 2.8g). In total, 26 different prey species were identified in the diets of gentoo penguins at Bird Island (Table 3).

Crustaceans were present in 732 samples (89 %). A total of six species from three families were identified (Table 3). Euphausiid crustaceans were dominant with *E. superba* occurring in 697 samples (85 %). Other species of euphausiid (*E. frigida* and *Thysanoessa* spp.; not always identified to species level so included here as a single prey group) were present in 39 samples (5 %). The hyperiid amphipod *Themisto gaudichaudii* was present in 164 samples (20 %), although 62 of these samples contained only trace amounts.

Fish remains were present in 652 diet samples (79 %). A total of 17 species of fish from six families were identified, with *Champsocephalus gunnari* and *Lepidonotothen larseni* the most frequently recorded species, present in 423 (51 %) and 270 (33 %) diet samples respectively (Table 4). Mean estimated standard lengths of all fish consumed were between 43 mm (*Protomyctophum bolini*) and 364 mm (*Chaenocephalus aceratus*) (Table 3).

Cephalopod remains were present in 25 diet samples (3 %). A total of three species of cephalopod (one octopus, two squid) from three families were identified, with the octopod *Pareledone turqueti* the most frequently recorded cephalopod species (Table 3).

*1b. Meal mass and energy derived from diet*

The mean meal mass ± standard deviation of all individual diet samples was 558 ± 368 g (Table 1; Figure 2a). The diet by mass was composed of crustaceans (285 ± 334 g), mostly krill (280 ± 335 g), fish (272 ± 346 g) and cephalopods (0.3 ± 2.6 g). The mean energy content of all individual diet samples was 2719 ± 1813 kJ (Table 1). The number of prey species recorded per sample was between 1 and 7 (mean = 2.4 ± 1.16) (Figure 2b).The proportion of *E. superba* in diets showed a bimodal distribution, with 127 samples (15 %) containing zero krill and 158 (19 %) containing 100 % krill (Figure 2c).

*1c. Annual patterns of diet variability*

During the 22 year period of the study, *E. superba* and *C. gunnari* were the dominant prey species, contributing more than 50% of the diet by mass in 10 years and 11 years respectively. In 2006, there was no dominant prey species and the diet comprised 46 % *E. superba*, 16% *C. gunnari* and 37 % *L. larseni* (Table 4).

Mean annual meal mass (mean ± standard deviation) ranged between 82 ± 74 g (in 1994) and 931 ± 451 g (in 2002). Mean annual meal energy ranged between 419 ± 390 kJ (1994) and 4538 ± 2252 kJ (2000) (Table 1). When all individual samples were compared (N = 824), meal mass was equivalent to meal energy (r = 0.997, P < 0.001). *E. superba* was recorded in diet samples in all 22 years, *T. gaudichaudii* was present in 19 years (Table 3), and other crustacean species were present in 1 to 10 years (Table 3). Fish were recorded in the diet in all 22 years, with otoliths recovered and species identified in 20 years (no species data were available for 1989 or 1990; and see Table 3). *C. gunnari* was present in 20 years and *L. larseni* in 19 years (Table 4). The fish component of diets (mass estimated by back calculation from otolith measurements) was dominated *by C. gunnari* in all years between 1991 and 2010 except 2006, when *L. larseni* was the dominant fish species (Table 4). The proportion by mass of *C. gunnari* was strongly negatively correlated with the proportion of *E. superba* in the diet (r = -0.891, P < 0.001); but the proportion of *L. larseni* was not related to the proportion of *E. superba* (r = -0.043; P = 0.858) or *C. gunnari* (r = -0.360; P =0.019). Cephalopod flesh was identified in 14 years (Table 1), with cephalopod beaks recovered in three years (1994, 2000, 2009; Table 3). There was no time-trend in the proportion of fish (r = 0.144, P = 0.524), *E. superba* (r = -0.17, P = 0.46), or all crustaceans combined (r = -0.14, P = 0.535) over the period of the study.

*1d. Variability in prey dominance*

Variability in prey dominance was determined by combining data into three main prey groups; ‘euphausiids’ (*E. superba, E. frigida, Thysanoessa spp*.), ‘fish’ (see Table 3 for species present) and ‘other’ (non-euphausiid crustaceans and cephalopods; see Table 3). A total of 253 samples (31 %) were composed entirely of a single prey type (161 were euphausiids; 89 fish; 3 amphipods). A further 349 diet samples (42 %) had a single prey type comprising at least 90 % of their mass (134 euphausiids; 212 fish; 2 amphipods; 1 cephalopods). These types of diet are categorised as ‘dominated’ by the majority prey type. The remaining 222 samples (27 %) had no dominant (> 90 %) prey type and are categorised as ‘mixed’ diets.

Inter-annual patterns of prey dominance are shown in Figure 3. Euphausiid-dominated diets were most common (> 50 % of diets) in four years (1989, 1993, 1998, 2002). Fish-dominated diets were most common in six years (1991, 1994, 1999, 2005, 2008 and 2009) and mixed diets in one year (2007). In the remaining eleven years, the average proportion of euphausiid-dominated, fish-dominated and mixed diets were similar (37 %, 32 % and 31 % respectively).

*2. Relationships between diet and breeding success*

Breeding success varied between zero and 1.7 chicks per year (mean = 0.92; Figure 4). There was no time trend in this variable (r = -0.071; P = 0.753), but breeding success was positively correlated with the proportion of krill or krill and fish in the diet (Table 5). AICc provided the most support for a two-parameter non-linear least squares model with the mass/energy of krill as the independent variable. The correlation between model-predicted and observed values for breeding success was 0.58 for both of these models (Figure 5; Table 5). The assumed relationship between mass and energy content was linear within each prey group, but varied across groups. Consequently, AICc did not distinguish between mass and energy models except when the independent variable included more than one prey group (e.g. all prey groups or all crustaceans).

*3. Comparison of gentoo and macaroni penguin diets*

The annual means of meal mass and meal energy for gentoo penguins were positively correlated with the equivalent values for macaroni penguins (r = 0.532, P = 0.011 and r = 0.587, P = 0.004 for mass and energy respectively, n = 22 years; 1989 to 2010). There were no correlations between the two penguin species for the mass or frequency of all fish or all crustaceans in the diets. There were, however, positive correlations for mass (r = 0.474, P = 0.026; Figure 6) and frequency (r = 0.567, P= 0.005) of *E. superba* in the diets of the two penguin species (Table 6).

**DISCUSSION**

*Diet composition of gentoo penguins at Bird Island*

This work presents data from 22 years of diet sampling of gentoo penguins *Pygoscelis papua* breeding at Bird Island, South Georgia. Along with previously reported data on macaroni penguins (Waluda et al. 2012), this is one of the longest and most comprehensive time series of penguin diet data available globally. Gentoo penguins feeding at Bird Island can be described as generalist predators with their diets consisting of an approximately equal proportion of crustaceans (51 %) and fish (49 %) (Table 1). Diets were dominated by Antarctic krill *Euphausia superba*, and krill-eating fish (Kock et al. 2012), particularly *Champsocephalus gunnari*, which together contributed more than 95 % of the overall diet by mass (Table 4). In a given year, gentoo penguin diets usually contained at least 50 % of either *C. gunnari* or *E. superba* by mass, except for in 2006 when diets comprised 46 % *E. superba*, 16 % *C. gunnari* and 37 % *Lepidonothen larseni*.

The diet composition of gentoo penguins at Bird Island (Table 3) is consistent with birds foraging inshore in shallow areas with possible benthic feeding, which might also explain the small stones found in 16% of the stomach samples. The most common fish species found in gentoo penguin diets belong to species and size classes that occupy a bentho-pelagic habitat, inhabiting the kelp beds around the coast of the island (Burchett et al. 1983; Kock et al. 2012). Additionally, shallow-water benthic cephalopods such as *Paraledone turqueti* (Collins et al. 2004) were occasionally observed (Table 3).

There was no evidence for a decline in the occurrence of fish or krill in the diet over the 22 years studied. This is consistent with Fielding et al. (2014) who showed variability, but no trend in krill density, using acoustic methods to document inter-annual variation in krill density in the waters to the north of Bird Island. Our results show coherence with earlier studies of gentoo penguin diets from the same location (e.g. Croxall and Prince 1980; Croxall et al. 1988b), except for the presence of *L. larseni* as a significant prey species (contributing > 10% of the diet in 4 years). These earlier studies (Croxall and Prince 1980; Croxall et al. 1988b) suggest that the contribution of species such as *Notothenia rossii* and *N. neglecta* were higher during the late 1970s and early 1980s, but these species were rarely observed in our study (Table 3). This may be due to a reduction in the availability of these species within the ecosystem due to predation or fishing pressure (Trathan and Reid 2009; Ainley and Blight 2010). This period corresponds with an increase in the abundance of Antarctic fur seals *Arctocephalus gazella* at South Georgia (Boyd 1993), with a similar change in fish species dominance described in their diets (Reid et al. 2006).

The proportion by mass of *C. gunnari* was significantly negatively correlated with the proportion of *E. superba* in the diet (see also Reid et al. 2005a). This suggests that gentoo penguins are likely to feed on whichever prey is more abundant within their foraging range, reflecting what is available in the local ecosystem. It is not clear if this is driven by the availability of krill or fish, but the years in which *E. superba* were particularly scarce in the diet of gentoo penguins (1994, 2009) are consistent with diet studies of other predators breeding at Bird Island (Croxall et al. 1999; Waluda et al. 2012; BAS unpublished data) and acoustic data on krill abundance (Croxall et al. 1999; Reid et al. 2010; Cury et al. 2011; Fielding et al. 2014), suggesting that krill availability in the South Georgia ecosystem was reduced in those years.

Our results show similarities with studies of gentoo penguins at other locations which have diets consisting of approximately equal proportions of fish and crustaceans (e.g. Falkland, Crozet, Laurie, and Marion Islands). However, fish (Kerguelen, Macquarie and Heard Islands) or crustaceans (Kerguelen and the South Shetland Islands) can predominate in some regions (Table 7; and see Lynch 2012). Cephalopods are generally rare in the diet, but, in certain years can comprise between 10 and 12 % of the diet by mass at Kerguelen, Macquarie and the Falkland Islands (Table 7). Diet plasticity is evident throughout the species range, with birds feeding opportunistically on the most readily available prey in the waters surrounding the breeding site (Lescroël et al. 2004), reflecting the restricted foraging range of gentoo penguins during chick rearing. However, some degree of prey selection and avoidance behaviour has been shown, for example, Clausen et al. (2005) compared data on penguin diets with contemporaneous trawl data from Falkland Islands waters and showed that gentoo penguins preferred squid and fish diets over lobster krill and other crustaceans, and tended to avoid small demersal sharks despite their apparent availability within the main foraging region.

*Prey preferences*

Within an individual diet sample, we found that gentoo penguins had similar probabilities of feeding exclusively on fish or krill or taking a mixture of prey types. Other studies also show this variability, although the frequency of each diet type varies between locations, and between studies at the same location. For example, of 46 gentoo penguins sampled repeatedly at King George Island, 24 (52 %) specialised in krill, 7 (15 %) in fish and 15 (33 %) a mixture of both (Jablonski, 1985). Croxall et al. (1988a) found that fewer than 10 % of gentoo penguin diets at Bird Island in 1985 and 1986 contained significant quantities of both fish and krill, suggesting specialisation of individual birds (at least within single trips) whereas in our study the percentage of mixed diets varied between 10% (1993) and 53% (2007). In 1993, an exceptional 80 % of diets were krill-dominated; suggesting krill availability was high in that year. The occurrence of krill was also high in the diets of other species at South Georgia during 1993, with macaroni penguin diets comprising 90% krill by mass (Waluda et al. 2012), and Antarctic fur seal diets containing 100% krill by frequency (Reid and Arnould 1996) respectively. In addition, data from acoustic surveys showed that krill abundance was above average at South Georgia in 1993 (based on data from 1981-1998; Brierley et al. 1999).

*Relationships between diet and reproductive performance*

The amount of krill in the diet of gentoo penguins was a better predictor (than any other prey combination) of reproductive performance as indicated by breeding success (number of chicks fledged per nest). A previous study of macaroni penguins (Waluda et al. 2012) used fledging weight as an indicator of reproductive performance. This is appropriate for macaroni penguins which typically raise only one chick, and for which survival to fledging appears relatively insensitive to nutritional status (Waluda et al. 2012). In contrast, gentoo penguins typically attempt to raise two chicks (Williams 1990) and, as is apparent from the current study, breeding success is a reasonably sensitive variable. As they are capable of producing two chicks per brood, fledging weight is likely to be a less suitable indicator for gentoo penguins because during ‘good’ years both chicks may achieve an average fledging weight and survive, whereas in ‘poor’ years the lighter chicks of the brood are more likely to die, such that a greater number of heavier chicks survive and the mean fledging weight is higher (Bost and Jouventin 1991). The product of fledging weight and breeding success could provide a more comprehensive index of reproductive performance (Reid and Croxall 2000), but as data on fledging weights are routinely collected from the Johnson Cove colony (approximately 750m distant; Figure 1c), rather than the Square Pond colony, this index was not used in the current study.

While variability in krill availability is clearly the main dietary influence on the reproductive performance of gentoo penguins at Bird Island, our results show that other prey items, especially fish, are also important. In four of the study years gentoo penguin breeding success was almost zero (< 0.01 chicks per nest) and in three of these years (1991, 1994, 2009) the amount of krill in the diet was very low (< 20 % by mass). In the remaining year (1998) the amount of krill was reasonably high in both absolute (mean 347 g) and proportional (> 90 %) terms, suggesting an additional source of mortality influenced breeding success in that year. Previous work has suggested that warmer sea surface temperatures at South Georgia are associated with reduced gentoo breeding success at Bird Island, and that the 1998 breeding season was amongst the warmest in the period 1989 to 2003 (Trathan et al. 2006). Further work is needed to establish the detailed relationship between environmental variability, gentoo penguin diet and reproductive performance.

*Comparisons between gentoo and macaroni penguin diets at Bird Island*

Gentoo penguinsare diurnal predators and make the majority of their dives to depths of between 20 and 100 metres (Croxall et al. 1988b; Kokubun et al. 2010; Wilson 2010). During chick-rearing most foraging trips are inshore with penguins generally travelling less than 50 km from land, while multi-day trips are undertaken only rarely (Williams et al. 1992; Kokubun et al. 2010; Ratcliffe and Trathan 2011). In comparison, macaroni penguins have a maximum foraging radius of around 150km, and tend to feed on the shelf-break region to the north of Bird Island during chick rearing (Waluda et al. 2010, Ratcliffe and Trathan 2011). The diets of the two species apparently reflect differences in preferred habitat. We found that 73 % of individual gentoo penguin diets were dominated by a single prey item, which is the same proportion as for macaroni penguins at the same location (Waluda et al. 2012). However, whereas 59 % of macaroni penguin diets were euphausiid dominated (Waluda et al. 2012), only 36 % of gentoo penguin diets were.Gentoo penguins appear to be less dependent on euphausiids and more dependent on fish, particularly *C. gunnari*, than are macaroni penguins breeding at the same location (Waluda et al. 2012). The overall diversity of prey items was the same (26 species) for both penguin species, but gentoo penguins ate fewer species of crustaceans and cephalopods and a more diverse range of fish species than macaroni penguins. The diets of the two penguin species included five crustacean species, ten fish species and two cephalopod species in common (Table 3), with the majority of species present in gentoo penguin diets but absent from macaroni penguin diets occupying a benthic or bentho-pelagic habitat (Table 3). More pelagic species were present in the diets of macaroni penguins (Waluda et al. 2012), consistent with the foraging habitat of the two penguin species (Croxall et al. 1988b; Ratcliffe and Trathan 2011). Gentoo penguins were less likely to consume small euphausiids or amphipods, which were a key prey item for macaroni penguins in three out of the 22 years studied but were also associated with reduced fledging weights in those years (Waluda et al. 2012). The scarcity of these prey species in gentoo penguin diets might be due to reduced availability in their foraging range, but it might also indicate the greater availability of more energy-rich food items within this range. While less than 1 % of gentoo penguin diet samples contained more than 90 % amphipods by mass, 38 % of those samples containing amphipods comprised only trace amounts. This suggests that their presence may be as a result of secondary consumption from fish, rather than from direct consumption by penguins. Fish occurred in the majority (79%) of gentoo penguin stomach samples compared to around half (46 %) of macaroni penguin samples. Fish (mainly myctophids) were the most common prey in macaroni penguin diets in 2004 (Waluda et al. 2010; Waluda et al. 2012), but this did not correspond to a year of particularly high fish consumption by gentoo penguins (Table 1).

Correlations between gentoo and macaroni penguins for metrics such as the mean mass of krill and mean total meal mass suggest that the diets of both species indicate the same source of variability, i.e. the availability of krill. The current study alongside Waluda et al. (2012) shows differences in the range of prey items in the diets of these two species and suggests that they have different strategies for dealing with this variability. Previous work suggests that macaroni penguins have a Type III (sigmoidal) functional response to Antarctic krill (Waluda et al. 2012) whereas gentoo penguins are more likely to exhibit a Type II (asymptotic) response (Reid et al. 2005b; Cury et al. 2011). The diet data for sympatric gentoo and macaroni penguins provide a promising source of information for investigating different foraging strategies in sympatric species and further examining functional responses.

Understanding how changes in penguin diet reflect changes in the ecosystem, particularly the amount of krill and fish available to predators and to the commercial fishery is critical for interpreting monitoring data. Gentoo penguin diets in particular allow us to sample inshore regions which are not occupied by the commercial finfish or krill fisheries operating around South Georgia (Agnew 2004). With the cessation of stomach lavage sampling for gentoo penguins in 2010, there is a need for alternative sampling methodology for further study. Such techniques might include DNA sampling of prey remains in guano (Deagle et al. 2007; McInnes et al. 2016), or the use of stable isotope analyses (Chiaradia et al. 2010; Stowasser et al. 2012). These methods are promising tools for the analysis of penguin diets, but their efficacy needs to be fully assessed before they can be fully adopted as alternative methodologies to stomach lavage sampling. Gentoo penguins are an important indicator species, and are one of the key species considered by the CCAMLR Ecosystem Monitoring Programme (CEMP) (Agnew 1997), so it is important to continue to understand and assess their role in the Southern Ocean ecosystem.

**Compliance with Ethical Standards**

The authors declare that they have no conflict of interest. All diet sampling procedures used were regulated by the British Antarctic Survey Ethical Review Committee in collaboration with Cambridge University and the UK Home Office. Permission for this scientific study was given by the Government of South Georgia and the South Sandwich Islands.

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Table 1. Summary of diet samples obtained from gentoo penguins breeding at Square Pond, Bird Island 1989-2010 (n = 824). Data are by percentage mass and percentage frequency of occurrence of main taxa. Data summarised by year, overall mean values (in bold) calculated for all individual samples. (-) Prey type not recorded.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | Date of first | N diet | N prey | Meal | Crustacean | Fish | Cephalopod |
| Year |  sample | samples | species | mass *g* | Energy *kJ* | %mass | *%freq* | %mass | *%freq* | %mass | *%freq* |
| 1989 | 04-Jan-89 | 41 | 3 | 683 | 3236 | 80.8 | *100.0* | 19.2 | *68.3* | 0.1 | *7.3* |
| 1990 | 04-Jan-90 | 40 | 3 | 451 | 2168 | 66.7 | *85.0* | 33.3 | *62.5* | <0.1 | *2.5* |
| 1991 | 28-Jan-91 | 37 | 8 | 317 | 1591 | 28.6 | *75.7* | 71.4 | *94.6* | <0.1 | *2.7* |
| 1992 | 17-Jan-92 | 40 | 5 | 643 | 3107 | 50.4 | *97.5* | 49.6 | *80.0* | - | *-* |
| 1993 | 21-Dec-92 | 40 | 6 | 421 | 1992 | 84.1 | *97.5* | 15.9 | *32.5* | - | *-* |
| 1994 | 17-Jan-94 | 26 | 11 | 82 | 419 | 13.4 | *80.8* | 85.4 | *100.0* | 1.2 | *7.7* |
| 1995 | 18-Jan-95 | 40 | 6 | 679 | 3304 | 58.9 | *75.0* | 40.9 | *80.0* | 0.1 | *5.0* |
| 1996 | 12-Jan-96 | 15 | 5 | 720 | 3546 | 24.3 | *53.3* | 75.3 | *100.0* | 0.4 | *6.7* |
| 1997 | 16-Jan-97 | 42 | 12 | 828 | 4130 | 36.3 | *90.5* | 63.7 | *92.9* | <0.1 | *2.4* |
| 1998 | 15-Jan-98 | 39 | 8 | 382 | 1792 | 91.0 | *94.9* | 8.9 | *33.3* | 0.1 | *2.6* |
| 1999 | 28-Dec-98 | 39 | 5 | 286 | 1427 | 36.8 | *69.2* | 63.2 | *71.8* | <0.1 | *7.7* |
| 2000 | 20-Jan-00 | 40 | 12 | 922 | 4538 | 44.4 | *80.0* | 55.5 | *87.5* | <0.1 | *7.5* |
| 2001 | 01-Jan-01 | 39 | 9 | 785 | 3910 | 35.4 | *84.6* | 64.6 | *79.5* | - | *-* |
| 2002 | 30-Dec-01 | 40 | 8 | 931 | 4490 | 64.3 | *97.5* | 35.7 | *82.5* | - | *-* |
| 2003 | 01-Jan-03 | 40 | 10 | 658 | 3198 | 41.8 | *92.5* | 58.2 | *82.5* | <0.1 | *2.5* |
| 2004 | 29-Dec-03 | 40 | 9 | 668 | 3298 | 54.2 | *95.0* | 45.8 | *100.0* | - | *-* |
| 2005 | 06-Jan-05 | 40 | 7 | 872 | 4297 | 32.2 | *82.5* | 67.6 | *100.0* | 0.2 | *7.5* |
| 2006 | 03-Jan-06 | 39 | 5 | 411 | 1967 | 46.2 | *100.0* | 53.8 | *82.1* | - | *-* |
| 2007 | 04-Jan-07 | 40 | 8 | 448 | 2147 | 58.7 | *100.0* | 41.3 | *100.0* | - | *-* |
| 2008 | 10-Jan-08 | 40 | 8 | 365 | 1808 | 42.8 | *90.0* | 57.2 | *77.5* | <0.1 | *2.5* |
| 2009 | 06-Jan-09 | 30 | 16 | 299 | 1482 | 34.1 | *90.0* | 65.9 | *86.7* | <0.1 | *6.7* |
| 2010 | 28-Jan-10 | 37 | 12 | 218 | 1034 | 67.0 | *97.3* | 33.0 | *67.6* | - | *-* |
| **Mean** |  |  | **2.4** | **558** | **2719** | **51.1** | ***88.8*** | **48.8** | ***79.1*** | **<0.1** | ***3.0*** |

Table 2. Energy content (kilojoules per gram) for key prey species of gentoo penguins.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Family | Species | Energy (kJ g-1) | Source |
| Cephalopods | [*see Table 3 for species names*] | 4.27 | Clarke et al. (1985) |
| Fish | Channichthyidae | *Chaenocephalus aceratus* | 5.38 | Vanella et al. (2005) |
|  |  | *Champsocephalus gunnari* | 5.21 | Vanella et al. (2005) |
|  |  | *Pseudochaenichthys georgianus* | 4.55 | Vanella et al. (2005) |
|  | Myctophidae | *Electrona antarctica* | 7.93 | Donnelly et al. (1990) |
|  |  | *Electrona carlsbergi* | 6.57 | Clarke and Prince (1980) |
|  |  | *Gymnoscopelus nicholsi* | 9.80 | Lea et al. (2002) |
|  |  | *Krefftichthys anderssoni* | 8.23 | Cherel and Ridoux (1992); Tierney et al. (2002) (mean value) |
|  |  | *Protomyctophum bolini* | 6.10 | Data for *P. tenisoni* used (Lea et al. 2002) |
|  |  | *Protomyctophum choriodon* | 6.10 | Data for *P. tenisoni* used (Lea et al. 2002) |
|  | Nototheniidae | *Gobionotothen gibberifrons* | 4.89 | Vanella et al. (2005) |
|  |  | *Lepidonotothen larseni*  | 4.90 | Staniland et al. (2007) |
| Crustaceans | Euphausiidae | *Euphausia superba* | 4.65 | Clarke (1980) (mean of male and female) |
|  |  | *Thysanoessa macura* | 5.04 | Torres et al. (1994) |
|  | Hyperiidae | *Themisto gaudichaudii* | 3.10 | Ciancio et al. (2007) |

Table 3. Prey species recorded in the diet of gentoo penguins at Square Pond, Bird Island 1989-2010. Prey habitat is defined as benthic (B), bentho-pelagic (BP) or pelagic (P). Mean length is given as standard length for fish and mantle length for cephalopods. (-) Data not available (\*) Also found in macaroni penguin diets sampled at Goldcrest Point, Bird Island over the same 22-year period (see Waluda et al. 2012).

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|   | Family | Species | Prey habitat | N years | N samples | % frequency | mean length | Years present in diet |
| Cephalopods | Brachioteuthidae | *Brachioteuthis picta\** | P | 1 | 1 | 0.12 | - | 1994 |
|  | Octopodidae | *Pareledone turqueti* | B | 2 | 2 | 0.24 | - | 2000, 2009 |
|  | Onychoteuthidae | *Kondakovia longimana\** | P | 1 | 1 | 0.12 | - | 2009 |
| Fish | Bathydraconidae | *Parachaenichthys georgianus\** | B | 7 | 14 | 1.70 | 247 | 94,97,98,01,07,09,10 |
|  | Channichthyidae | *Chaenocephalus aceratus* | B | 1 | 1 | 0.12 | 374 | 2000 |
|  | Channichthyidae | *Champsocephalus gunnari\** | BP | 20 | 423 | 51.33 | 171 | 1991-10 |
|  | Channichthyidae | *Pseudochaenichthys georgianus\** | BP | 3 | 8 | 0.97 | 274 | 1997,00,09 |
|  | Harpagiferidae | *Harpagifer georgianus* | B | 1 | 1 | 0.12 | - | 2002 |
|  | Muraenolepididae | *Muraenolepis microps\** | P | 4 | 5 | 0.61 | 175 | 00,07,09,10 |
|  | Myctophidae | *Electrona antarctica\** | P | 7 | 10 | 1.21 | 60 | 94,00-04,09 |
|  | Myctophidae | *Electrona carlsbergi\** | P | 6 | 31 | 3.76 | 90 | 00,01,03,04,05,10 |
|  | Myctophidae | *Gymnoscopelus nicholsi* | P | 2 | 3 | 0.36 | 151 | 1997,2009 |
|  | Myctophidae | *Krefftichthys anderssoni\** | P | 4 | 4 | 0.49 | 66 | 97,04,07,10 |
|  | Myctophidae | *Protomyctophum bolini\** | P | 1 | 1 | 0.12 | 43 | 2009 |
|  | Myctophidae | *Protomyctophum choriodon\** | P | 6 | 20 | 2.43 | 62 | 94,97,03,08,09,10 |
|  | Nototheniidae | *Gobionotothen gibberifrons* | B | 3 | 5 | 0.61 | - | 00,01,10 |
|  | Nototheniidae | *Lepidonotothen larseni \** | BP | 19 | 270 | 32.77 | 89 | 1991-99,01-10 |
|  | Nototheniidae | *Notothenia coriiceps* | B | 1 | 1 | 0.12 | - | 1998 |
|  | Nototheniidae | *Notothenia rossii* | BP | 1 | 1 | 0.12 | - | 2002 |
|  | Nototheniidae | *Trematomus hansoni* | B |  2 | 2 | 0.24 | - | 2008,09 |
| Crustaceans | Crangonidae | *Notocrangon spp.\** | B | 10 | 20 | 2.43 | - | 1991-98, 2003, 2009 |
|  | Euphausiidae | *Euphausia superba\** | P | 22 | 698 | 84.71 | 49 | 1989-2010 |
|  | Euphausiidae | *E. frigida\*/Thysanoessa\**  | P | 6 | 39 | 4.73 | - | 1991, 1994, 2000, 2002, 2009, 2010 |
|  | Hyperiidae | *Themisto gaudichaudii\** | P | 19 | 164 | 19.90 | - | 1991-95, 1997-2010 |
|  | Hyperiidae | *Hyperiella antarctica* | P | 1 | 4 | 0.49 |  | 2004 |

Table 4. Frequency occurrence and percentage mass of the main crustacean (*Euphausia superba*) and fish (*Champsocephalus gunnari* and *Lepidonotothen larseni*) prey. No data are available on fish species present in 1989 and 1990. Data are summarised by year, with overall mean values (in bold) calculated for all individual samples.

|  |  |  |  |
| --- | --- | --- | --- |
|  | *E. superba* | *C. gunnari* | *L. larseni* |
| Year | % mass | *% freq* | % mass | *% freq* | % mass | *% freq* |
| 1989 | 80.8 | *100.0* | - | *-* | - | *-* |
| 1990 | 66.7 | *85.0* | - | *-* | - | *-* |
| 1991 | 20.0 | *62.2* | 70.4 | *24.3* | 1.1 | *5.4* |
| 1992 | 50.1 | *97.5* | 33.9 | *55.0* | 15.6 | *45.0* |
| 1993 | 83.8 | *97.5* | 15.4 | *20.0* | 0.5 | *12.5* |
| 1994 | 9.0 | *42.3* | 84.5 | *38.5* | 0.7 | *3.8* |
| 1995 | 58.8 | *75.0* | 39.5 | *55.0* | 1.5 | *10.0* |
| 1996 | 24.3 | *53.3* | 57.7 | *66.7* | 17.6 | *80.0* |
| 1997 | 36.2 | *88.1* | 60.4 | *81.0* | 3.2 | *57.1* |
| 1998 | 90.9 | *92.3* | 7.8 | *23.1* | 1.1 | *12.8* |
| 1999 | 36.4 | *61.5* | 63.2 | *51.3* | 0.0 | *0.0* |
| 2000 | 43.3 | *77.5* | 51.0 | *62.5* | 2.2 | *35.0* |
| 2001 | 35.4 | *84.6* | 61.0 | *71.8* | 3.6 | *66.7* |
| 2002 | 64.2 | *97.5* | 35.0 | *67.5* | 0.8 | *37.5* |
| 2003 | 40.6 | *92.5* | 53.4 | *67.5* | 4.7 | *42.5* |
| 2004 | 53.2 | *92.5* | 39.6 | *45.0* | 4.6 | *35.0* |
| 2005 | 32.2 | *82.5* | 63.1 | *52.5* | 4.5 | *52.5* |
| 2006 | 46.2 | *100.0* | 16.4 | *7.7* | 37.4 | *25.6* |
| 2007 | 58.4 | *97.5* | 36.7 | *52.5* | 4.6 | *47.5* |
| 2008 | 42.8 | *90.0* | 55.3 | *42.5* | 1.9 | *12.5* |
| 2009 | 11.9 | *50.0* | 59.1 | *33.3* | 5.9 | *26.7* |
| 2010 | 67.0 | *97.3* | 18.7 | *35.1* | 13.7 | *48.6* |
| **Mean** | **50.1** | ***84.6*** | **45.1** | ***51.3*** | **3.3** | ***32.8*** |

Table 5. Results of model fitting (diet versus breeding success) using linear regression [ $y=ax+b$] and two parameter non-linear least squares analysis [$y=b(1-e^{-ax})]$. *X* is calculated as (I) wet mass (g) (II) energy derived from prey (kJ) for each prey group and all diet components combined*.* Best fit for each parameter (corrected Aikaike Information Criteria (AICc)) indicated in bold. The correlation between model-predicted and observed values for breeding success is also given for each model.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
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|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | Wet mass (g) |  |  | Energy (kJ) |  |
|  | AICc | Correlation |  | AICc | Correlation |
| *Non linear model*  |  |  |  |  |  |
| All diet components | 37.17 | 0.46 |  | 37.33 | 0.46 |
| All crustaceans | 36.59 | 0.47 |  | 36.61 | 0.49 |
| **Krill (*E. superba*)** | **33.86** | **0.58** |  | **33.86** | **0.58** |
| All euphausiids | 36.96 | 0.47 |  | 36.36 | 0.49 |
| All fish | 40.06 | 0.31 |  | 40.13 | 0.31 |
| Fish + krill | 36.21 | 0.50 |  | 36.43 | 0.49 |
| *Linear model*  |  |  |  |  |  |
| All diet components | 38.60 | 0.40  |  | 38.06 | 0.39 |
| All crustaceans | 38.82 | 0.39 |  | 38.80 | 0.39 |
| **Krill (*E. superba*)** | **38.03** | **0.42** |  | **38.02** | **0.42** |
| All euphausiids | 39.00 | 0.38  |  | 38.70 | 0.39  |
| All fish | 41.11 | 0.24 |  | 41.11 | 0.23  |
| Fish + krill | 38.06 | 0.42 |  | 38.29 | 0.41  |

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|  |

Table 6. Comparison of annual variability in diets of gentoo (data from Square Pond, Bird Island) and macaroni penguins (data from Goldcrest Point, Bird Island; see Waluda et al. 2012), 1989 – 2010. Bold = result significant to P < 0.05.

|  |  |  |
| --- | --- | --- |
| Parameter | r | P |
| **Meal mass** | **0.532** | **0.011** |
| **Meal energy** | **0.587** | **0.004** |
| Crustacean mass (%) | 0.066 | 0.771 |
| Frequency of crustaceans (%) | -0.111 | 0.622 |
| Fish mass (%) | 0.071 | 0.754 |
| Frequency of fish (%) | 0.079 | 0.726 |
| **Krill (*Euphausia superba*) mass (%)** | **0.474** | **0.026** |
| **Frequency of krill (*E. superba*)(%)** | **0.576** | **0.005** |

Table 7. Summary of diet studies on gentoo penguinsduring the breeding season. Data are the percentage of diet by mass; this is given as an approximate mean value if the original study examined data over multiple years. (-) Prey type not recorded. \* Data from Lescroël et al. (2004) comprises diet samples during both winter and summer.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Location | Year(s) | Crustaceans | Fish | Cephalopods | Reference |
| Crozet (Posession Island) | 1980/81 | 54.2 | 43.9 | 1.8 | Ridoux (1994) |
| Falkland Islands (various sites) | 1986/87 to 1999/00 | 34 | 56 | 10 | Clausen and Pütz (2002) |
| Falkland Islands (various sites) | 1986/87 to 1998/99 | 36 | 53 | 11 | Pütz et al. (2001) |
| Falkland Islands (Cow Bay) | 2002/03/04 & 2011/12/13 | 4 | 80 | 14 | Handley et al. (2016) |
| Heard Island | 1986/87 | 7.8 | 90.5 | 1.7 | Klages et al. (1990) |
| Kerguelen | 1987, 1989 | 97.3 | 2.5 | - | Bost et al. (1994) |
| Kerguelen (Cape Ratmanoff) | 1987, 1989 | 60.8 | 24.8 | 12.5 | Lescroël et al. (2004)\* |
| Kerguelen (Morbihan Gulf) | 1987, 1989 | 16.2 | 79.2 | 0 | Lescroël et al. (2004)\* |
| Laurie Island | 1993, 95, 96 | 42 | 56 | 2 | Coria et al. (2000) |
| Macquarie Island | 1993/94 | 0.1 | 91.6 | 8.3 | Robinson and Hindell (1996) |
| Marion Island | 1984-85 | 44.4 | 53.5 | 2.1 | Adams and Klages (1989) |
| Marion Island | 1982, 84, 85 | 37 | 62 | 1 | Brown et al. (1990) |
| South Georgia (Bird Island) | 1977, 80, 85, 86 | 65.4 | 34.6 | - | Croxall et al. (1988b) |
| South Georgia (Bird Island) | 1988/89-2009/10 | 51.0 | 48.9 | 0.1 | Present study  |
| South Shetlands (King George Island) | 1978/79 - 1980/81 | 88.5 | 11 |  | Jablonski (1985) |
| South Shetlands (King George Island) | 1997/8-2003/4 | 98.4 | 1.6 | - | Miller et al. (2010) |
| South Shetlands (Livingston Island) | 1997/8-2003/4 | 70.8 | 28.8 | - | Miller et al. (2010) |
| South Shetlands (Livingston Island) | 2002-05, 2008 | 77 | 23 | - | Miller et al. (2009) |
| South Shetlands (Livingston Island) | 2007-2011 | 79 | 21 | - | Polito et al. (2015) |

FIGURE LEGENDS

1. Northern Scotia Sea with (a) South Georgia and the major fronts of the Antarctic Circumpolar Current (light grey) (b) Bird Island with location of 200 and 1000 m bathymetric contours (dark grey), and (c) Bird Island showing locations of gentoo penguin colonies at Square Pond and Johnson Cove.

2. Frequency occurrence of: (a) diet sample mass (b) number of species per sample (c) proportion of krill (*Euphausia superba*) in gentoo penguin diet samples from Square Pond, Bird Island 1989-2010.

3. Composition of gentoo penguin diets from Square Pond, Bird Island, 1989 to 2010. Diets are categorised as dominated by (> 90 % by mass of a diet sample) euphausiids, fish or ‘other’ (one sample dominated by cephalopods in 1994; one sample (per year) dominated by amphipods, *Themisto gaudichaudii* in 1991, 1999, 2003, 2004 and 2009) or as ‘mixed’ diets where no individual prey group contributed > 90 %.

4. Mean (±SD) annual breeding success (number of chicks fledged per nesting pair) of gentoo penguins at Square Pond, Bird Island from 1989 to 2010. Horizontal dashed line shows overall mean 1989-2010 = 0.92 chicks/nest.

5. Relationship between meal mass and breeding success (number of chicks fledged per nesting pair) for gentoo penguins breeding at Square Pond, Bird Island. Solid line shows fitted 2-parameter non-linear least squares model; $y=b(1-e^{-ax})$, where *X* = mean mass of krill in diet and *Y* = number of chicks fledged per nest.

6. Observed proportion of Antarctic krill in gentoo versus macaroni penguin diets at Bird Island, 1989 to 2010. Diet samples taken from Square Pond and Goldcrest Point colonies respectively. Regression (solid line) and 95 % confidence intervals (dashed line) shown; r = 0.47, P = 0.026.









