

PENGUINS: PARADOXES AND PATTERNS

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SUMMARY

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Penguins are often considered to be as ecologically and behaviourally homogenous as their morphology. Their structural morphology and associated physiological adaptations are governed by the demands of operating as flightless, subsurface marine predators. However, within the very strict constraints of this life-form, penguins show considerable ecological and behavioural heterogeneity, although some of this undoubtedly relates to the range of latitudes and biotopes in which penguins breed. In this paper we: (i) briefly summarise and review some of the main features of the breeding biology, ecology and demography of penguins; (ii) identify consistent patterns across species in the grouping of these features – and highlight anomalies; (iii) suggest explanations/hypotheses for some of the potential links between ecology, behaviour and demography within these groupings; (iv) investigate six topics containing potential paradoxes, namely: migration, fasting, mate fidelity, brood reduction, demography and duration of breeding seasons. We conclude that in many biological and ecological traits penguins can be divided into two groups: (i) resident species, feeding inshore with short fasts ashore, breeding at an early age and having low divorce rates, and; (ii) migrant species, feeding offshore with long fasts ashore, breeding at older ages and having higher divorce rates. The placement of Magellanic *Spheniscus magellanicus* and Gentoo *Pygoscelis papua* Penguins in opposite groups to their congeners is particularly intriguing. We suggest that trade-offs between the year-round abundance and predictability of prey and the latitudinally-influenced time available for breeding are important determinants of these patterns. Considerably improved basic biological and ecological data on penguins and careful testing of explicit hypotheses will be required to investigate further both the suggested patterns and the remaining paradoxes.

INTRODUCTION

Penguins are often considered to be as ecologically and behaviourally homogenous as their morphology. Their structural morphology and associated physiological adaptations are governed by the demands of operating as flightless, subsurface marine predators. However, within the very strict constraints of this life-form, penguins in fact show considerable ecological and behavioural heterogeneity. Some of this undoubtedly relates to the range of latitudes and biotopes in which penguins breed, ranging from Antarctic ice-shelves, through cool temperate sub-Antarctic islands to warm temperate, even subtropical, coasts, and to the equator itself. Nevertheless, even allowing for this, in some of their potentially more fundamental ecological and demographic attributes, penguins show a surprising degree of interspecies variation. This variation contains a number of apparent paradoxes.

Paradoxes

1. Migration

Except in the very highest latitudes, where breeding sites are ice-bound during winter, open water feeding habitat surrounds penguin breeding sites at all times. At similar latitudes and in broadly equivalent biotopes, some penguin species are migrants, visiting their colonies only for breeding (e.g. Emperor *Aptenodytes forsteri*, Magellanic *Spheniscus magellanicus*, crested *Eudyptes* spp.), whereas other species are year-round

residents (e.g. African *S. demersus*, Gentoo *Pygoscelis papua*, Little *Eudyptula minor*, Yellow-eyed *Megadyptes antipodes*).

2. Fasting

Penguins have very substantial capacities for storing body reserves while at sea and then fasting ashore for lengthy periods. All species fast throughout moult for periods ranging from 13–40 days. However, during the breeding season, fasts ashore in the pre-laying and/or incubation periods regularly last 25–40 days in some species (e.g. Adélie *P. adeliae*, Magellanic, King *A. patagonicus* and all crested penguins – not to mention c. 100 days in male Emperor Penguins), whereas other species of similar size (e.g. Gentoo, Yellow-eyed *Megadyptes antipodes*) undertake only very short (< 3-day) fasts during these periods, even though they are clearly physiologically capable of much longer fasts.

3. Mate fidelity

It is virtually a tenet of behavioural ecology that for long-lived vertebrates the maintenance of a pair-bond with the same individual across years enhances reproductive success. However, while mate fidelity is indeed high for most penguin species, there is a great deal of variation, with 'divorce' rates ranging from <20% (e.g. Galapagos *S. mendiculus*, Gentoo, Magellanic, Yellow-eyed) to >80% a year (e.g. Emperor, King). Furthermore, there is little evidence that penguins that retain their partners enjoy improved reproductive success. Any

attempt to explain the levels of mate fidelity in penguins must, therefore, provide a reason that would promote partners reuniting, and explain the high degree of variation between species.

4. Brood reduction

All penguins, except Emperor and King, lay two eggs, often of different sizes, usually three days apart. The likelihood of chicks of different sizes hatching asynchronously, with the resulting potential competitive advantage to the first-hatched chick, is a classic basis for subsequent brood reduction (i.e. a situation where the second-hatched chick only survives in years when it can receive adequate food after its older sibling has been satisfied). However, despite their common basis, penguin species show a wide variety of outcomes, including brood reduction during incubation, invariable loss of one chick, typical, flexible brood reduction, and no evidence of brood reduction at all.

5. Demography

Longevity and the age at which breeding starts are usually closely linked, with species that start breeding later in life normally having higher survival and vice versa. Lifespan and the duration of sexual immaturity are also often closely related to the size of animals. In penguins, although the largest two species, Emperor and King, have higher annual adult survival rates (0.90–0.95) than the rest (0.80–0.85), there is no clear pattern within the latter group. Furthermore, variation in mean age at first breeding, ranging from three years (Gentoo, Little, Yellow-eyed) through five-to-six years (Adélie, Emperor, King, Magellanic) to more than seven years (Macaroni *Eudyptes chrysolophus*, Royal *E. schlegeli*, Snares Crested *E. robustus*), seems inconsistent with survival rate and lacking any relationship with size.

6. Time taken for breeding

It might reasonably be expected that the time taken for breeding would change with latitude, reflecting the smaller window of opportunity available at higher latitudes. Whereas this may indeed be the case for penguins breeding during the summer at the very highest latitudes (e.g. Adélie), no such correspondence is immediately apparent at latitudes lower than Antarctica. For example, Yellow-eyed Penguins take from 38–50% longer to incubate their eggs and rear their chicks to fledging than do the similarly-sized Fiordland Crested *E. pachyrhynchus*, Snares Crested and Magellanic Penguins breeding at similar latitudes.

Patterns

In this paper we try to:

- a. briefly summarise and review some of the main features of the breeding biology, ecology and demography of penguins;
- b. identify consistent patterns across species in the grouping of these features – and highlight anomalies;
- c. suggest explanations/hypotheses for some of the potential links between ecology, behaviour and demography within these groupings;
- d. assess which of the ‘paradoxes’ above may now be more explicable and which still require further research even to construct adequate hypotheses.

Our approach to this paper – as to the opening keynote address to the Third International Penguin Conference in Cape Town, South Africa in September 1996, on which it is based – is,

against the background of current knowledge of the biology and ecology of penguins, to highlight interesting problems and suggest hypotheses in order to stimulate new research. We do not intend to provide any rigorous analysis of available numerical data for penguins, but simply to provide sufficient empirical evidence to justify our assertions and conclusions. In the interests of clarity and readability we have mainly confined references to papers and data not already summarised or included in Williams (1995).

METHODS

General

Data, summarised in Appendix 1, are derived chiefly from Williams (1995), additionally from the sources indicated. We used the same species concept as Williams (1995). In general we used the midpoint of values presented as ranges and took the average of means where data for several years were available for the same site. Where data with broadly similar values were available for several sites, we used those with the largest sample size or from the site with the most complete set of data for other parameters.

In selecting data for analysis we used, wherever possible, comprehensive data from a single study and/or site. There are quite substantial intersite differences in some parameters, particularly between latitudinally well-separated populations (e.g. Adélie Penguin at sites on the Antarctic Continent and Antarctic Peninsula, Magellanic Penguin between northern and southern Argentina, King, Gentoo and Macaroni Penguins between Atlantic and Indian Ocean sites, the different subspecies of Rockhopper Penguin *E. chrysocome*) but published data are at present inadequate to assess critically the effects and significance of this.

Specific

For body mass, wherever possible we used values for breeding birds when they first arrived ashore at the beginning of the breeding season. This reduces the problem of selecting comparable values across species that show very different – and often very substantial – patterns of mass change during the breeding season. For six species (African, Erect Crested *E. sclateri*, Galapagos, Humboldt *S. humboldti*, Snares, Yellow-eyed) no such data are available and we had to use the next most comparable values.

For incubation shift we used the first shift after egg-laying where only one partner was ashore (i.e. excluding the first period of incubation by crested penguins when both sexes are in attendance).

With moult, we were interested in the duration of the fast ashore, not in the process of moult itself. These are not the same because at least Macaroni and Rockhopper Penguins come ashore when moult has already started, whereas Adélie and Gentoo Penguins appear to spend a day or two ashore before signs of moult become evident.

For resident species, as the longest fast ashore, excluding moult, we used the mean incubation shift.

The relationships we examine are primarily to illustrate some of the topics we investigate. They are not rigorous analyses, often due to lack of comprehensive data. They do not take into

consideration phylogenetic issues (e.g. the potential lack of independence of data from congeneric species). Because we are mainly dealing with broad-scale (often generic level) relationships we do not believe that our conclusions are misleading from this perspective. Given the small number of genus-level groups in the Spheniscidae, further analysis at this level may not be too productive.

RESULTS AND DISCUSSION

Availability of data

Despite the prodigious literature on penguins, data on many aspects of their biology and ecology remain either unstudied or unpublished. The species which are most poorly documented are Humboldt and Erect Crested Penguins. There are also substantial omissions in basic biological data even for well-studied species like African and Chinstrap *P. antarctica* Penguins. For rather few species are data on survival rates and other demographic parameters more than indicative of likely values prevailing and this whole area needs critical study. The compilation in Appendix 1 should at least highlight some of the current gaps in our knowledge of the basic elements of penguin biology and, we hope, stimulate those with, or able to collect, such data to make them available.

Patterns

Although we use much of the data in Appendix 1 in exploring interactions between different variables, gaps in data mean that different, and by no means all, species appear in the various graphical presentations. Furthermore the variability inherent in some of the relationships makes it difficult to discern broad-scale patterns. Therefore, in Table 1 we have tried to categorise very simply the status of penguin species in respect of a range of biological, ecological and behavioural variables, relevant to the paradoxes we are trying to examine.

Table 1 suggests that penguins fall broadly into one of two groups. One group of species (African, Galapagos, Gentoo, Little, Yellow-eyed – and presumably also Humboldt) are

essentially resident at their breeding sites, undertake only short foraging trips to sea and correspondingly brief fasts ashore, breed at an early age and have a low divorce rate thereafter. In contrast, the other species in the family migrate away from their breeding sites for part of the year, make longer foraging trips to sea and undertake long fasts ashore during the courtship and/or incubation period. They start breeding when older and, except for Magellanic Penguins, have higher divorce rates. Overall, the positions of Gentoo and Magellanic Penguins are of particular interest, in that both fit in the opposite group to that with the rest of their congeners, suggesting that ecological rather than phylogenetic factors may be the most important determinants of the life history and behavioural patterns exhibited by penguins.

The ecological feature that most clearly differentiates the two groups is that the members of the resident group are generally inshore feeders, whereas the others are offshore feeders. This difference is especially apparent during the incubation period. Foraging trip duration is apparently a reasonable predictor of distance travelled from the nest site (Wilson 1995), and the mean duration of the first foraging trip during incubation is significantly less for the resident group (1.6 d, SD = 0.5, median = 1.7, n = 6) compared to the migrants (18.3 d, SD = 16.5, median = 13.0, n = 10) (Mann-Whitney U-test: Z = 3.26, P = 0.001). The necessity to feed chicks regularly places limits on how long a parent can be away from the nest during chick-rearing. Nevertheless, penguins constituting the migrant group are away significantly longer (3.0 d, SD = 4.0, median = 1.55, n = 8) than those in the resident group (0.5 d, SD = 0.07, median = 0.5, n = 5) (Mann-Whitney U-test: Z = 2.95, P < 0.01), suggesting that they forage farther afield even then. Data from electronic positioning devices attached to foraging penguins generally confirm this relationship (Appendix 1), with breeding birds from the resident group seldom travelling more than 20 km from the colony, while breeding birds from the migrant group can travel hundreds of kilometres from their breeding sites during incubation.

Having classified penguins as either inshore or offshore feeders, we can now evaluate their adaptations in relation to theoretical predictions about life history and behavioural

TABLE 1

Diagrammatic representation of distribution of biological and ecological characteristics amongst the species of penguins. ● = characteristic present; ○ = characteristic absent; Ⓛ = characteristic intermediate. ?: conclusive data unavailable. Note that all entries are for single species, except Crested, which covers all species in the genus *Eudyptes*

Penguin species	Resident	Inshore	Short fast	Breed young	Faithful	Long fledge	Egg dimorphism	Lay interval	Brood reduction
Gentoo	●	●	●	●	●	●	○	○	○
Yellow-eyed	●	●	●	●	●	●	○	○	○
Little	●	●	●	●	●	○	○	○	○?
Galapagos	●	●	●	●	●	○	○	●	●
African	●	●	●	●?	★	★	○	●	●
Humboldt	●	●	●				○	○	○
Chinstrap	○	★	★			○	○	○	○
Adélie	○	○	○	★	★	○	●	★	○●
Magellanic	○	○	○	★	●	○	○	●	●
Crested	○	○	○	○	★	○★	●	●	●
Emperor	○	○	○	★	○	○	–	–	–
King	○★	○	○	★	○	●	–	–	–

differences between inshore and offshore feeders, developed for flying seabirds (Lack 1968, Furness & Monaghan 1987, Ricklefs 1990). Briefly, offshore feeders tend to breed in larger and more widespread colonies, have smaller clutches, longer incubation periods, fledging periods, incubation shifts and foraging trips, start breeding at older ages and have lower adult mortality.

Migration

Remaining around the breeding site all year is characteristic of the six inshore-feeding species (African, Galapagos, Gentoo, Humboldt, Little, Yellow-eyed). Although it seems reasonable that access to a close year-round food supply should be a prerequisite for being resident, it is not at all clear why inshore feeders should necessarily be residents. Certainly the most southerly populations of Gentoo (their breeding sites being ice-bound during winter) and Little Penguins are not strictly resident all year-round, and move away from the breeding areas for at least some of the non-breeding period. Most of the inshore-feeding species breed at lower latitudes where the environment presumably provides fewer constraints (e.g. in terms of seasonal availability of food and climate) necessitating birds leaving the area altogether. In addition there is a greater extent of continental shelves at lower latitudes in the southern hemisphere, presumably assisting year-round exploitation of this habitat (M. de L. Brooke *in litt.*). Nevertheless, whereas some inshore-feeding penguins have been recorded to breed in almost all months of the year, Gentoo, Yellow-eyed and, in most locations, Little Penguins are highly seasonal breeders. Furthermore, all sub-Antarctic populations of Gentoo Penguins are resident, contrasting markedly with the various species of crested penguins which breed with them and are strictly migratory.

Apart from the situation where Antarctic species like Adélie Penguins are forced to migrate because their sites become surrounded by impenetrable pack-ice, one might nevertheless expect the prey species to be most susceptible to seasonal changes at higher latitudes. It may be that at higher latitudes the highly seasonal reproduction or availability of the prey species means that they are only found close to shore in sufficient quantities for a very limited period of time: sufficient to support chick rearing, but otherwise forcing the penguins to forage farther offshore outside the chick-rearing period. Thus, species in higher latitudes will generally have shorter breeding seasons and be more liable to migrate.

Where there are apparent paradoxes such as that between sympatric populations of the inshore and resident Gentoo Penguins and the offshore and migrant crested penguins that co-exist in the sub-Antarctic, it should be instructive to examine differences in their diets.

At South Georgia (based on 12 years of diet sampling) both Macaroni and Gentoo Penguins predominantly feed on Antarctic Krill *Euphausia superba* and of very similar length-frequency distribution (although Macaroni Penguins also sometimes take size classes of krill smaller than those taken by Gentoo Penguins). For Macaroni Penguins krill forms a greater and more consistent proportion of the diet (95%) than for Gentoo Penguins (69%). In years when krill is scarce around South Georgia, Macaroni Penguins take increased proportions of the amphipod *Themisto* (one-third the length, one-tenth the mass of adult krill); in such years they can usually catch sufficient prey to achieve comparable breeding success to years of normal krill availability, but with meal mass and

chick mass at fledging significantly reduced. In contrast, when krill is scarce Gentoo Penguins increase the proportion of fish in their diet but the size of meals decreases substantially and comprehensive breeding failure usually results (Croxall *et al.* 1999).

Data on zooplankton distribution and abundance at South Georgia do not suggest that *Themisto* is more abundant offshore but the main fish species eaten by Gentoo Penguins (icefish *Champsocephalus* sp., notothenioids) are confined to the continental shelf. It would be tempting to suggest that the virtual absence of (and lack of obvious adaptations for) piscivory in Macaroni Penguins is responsible for their offshore distribution, and that in winter they need to range farther afield to subsist on scarcer/more dispersed crustacean resources. However, in winter Gentoo Penguins take as much, if not more, krill than in summer (Williams 1991, S. Berrow unpubl. data) and the krill fishery around South Georgia typically occurs in winter, so this hypothesis is difficult to sustain. One might speculate that the original co-existence between these species may have been based on piscivory in Gentoo Penguins and planktivory in Macaroni Penguins, but that both can subsist on a common resource (krill) at a location where it is consistently highly abundant.

While it is very probable that species which migrate do so to maintain access to adequate food supplies, there has only been one study of the diet of a migratory penguin species outside the breeding season. Ainley *et al.* (1992, 1994) found that the diet of Adélie Penguins wintering in the Marginal Ice Zone comprised more fish and squid than krill (their staple summer diet). Quantifying changes in food availability around breeding sites and the nature of penguins' diet in their wintering areas will be important requirements to understanding why there is such a marked dichotomy between migratory and resident species of penguins. It is certainly one which cannot solely be explained by invoking the effects of the physical environment.

Fasting

Larger birds can store proportionately more reserves than smaller ones and consume them at a proportionately slower

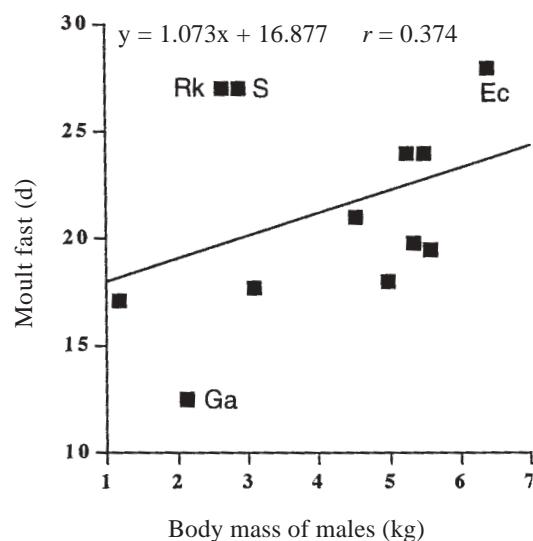


Fig. 1. Relationship between body mass (males) and duration of moult fast in penguins (excluding *Aptenodytes* spp.).

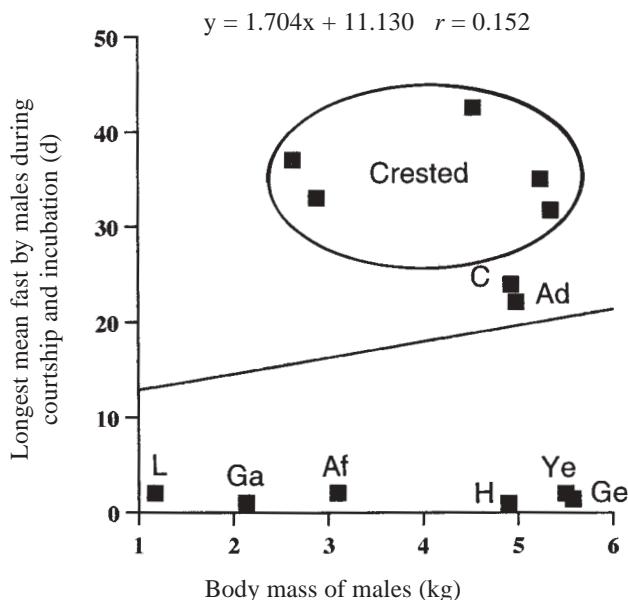


Fig. 2a. Relationship between body mass (males) and longest mean fast by males during incubation and courtship (excluding *Aptenodytes* spp.).

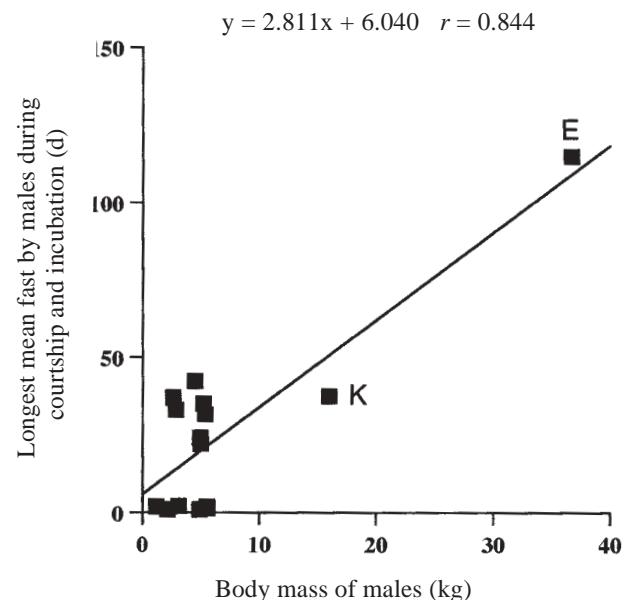


Fig. 2b. Relationship between body mass (males) and longest mean fast by males during incubation and courtship.

rate. If Emperor and King Penguins are excluded, then body mass explains less than 15% of the variation in the duration of the moult fast (Fig. 1). For their mass, Erect Crested, Rockhopper and Snares Crested Penguins appear to have relatively long moult fasts and Galapagos Penguin a disproportionately short one. Furthermore, body mass explains less than 3% of the variation in duration of the longest fasts undertaken by species as part of the rest of their breeding cycle (Fig. 2a). Therefore we conclude that the typical fast durations shown by penguins, with the probable exception of the Emperor Penguin and crested penguins (Fig. 2b), do not relate to constraints imposed on body reserves by the size of the bird. Figure 2a shows clearly the distinction between the six inshore-feeding resident species with short fasts and the remainder.

In addition, there is a strong relationship ($r^2 = 0.71$, $df = 9$, $P < 0.05$) between the duration of the fast of the first incubation shift (which is also a measure of the duration of the partner's first foraging trip during incubation) and foraging trips to sea during chick-rearing (Fig. 3). This reinforces the notion that those species which regularly store large energy reserves as essential components of lengthy incubation shifts, are basically offshore foragers: those species that go farthest during incubation to get food, also travel farthest during chick-rearing.

The time spent at sea prior to moult does not seem to relate to the duration of previous foraging trips (Fig. 4a), nor does it appear to relate to the subsequent duration of the moult fast itself (Fig. 4b), though there are trends in these directions.

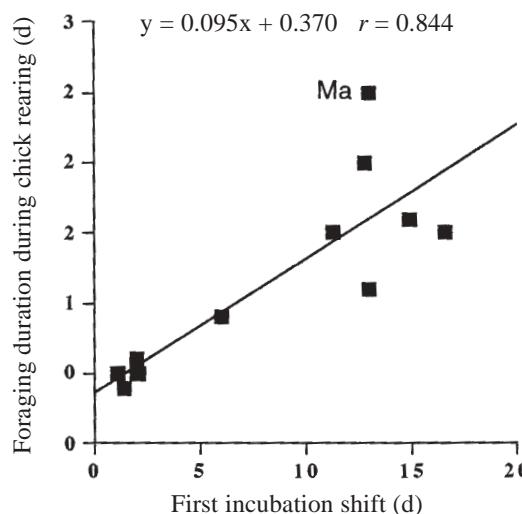


Fig. 3. Relationship between duration of first incubation shift and foraging trip duration during chick rearing (excluding *Aptenodytes* spp.).

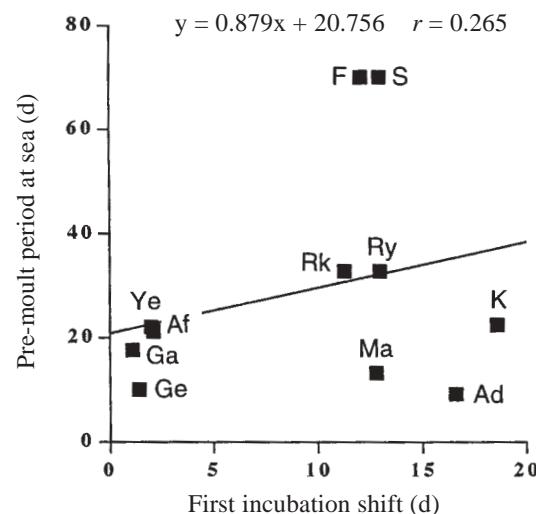


Fig. 4a. Relationship between duration of first incubation shift and pre-moult period at sea.

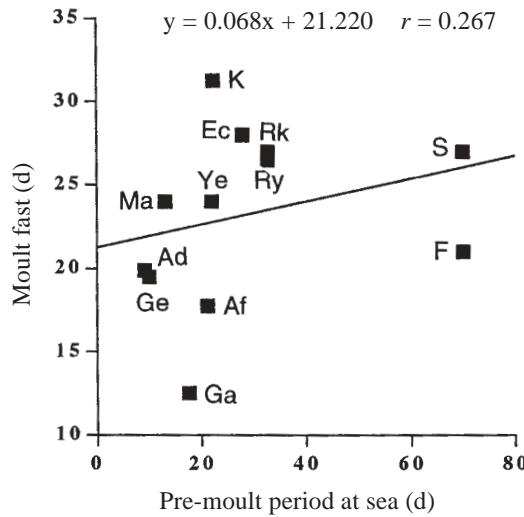


Fig. 4b. Relationship between duration of pre-moult period at sea and duration of moult.

Nevertheless other considerations must be involved, possibly relating to some combination of reserve replenishment after breeding and/or additional reserve acquisition for the post-moult recovery at the onset of winter. In addition the premoult period at sea does not appear to be obviously influenced by the time available for breeding inasmuch as it bears no relationship either to the time taken for breeding (Fig. 5a) or to latitude (Fig. 5b). This might suggest that foraging during the pre-moult period is governed by factors independent from the breeding period, perhaps indicating that birds are foraging in different locations or affected by temporal changes in the availability of prey. Unlike other fasts, that during moult cannot be abandoned prematurely without risk of prejudicing survival, so the acquisition of adequate body reserves is probably a greater priority than at any other time in the annual cycle. The complete lack of data on differences in prey, foraging location and foraging intensity between incubation/chick-rearing birds and pre-moult ones makes further speculation difficult.

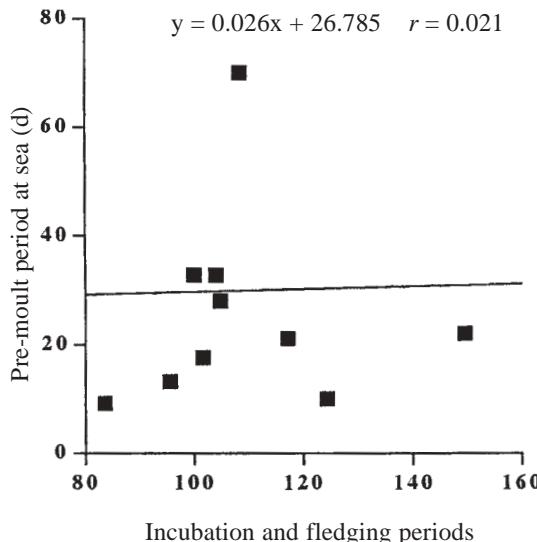


Fig. 5a. Relationship between combined duration of incubation and fledging periods and duration of pre-moult period at sea (excluding Aptenodytes spp.).

The presence of predators on penguins in the vicinity of breeding colonies has been suggested as a reason why some species should reduce the number of times they transit to and from their colony. However the frequent occurrence at the same site of species showing both extremes of fasting patterns (e.g. Gentoo and crested penguins) makes this an unlikely explanation.

Further investigation of why penguins which are physiologically capable of lengthy fasts (e.g. during moult) do not use this ability during the rest of the breeding cycle, may need to await quantitative data on the distribution and rate of acquisition of food, the nature of foraging tactics (e.g. in terms of patch location and exploitation times), the relationship between body shape and mass and the energy cost of transport and the costs of transferring material to and from reserve stores.

Mate fidelity

The main advantage to penguins of reuniting with a previous partner comes not from the benefit of improved reproductive output but from avoiding the costs of finding a new mate. Studies have shown that penguins which separate from their previous partner (either because of death, absence or 'divorce') have a lower probability of mating than do birds that re-unite with their former partners. According to models (Davis & Speirs 1990) used to predict the pattern of pair formation in Adélie Penguins for established breeders (i.e. penguins that have bred the previous season), males have a high degree of nest-site fidelity and return to the nests they used the previous season. Males are non-discriminating in their choice of partner and will remain on their nest and court any available female until paired. Females, in contrast, will return to the vicinity of their previous nest-sites and will mate with last season's partner if he is there, but otherwise they will choose a new partner nearby. This model appears to hold true for other penguins with fixed nest sites such as Macaroni (Williams & Rodwell 1992) and Fiordland Crested Penguins (L.S. Davis *et al.* unpubl. data).

The most extreme situation that has so far been well-documented is that for the King Penguin (Olsson 1998), which

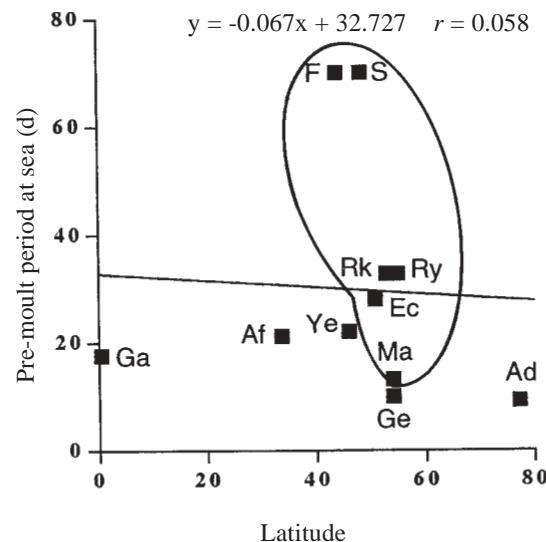


Fig. 5b. Relationship between mean breeding latitude and duration of pre-moult period at sea.

lacks a fixed nest site. Divorce was highly correlated with the degree of asynchrony in arrival, being *c.* 50% if birds arrived <5 days apart, compared with 100% if arrival was separated by >14 days. There was a significantly higher divorce rate for birds failing at their previous breeding attempt (84%) than for those that had successfully reared a chick (64%). Nevertheless divorce rates are still relatively high, even for birds which return more or less simultaneously having bred successfully previously. The high frequency of mate change is suggested to result from stochastic features of the pattern of arrival, promoting a situation where acquisition of a partner is more important than taking time to undertake mate quality assessments; this results in many birds changing partners at the next opportunity.

Hence, the factors that determine whether a female re-unites with her previous partner will be: (a) her ability to return to her former nest site; and (b) the probability that the male will already be in attendance when she arrives.

From the above we can predict:

- That mate fidelity will be high for the inshore-feeding residential species of penguins. If the nest site provides the mechanism by which penguins can reunite, then the prospects of mate retention are enhanced by never being away from the nest site for very long throughout the breeding period and by continuing to remain residents throughout the non-breeding period. Although sample sizes are small due to a lack of appropriate data from some species, there is nevertheless a tendency for the resident species to have lower divorce rates ($\bar{x} = 11.3\%$, $SD = 5.3$, $n = 4$) than the migratory species ($\bar{x} = 39.7\%$, $SD = 31.8$, $n = 6$) (Mann-Whitney U-test: $Z = 1.706$, $P < 0.1$).
- Migratory species (offshore feeders) without fixed nesting territories (i.e. Emperor and King Penguins) are predicted to have extremely low levels of mate fidelity because they lack any mechanisms to provide an accurate rendezvous point. Divorce rates in these two species exceed 75%.
- That for migratory species with fixed nesting territories, the amount of time a female initially spends on a nest territory

will influence her ability to return to that nest site the following season (i.e. the degree of nest-site attachment that she shows). Where females initially spend long amounts of time at the nest (as measured by the period of fasting between arrival at the colony to breed and first departure), they develop strong nest-site attachment and exhibit high mate fidelity (Fig. 6a).

- Further, the probability of the male being there when the female arrives will depend upon the degree of asynchrony in the mean arrival dates of males and females for migratory species that use fixed nesting territories. Where males arrive much earlier than females, there will be an increased likelihood of the male being there when the female arrives and, therefore, a higher probability of reuniting (Fig. 6b).

Brood reduction

The available data (Appendix 1) indicate that substantial (>5%) egg size dimorphism occurs only in the Adélie Penguin (first egg 8% larger) and crested penguins (first egg 17–44% smaller). All species show a substantial (the longest in any group of birds) interval between laying the first and second egg. This interval is longest (>4 d) in the Yellow-eyed and crested penguins (despite the latter's first egg being proportionately so much smaller than in other penguins) and shortest (<3 d) in the Little Penguin (which has the largest eggs relative to its body mass of any penguin). This suggests that rate of egg production is unlikely to be the limiting step in determining laying interval.

Hatching intervals are much shorter than laying intervals in all species, except African (where they are the same) and Galapagos Penguins, being about one half as long in *Pygoscelis* spp. (especially Adélie), Little and Magellanic Penguins. In crested penguins, when both eggs hatch the second usually does so before the first. The reasons for these differences amongst species are unclear (see St Clair 1996), though some relationship with environmental temperature might be possible. One might predict that in high latitudes incubation should start as soon as the first egg is laid (to avoid risk of chilling); in lower latitudes ambient temperatures may be high enough

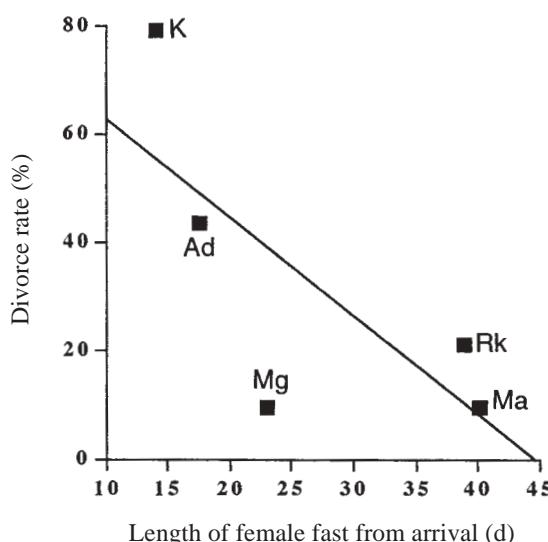


Fig. 6a. Relationship between duration of the initial period females spend on the nesting territory (i.e. excludes Emperor Penguin) and mean annual divorce rate for migratory species of penguins.

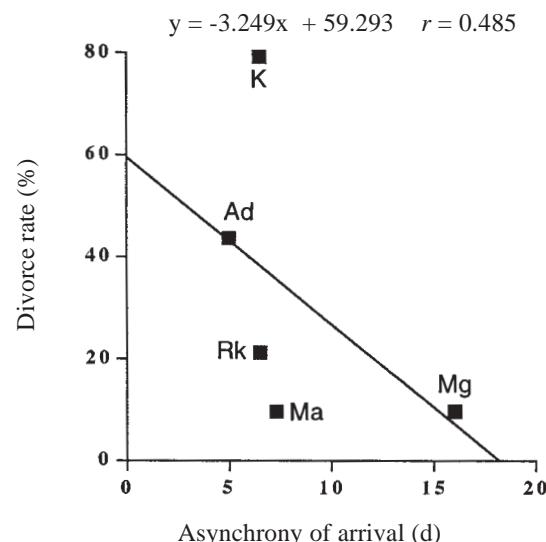


Fig. 6b. Difference in mean arrival dates of males and females for migratory species that use nesting territories (i.e. excludes Emperor Penguin) and mean annual divorce rate.

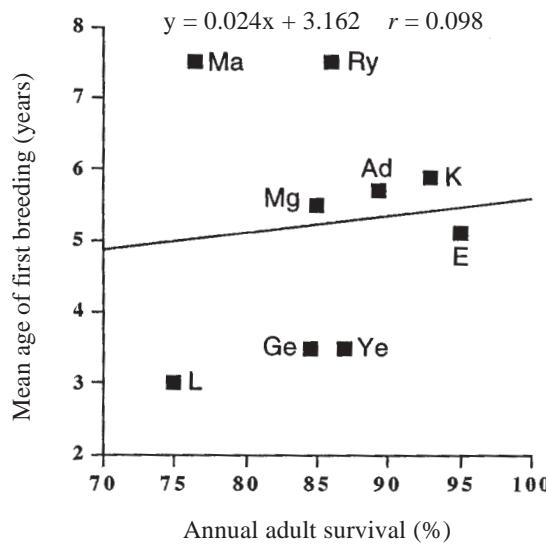


Fig. 7a. Relationship between mean annual adult survival rate and mean age of first breeding.

to avoid parents having to incubate immediately. However the reduced hatching interval in *Pygoscelis* species and the differences between African, Galapagos and Magellanic Penguins do not support this.

Nevertheless, hatching intervals ranging from 1–3 days still offer scope for potential brood reduction. Excluding crested penguins, the three species with best evidence for brood reduction (African, Galapagos, Magellanic) have the longest hatching intervals (3.2, 3 and 1.9 days, respectively) compared with intervals of 0.75, 1.4 and 1.5 days in Little, Yellow-eyed and Gentoo Penguins, respectively, the species for which there is the best evidence for lack of brood reduction. Although this may indicate some potential (albeit rather tenuous) relationship between incubation behaviour influencing hatching interval to assist (or not) the development of sibling size differences at hatching, this difference will only persist if there is sibling competition or differential parental investment. Furthermore it remains unclear why the mechanism should be confined to *Spheniscus* species and absent in other species,

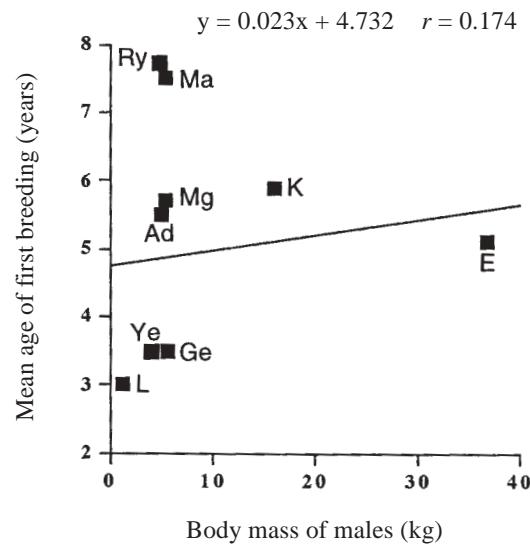


Fig. 7b. Relationship between mean body mass (males) and mean age of first breeding.

some of which are broadly similar in terms of ecology and breeding habitat/environment.

The enigma of brood reduction in crested penguins, whereby the second egg is the large one, and many (most, if not all, in Macaroni and Royal Penguins) first eggs are lost before hatching and two chicks are rarely reared to fledging, still eludes any convincing overall explanation. The numerous hypotheses advanced (reviewed in Williams 1995) all have either proved invalid when tested in the field or clearly inapplicable to all species of crested penguins, particularly the Macaroni Penguin, which shows the most extreme pattern in the group. Even the discovery of deliberate ejection of the small first-laid eggs (St Clair *et al.* 1995) and detailed experimental investigation of the reversed hatching asynchrony (St Clair 1996), which may help understand the mechanisms involved, do not explain the phenomenon. Furthermore, recent phylogenetic work (Edge *et al.* 1996) indicates that delays in incubation and brood patch formation have arisen independently of reduction in size of the first laid egg.

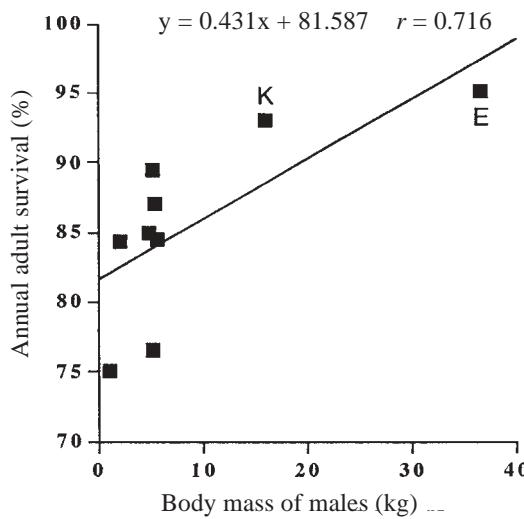


Fig. 8a. Relationship between mean body mass (males) and mean annual adult survival rate.

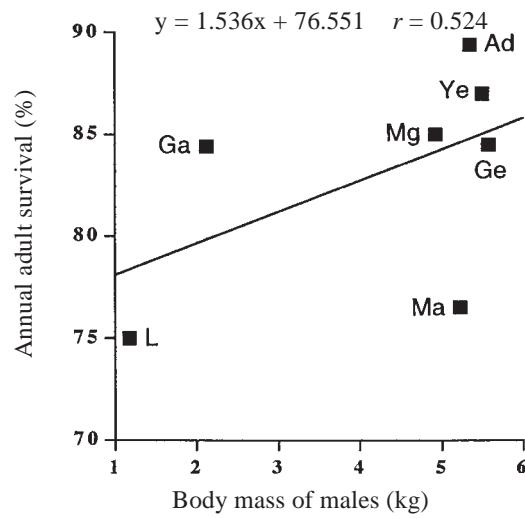


Fig. 8b. Relationship between mean body mass (males) and mean annual adult survival rate (excluding *Aptenodytes* spp.).

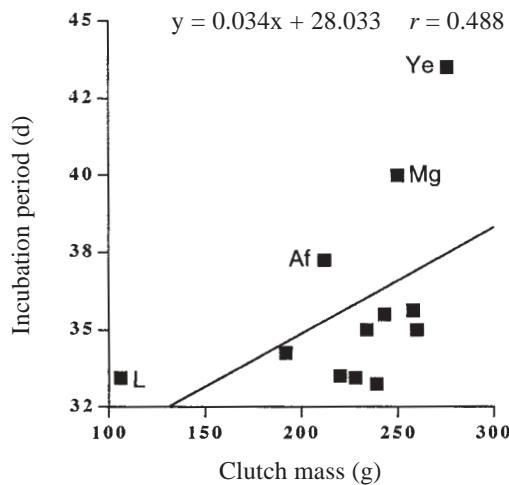


Fig. 9. Relationship between mean clutch mass and duration of incubation period (excluding *Aptenodytes* spp.).

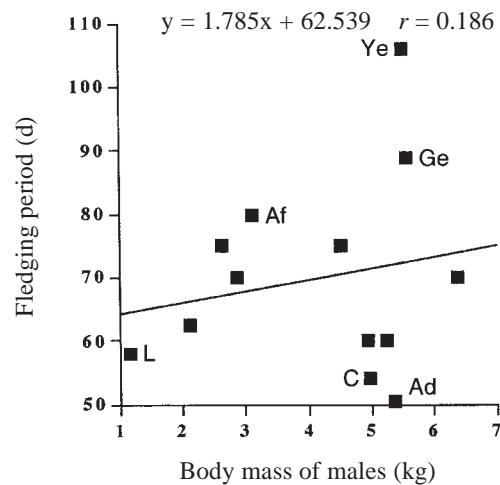


Fig. 10. Relationship between mean body mass (males) and mean duration of fledging period (excluding *Aptenodytes* spp.).

Demography

There is no clear relationship between mean annual adult survival rate and age of first breeding (Fig. 7a), nor is there any significant relationship between the latter and body size (Fig. 7b), although there are trends in these directions. However, annual survival is higher in larger penguins (Fig. 8a) and this relationship appears to hold even when Emperor and King Penguins are excluded (Fig. 8b), although data for most species are still relatively imprecise.

Mean age of first breeding is highly variable and species seem divisible into two distinct groups. Resident, inshore species breed at an earlier age ($x = 3.3$ years, $SD = 0.3$, $n = 3$) than the off-shore, migratory species ($x = 6.2$ years, $SD = 1.0$, $n = 6$) (Mann-Whitney U-test: $Z = 2.34$, $P < 0.02$).

Time taken for breeding

Appropriate and indicative relationships between date of return to the colony and breeding latitude in Adélie Penguins (Williams 1995) and between egg-laying date of Rockhopper

Penguins and mean sea surface temperature (Warham 1975) already exist. However relationships involving the duration of incubation and fledging (chick-rearing) period are more complex, not least because the potential effect caused by differences in species' body size needs to be taken into account.

Thus the duration of incubation is significantly affected by clutch mass, which accounts for 75% of the variation if Emperor and King Penguins are included and 25% if they are excluded (Fig. 9). Body size has only a very weak relationship with the duration of the fledging period (Fig. 10). It might be expected that fledging period should decrease with increasing latitude, given the more abrupt seasonality at higher latitudes. However, relating latitude to fledging period accounts for less than 5% of the variation in fledging. Nevertheless, if the two extreme penguins in terms of body size (Emperor and King) are excluded, migratory offshore feeding species of penguins do exhibit shorter fledging periods at higher latitudes (Fig. 11a). By contrast, for the resident inshore-feeding species, fledging periods tend to increase with increasing latitude (Fig. 11b).

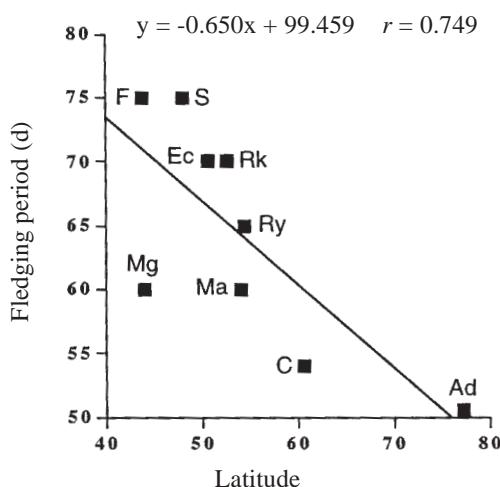


Fig. 11a. Relationship between mean breeding latitude for migratory offshore-feeding penguin species (excluding *Aptenodytes* spp.) and mean duration of fledging period.

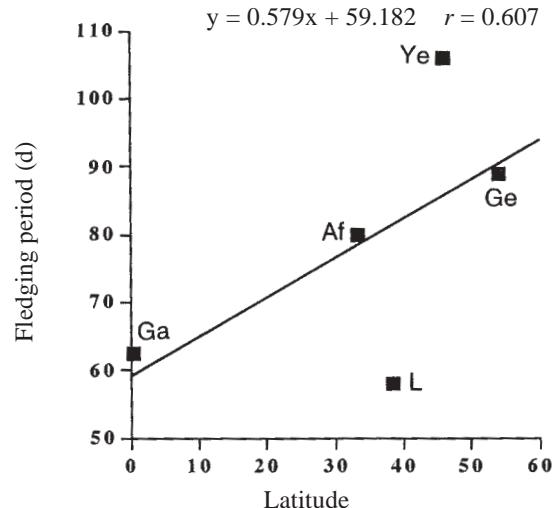


Fig. 11b. Relationship between mean breeding latitude for resident inshore-feeding penguin species (excluding *Aptenodytes* spp.) and mean duration of fledging period.

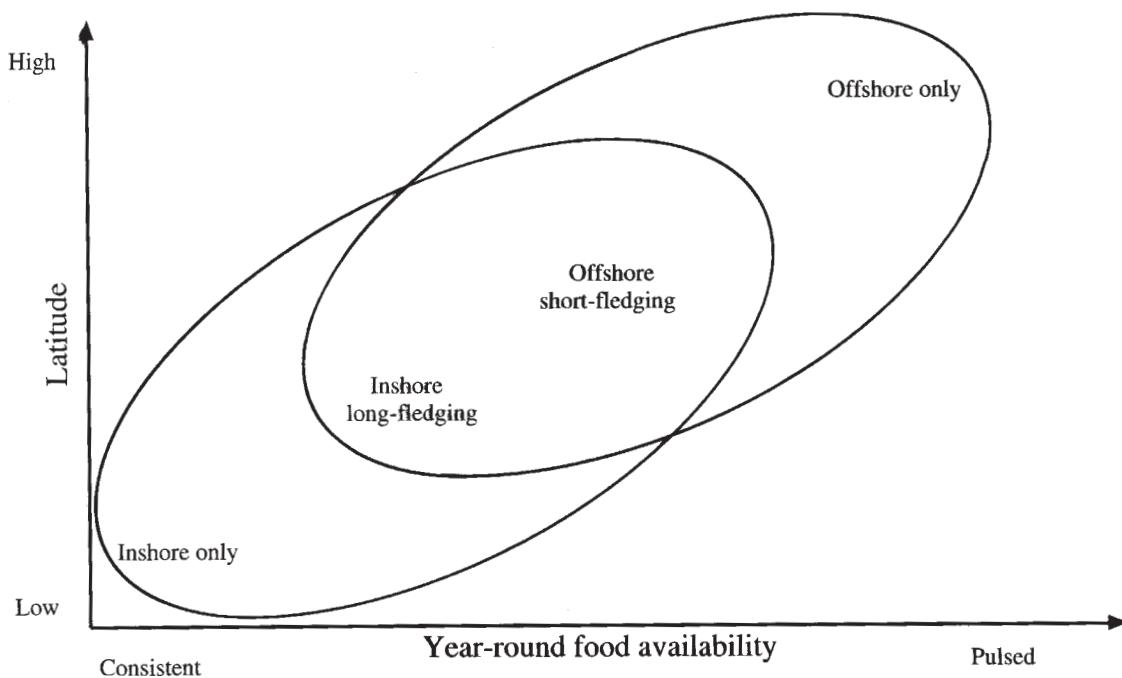


Fig. 12. Diagrammatic representation of potential relationships between prey availability, breeding latitude and duration of breeding season events in penguins.

Perhaps this provides an insight into the distribution and occurrence of the two main penguin strategies: whereas inshore-feeding may be more efficient when a concentrated and consistent food source is available near to the breeding area, at higher latitudes the seasonal nature of the environment and food supply reduces the efficiency of such a strategy for transferring food to chicks. Under such a scenario, we would expect inshore-feeding to occur exclusively at the lowest latitudes, off-shore feeding to occur exclusively at the highest latitudes, and for both strategies to occur at intermediate latitudes but with the inshore feeders taking relatively longer to rear their chicks to fledging (Fig. 12). This is exactly the pattern observed, with Gentoo and Yellow-eyed Penguins taking 89 and 106 days, respectively, to rear their chicks: two weeks to a full month longer than the longest time taken by comparably-sized off-shore feeding penguins at similar latitudes. Perhaps the breeding and life history tactics of penguins are not so paradoxical after all?!

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APPENDIX 1

Average values for various biological and ecological attributes of penguins. Main source is Williams (1995); additional sources are as referenced

Species	Latitude (°S)	Body mass (g)		Post-arrival fast (d)		Courtship period		Laying interval (d)	Clutch mass (g)	Egg dimor- phism
		Male	Female	Male	Female	Male	Female			
King	K	54.2	16 000	14 300	37.6	14.0	19.0	14.0	319	
Emperor	E	66.7	36 700	28 400	115.0	40.0	50.0	40.0	469	
Gentoo	Ge	54.0	5575	5150	1.0	5.3	25.0	25.0	258	0.99
Adélie	Ad	77.2	5350	4740	31.7	17.6	13.1	8.4	239	1.08
Chinstrap	Ch	60.6	4980	4770	22.1	23.4	22.1	17.4	228	1.03
Rockhopper	Rk	52.6	2880	3080	33.0	39.0	16.9	11.6	192	0.71
Fiordland Crested	Fi	43.9	4530	4030	42.5				220	0.83
Snares Crested	Sn	48.1	2630	2484	37.0	39.0	21.7	13.5	4.1	0.80
Erect Crested	Ec	50.7	6382	5434			23.0		234	0.56
Macaroni	Mc	54.0	5240	5310	35.0	40.1	19.1	10.5	243	0.62
Royal	Ry	54.5							260	0.63
Yellow-eyed	Ye	45.9	5500	5100			30.0	30.0	276	
Little	L	38.5	1172	1048			30.0	30.0	53	1.00
African	Af	33.4	3099	3099			25.0		212	1.02
Humboldt	Hu		4900	4500						
Magellanic	Mg	44.0	4930	4590	24.0	23.0	24.0	8.0	3.8	1.00
Galapagos	Ga	0.3	2135	1730					3.5	

Species	Incubation period (d)	Incubation shift duration (d)		Hatch asynchrony (d)	Fledging period (d)	Foraging trip (d)	Pre-moulting at sea (d)	Moulting fast (d)	Nest site fidelity (%)	Divorce rate (d)
		First	Second							
King	K	53.8	18.6	18.7		334.0	12.8	22.2	31.2	83.0
Emperor	E	64.4	64.4			150.0			35.0	0.0
Gentoo	Ge	35.6	1.4	1.3	1.5	89.0	0.4	10.0	19.5	92.5
Adélie	Ad	33.2	16.6	12.3	1.4		1.5	9.0	19.8	43.5
Chinstrap	Ch	33.4	6.0	9.8	1.0	54.0	0.9		18.0	
Rockhopper	Rk	34.2	11.3	13.9	1.1	70	1.5	32.5	27	
Fiordland Crested	Fi	33.5	13	13		75	1.1	70	21	
Snares Crested	Sn	33.5	12.1	12		75		70	27	
Erect Crested	Ec	35				70		28	28	
Macaroni	Mc	35.5	12.8	10.4		60	2	13	24	84
Royal	Ry	35	13	13		65	2.5	32.5	26.5	
Yellow-eyed	Ye	43.5	2	1.8		106	0.5	22	24	30
Little	L	33.4	2	2	0.75	58	0.6		17.1	65.9
African	Af	37.2	2.1	2	3.2	80	0.5	21	17.7	59.8
Humboldt	Hu	40.7	1	1	2.6					
Magellanic	Mg	40	14.9	17.4	1.9	60	1.6		75	9.6
Galapagos	Ga	39	1.09	2	3	62.5	0.5	17.5	12.5	98
										6.7

Mean age first breeding (yrs)

Species		Male	Female	Overall	Annual survival (%)		References
King	K	5.9			93		3,4
Emperor	E		5.2	5	95.1		
Gentoo	Ge		3.5		84.5		8
Adélie	Ad		6.5	4.85	89.4		1,2
Chinstrap	Ch						5
Rockhopper	Rk						
Fiordland Crested	Fi						
Snares Crested	Sn						6
Erect Crested	Ec						
Macaroni	Mc	7.5			76.5		
Royal	Ry		8	7	86		
Yellow-eyed	Ye		4	3	87		9
Little	L	3			75		10
African	Af						
Humboldt	Hu						11
Magellanic	Mg						
Galapagos	Ga		6.5	4.5	85		7
					84.4		12

References: **1:** Ainley *et al.* 1983; **2:** Taylor 1962; **3:** Weimerskirch *et al.* 1992; **4:** Olsson 1998; **5:** Marchant & Higgins 1990; **6:** C. Miskelly pers. comm.; **7:** Boersma 1991; **8:** Trivelpiece & Trivelpiece 1990; **9:** Darby & Seddon 1990; **10:** Dann & Cullen 1990; **11:** Seddon & van Heezik 1991; **12:** Boersma 1976.