

## FIRST INTERNATIONAL CONFERENCE ON PENGUINS

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### ABSTRACTS OF PRESENTED PAPERS AND POSTERS

CONVENORS : L.S. DAVIS & J.T. DARBY

#### ENERGETICS OF MOULT IN PENGUINS

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Moult involves the production of new tissue and therefore moulting birds incur some energy cost above that required for maintenance. In contrast to most avian species, penguins have an intense moult when they are confined to land and consequently unable to feed. Therefore, this period may impose some physiological stress. Estimates of energy cost of moult based on mass loss indicate daily moult costs are around 2 x BMR. Measurements of oxygen consumption of five species of penguins through moult suggest the process is generally less energy expensive. The pattern of metabolism may reflect the different biochemical processes associated with moult. The use of isotope turnover techniques in determining energy cost of moult has been restricted to one species of penguin and this study indicated a cost of 1,5 x BMR, close to that determined from laboratory measurements of oxygen consumption. The reasons for adopting an intense moult as opposed to a slow progressive moult are not clear but may be related to increased thermal conductance and decreased swimming proficiency during feather synthesis.

#### A METHOD TO OBTAIN HAND-REARED ADELIE PENGUINS FOR PHYSIOLOGICAL EXPERIMENTS

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Man-made stress influences physiological measurements and leads to wrong results. Adélie Penguins *Pygoscelis adeliae* are highly stressed by man and captured penguins can die by shock. The best method to obtain unstressed penguins for laboratory experiments is to rear them from chicks and imprint them onto man. For rearing them under Antarctic field conditions with minimum effort, 14-day old chicks with stable thermoregulation were kept in a fenced area with wooden shelters to protect them against bad weather. A suitable diet had to be developed because krill as a natural food source was not easily available. The best diet, developed over three seasons, consists of a mixture of deboned fish, minced kelp or duck food pellets, oil, gelatine and water in a relationship of 25:5.1,25:1:7,5. After a halt in growth during the first three days of accommodation the chicks grew up as fast as the best fed chicks under natural conditions. The feeding frequency was reduced from three to two times per day after one week. The gain of body mass was 90 g/d and the total mass during moulting 2 600-3 750 g. Even after moulting the penguins remained tame. There was no mortality and all chicks showed normal development.

#### VIROLOGICAL STUDIES ON ADELIE PENGUINS

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In temperate regions many wild birds are asymptotically infected with a number of different viruses including paramyxoviruses and influenza A viruses. Evidence on the extent of

these infections and on the emergence of virus strains which are pathogenic for other species has led to the suggestion that birds represent a large natural reservoir of viruses from which strains which are pathogenic for other species emerge. If this is so then it is important in studying the ecology of these viruses and the relationship between virulent and avirulent strains to discover the extent to which viruses occur in birds in all regions, including those in the relative isolation of Antarctica. Samples were collected from Adélie Penguins *Pygoscelis adeliae* at Cape Bird on Ross Island and tested for viruses and for antibodies. There was no evidence of influenza virus infection in the population but paramyxovirus infection was demonstrated by virus isolation and the detection of specific antibodies.

#### REPRODUCTIVE VARIABILITY AND HISTORICAL CHANGE OF MAGELLANIC PENGUINS AT PUNTA TOMBO, ARGENTINA

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Reproductive success at the largest continental colony of Magellanic Penguins *Spheniscus magellanicus* located at Punta Tombo, Argentina, is highly variable between years. During five breeding seasons, reproductive success (the mean number of chicks fledged per breeding pair) ranged from less than 0,02 in 1984 to approximately 0,50 in 1983 and 1985. In years of higher reproductive success, eggs are larger, and are laid earlier. Chicks are fed more frequently and grow faster as well. These patterns indicate that variability in Magellanic Penguins' reproductive success is determined by changes in food resources. Mainland colonies of Magellanic Penguins along the northern Patagonian coast probably did not exist in the late 1800s. During the first half of the 20th century Magellanic Penguins increased in number. The colony at Punta Tombo, consisting of several hundred

thousand birds, has existed for less than 80 years. The most northerly colonies, which occur on the Peninsula Valdes, have existed only since the 1960s. Changes in food availability along with changes in predation, may explain historic fluctuations in continental colony location and size. Both the high variation in annual reproductive success and the historical changes in colony size suggest that Magellanic Penguin populations are not at equilibrium and are potentially fragile.

#### EVOLUTIONARY ECOLOGY AND ETHOLOGY OF PENGUINS; WITH SPECIAL REFERENCE TO THE GENTOO PENGUIN

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Of all seabirds, penguins have evolved the most elaborate morphological adaptations to an oceanic existence. With the penguin family, however, ecological and behavioural heterogeneity exists between species and between populations. An interspecific comparison of penguins nesting inside burrows, on sand or icebank shows that breeding biology and behaviour may be adapted to very different constraints. Different populations of the same species likewise show adaptations to the particular constraints of their environment. The Gentoo Penguin *Pygoscelis papua* makes an interesting case study because of its wide geographical distribution and its extended laying period.

#### RE-UNITING IN THREE CAPTIVE PENGUIN SPECIES: PERSPECTIVES ON THE FACTORS PROMOTING LONG-TERM PAIR BONDS IN THE WILD

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We have monitored pairing and reproductive success of adult penguins (48 Emperor *Aptenodytes forsteri*, 21 King *A. patagonicus*, 80 Adélie *Pygoscelis*

*adeliae* Penguin pairs in a captive colony at Sea World since 1979 and intensively since 1984. Eighty-eight percent of the Adélie Penguin pairs reunited from one season to the next, much higher than in the wild. Emperor Penguins also remated somewhat more often in captivity than in the wild, 30% vs 15%. The remating rate for wild King Penguins is 29%, in captivity it was approximately 18% of the birds that produced eggs. These rates are still relatively low when compared with other species of penguins, even though the captive pairs are not separated during migration, do not experience food shortages and do not suffer significant mortalities. Apparently, *Aptenodytes* penguins are not motivated to take the same partner year after year, a finding supported by our observations that established pairs often do not stop associating until just prior to breeding. In captivity, remated Adélie Penguin pairs were slightly more successful than new pairs. Successful partnerships exchanged more mutual displays and spent more time together than unsuccessful ones during brood rearing, although their courtship was often perfunctory in keeping with reports on wild Adélie Penguins. Unexpectedly, in captivity new King and Emperor Penguin pairs laid and reared young more often than did remated pairs (total n of 35 and 59 pairs respectively). In the Emperor Penguin, this difference was significant (Fisher's Exact Test,  $P < 0.05$ ). We quantified courtship behaviours of Emperor Penguins to determine the possible reasons for this unexpected result. New pairs displayed more often and fought with competitors more during pairing. All copulation attempts were by new pairs. Both rates of behaviours and a brief pilot project to measure levels of sex steroids suggested marked asynchrony in reproductive readiness between partners in unsuccessful pairs. Our data suggest that displays and competition for mates or other factors associated with courtship stimulate reproductive readiness and synchrony in *Aptenodytes* penguins to a much greater degree than they do in the Adélie Penguin.

#### PERIODIC RETURN OF WHITEFLIPPED PENGUINS TO THEIR BREEDING SITE AND ITS INFLUENCE ON TIMING OF LAYING

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Adult Whiteflipped Penguins *Eudyptula minor albosignata* return to their breeding area periodically from early winter until laying in September-November. Systematic observations made over 12 years (1976-1987) at colony on Banks Peninsula, New Zealand have shown that the return of birds is synchronized. During the winter the numbers ashore and the timing of peaks varies, becoming more regular and pronounced as the breeding season nears. Most of the breeding birds come ashore during or just after the new moons in August and September, but few if any are ashore during the intervening full moon. Laying is synchronized and bimodal. The first mode typically occurs just before the new moon that falls between mid-September and mid-October, and 20-25 days after a peak presence of birds ashore. The second mode occurs 20-25 days after the first. This pattern is consistent from year to year. Apparently the penguins are using the new moon as a cue to synchronize their return ashore prior to breeding, and that in turn determines the timing of laying.

#### WIND AND TEMPERATURE EFFECTS ON METABOLISM OF CHICKS AND ADULTS OF ADELIE PENGUINS

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Convective exchange is a potentially important pathway for heat loss in penguins. Using temperature-controlled metabolism chambers and recirculating wind tunnels, we measured metabolic rates ( $O_2$  consumption;  $VO_2$ ) for Adélie Penguins *Pygoscelis adeliae* subjected to three wind speeds (no forced convection, 2.5-3 m/s, and 6-8 m/s) at

ambient temperatures ( $T_a$ ) from  $-20$  to  $20^\circ\text{C}$ . Individuals from five age classes were studied: one, two and three kg chicks; fledglings (3-4 kg), and adults (3-4 kg), and adults (3,5-4,5 kg). In all age groups  $\text{VO}_2$  increased with decreasing  $T_a$  at all wind speeds; mass-specific  $\text{VO}_2$  and the proportional change in  $\text{VO}_2$  decreased with increasing age. The effects of wind on  $\text{VO}_2$  were generally significant only at  $T_a$  of  $0^\circ\text{C}$  and lower, and also varied with age. The strongest convective effects were observed in fledglings and adults: at  $-20^\circ\text{C}$ ,  $\text{VO}_2$  was two to three fold larger at high wind speed than in the absence of forced convection. Considerably smaller but nevertheless significant changes occurred in downy chicks. We attribute this difference to the poorly insulated flippers of older birds, which must be kept above freezing to protect against frostbite injury and hence act as thermal windows at  $T_a$  below  $0^\circ\text{C}$ . In small chicks, the flippers are covered with highly insulative natal down.

#### MELATONIN AND CIRCADIAN RHYTHMS IN THE ADELIE PENGUIN

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Adélie Penguins *Pygoscelis adeliae* in Antarctica live in an unusual environment in which they are exposed each summer to four months of continuous daylight. Various behaviour patterns of Adélie Penguins have been reported as showing either diurnal rhythmicity with activity peaks around midnight or midday, or else no rhythmicity at all. The physiology of circadian rhythms in the Adélie Penguin has been studied at Cape Bird ( $77^\circ\text{S}$ ) using plasma melatonin and body temperature as indicators of the behaviour of the underlying biological clock of the bird. Melatonin is a hormone secreted by the pineal gland, with melatonin levels in the plasma of birds normally showing a circadian rhythm with high levels during the night and low levels during the day. No clear

24-h rhythm of plasma melatonin was found in penguins held in captivity in January, although in December one bird did have a low amplitude diurnal rhythm. A 24-h rhythm appeared in some birds held for three days in constant darkness. A clear melatonin rhythm was present after three days of an LB 12:12 light/dark cycle. Thus the pineal gland of the Adélie Penguin is capable of secreting melatonin rhythmically. The body temperature of penguins under natural lighting in January showed no clear rhythmicity, whereas a rhythm was seen when penguins were exposed to an LD 12:12 light/dark cycle. The continuous light of the Antarctic summer interferes with the expression of an endogenous circadian clock that continues to run during the summer. These results, together with previous observations of the behaviour of Adélie Penguins, are discussed in relation to the adaptive significance of circadian rhythms to penguins in the Antarctic environment.

#### FOOD AND FEEDING HABITATS OF CRESTED PENGUINS

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Crested penguins *Eudyptes* have a wide distribution at sub-Antarctic and cold temperate islands. Quantitative dietary information now exists for six of the seven taxa at 14 widely separated breeding localities. Use of stomach-flushing techniques and identification keys allow data to be comparable. Relative proportions of crustaceans, squid and fish vary between species, localities and years and seasonally. Euphausiid crustaceans dominate at many, but not all, localities. Some prey species are common to different species and localities. It seems that the ability to take relatively large fish and cephalopods has resulted in Macaroni and Royal Penguins *E. chrysolophus* and *E. schlegeli* occurring in greater numbers at most sympatric

breeding localities than the smaller Southern Rockhopper Penguin *E. c. chrysochome*. Where a larger crested penguin is absent, Southern Rockhopper penguins occur (Falkland Islands) and have occurred (Campbell Islands) in far greater numbers than at sympatric breeding localities. These findings suggest that ecological segregation in terms of diet (and foraging ranges and depths) is incomplete, and that differences in the timing of breeding of sympatric crested penguins may also be an important segregating mechanism.

#### ENERGY EXPENDITURE AND TRAVELLING SPEEDS OF FREE-RANGING LITTLE PENGUINS

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Onshore and at-sea CO<sub>2</sub> production and water turnover of Little Penguins *Eudyptula minor* were measured during the incubation phase of reproduction during September 1986 on Phillip Island, Australia, using the doubly-labelled water method. In addition, measurements of swim speed and dive duration were collected by radiotelemetry and strip-chart recorder of four birds swimming within three kilometres of the colony. Mean CO<sub>2</sub> production of seven penguins fasting ashore was  $0,784 \pm 0,08$  ml CO<sub>2</sub>/g/h, which yields  $485 \pm 48$  kJ/kg/d of energy. Mean CO<sub>2</sub> production of five birds ashore and at sea was  $1,495 \pm 0,32$  ml CO<sub>2</sub>, which yields  $925 \pm 196$  kJ/kg/d of energy. Over this measurement interval these birds spent approximately 33% of their time at sea. Correcting for the amount of energy spent onshore, we estimate that these birds expended  $1\ 800 \pm 680$  kJ/kg/d while at sea. This is 4,2 times the measured SMR previously reported for this species. The mean swimming velocity for birds travelling to or from the colony was  $7,6 \pm 1,2$  km/h, with a

mean dive time of  $3,6 \pm 0,4$  s and a maximum of 65 s. Tracks of penguins before signal loss at three kilometres reflected primarily travelling behaviour.

#### ENERGY BUDGETS AND FORAGING BEHAVIOUR OF FREE-RANGING PYGOSCELIS AND EUDYPTES PENGUINS

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We review the techniques used in and data acquired from recent research on foraging behaviour and energetics of *Pygoscelis* and *Eudyptes* penguins, including comparison with *Spheniscus* species as appropriate. Diving depth and duration, swimming speed and activity and energy budget data are treated in full. Inter-relationships between these parameters are investigated, particularly to see how various aspects of foraging activity relate to trip duration. From limited data we conclude that meal mass (as delivered to chicks), diving and swimming activity and energy expenditure do not increase proportionately with longer foraging trips. This may reflect the uncertainties associated with exploiting patchily distributed swarming crustacean prey, whereby activity rates are kept fairly constant and trip duration varied. Minimum prey capture rates are deduced and compared with recorded krill densities; the presence of swarms may be crucial for successful provisioning of offspring. Appropriate lines of further research are indicated.

#### FLOURIDE TOXICITY IN ANTARCTIC PENGUINS: PROBLEMS ASSOCIATED WITH A KRILL DIET

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Fluoride concentrations in whole Antarctic Krill *Euphausia superba* are in the order of 300-500 mg/kg (wet mass). Antarctic penguins relying almost exclusively on krill as a food source consume more than 200 mg F/d. Whereas 1-2 mg F/d are recommended for caries prevention in humans, 20-80 mg/kg.d are toxic if consumed over long periods. Fluoride concentrations in femurs of Adélie *Pygoscelis adeliae*, Gentoo *P. papua*, Chinstrap *P. antarctica* and Emperor *Aptenodytes forsteri* Penguins were in the order of 10 000 mg/kg (dry mass). Concentrations in the soft tissues ranged from 2 to 10 mg/kg (dry mass). By comparison, F concentrations in the femur and soft tissues of domestic ducks *Anas platyrhynchos* were 170 mg/kg and <0.1 mg/kg (dry mass) respectively, reflecting a fluoride poor diet. In Adélie Penguins, fluoride uptake is buffered by the skeleton where it has a half life of three to four weeks, the bioavailability of fluoride from krill is only 21-30% in the muscle and 48-60% in the femur compared to NaF (100%). The amount of F excreted via the cloaca (670 mg/kg wet mass) by far exceeds excretion via the salt glands (1,2-2,2 mg/kg wet mass).

#### DEMOGRAPHY OF LITTLE PENGUINS AT PHILLIP ISLAND, VICTORIA AUSTRALIA

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Twenty years' banding of Little Penguins *Eudyptula minor* has provided estimates of demographic parameters such as age of first breeding, adult mortality rate, philopatry of recruits and dispersal patterns of young and adults outside the breeding season (now being monitored also by telemetry). Survival during the first years of life is strongly influenced by fledging mass, and appears to favour males over females. Juveniles generally carry a higher parasite load than do adults and this is thought to be largely responsible for their heavier mortality. For adults, starvation, uncomplicated by parasitism, seems a more frequent cause. Over the

last two years offshore food sampling has demonstrated the importance of food for the timing and success of breeding at Phillip Island.

#### LIFE-TIME REPRODUCTIVE OUTPUT OF THE LITTLE PENGUIN

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Studies of the breeding success and survival of Little Penguins *Eudyptula minor* began on Phillip Island, Victoria, Australia in 1968 and are continuing. Individual breeding histories were obtained for periods up to 15 years but were considerably shorter for most individuals. The mean number of chicks produced per pair each year varied tenfold over the twenty-year period and annual variation in the mean number of young surviving the first year per pair was considerably greater. More than 60% of birds did not reach breeding age. A relatively small proportion of adults produced a large proportion of the young each year. Breeding success was analysed for age/experience and "quality" differences. The effects of annual variation were removed by comparing each individual's breeding success with the mean of the year. Success changed with increasing age/experience in both sexes in some of the measures examined but not in all. Removal of the variation due to both year to year and age/experience differences showed that differences in "quality" between individuals were evident only for hatching success. Life-time reproductive output was examined in relation to population changes in the study area over the last 20 years.

#### THE BREEDING BIOLOGY OF THE YELLOWEYED PENGUIN

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The former nesting habitat of the Yelloweyed Penguin *Megadyptes antipodes* was the cool, coastal podocarp/hardwood forests of southern New Zealand. Nest sites are characterized by dense vertical cover and a high degree of concealment. Breeding pairs are usually visually isolated from each other and where this does not obtain one or both pairs usually fail to breed successfully. Most birds nest within aural distance of each other, however, this is not obligatory. We believe that this behaviour confirms that the Yelloweyed Penguin is the only noncolonial species of penguin. Large-scale land clearance along the southeast coast of the mainland has directly influenced breeding success. Over 650 nesting attempts by banded pairs of Yelloweyed Penguins during six breeding seasons were monitored on the Otago Peninsula. The present study shows that breeding success differs markedly between breeding areas, ranging from 0-100% of eggs laid. Comparison with earlier studies suggest that chick mortality has almost doubled in the last 30-50 years. We identified the major cause of breeding failure as predation of guard-stage chicks by mustelids and feral cats *Felis catus*. The present population of Yelloweyed Penguins throughout its range is estimated at 4 500 individuals. We believe that this represents about one quarter to one fifth of former numbers.

#### MATE CHOICE IN PENGUINS

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There are several reasons to expect the intensity of sexual selection to be low in penguins: they are monogamous, exhibit little sexual dimorphism, and are obligate biparental incubators. Yet female choice could occur in monogamous bird species where early breeding is likely to result in greater reproductive success and more extra-pair copulations for favoured males. Here I examine the courtship patterns in a colony of Adélie Penguins *Pygoscelis adeliae* over four consecutive breeding seasons (1984/85 - 1987/88). Males were more faithful to their nest sites than to their

previous partners: they seldom changed nest sites between seasons, and courted females indiscriminately until paired. Males did not appear to compete directly for access to females. Females paired soon after arriving at the colony and would sometimes compete for access to a male. I tested the influence of previous partner, synchrony of arrival, proximity to old nest site, nest type, and ecstatic calls on the mating patterns of females. I argue that females should select males on the basis of body size, and compare the level of dimorphism and incubation patterns in different species of penguins.

#### BEHAVIOURAL INFLUENCES ON INCUBATION SUCCESS IN CAPTIVE ADELIE PENGUINS

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Incubation behaviour in 40 pairs of Adélie Penguins *Pygoscelis adeliae* was monitored via time-lapse video recording and direct observation at Sea World of California in San Diego. Incubation bouts ranged from 5 h 35 min to 32 h. Unlike wild Adélie Penguins in which males perform 60% of incubation duties, females performed slightly more total incubation (52%) than did males in this study. Although cross-fostering provided each pair with a fertile egg, birds hatching offspring successfully had significantly shorter incubation bouts. These birds also spent significantly more non-incubating time at the nest with their partners and had less disparate incubation bout lengths. Whereas mate fidelity strongly influenced synchrony of within-pair interactions, it did not affect ultimate success in incubation. These data suggest that those birds deviating the most from the wild pattern tend to be those that successfully hatch offspring in this zoo environment.

#### NEW FOSSIL PENGUIN MATERIAL FROM NEW ZEALAND AND THE EARLY HISTORY OF PENGUINS

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Fossils suggest that penguin evolution has been restricted to the southern hemisphere. Penguin origins are still uncertain despite long study; recent opinion suggests relationships with Gaviiformes. The oldest penguin-like diver, a partial skeleton from New Zealand (Paleocene or Early Eocene, ~55-60 million years) may ultimately clarify penguin origins. Younger penguins from the Late Eocene (~40 m y) and Oligocene (23-38 m y) are geographically widespread, rather highly derived and like modern penguins in many aspects, yet with a structural diversity not seen in Neogene (0-23 m y) taxa. Fossils collected since Simpson's reviews of New Zealand penguins include some potentially useful in evolutionary studies. Of note are a large *Palaeudyptes*-like species from a suite of taxa of late Early-Late Oligocene (~28-32 m y) age, and the somewhat laterally compressed *Platydyptes* and a diminutive bird identical in size to *Eudyptula* (Late Oligocene-earliest Miocene, ~23 m y). The first fossil species described, *Paleudyptes antarcticus* Huxley, is still known only from a tarasometatarsus of probable Oligocene age. Its relationships with other penguins are uncertain, which complicates the nomenclature of Palogene fossils. Future work on fossils could usefully focus on cladistic analysis, constructional morphology (e.g. implications of body size, analysis of feeding and locomotion), interactions with other marine homeotherms, the rather poor earlier Miocene record, and contrasts between Paleogene and Neogene taxa.

#### FREE-LIVING ENERGETICS OF LITTLE PENGUINS DURING THE ANNUAL CYCLE

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The energetics of free-living Little Penguins *Eudyptula minor* in Tasmania were evaluated using

tritium, <sup>22</sup> sodium and doubly-labelled water turnovers. Preliminary results of total body waters, water influx and metabolic rates over the annual cycle are presented. Sea water ingestion rates are assessed and the implications discussed. The metabolic rates of adult penguins varied over the annual cycle and reflect the increase in energy demands during the breeding season. The energetics of chick growth are also described. Bass Strait is the stronghold of the species in Australia and by combining population estimates and food consumption rates, the biomass of prey consumed by the penguins in this area is calculated. Initial results of foraging behaviour (diving depth and swimming speed vs time), using a new archival activity recorder, will also be presented.

#### COMPARATIVE BREEDING ENERGETICS OF PENGUINS AT MACQUARIE ISLAND AND HEARD ISLAND

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Macquarie and Heard Islands are located north and south respectively of the Antarctic Polar Front and are substantially different in their surrounding oceanographic characteristics. The energy requirements of free-living Gentoo *Pygoscelis papua*, Macaroni *Eudyptes chrysolophus*, Royal *E. schlegeli* and Rockhopper *E. chrysocome* Penguins were assessed during the breeding season, simultaneously at both locations during 1986/87, by means of isotope turnover techniques. The energy requirements of adults while incubating, brooding and foraging will be presented, as well as the energy requirements of chicks. Intraspecific and locational comparisons are discussed with respect to feeding ecology.

#### THE BREEDING ENERGETICS OF ADELIE PENGUINS AT CAPE BIRD, ROSS ISLAND



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Isotope turnover techniques were used to determine the water and sodium influxes, metabolic rates and food consumption rates of free-living adult and chick Adélie Penguins *Pygoscelis adeliae* throughout the breeding season. These data allow assessments to be made of the total food and energy requirements of Adélie Penguins during the breeding and nonbreeding seasons.

#### **WATER, SODIUM AND ENERGY TURNOVER IN FREE-LIVING PENGUINS: A REVIEW**

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Isotope turnover studies on free-living penguins are reviewed with particular emphasis on the doubly-labelled water technique and estimated food consumption rates. The energetic costs of incubation, moult and foraging are compared along with the growth energetics of chicks. Sodium influx rates are discussed with reference to the sodium status of diets, sea-water ingestion and nasal salt-gland function.

#### **METABOLIC ADAPTATION TO FASTING IN PENGUINS**

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The ability to survive prolonged periods of fasting during breeding is one of the most remarkable adaptations of penguins to their environment. Lowering of energy metabolism to basal levels during incubation seems a common way to save

energy stores in various penguin species. Fat contributes to 96% of energy production in Emperor Penguins *Aptenodytes forsteri*, allowing protein sparing. Maintenance of the plasma levels of most metabolites (glucose, free fatty acids, lipids, uric acid amino acids, proteins, etc.) and hormones (thyroid hormones, corticosterone, insulin) in breeding fasting Emperor or King Penguins *A. patagonicus* suggests the achievement of a remarkable fuel and endocrine balance. A selective mobilization of the various fatty acids deposited in adipose tissues, and a decrease in fat cell size but likely not number, are also two major characteristics of fat store utilization in fasting penguins. A shift from lipids to proteins as the main energy fuel towards the end of the fast probably contributes to the triggering of nest or egg abandon, and of refeeding. This illustrates the close inter-relations between breeding and feeding behaviour, and fuel store availability in penguins.

#### **THE PROTRACTED BREEDING REGIME OF LITTLE PENGUINS IN WESTERN AUSTRALIA**

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An island population of about 1 000 breeding Little Penguins *Eudyptula minor* in the Perth metropolitan area of Western Australia was studied throughout two consecutive breeding cycles (1986-1988). This relatively isolated colony, at the northernmost limit of the species' range, had a laying period (May to October/November) much longer than elsewhere. Breeding and moulting took place two months earlier than in southeastern Australia and New Zealand. Penguins at this colony were substantially larger (1.5 kg) than conspecifics elsewhere. They nested under bushes rather than in burrows but their reproductive success was similar to other colonies of the species studied. They fed mainly inshore on four species of bait fish. The anomalous size and breeding regime

of these penguins is thought to be linked to the favourable climate and food supply resulting from the Leeuwin Current, warm tropical water flowing southwards down the coast each winter.

#### PHYSIOLOGY OF DIVING IN KING AND EMPEROR PENGUINS

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Recent observations of dive behaviour of King *Aptenodytes patagonicus* and Emperor *A. forsteri* Penguins raises some perplexing questions about the physiological responses to diving in these birds. Both King and Emperor Penguins frequently dive to depths greater than 100 m. Furthermore, such deep dives in Emperor Penguins often last for 5 to 10 minutes. Since gas tension in the air sacs is directly related to pressure (Dalton's law of partial pressures) and solubility of gases in the blood is directly related to blood gas tensions (Henry's law) there is the potential for very high amounts of  $N_2$  in the blood and tissue of these birds while diving. The amount of dissolved  $N_2$  is dependent upon how freely gas exchange occurs between the air sacs/lungs and blood in the pulmonary capillaries. If the King and Emperor Penguin gas exchange at depth is as great as that shown for other species of penguins, then they should be exposed to transiently high  $O_2$  and  $N_2$  in the course of the dive. These  $N_2$  tensions could be at levels that in theory are high enough to induce gas bubble formation in blood and tissue upon ascent. If it is assumed that while birds are at depth gas exchange between the lung and blood is hindered to such an extent that blood  $N_2$  tension remains low, then a major source of  $O_2$  (the air sac) may be inaccessible for uptake as well. This would seem unlikely because the dive durations and swim velocities indicate an  $O_2$  consumption rate that theoretically exceeds the calculated  $O_2$  store available during the dive.

#### HATCH ASYNCHRONY AND BROOD REDUCTION IN PENGUINS

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Many birds lay more eggs than they can raise in an average year. It has been suggested that this apparent over-production of eggs is a strategy to maximise parental reproductive success in the face of environmental unpredictability, in particular, food availability. In bountiful years all young survive, but when food is scarce one or more chicks die until the remaining brood size matches available conditions. Which chick is to be the "victim" of brood reduction is decided by asymmetries in the competitive abilities of brood members due to initial (egg) size differences and/or temporal advantages resulting from an asynchronous hatch. Typically it is the youngest and smallest brood member that is lost. All but the two largest species of penguins normally lay two or more eggs per clutch. However, survival of more than one chick per pair is unusual for many species. In the most extreme case, crested penguins *Eudyptes* raise a maximum of one chick, despite always laying two eggs. Data on intraclutch egg-size variation, hatch asynchrony and reproductive success for several species of penguins are examined in the light of current brood reduction theory. The discussion focuses on the possible benefits of extreme egg-size dimorphism, hatch asynchrony and obligate brood reduction in crested penguins.

#### THE PLIOCENE PENGUIN *TEREINGAORNIS MOISLEYI*: DISTRIBUTION AND PREDATION BY OTHER VERTEBRATES

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*Tereingaornis moisleyi* Scarlett (1983) is the only New Zealand fossil penguin known definitely to be of Pliocene age. Recently, material from two further specimens of this penguin have been

discovered. One at the type locality (Northern Hawkes Bay) and at Hawera (Taranaki). During Pliocene times an extensive sea-way extended across the lower half of the North Island, covering both localities. *T. moiseleyi* was probably distributed throughout this sea-way. The Hawera material shows toothmarks, indicating predation of this penguin by another vertebrate. A number of vertebrates are known from both localities: pseudodontorns, seals cetaceans, sharks and a number of fish. The toothmarks on the Hawera humerus suggest that the animal responsible had either small jaws or long narrow jaws. One can speculate as to the possible identity of the predator. However, it is unlikely that a seal was responsible.

#### SNARES CRESTED PENGUINS : A PRELIMINARY LIFE HISTORY TABLE

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Banding of adult and fledgling Snares Crested Penguins *Eudyptes robustus* has been conducted since 1967. Total counts of chicks fledging from Main Island were made in the years 1968/69, and 1982/83 through 1986/87 inclusive. The islands were not visited in all years, and there has been variation in the amount of time spent searching for banded birds, however, we have used all available data to calculate a preliminary life table, and to comment on several aspects of behaviour which vary with age. The numbers of chicks fledged (which are correlated with the numbers of breeding adults) increased from 6 000 in 1968/69 to over 19 000 in 1984/85. Numbers appear to have stabilized since that time; the current population estimate is 66 000 birds. The oldest bird recorded to date was 21+ years. Minimum annual survivorship of chicks to one year varied significantly between years from a maximum of 39.2% (1983/84) to a minimum of 4.9% (1982/83). Annual survivorship of one to five old birds is generally >50% but data are still too few for a detailed analysis. Annual survivorship of adults is

high. Less than 50% of yearlings found to be alive in subsequent years are sighted in their yearling year. Yearlings only come ashore to moult (in January and February), whereas older subadults appear in November and are often seen on the edges of breeding colonies well before the moult.

#### LOWER TERTIARY FOSSIL PENGUINS FROM SEYMOUR ISLAND, ANTARCTIC PENINSULA

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Since the first few specimens of fossil penguins from the late Eocene, La Mesta Formation of Seymour Island were collected by a Swedish expedition in 1903, various British, Argentinian and United States expeditions have accumulated more than 1 000 additional specimens of penguins, the first elements of other marine and terrestrial birds and of terrestrial mammals, and considerable cetacean material. Despite such relative abundance of spheniscid remains, attempts to provide a more definitive taxonomic scheme than those of Wiman, Marples or Simpson continue to be hindered by a lack of associated skeletal elements. The Seymour Island fossil penguins vary widely in size and form and to accommodate such a diverse assemblage even the most parsimonious taxonomic scheme (as given here, based largely on tarsometatarsal elements) includes seven genera (two of them new) and some 14 species (seven of them new). Biogeographically, the Seymour Island penguins appear more closely related to Eocene/Oligocene New Zealand and Australian taxa (particularly in sharing the important genus *Palaeudyptes*) than to the Oligocene/Miocene South American faunas. The few non-spheniscid avian remains so far found are all isolated elements of fragments and, apart from some distinctive elements of pseudodontorns, cannot be identified with confidence even to ordinal level. However several are clearly of marine birds, some with similarities to sulids, others to procellariids. Several tarsometatarsal fragments of

terrestrial birds show similarity to those of various generalized gruiforms.

#### REPRODUCTIVE SUCCESS AND MASS CHANGES DURING FORAGING OF ADELIE PENGUINS

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The timing of the nest-relief cycle (especially for the first two foraging trips) is one of the most important factors affecting reproductive success in Adélie Penguins *Pygoscelis adeliae*. If the bird that is foraging fails to return in time to relieve its partner, the breeding attempt will fail. In this study, we investigated the relationships between masses (as a measure of physiological condition), the timing of nest relief, and reproductive success in marked birds at Cape Bird, Antarctica. Penguins were weighed at the beginning of the season and/or within 12 h of their return from foraging. Four groups were compared. First, a control group that was left undisturbed except for the weighings, second, the 'removal group' in which the first egg was removed from a set of nests, third, a 'penned group' in which nine females were captured as they left the nest and were penned for 4 d, and fourth, 15 birds (seven males, eight females) were fitted with a mock transmitter to create drag on them while they swam. Fasting females lost an average of 85 g/d. There were no significant differences in the overall reproductive success (chicks fledged/egg laid) among the controls or experimental groups. Furthermore, there were no differences in the foraging trip times of successful birds, but birds carrying mock transmitters were delayed significantly, returned lighter than other birds, and mostly failed to complete their foraging trips before their mate deserted their nest. Eleven of 15 and six of 16 'removal group' females laid a replacement egg in 1986/87 and 1987/88 respectively. We conclude that short delays in foraging trips and the need to lay an additional egg do not affect the timing of nest relief, but

substantial decreases in foraging efficiency can cause long delays that can affect reproductive success.

#### LITTLE PENGUIN DIETS

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Two and a half thousand stomach samples have been taken from Little Penguins *Eudyptula minor* nesting at colonies along the Victorian coast since 1979. Analysis showed that Little Penguins are primarily piscivores preying on small fish (<20 cm standard length). Species composition of the diet varied significantly from location to location within and between years, and species most commonly eaten are known to school. This suggests Little Penguins feed on fish with certain size and behaviour characteristics rather than on any one species in particular. A number of different methods have been used by workers to quantify penguin diets, given the stomach samples available. These are reviewed and compared.

#### DEATHS OF ROCKHOPPER PENGUINS AT CAMPBELL ISLAND FROM BACTERIAL INFECTION BY *PASTEURELLA MULTOCIDA*

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During the last 40 years the number of Rockhopper Penguins *Eudyptes chrysocome* breeding at Campbell Island has decreased by about 90%. During the 1985/86 breeding season chicks and adults were dying from a disease with rapid onset and mortality. The cause of death for seven chicks and one adult in a sample of 13 was shown to be infection by *Pasteurella multocida*, an infection not previously reported from wild penguins. In the 1986-87 breeding season mortality was lower than in 1985-86, but *P. multocida* was isolated from two of 19 dead chicks and histological evidence of this

infection was found in five of another 34 samples. Pasteurellosis has the potential to cause many deaths of Rockhopper Penguins, but at present there is no evidence to indicate it has been the main cause of the population decrease at Campbell Island. No viruses were found in the autopsied penguins, but an enveloped RNA virus has been isolated from ticks *Ixodes uriae* collected from moulting subadults. The identity and potential pathogenicity of this virus are being investigated using tick and blood samples collected in February 1988.

#### VOCALIZATION OF THE YELLOWEYED PENGUIN

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Yelloweyed Penguins *Megadyptes antipodes* breed in loose aggregations on the coasts of New Zealand. The need for recognition between mates as well as parents and chicks by vocal cues alone is not as critical for the Yelloweyed Penguins as it is for other penguin species that breed in dense colonies. The vocalizations and associated behaviours of adults and chicks were recorded during the 1987/1988 breeding season. Sonograms from three main stages of chick development up to fledging were analyzed to determine if there are components within the vocalizations that allow for individual recognition at any of the three stages. In addition, a playback experiment of adult vocalizations to chicks was conducted to determine if >60 day old chicks were able to distinguish their parents calls from the calls of a strange breeding adult. The results of both of these aspects will be presented and discussed.

#### CHICK RECOGNITION OF PARENTS' CALLS IN SNARES CRESTED PENGUINS

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Anecdotal evidence suggests that adult Snares Crested Penguins *Eudyptes robustus* recognize their chicks. One would therefore expect selection for chicks to discriminate between parents and non-parents, rather than begging indiscriminantly. Natural observations (n=18) made during the early creche stage indicate that chicks can recognize their parents. Chicks seem to respond initially to their parents' calls, although visual cues and nest recognition may also be involved. The nest site appears to serve as a meeting place for parents and their chicks during the early creche state. Playback experiments were used to test recognition of parents' "mutual trumpet" calls by 24 chicks in one colony on Main Island. Experiments were carried out in the first and second weeks of the creche stage and the late creche stage (data for the latter are not presented). Comparisons were made between: (1) responses of chicks during playbacks of parents' and non-parents' calls, (2) responses during playbacks from the nest and a neighbouring nest, and (3) two orders of playbacks. No significant order effects were found. There was one significant nest effect, indicating that chicks are more likely to orient or move toward calls coming from their own nest. Significant results for some behaviours indicate that chicks recognize their parents' voices, independently of nest location, at all three stages of development. Thirteen parameters were measured from sonograms of the "trumpet" calls of ten adults and were analysed for between- and within- individual variability. Calls were found to be individually distinctive, thus providing a proximate basis for chick recognition of parents' calls.

#### FORAGING MOVEMENTS OF PENGUINS, WITH EMPHASIS ON A STUDY OF ADELIE PENGUINS

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Radio transmitters were fitted to Adélie Penguins *Pygoscelis adeliae* at the Cape Bird Colony, Ross Island, during incubation (1987) and chickfeeding (1986). During 1986 birds were tracked from two receiving stations located 2,7 km apart. On one to two day foraging trips birds could only be located accurately close to the colony. Many birds moved outside accurate tracking range where their direction from the stations, but not distance, could be recorded. Most birds moved north west to the centre of McMurdo Sound and some travelled north then east of Beaufort Island thus out of radio range. During 1987 birds were tracked from stations on each side of McMurdo Sound 75 km apart. Foraging trips which lasted from 13-19 days showed a moderately concentrated pattern. Birds moved to the central northern area of McMurdo Sound about 50 km off the coast. For the first five to seven days individuals foraged inside 10-km diameter ranges during 12-hour periods which were closely adjacent. After this birds swam rapidly north out of radio range. A few were tracked during this movement and their signals were detected more than 150 km from the receiving stations.

**THE RESPECTIVE ROLE OF MALE AND FEMALE IN ESTABLISHING NEST-SITES AND PAIR-BONDS IN THE HUMBOLDT PENGUIN AT EMMEN ZOO, THE NETHERLANDS**

*C.J. Scholten, Emmen Zoo, Postbus 1010, 7801 BA Emmen, The Netherlands*

In Humboldt Penguins *Spheniscus humboldti* it seems to be the male who determines the location of the nest-site. Ecstatic displays are performed nearly always by males and are done a great deal in the immediate surroundings of the nest. When a change of nest-site occurs, the male sometimes starts giving ecstasies at the new nest-site a year or more before actual nesting occurs. It is mostly the male who brings the nesting material to the nest. The results obtained in the Zoo confirmed observations I have made in the wild. The female seems to be the one who is decisive concerning the

matter of mate choice. That this seems likely I will try to explain from several case studies made in the Zoo: 1) A case where I could follow the process of becoming a pair very closely, 2) one case where a male had a relationship with two females and, 3) five cases where partner-changes occurred. Observations on what happened in the Zoo in times of a surplus of males and in times of a surplus of females seem to agree with the role of male and female as mentioned above.

**NEST SITE SELECTION IN YELLOWEYED PENGUINS**

*P.J. Seddon, Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand*

The traditional nesting habitat of the Yelloweyed Penguin *Megadyptes antipodes* is believed to be coastal forest. Logging and land clearance for farming has meant that today only isolated patches of regenerating coastal forest persist along the Yelloweyed Penguin's breeding range on the mainland of New Zealand and Yelloweyed Penguins are to be found nesting in a variety of alternative vegetation types. I examined nest site selection in breeding areas representing three vegetation types: flax tussockland, scrub, and forest. The features at totals of 80 nest sites and 80 random sites were compared. Selection of nests is influenced primarily by vegetation. Yelloweyed Penguins selected nests with a dense vegetative cover, particularly between 50 and 100 cm above the ground, and a high degree of lateral concealment, regardless of vegetation type. Forest cover once provided a cool, damp terrestrial environment for breeding, but the loss of this cover has exposed the Yelloweyed Penguin to high levels of heat stress on land. Vertical vegetative cover at nests provides protection from the sun for both chicks and breeding adults. Lateral concealment due to solid nest-backs and surrounding vegetation may hinder access by predators, and may result in nests that are visually isolated from their neighbours. Inter-nest distances decrease with increasing density of vegetation, probably reflecting

the availability of sites with suitable cover and concealment.

#### THE PENGUIN ENVIRONMENT AT STEINHART AQUARIUM : A MODEL FOR SUCCESSFUL CAPTIVE REARING

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Since 1983, the Penguin Environment has functioned as a cost-effective, reproductively successful display of Jackass Penguins *Spheniscus demersus*. Constructed with minimal financial expenditure and exhibit space, this display is a self-sustaining breeding colony of 20 birds, including five mated pairs. By creating a habitat designed to enhance behavioural complexity, in conjunction with intensive keeper/bird interaction, colony health has been maximized. The Environment has never experienced an adult mortality. Utilizing a programme of hand-rearing, parent-rearing, and triple and quadruple clutching, 17 fertile eggs were produced in the most recent 1987/1988 breeding season, with a hatch to fledge success rate of 76%.

#### MODELLING THE NICHE REQUIREMENTS OF THE YELLOWEYED PENGUIN

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The Yelloweyed Penguin *Megadyptes antipodes* population has undergone a severe decrease in numbers and is now rare and regionally threatened on the New Zealand mainland. Its breeding area is restricted to patches of the east coast of the South Island. An analysis of the niche requirements of this penguin, both at the macroscale (including oceanographic and climatic factors) and at the local scale (including aspect, slope, vegetation structure and the accessibility of the habitat) was conducted to provide an explanation of the penguins' distribution and by extrapolation to determine the mechanisms of the populations' decrease. These

environmental parameters were incorporated into a model summarizing the niche requirements of the Yelloweyed Penguin. Whereas the model required clarification at the local scale it can be broadly applied to estimate the mainland range of the Yelloweyed Penguin. The model was also used to postulate the potential range of the Yelloweyed Penguins in the early European period and also for contemporary conditions. A comparison of these postulated ranges suggest that the main causes of population decrease were firstly a loss of habitat and secondly a decreased food supply.

#### MUTUAL CALLS AND MATE RECOGNITION IN ADELIE PENGUINS

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Preliminary analysis of sonograms of mutual calls of the Adélie Penguin *Pygoscelis adeliae* show significantly less intra-individual variation than inter-individual variation. This call apparently serves as a basis for discrimination between mate and other members of the colony during nest relief. Playback experiments were conducted during the incubation period to test the responses of 24 Adélie Penguins to recordings of the mutual calls of their mates, neighbours and strangers. Their behavioural responses were recorded and a hybrid-index scale was constructed to analyse the data. Both males and females could discriminate between their mates and strangers. Both males and females differed in their responses to the calls of their neighbours. Order of presentation on the calls did not affect the responses.

#### STATUS AND TRENDS OF ADELIE PENGUIN POPULATIONS IN THE ROSS SEA REGION

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Aerial reconnaissance and photography are being used in the Ross Sea sector of Antarctica to determine the breeding locations of Adélie Penguins *Pygoscelis adeliae*, and to count the numbers of nests occupied during the early incubation period. The study aims to provide adequate baseline information on Adélie Penguin populations that may be used in future to monitor large scale changes in krill abundance. Over the years 1981 to 1987, all islands and sea coasts (of Victoria Land and part of Oates Land) between 158E and 175E were searched, and 10 previously unreported breeding sites discovered. The region now has 38 known Adélie Penguin colonies with a total of over 1 000 000 breeding pairs : almost half of the world population. A sample of colonies selected for different size, topography, and latitude was photographed in each of the seven seasons to study the pattern of natural fluctuations in Adélie Penguin populations. Most other colonies have been surveyed more than once, and comparisons have been made with population estimates in earlier accounts. The relative advantages and efficiency of aerial photographic and ground censuses are discussed. Nearly all colonies have increased in size over the last 10-20 years. Possible reasons for this trend and for annual fluctuations in the numbers of penguins breeding, include climatic change, weather conditions, and the seasonal distribution of sea ice.

#### THE COURTSHIP PERIOD OF ADELIE, GENTOO, AND CHINSTRAP PENGUINS

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We studied the courtship period of sympatrically breeding Adélie *Pygoscelis adeliae*, Gentoo *P. papua*, and Chinstrap *P. antarctica* Penguins at Admiralty Bay, King George Island, South Shetland Islands, over six breeding seasons between 1981-82 and 1987-88; detailed observations and mass measurements were made during the 1982-83 and 1984-85 years. Adélie and Chinstrap Penguins are

migratory species that fasted from the time they arrived at the colony in spring until egg laying, unlike the sedentary Gentoo Penguin which made daily foraging trips to sea prior to egg laying. Male Adélie Penguins were highly nest-site tenacious, retaining their former territory 99% of the time in consecutive years. Gentoo Penguins had weak site affinities but very high mate fidelity, retaining mates 90% of the time, whereas Chinstrap Penguins exhibited both high nest-site tenacity (94% in males) and mate fidelity (82% of pairs remained together). Each species had significantly different frequencies of behavioural interactions during courtship with Adélie Penguins having the highest agonistic encounter rates and Gentoo Penguins the highest social display rates. Mass loss during courtship was significantly less in males than in females in all species on a g/d basis. Adélie Penguin pre egg-laying mass losses (49 g/d) were significantly lower than were those of Chinstrap Penguins (63 g/d) which were significantly less than those of Gentoo Penguins (85 g/d). Patterns of attendance, nest site and mate fidelity, behavioural interactions and mass changes are discussed in the context of the different environmental variables affecting the species in the centre of their respective breeding distributions.

#### EFFECTS OF A CHANGE IN FOOD SUPPLY ON GROWTH RATES, FLEDGING SIZES AND REPRODUCTIVE SUCCESS IN THE YELLOWEYED PENGUIN

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Diet, growth rates, morphometry and reproductive success of Yelloweyed Penguins *Megadyptes antipodes* were studied at two mainland breeding areas during two breeding seasons. Low adult body masses, delayed moult, high mortality of adults and chicks and depressed growth rates in the 1985-86 season indicated an adverse trend in food supply, and quantities of some prey species in the diet were found to differ. Growth rates of mass and some morphometric parameters varied between seasons



at one breeding area. Growth rates of one and two chick broods were found to differ only when food quality was apparently so poor as to cause mortality. Growth rates of first and second hatched chicks and of survivors and non-survivors within a brood were not significantly different. These largely invariant growth rates and the lack of brood reduction mechanisms suggest that Yelloweyed Penguins usually exploit a predictable food supply, and rarely face feeding conditions as unfavourable as those during the 1985-86 season.

#### THE FOOD, OVER SEVEN BREEDING SEASONS, OF THE ADELIE PENGUIN IN PRYDZ BAY, ANTARCTICA

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The breeding season stomach contents of adult Adélie Penguins *Pygoscelis adeliae* were sampled annually between 1981/82 and 1987/88 at colonies in the Vestfold Hills and Rauer Islands in Prydz Bay, Antarctica. Sampling techniques were improved over the study period; initially emetic induced vomiting and single flush water off-loading methods were used, until 1985/86, from which time the multiple-flush water offloading technique was used to extract food items. A comparison of the single and multiple flush techniques is made with data from the 1987/88 season. The euphausiids, *Euphausia crystallorophias* and *E. superba*, and the pelagic fish *Pleuragramma antarcticum*, were consistently dominant food items over the study period. Amphipods occurred in small numbers in most samples. Squid was a rarely encountered food item. Samples obtained prior to hatching were always small and contained mostly amphipods and *E. crystallorophias*. Following hatching, sample mass increased, *E. crystallorophias* remaining an important item during the remainder of the chick growth period. *E. superba* also increased in importance at this time. The fish component of the diet typically became more significant during the latter half of chick growth. Between season

fluctuations in composition of the diet also existed. In 1982/83 *E. crystallorophias* was the dominant euphausiid in the diet, occurring twice as frequently as *E. superba*. In the 1983/84 and 1984/85 seasons this ratio was reversed, with *E. superba* dominating by 2:1. Data on the distribution and abundance of the two krill species over the local continental shelf region for the 1982/83 and 1985/86 seasons are presented. Factors which may contribute to the fluctuating food availability are discussed.

#### MOVEMENTS AT SEA OF LITTLE PENGUINS FROM PHILLIP ISLAND, VICTORIA

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Little Penguins *Eudyptula minor* from Phillip Island, Victoria have been radiotracked to discover the range of their movements at different time of the year and to attempt to identify their feeding areas. At two-monthly intervals between February 1987 and April 1988, about 10 penguins on each occasion were fitted with radiotransmitters (total c. 60 individuals). Each penguin was tracked for periods of three days to two months. Penguins that remained within about 20 km of their burrow site during a tracking period were precisely located at 30-min intervals throughout each day with a land-based antenna system (typically three intercepts/location). Birds that travelled greater distances were located with a light aircraft at two-four day intervals. Movements of penguins were varied and the variation may be attributed to the seasonal occupation of the bird (e.g. breeding or nonbreeding) or the distribution and availability of prey species. One female penguin that had been recorded 'breeding' at Phillip Island in February 1987 was tracked to a range of more than 700 km from Phillip Island in June-July 1987.

#### FLUCTUATIONS IN THE ADELIE PENGUIN POPULATION AT CAPE BIRD, ANTARCTICA

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The results of a monitoring study of three Adélie Penguin *Pygoscelis adeliae* colonies at Cape Bird, Antarctica, are presented. Occupied nests have been counted immediately after egg laying most years between 1965 and 1970, and annually since 1974. The population has not shown the degree of stability that might be expected of a long-lived species with a low reproductive rate. The population has twice deviated significantly from its mean value (c. 37 500 pairs). Numbers dropped by about 16% in 1967 and a further 30% in 1968, when in November fast-ice extended from Cape Bird to the horizon. The 1968 decrease has been attributed to the fast-ice, but numbers were unaffected in two subsequent years with similar ice conditions. After eight years of relative stability around the pre-1967 level, a period of unprecedented growth began in 1982 and 1983. The 1987 count of 54 000 pairs was the highest ever made at Cape Bird. The results of this study stress the need for great caution when using marine bird populations to detect man-induced changes in the marine environment.

#### THE FORAGING ECOLOGY OF SPHENISCID PENGUINS

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The four penguin species comprising the genus

*Spheniscus*, the Humboldt Penguin *S. humboldti*, Magellanic Penguin *S. magellanicus*, Jackass Penguin *S. demersus* and Galapagos Penguin *S. mendiculus*, inhabit tropical or temperate areas. There are few data on the foraging behaviour of nonbreeding birds, but nesting *Spheniscus* penguins feed almost exclusively on pelagic school fish such as sardines and anchovies. Penguins leave their breeding islands in the morning and return, after foraging, at dusk. Most foraging trips are one day but may extend up to five days when the birds have large chicks. *Spheniscus* penguins at sea occur most frequently as singletons with larger groups being exponentially less common. Penguins normally travel by swimming just below the water's surface at speeds between 7 - 9 km/h, interspaced with rests on the surface where they swim at c. 1.5 km/h. Overall, the travelling speed is between 3 - 7 km/h. Almost all birds appear to forage inshore within 25 km of their breeding locality. In contrast to travelling birds, which normally dive for 15-30 s, foraging penguins may remain underwater for up to 240 s. The deepest dive recorded is 130 m, however, most time underwater is spent at less than 10 m depth. Normal foraging dives consist of simple 'bounce' dives. When a school of fish is encountered, penguins in groups hunt co-operatively. The birds swim rapidly round the fish herding them into a dense, depolarized group. Individual penguins leave the encircling group to plunge through the fish below the school. Prey are caught and swallowed underwater while the birds continue circling. The conspicuous colouration of *Spheniscus* penguins is thought to facilitate prey capture by confusing the schooling fish.