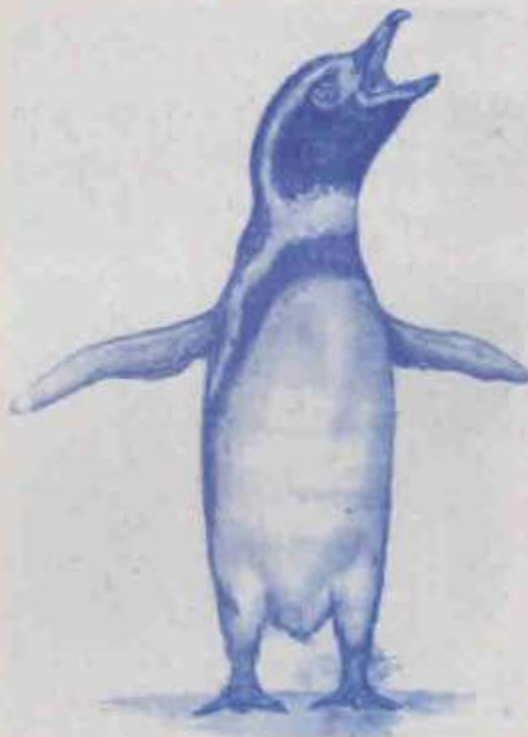


THE FOURTH INTERNATIONAL PENGUIN CONFERENCE

4 - 8 SEPTEMBER 2000



BOOKS OF PROGRAMME AND ABSTRACTS



DEPARTAMENTO DE BIOLOGIA MARINA
FACULTAD DE CIENCIAS DEL MAR
UNIVERSIDAD CATOLICA DEL NORTE
COQUIMBO, CHILE

GALAPAGOS

Fourth International Penguin Conference

**Caja de Compensación de Los Andes,
La Serena, Chile
4 – 8 September 2000**

Programme and Abstracts

Sponsored by:

**Universidad Católica del Norte Sede Coquimbo
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**Laboratorio de Vertebrados Marinos
Departamento Biología Marina
Facultad Ciencias del Mar
Universidad Católica del Norte
Larrondo 1281, Coquimbo
Chile**

August 2000

PENGUIN CONFERENCE PROGRAMME

3 September

- 1830 Registration, Conference Room Foyer, Caja de Compensación de Los Andes.
2030 Informal ice-breaker, Caja de Compensación de Los Andes.

4 September

- 0915 Registration, Conference Room Foyer, Caja de Compensación de Los Andes.
0930 Welcome and introductory remarks.

LECTURE

Chair: Rory Wilson

- 1030 Gerald Kooyman: "Closing the circle on the annual cycle of the emperor penguin: 1902 - 2001".
1100 Morning tea.

SESSION I: Breeding Biology I

Chair: Alejandro Simeone

- 1125 Davis, L.S., Renner, M. and Houston, D : Brood reduction and behaviour in Erect-Crested Penguins (*Eudyptes sclateri*).
1150 Saez D. & J. Valencia : Effects of nest group size and physical parameters on reproductive success of *Pygoscelis papua*, Ardley Island, South Shetland, season 1997-98.
1215 Barham P., R. Murphy, D. Bolton and N. Simpson: Incubation of African penguin eggs: finding out how the birds do it.
1240 Simeone, A, B. Araya, M. Bernal, E. N. Diebold, K. Grzybowski, M. Michaels, J. A. Teare, R. S. Wallace & M. J. Willis. : Breeding and attendance patterns of Humboldt penguins (*Spheniscus humboldti*) at a colony in central Chile.
1400 Lunch.

SESSION II: Population Trends

Chair: Braulio Araya

- 1425 Araya B. & M. Bernal : Humboldt Penguin censuses in Chile
1450 Bingham M.: Penguins of the Falkland Islands www.seabirds.org
1515 Jessop R., P. Dann, A. Chiaradia and M. Cullen : The effects of pilchard mortalities on Little Penguins *Eudyptula minor*
1540 Ellis S., Lacy R., Crawford, R.J.M., Underhill, L.G., Whittington, P.A.: Whither the Spheniscus penguins - How many will be extant in the wild in 2100?
1610 Afternoon Tea.



SESSION III: Conservation and Captivity

Chair: Patricia Majluf

- 1610–1635 P. Dee Boersma, and D. L. Stokes : Magellanic penguins and marine protection: using behavior and ecology for conservation.
- 1635–1700 Govers J.: Black-Footed Penguins (*Spheniscus demersus*) in European zoos and the link to wildlife conservation.
- 1700–1725 Majluf P., Babcock B. & Riveros J.C. : Penguin-fishery interactions off Punta San Juan, the main Humboldt Penguin colony in Peru.
- 1725–1750 George, H. The Otway Foundation: Ten years protecting penguins in Chile.
- 1750–1815 Tsuda T.T., M. Tsuda, M. Fukada, M. Kurita and H. Inoko : Phylogenical Analysis of Penguin (Spheniscidae) based on genetic polymorphism in the MHC.
- 1815–1840 Schiavini A. : Staten Island, Tierra del Fuego: The unrevealed and largest breeding ground for Southern Rockhopper Penguins?
- 1930–2200 Cocktail party (Caja de Compensación de Los Andes).

Tuesday 5 September

0855–0900 Announcements.

SESSION IV: ENSO

Chair: Boris Culik

- 0900–0925 Culik B., J. Hennicke & T. Martin: Humboldt penguins outmanoeuvring El Niño.
- 0925–0950 Elaine P. Akst, P. Dee Boersma and Robert C. Fleischer: The effect of El Niño events on penguin genetic diversity
- 0950–1015 Fortescue M.: The effect of El Niño Southern Oscillation (ENSO) on foraging behaviour and breeding success of the Little Penguin *Eudyptula minor* on Bowen Island, Jervis Bay.
- 1015–1040 Vargas H.: Efectos de El Niño en los pingüinos de Galapagos y tendencia poblacional.
- 1040–1100 Morning tea.

SESSION V: Behaviour

Chair: Joseph R. Waas

- 1110–1135 J.M.Cullen : Divorce in Little Penguins
- 1135–1200 Hennicke, J., B. Culik : Parental investment in Humboldt Penguins
- 1200–1225 Miyazaki M. and J.R. Waas : Correlations between body size, defensive behaviour and reproductive success in male Little Blue Penguins *Eudyptula minor* : implications for female choice.
- 1230–1400 Lunch.



SESSION VI: Foraging Ecology I

Chair: Robert J. M. Crawford

- 1400 – 1425 Crawford R.J.M., J. H. M. David & L. J. Shannon: African penguins as predators and prey. - Coping (or not) with change
- 1425 – 1450 Wienecke B. & G. Robertson: Variability of foraging behaviour of King Penguins at Macquarie Island
- 1450 – 1515 Ainley D.G. C.A. Ribic, G. Ballard, P.R. Wilson, K.R. Barton.: "Foraging-area overlap among neighboring colonies of Adelie Penguins: does competition play a role?"
- 1515 – 1540 Tremblay Y. & Y. Chérel : Flexible diving behaviour, foraging effort and foraging success in Rockhopper Penguins (*Eudyptes chrysocome*) living in different marine environments.

1610 – 1730 First formal poster session. (odd numbers)

2000 – 2200 Special session for open contributions.

Wednesday 6 September

Excursions to a Humboldt penguin colony.

Thursday 7 September

0855 – 0900 Announcements.

SESSION VII: Breeding Biology VII

Chair: Carlos Zavalaga

- 0900 – 0925 Chiaradia A.: Changes in parental care, chick provisioning and chick growth rates of Little Penguins *Eudyptula Minor* in years of high and low breeding success.
- 0925 – 0950 Clarke J. & K. Knowles : Breeding success of Adelie Penguins in relation to diet and foraging behaviour: an overview of eight seasons of data.
- 0950 – 1015 Wolfaardt A.C., A.J. Williams & L.G. Underhill : Breeding success and productivity of rehabilitated African Penguins following the *Apollo Sea* oil spill
- 1015 – 1040 Zavalaga C.B. and R. Paredes : The breeding biology of the Humboldt Penguin at Punta San Juan, Peru
- 1040 – 1100 Morning tea.

SESSION VIII: Foraging & Breeding

Chair: Klemens Pütz

- 1100 – 1125 Cannell B. R. Wooller and S. Bradley: Do nearby nursery areas for clupeoid fish dictate the breeding locations Of Little Penguins *Eudyptula minor*.
- 1125 – 1150 Pütz K.: Winter foraging of King Penguins breeding in the Falkland Islands compared breeding sites elsewhere



1150 – 1215 Vergani D F , Stanganelli ZB : Analysis of breeding success fluctuation of Adelie Penguins in the Scotia Arc. Environmental warming or ENSO effect?

1230 – 1400 Lunch.

SESSION IX: Conservation

Chair: Esteban Frere

1400 – 1425 Gandini P., E. Frere, S. Ferrari & M. Perroni : Magellanic penguin mortality in a gillnet fishery of southern patagonia, Argentina.

1425 – 1450 Houston D.M. : The impact of tourism on Blue Penguins.

1450 – 1515 Dann P., R. Jessop, M. Cullen, L. Renwick, M. Healy, P. Collins and B. Baker.: The effects of flipper bands on the survival of Little Penguins, *Eudyptula minor*.

1515 – 1540 Crawford, R.J.M., S.A. Davis, R. Harding, L.F. Jackson, T.M. Leshoro, M.A. Meyer, R.M. Randall L.G. Underhill, L. Upfold, A.P. van Dalsen, E. van der Merwe, P.A. Whittington, A.J. Williams & A.S. Wolfaard : Assessment of the initial impact of the "Treasure" oil spill on the African Penguin off Western Africa.

1540 – 1605 Woolfaardt, A.C., Whittington, P.A., Nel, D.C. & Crawford, R.J.M.: The "Apollo Sea" revisited. The fortunes of victims from this and other oil spills.

1610 – 1700 Second formal poster session. (pair numbers)

1730 – 1830 The Second International Penguin Fun Run (5 km).

2100 – 2200 Special sessions of the Penguin Conference Standing Committee.

Friday 8 September

0855 – 0900 Announcements.

SESSION X: Foraging Ecology II

Chair: John Croxall

0900 – 0925 Radl, A., B. Culik: Foraging strategies in Magellanic Penguins (*Spheniscus magellanicus*); habitat use and diving behaviour.

0925 – 0950 Y Ropert-Coudert, A. Kato, J. Baudat, C-A. Bost, Y. Le Maho and Y. Naito : Underwater feeding behaviour study by multiple data recording on free-ranging Adélie Penguins

0950 – 1015 Wilson P.R. & Antje Steinfurth: The ups and downs of diving In Magellanic Penguins: new angles on the effort of being at depth.

1015 – 1040 Barlow K.E., J.P. Croxall, I.L. Boyd & I.J. Staniland : Foraging ecology of breeding Macaroni penguins at South Georgia. Are penguins in competition with seals?

1040 – 1100 Morning tea.



SESSION XI: Physiology and Energetics I

Chair: Pat Butler

- 1100 – 1125 Butler P.J., Richard M. Bevan, Anthony J. Woakes & Ian L. Boyd.: Field metabolic rate of Gentoo Penguins throughout the breeding season.
- 1125 – 1150 Winter, S. J. & Waas, J. R. : Heart rate as a measure of individual recognition in Little Blue Penguins (*Eudyptula minor*).
- 1250 – 1215 Froget, P.J. Butler, A.J. Woakes, Y. Handrich and Y Le Maho : The use of heart rate to estimate field metabolism of King Penguins
- 1215 – 1240 J.A. Green, P.J. Butler, A.J. Woakes And I.L. Boyd : Behaviour and energetics of Macaroni Penguins (*Eudyptes chrysolophus*) at South Georgia.
- 1230 – 1400 Lunch.

SESSION XII: Physiology and Energetics II

Chair: Gene Fowler

- 1400 – 1425 Boggs D.F., P.J. Butler, R.V. Baudinette and P.B. Frappell.: Differential air sac pressures in swimming Little Penguins.
- 1425 – 1450 Peters G. : Digestive regulation and resource partitioning in penguins – implications for optimized foraging.
- 1515 – 1540 Bannash, R. & Santivañez-Koref : New results from the hydrodynamic approach to the energetics of penguins swimming.
- 1605 – 1630 Fowler G.S., E. Frere and P. Gandini : Stress responses to human disturbance in Magellanic Penguins under conditions of low vs. Moderate levels of visitation.
- 1655 – 1720 Turner, E.K. and R.G. Harcourt.: The effects of human activity on the behavioural and hormonal stress response of Little Penguins (*Eudyptula minor*).
- 1750 – 1800 Conference closure.
- 2000 – 2400 Banquet, Casino de Peñuelas de Coquimbo.

POSTERS

Breeding Biology

1. Groscolas R., M.A. Thil, C. Fayolle, F. Decrock, S. Côté, A. Lacroix, J.P. Robin: Triggering of egg abandon below a body mass threshold in fasting-incubating King penguins
2. Vallance N., L.S. Davis & J. Valencia. Moulting of Adelie Penguin chicks.
3. Sclaro J.A., R.P. Wilson, S. Laurenti, H. Gallelli & J. Upton: Sex identification in the monomorphic Magellanic Penguin.
4. Shindo J.: Annual changes in the quality of semen in Humboldt Penguin (*Spheniscus humboldti*)



5. Paredes R., C. Zavalaga & D. Boness: Patterns of egg laying and breeding success in Humboldt Penguins (*Spheniscus humboldti*) at Punta San Juan, Peru.
6. Moreno J., P. Yorio, P. García Borboroglu and J. Potti : Health state, condition, immunocompetence and reproductive performance in Magellanic Penguins *Spheniscus magellanicus*
7. Chiaradia A. : Waddling in the dark – annual cycle of arrival and departure of Little Penguins *Eudyptula Minor*
8. Mangin S., M. Gauthier-Clerc, Y. Le Maho: Parasitism of the King Penguin by the tick *Ixodes uriae*: effects on breeding performance and relation with the breeding site in the colony

Breeding Biology and Foraging Ecology

9. Gauthier-Clerc M., Y. Le Maho, J. Gendner, J. Durant & Y. Handrich: State-dependent decisions in long-term fasting King Penguin during courtship and incubation
10. Robertson G. & B. Wienecke : The fatter the better.
11. Clausen A. and K. Pütz, : Recent trends in diet composition and productivity of Gentoo, Magellanic And Rockhopper Penguins in the Falkland Islands

Foraging Ecology

12. Dyer B.M., R. Crawford and L. Upfold: Bias attributable to prey size in estimating diet of African Penguins by stomach flushing.
13. Ballard G., D. Ainley, C. Ribic, K. Barton, S. Heath, I. Gaffney, S. Webb, P. Wilson, M. Beigel and N. Polish: Effect of instrument attachment on foraging trip duration of Adélie Penguins At Ross Island, Antarctica.
14. Charrassin, J.B. and C.A. Bost: Foraging behavior of penguins in relation to hydrographic features
15. Coria N., M. Libertelli, P. Berón, R. Casaux and M. Favero: Comparison of the autumn diet Of Gentoo Penguin (*Pygoscelis Papua*) on Laurie Island, Antarctica, over six years
16. Schiavini, A.C.M., Rajlevsky, J. : La dieta del pingüino Penacho Amarillo en el Mar Argentino Austral. Resultados preliminares.

Physiology:

17. Rudolph, W., C. Godoy, M. Herrera, C. Rios and J. Valencia.: Plasma chemistry changes of chicks and adults Gentoo Penguins (*Pygoscelis papua*).
18. Nakagawa S., J. Waas & M. Miyazaki.: Heart rate as a measure of social recognition: do Little Blue Penguin chicks use unique vocal signatures to distinguish siblings from other chicks?
19. Lawless R, Buttemer Wa, Astheimer Lb, Kerry Kr: Cool chicks: the influence of thermoregulatory demand on contact creching behaviour in Adelie Penguin chicks.
20. Gerrit P., J. A. Scolaro, J. Upton, S. Laurenti, H. Gallelli: Monitoring of seabird behaviour and physiology at the nest site using autonomous UHF-video-transmission.



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21. Handrich, Y., A. Ancel, M. Gauthier-Clerc, Y. LeMaho & Y. Naito: Tracheal temperature changes associated with diving behaviour in free-ranging King Penguins.
 22. Charrassin, J.-B., A. Ancel, M. Gauthier-Clerc, C. Bost, Y. Naito, and Y. Handrich.: Activities at sea that affect oesophageal temperature in free-ranging King Penguins
 23. Kubetzki, U. J. Muñoz S., S. Garthe, G. Luna-Jorquera and R.P. Wilson : Thermoregulation of Humboldt Penguin chicks as related to the thermal characteristics of the nest-sites.

Penguin Diseases

24. Laurenti S., and G. Pazos : Helminth fauna of Magellanic Penguins in a colony of Peninsula de Valdés, Chubut, Argentina.
25. Fredes, F., M. Herrera, C. Madariaga, C. Godoy, J. Valencia, H. Alcaino: Preliminary findings of the intestinal parasite fauna of Gentoo Penguin (*Pygoscelis Papua*) at waterboat point, Paradise Bay, Antarctica.
26. Miller G., B. Hofkin, and R. Miller.: Avian malaria in some wild populations of penguins.
27. Miller G., B. Hofkin, and R. Miller.: Testing for some diseases in penguins and skuas.

Population Trends

28. Miller G., B. Hofkin, and R. Miller.: Genetic diversity of Galapagos Penguins (*Spheniscus mendiculus*).
29. Descamps S., M. Gauthier-Clerc, J. Gendner, V. Motsch and Y. Le Maho : Long-term study of King Penguin population using an automatic identification system
30. Woehler, E. & M. Riddle : Recent trends in Adélie Penguin populations at Casey, East Antarctica
31. Woehler, E., J. Cooper, Jp. Croxall, Wr. Fraser, G. Kooyman, Gd. Miller, Dc. Nel, D. Patterson, H. Peter, Ca. Ribic, K. Salwicka, Wz. Trivelpiece & H. Weimerskirch : The montana report
32. Woehler E. & Y. Claypole, H. Brotsma & M. Riddle : Increases in Adélie Penguin populations in the Australian Antarctic Territory
33. Woehler, E. K. Stove, H. Brotsma & Martin Riddle : Counting penguins
34. Horner M., R. Miller And G. Miller.: A molecular phylogeny of penguins based on MTDNA *cytochrome-b* gene sequences
35. Black A., R. White and K. Gillon : The dispersion of penguin species in the waters of the Falkland Islands
36. Clarke J., Lyn Irvine & K. Knowles: Changes in Adélie penguin colony occupation patterns over ten seasons: a demographic perspective.

Conservation

37. DeNapoli N. and H. Urquhart : Analysis of molt wing swelling in a captive colony of African Penguins



38. Walker B., P. Boersma and J. Wingfield : Penguins and people in patagonia: an example of sustainable nature tourism
39. Wolfaardt A., A. Williams & D. Nel: Entanglement of African Penguins at Dassen Island – how severe is the problem?
40. Márquez M., C. Vodopivec, R. Casaux, A. Curtosi : Comparison of total mercury concentration in tissues of chick and Adult *Pygoscelis Adeliae* and *Pygoscelis Papua* at Potter Peninsula, South Shetland Islands, Antarctica.
41. Barham P., J. Wilcox, Tania Longman, Sarah Bracher : Design of improved flipper bands for penguins
42. Leshoro M., R. Crawford, L. Shannon, P. Whittington, Van der Merwe, M. Kroese and J. Kieser : Management of the African Penguin colony at Robben Island, 1997-1999
43. Fowler G., R. A. Sosa, J. C. Wingfield & P. D. Boersma: Seasonal and sex-based variation in the adrenocortical response to capture and handling in the Magellanic Penguin

ABSTRACTS

Triggering of egg abandon below a body mass threshold in fasting-incubating King Penguins

R. Groscolas¹, M.A. Thié¹, C. Fayolle¹, F. Decrock¹, S. Côté¹, A. Lacroix², J.P. Robin¹
¹Centre d'Ecologie et Physiologie Energétiques, CNRS, Strasbourg, France; ²Centre d'Etudes Biologiques de Chizé, CNRS, Villiers-en-Bois, France

Like other penguin species, the king penguin (*Aptenodytes patagonicus*) fasts while incubating, relying on fat stores as the main energy source. The observation that some birds spontaneously abandon their egg before being relieved by their mate has led to the suggestion that an endogenous refeeding signal stimulates departure to sea. This hypothesis was tested by monitoring the behavior of incubating birds prevented relief and by determining their metabolic and endocrine status at egg abandon. The recording of egg temperature by biotelemetry showed that birds incubate continuously until they begin to leave the egg temporarily and eventually desert it. On average, definitive egg abandon was preceded by twenty transitory abandons spread over two days. Video analysis of behavior showed that the duration of transitory abandons and the distance between the bird and the egg during these abandons increased progressively throughout the abandon process, reflecting a decrease in the drive to incubate. Body mass at egg abandon was lower than the critical body mass characterizing the phase II-phase III transition in fasting king penguins (shift from protein sparing to increased protein catabolism at a threshold adiposity). The plasma levels of various metabolites (uric acid, NEFA, triglycerides) and corticosterone were also indicative of a phase III. Plasma prolactin was markedly depressed in abandoning birds, contributing to explain the decreased drive to incubate. All the birds that abandoned their egg and departed to refeed at sea in a poor body condition were resighted and rapidly regained their deficit in body mass. We conclude that in incubating king penguins an endogenous signal linked to a critical depletion of energy stores triggers egg abandon and refeeding before the bird's life is endangered.

The Effect of El Niño Events on Penguin Genetic Diversity

Elaine P. Akst, P. Dee Boersma and Robert C. Fleischer

There remains little doubt that severe bottleneck events decrease genetic diversity. However, most studies have focussed on human observed, recent bottleneck events. An examination of the effects of multiple historic and pre-historic bottlenecks would add to the existing knowledge about the consequences of small and fluctuating population sizes. The penguin genus *Spheniscus* is a good system for studying the effects of historic bottlenecks because it is comprised of two species (Galápagos and Humboldt) that have probably

undergone El Niño induced bottlenecks for thousands of years, and two species (African and Magellanic) that are not as affected by El Niño events and may have more historically stable population sizes. In order to infer the amount of genetic diversity in *Spheniscus* penguins, we developed microsatellite markers for each of the four species. Microsatellites are repetitive, non-coding regions of DNA randomly distributed throughout the genome. To date, we have worked with 7 microsatellite loci which we have analyzed in all four species. As expected, preliminary data suggests that the Galápagos Penguins, which have the smallest population size, have almost no genetic diversity. Magellanic Penguins, which have the largest populations, have the most genetic diversity and heterozygosity.

Breeding and attendance patterns of Humboldt penguins (*Spheniscus humboldti*) at a colony in central Chile

A. Simeone¹, B. Araya², M. Bernal³, E. N. Diebold⁴, K. Grzybowski⁵, M. Michaels⁵, J. A. Teare⁶, R. S. Wallace⁵ & M. J. Willis⁷

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⁵Milwaukee county zoo, milwaukee, wi, usa, e-mail: rwallace@execpc.com

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⁷Denver zoological gardens, denver, co, usa, e-mail: superbird@denverzoo.org

Since 1995 we have been monitoring the humboldt penguin (*Spheniscus humboldti*) colony on pajaro niño island (33°21's; 71°41'w) Algarrobo, central Chile. Breeding activity was recorded at 2 week-intervals in three sections of the island, each partitioned using 10 x 10 m grids: roosting birds were counted from vantage points at dusk when most birds return from foraging. Breeding occurs throughout most of the year with two peaks, one during autumn (may) and another in spring (october). Autumn breeding seasons are heavily affected by rains, resulting in flooding of most nests and subsequent nest desertion. During winter (june to august) penguins abandon the colony until the following spring season. Maximum numbers of roosting birds are observed during february when most penguins moult. Juveniles are present in the colony only between november and march, with maximum numbers during the moult in january. Compared with non-el niño years, the unusual rains during the 1997-1998 el niño delayed the spring breeding season by ca. 45 days and nesting pairs were reduced by ca. 70%; during the autumn of 1998 rains stopped all breeding attempts. A similar pattern has been reported for Cachagua island (32°s) also in central chile. However, at the more northerly colony at Pan de Azúcar island (26°s) breeding is more continuous and birds do not completely abandon the colony during winter. This comparison suggests latitude-related variations in the breeding and attendance patterns between colonies, attributable to some extent to differential rainfall regimes.

Effect of Instrument Attachment on Foraging trip duration of Adélie penguins at Ross Island, Antarctica

Grant Ballard*, David G. Ainley*, Christine A. Ribic+, Kerry Barton#, Sacha Heath*, Ian Gaffney*, Sophie Webb*, Peter R. Wilson#, Mike Beigel^ and Nat Polish^

*H.T. Harvey & Associates, + University of Wisconsin, #LandCare Research NZ,

^ Beigel Technology.

We compared foraging trip duration and breeding success of Adélie Penguins (*Pygoscelis adeliae*) carrying various combinations of small radio telemetry transmitters, flipper bands, implanted passively interrogated transponder (pit) tags, and/or time-depth recorders at two widely separated colonies of different size on Ross island, antarctica, during three seasons. Trip durations were timed by electronic devices rather than human observation. Breeding success was not affected. Instruments contributed only minor effects, which varied with timing within the nesting season. Most of the variation in foraging trip duration was attributed to individual, sexual, annual, and colony differences. Male trips were significantly shorter than females' in a subset of known-sex birds. If researchers use small, carefully-attached instruments, the effects of attachments on research results will be virtually nil.



Incubation of African Penguin eggs: Finding out how the birds do it

Peter Barham, Roger Murphy, Duncan Bolton*, Nigel Simpson*
H H Wills Physics Laboratory, University of Bristol, Bristol BS8 1TL, UK
*Bristol Zoo Gardens, Clifton, Bristol, BS8 3HA

Artificial incubation of bird's eggs is based on data gained from domesticated species, mainly *galliformes*. It is generally assumed that other species eggs will require similar conditions and exceptions are found through trial and error with no knowledge of the natural incubation parameters. This basic lack of data results in lower hatch rates than might be desirable, especially considering that some of the species involved may have high conservation significance.

We have designed and built instrumented eggs which can monitor both the orientation and the temperature during incubation. We have exchanged these eggs for infertile eggs of nesting African penguins (*Spheniscus demersus*) in Bristol Zoo and thus obtained data on the frequency and degree of turning of the eggs as well as the mean temperature and temperature gradient across the egg.

In general, we find that the penguins turn the eggs through a small angle (typically between 45 and 90°) rather often (the mean time between successive turns is typically only 5 to 10 minutes) with only a few long periods (more than 30 minutes) with no turning; the birds tend to turn the eggs much less at night than during the day. The core temperature of the eggs varies during a typical day by about 1°C and lies between about 35 and 36°C. The warmest part of the egg is usually at a temperature about 1.5°C higher and the coolest about 1.5°C lower than this core temperature. A further interesting observation is that the temperature is that the egg temperature is about 1°C lower in the first few days of incubation than it is later.

Design of improved flipper bands for penguins

Peter Barham*, James Wilcox, Tania Longman, Sarah Bracher
University of Bristol, H H Wills Physics Laboratory, Tyndall Avenue,
Bristol, BS8 1TL, UK

At the Cape Town Penguin Conference, Bernard Stonehouse raised the issue of using plastics for improved penguin flipper bands, a subject that led to considerable discussion. We have since carried out experiments to demonstrate that there are a range of polymeric materials covering a wide range of stiffnesses, that can withstand the environments in which penguins live and from which plastic bands can be made. We have also shown, using model systems, that bands of a conventional design can have a serious detrimental effect on the hydrodynamics of penguins (leading to increases in energy consumption of up to 30%). We have tested modified designs and will present results that suggest that a suitably shaped plastic band can be produced that has an energy cost of less than 5% (at least in our model tests).

The advantages, and potential disadvantages of different band designs and materials will be discussed as will the possibilities for producing "smart" bands containing active devices such as depth measuring and recording systems, etc.

The dispersion of penguin species in the waters of the Falkland Islands

Andrew D. Black, Richard W. White and Keith W. Gillon
Joint Nature Conservation Committee, South-west Atlantic Seabirds at Sea Team,
PO Box 705, Stanley, Falkland Islands
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The South-west Atlantic Seabirds at Sea Team (SWASAST) was formed in February 1998 to conduct at-sea surveys of seabirds and marine mammals in Falkland Islands waters. During these surveys six species of penguin have been recorded. The three most frequently recorded penguin species, Magellanic *Spheniscus magellanicus*, rockhopper *Eudyptes chrysocome* and gentoo *Pygoscelis papua* penguins, all breed in internationally important numbers in the Falkland Islands. However, the frequency of at-sea sightings does not reflect the population sizes of the species in the islands. On survey, Magellanic penguins outnumber rockhopper penguins, which suggests that rockhopper penguins might be under-recorded. Magellanic and

rockhopper penguins are seasonal visitors to the waters of the Falkland Islands, present between September and April, while gentoo penguins are resident. During the breeding season highest densities of Magellanic and gentoo penguins were recorded in inshore waters while rockhopper penguins are more widely dispersed. Following the post-breeding moult in March and April, the vast majority of Magellanic and a high proportion of rockhopper penguins depart from the Falkland Islands waters to over-winter in adjacent Patagonian Shelf waters off continental South America before returning to the survey area from September onwards. Gentoo penguins winter within Falkland Islands waters and were recorded throughout the winter months at higher densities, in larger groups and further offshore than during the breeding season. Three other species were recorded less frequently. Two of these, king *Aptenodytes patagonicus* and macaroni penguins *E. chrysolophus*, breed locally in small numbers. However, the frequency and timing of the sightings of these species suggests that these birds could be from the much larger South Georgian populations. Chinstrap penguins *P. antarctica* have been recorded on four occasions in the south of the main study area indicating that the Falklands are at the northern limit of their range. A sound knowledge of the at-sea distribution of penguins and other seabirds in these waters is important when assessing the potential impact of human activities, such as fishing and hydrocarbon exploration and exploitation.

Differential air sac pressures in swimming Little penguins.

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Both wing flapping in flying birds and foot paddling in diving ducks alter the pressures within air sacs. Therefore we sought to determine whether wing flapping in submerged swimming penguins would cause differential changes in air sac pressures that might induce a mixing of air sac air with lung air, accessing the respiratory system oxygen store during the breath hold. Differential and absolute air sac pressures were measured in interclavicular and posterior thoracic air sacs of four Little Penguins, *Eudyptula minor*, as they swam in a water flume (0.95 m s^{-1}). The mean change in differential pressure associated with downstroke was 0.053 kPa , due to a greater change in pressure in anterior (0.115 kPa) than posterior sacs (0.059 kPa). These changes in sac pressure with wing stroke are less than those observed in flying mappies (0.37 kPa); the differential pressure fluctuations are less than those observed in diving tufted ducks (0.49 kPa) and represent about a tenth of the driving pressure per breath at the surface. Although the impact of the wingbeat cycle on air movements must be volumetrically small in penguins, these pressure oscillations at 2.5 Hz may nonetheless enhance mixing by combined convective and diffusive mechanisms such as described for high frequency ventilators. Wing excursions were quite small at these shallow depths and slow speeds, thus our measurements probably underestimate the impact more forceful swimming efforts could have on air sac pressures. (Supported by EWU and the Australian Research Council)

Field metabolic rate of Gentoo Penguins throughout the breeding season

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We have calibrated heart rate (f_H) against rate of oxygen consumption (\dot{V}_{O_2}) in gentoo penguins and, by implanting heart rate and temperature data loggers (HRTDLs) into the abdominal cavity, f_H has been used with free-ranging gentoo penguins to estimate \dot{V}_{O_2} during their breeding period. The estimated rate of oxygen consumption when the birds were ashore during incubation and chick guarding was similar to that measured directly by respirometry for penguins resting on land ($12.1 \text{ ml kg}^{-1} \text{ min}^{-1}$) and to that determined by the doubly-labelled water (DLW) method for birds during incubation ($12.2 \text{ ml kg}^{-1} \text{ min}^{-1}$). However, the estimated \dot{V}_{O_2} for penguins at sea during incubation and chick guarding was almost 50% of that determined by the DLW method during chick rearing ($51.0 \text{ ml kg}^{-1} \text{ min}^{-1}$) and 64% of that for penguins swimming in a static water canal ($40.9 \text{ ml kg}^{-1} \text{ min}^{-1}$). Also, it is only 15% above the value obtained for gentoo penguins



resting in water ($22.7 \text{ ml kg}^{-1} \text{ min}^{-1}$). The discrepancy between the estimates from the f_{H} method and the DLW technique when the birds are at sea, could be mostly explained by a 40% over estimate by the latter when used with animals in water. The discrepancy between the estimate of $\dot{V}\text{O}_2$ for birds at sea from the f_{H} method and the value obtained from birds swimming on the water canal could be at least partly explained by the drop in abdominal temperature that occurs in these birds when they dive.

Activities at sea that affect oesophageal temperature in free-ranging King Penguins

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Determining when and how much penguins feed at sea still remains a major challenge in foraging studies. While the use of stomach temperature recorders has partially solved this problem, the deployment of such devices on king penguins has shown that the method is limited when birds eat small prey and when the stomach fills up. Furthermore, abdominal temperatures fluctuate in relation to diving per se. Recent studies on king penguins have shown that oesophageal temperature is a better tool for accurately detecting feeding events than stomach temperature. To determine what the different factors that affect oesophageal temperature in free-ranging King Penguins might be, we have measured this temperature simultaneously with these of four other tissues from the periphery to the core of the body : skin, trachea, abdomen and stomach. We have shown that oesophageal temperature is affected by four different activities at sea: (1) Diving per se, which also influences the four other temperatures according to the duration of the dive; (2) Breathing events, reflected by large drops of tracheal temperature during surfacing; (3) Water ingestion, characterised by fast and large drops occurring near the surface; (4) And finally feeding events, which also affect the tracheal and the stomach temperatures. Importantly, except for diving per se, stomach temperature is often unaffected by the events that induce a drop of oesophageal temperature. Keywords: Body temperatures - Energetics - Foraging ecology - Food intake - King Penguin.

Foraging behavior of penguins in relation to hydrographic features

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Penguins do not forage randomly at-sea as revealed by recent telemetric studies. We here examined the three-dimensional exploitation of the water mass in relation to hydrographic features by deep and long distance foragers such as King penguin, throughout the annual cycle. The study was conducted at different scale levels in the Polar Frontal Zone (Crozet and Kerguelen sectors) lying between two major fronts, the Sub-Antarctic and the Polar Front. We monitored over 3 years the foraging routes, diving behaviour of King penguins and simultaneously the thermal structure of the sub-surface layer. A total of 51 birds were instrumented with TDRs or PTTs. The penguins utilized specific oceanic areas and adjusted their diving behavior to the water mass visited. We identified two main foraging regions (the limit of the Polar Front and the Antarctic waters) and two distinct foraging modes (directional to predictably profitable areas, and erratic in spring). The foraging mode was related primarily to large-scale seasonal changes in hydrographic structure and prey availability. The day-by-day analysis of diving behavior over the annual cycle revealed that large differences occurred in the use of the water column, at meso to small scales (dive scale). Excepted in spring, all the birds avoided to dive in the surface mixed layer and mostly dived in and below the thermocline separating the surface mixed layer from the cold winter water. At any time of the year, the penguins tended to minimize dive depth by traveling toward areas of thinner surface mixed layer, suggesting that prey were more accessible. The preference for thermocline depths may result from enhanced local biological activity (« barrier effect ») leading to the concentration of the main prey.

Large plasticity in the use of the hydrographic features allows King penguin to be the unique seabird feeding on mesopelagic resources throughout the whole year.



Changes in parental care, chick provisioning and chick growth rates of Little penguins *Eudyptula minor* in years of high and low breeding success

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This research examined the breeding performance of little penguins *Eudyptula minor* at Phillip Island in south-east Australia. A major goal was to relate breeding success to fluctuations in parental care and chick provisioning rates within and between seasons. Data were collected on nest attendance patterns, chick growth rates and chick meal mass. Sampling extended over two reproductive cycles, one with good and other with poor reproductive success.

Penguins kept the mean length of their foraging trips below two days during the good breeding season. During the poor breeding season birds foraged longer than two days right from the beginning of the post guard. Compared with successful birds from the poor breeding season, successful birds from the good breeding season guarded their chicks for 6 days longer, the post-guard was 9 days shorter and their chicks grew faster. The later a little penguin started to breed in the season the poorer was its breeding performance.

Successful birds had shorter incubation shifts and undertook more foraging trips than failed birds during both incubation and chick guard periods. Chick provisioning rates were analysed in relation to chick age and over time. Chicks were fed on average 211 grams of food per day. The variation of chick body masses had similar fluctuations to the meal masses delivered by the parents. Chicks may need more food during their exponential growth from 1 to 6 weeks old which coincided with the highest mean meal masses delivered to them by their parents. After the age of 6 weeks, there was a decrease in meal mass delivered by the parents followed by a decrease in chick growth.

Although little penguins exhibited substantial temporal and seasonal variation in their time budget and foraging performance, our findings suggest that parents adjust their provisioning rates according to age of their chicks since chicks that fledged had similar changes in masses throughout both seasons of distinct breeding success.

Waddling in the dark – annual cycle of arrival and departure of Little penguins *Eudyptula minor*

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Little penguins *Eudyptula minor* come ashore and leave at a very defined time. Previous study reported that the majority of penguins arrive one to two hours after dusk and depart one hour before dawn. We investigated further to determine whether this pattern differs according to their breeding cycle at Phillip Island in south-east Australia. We also examined time of arrival and departure according to moon phases. An automated penguin monitoring system (APMS), developed by the Australian Antarctic Division, combined with implanted transponders were used to record daily the transponder number, date and time and direction of 315 birds as they entered or left the colony.

A total of 14109 crossings of transpondered birds were recorded from September 1995 to April 1997. The arrival time of the first penguin was 44 minutes (SD = 18 minutes) and mean arrival time was 92 minutes (SD = 32 minutes, range -5 to 454) after sunset. The departure of the last penguin was 65 minutes (SD = 23 minutes) and mean departure time was 100 minutes (SD = 31 minutes, range 22 to 360) before sunrise. Frequency of crossing was analysed according to each seven stages of breeding: pre-breeding, courtship, honeymoon, pre-laying, incubation, chick rearing and moulting. More than 70 percent of birds arrived in the first hour at pre-breeding, courtship, incubation and moulting. But crossings were spread along 3 hours at honeymoon, laying and chick rearing stages. This pattern did not differ at departure.

Arrival and departure times were compared to four phases of the moon: new, first quarter, full and last quarter. Birds tended to arrive later and departure earlier at full moon. There was no correlation between moon phase and numbers of birds at arrival or departure.

These results showed that arrival and departure patterns of little penguins varies according to breeding stages. Birds tend to spread arrival and departures times at busy times of breeding. This poster will present a graphical representation of arrival and departure patterns and discuss reasons for variations at different breeding stages.

Breeding success of Adélie Penguins in relation to diet and foraging behaviour: an overview of eight seasons of data.

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An 1800 breeding-pair Adélie penguin colony at Béchervaise Island near Mawson station, East Antarctica has been the site of a long-term ecosystem-monitoring programme since the summer of 1990-91. This presentation provides a summary of foraging trip durations and meal sizes for male and female penguins in relation to annual breeding success (chicks raised to crèche age) and fledging mass over eight breeding seasons. Significant interannual differences in length of foraging trip and food brought into the colony were observed. These parameters were correlated with breeding success and fledging mass, and may be useful as indicators of food availability during the breeding season. Diet composition varied between seasons; years of highest breeding success were associated with large proportions of mature-age krill in the diet. Although length-frequency distributions of krill varied between seasons, the vast majority of organisms consumed were mature or gravid females in every year of the study. Results are discussed in relation to environmental parameters and potential fishery activities.

Changes in Adélie Penguin colony occupation patterns over ten seasons: a demographic perspective.

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The 1800 breeding-pair Adélie Penguin colony at Béchervaise island near Mawson station, east antarctica, is comprised of 18 discrete sub-colonies. The numbers of occupied nests in each of these have been counted during mid-incubation every year since 1990. The colony as a whole has remained stable in size over the ten years of our study; however the distribution of birds among the various sub-colonies has changed over time. Nest numbers have decreased in four sub-colonies, remained stable in ten others, and increased dramatically in the remaining four sites. Human disturbance is the most likely cause of the loss of nests in those colonies that have reduced in size; decrease was most rapid over the first four seasons and the effect has been confined principally to the colony margins. The four expanding colonies are those closest to areas of loose stones, and their rate of increase has accelerated over time. Each year a total of approximately 300 fledging chicks from five sub-colonies (three decreasing and two stable) have been individually marked using implanted transponders. Over recent seasons a number of these chicks have returned to breed on the island. The majority of such birds have been detected within the four expanding sub-colonies. This poster illustrates the colony structure of the island and details the locations in which young breeders were tagged and to which they have returned to breed.

Comparison of the Autumn Diet of Gentoo Penguin (*Pygoscelis papua*) on Laurie Island, Antarctica, over six years

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Penguins are major consumers of Southern Ocean marine resources, mainly feeding on planktonic crustaceans, small fishes and squids. The Gentoo Penguin is an important component of the avifauna in many sub-Antarctic and Antarctic areas; the diet of this species has been studied at several localities over extended periods during the breeding season. Although there is some literature on the diet of the Gentoo penguins during the non-breeding season, most of these studies were carried out in sub-Antarctic regions. In this study we investigate the diet of Gentoo penguins at Laurie Island (60°46'S, 44°42'W), South Orkney Islands.



Antarctica, over six autumns to determine the nature and extent of the inter-annual variation in the type and amount of prey consumed. Fishes were the most important prey by mass in 1995 (81.1%) and 1996 (60.5%) while crustaceans predominated in 1993 (70%), 1997 (61%), 1998 (83% by mass) and 1999. Among fish, species of the family Nototheniidae predominated in the diet with *G. gibberifrons* as the most important prey by mass in 1993 (45%) and 1995 (74%) and *N. nybelini* in 1996 (45%), 1997 (88%) and 1998 (89%). Other nototheniid fish such as *L. nudifrons* and *T. newnesi* were also well represented in the six sampling periods. Krill (*Euphausia superba*) was largely the most important prey among the eleven crustacean taxa identified in the samples. A total of 1632 squid lower beaks was found, 97% identified as *Psychroteuthis glacialis*.

African penguins as predators and prey - Coping (or not) with change

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African Penguins *Spheniscus demersus* live in the Benguela and western Agulhas ecosystems off southern Africa. Their numbers decreased throughout the 20th century from at least 1.8 million to about 0.16 million adults, although different regional trends were apparent. African Penguins feed to a large extent on shoaling epipelagic fish, notably Anchovy *Engraulis capensis* and Sardine *Sardinops sagax*. Regional trends in the abundance of penguins are associated with trends in the abundance and distribution of these prey fish. Many first-time breeders emigrate from colonies where feeding or other conditions are unfavourable at the time to more favourable breeding localities. This has led to both the extinction and formation of colonies. Food now may limit colonies at relatively small sizes, which is thought to be attributable to industrial fisheries reducing the densities of forage fish. African Penguins share their habitat with several other predators, with which they compete for food and breeding space. One of these, the Cape Fur Seal *Arctocephalus p. pusillus*, increased throughout the 20th century to 1.5-2 million animals at its close. Predation by seals on seabirds has increased markedly in recent decades and threatens the continued existence of some small penguin colonies. Minimum viable size of colonies is investigated using both long-term empirical information and modelling that accounts for variability in demographic parameters.

Humboldt penguins outmanoeuvring El Niño

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We satellite-tracked five Humboldt penguins during the strong 1997-98 El Niño Southern Oscillation (ENSO) from their breeding island Pan de Azúcar (26°09'S, 70°40'W) in Northern Chile and related their activities at sea to satellite-derived information on sea-surface temperature (SST), sea-surface temperature anomaly (SSTA), wind-direction and wind speed, chlorophyll-a concentrations and statistical data on fishery landings. We found that Humboldt penguins migrated by up to 890 km as marine productivity decreased. Total daily dive duration was highly correlated with SSTA, ranging from 3.1 h, to 12.5 h when water was warmest (+4°C). Birds travelled between 2 and 116 km every day, travelling further when SSTA was highest. Diving depths (maximum = 54 m), however, were not increased with respect to previous years. Two penguins migrated South and independently of each other, located an area of high chlorophyll-a concentrations, 150 km off the coast. Humboldt penguins seem to use daylength, temperature gradients, wind-direction and olfaction to adapt to changing environmental conditions and to find suitable feeding grounds.



This makes Humboldt penguins biological *in situ* detectors of highly productive marine areas, with potential use in the verification of trends detected by remote sensors on board of satellites.

Divorce in Little Penguins

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Little Penguins breeding at Phillip Island, Australia have been studied since 1968, with six study areas within the colony monitored since 1994. The species is socially monogamous with most pairs separating during the winter and re-forming prior to the breeding season if the mates are still alive. Following divorce, both mates are equally likely to re-mate. Divorce is more frequent in younger birds, but after making allowance for age, failure to raise chicks also increases the likelihood of a split up of the pair before the next breeding season. The absence of any chicks to be fed, rather than their number appears to be the trigger for this. Pairs that re-form following a successful season the year before raise more chicks than divorced mates with new partners. This difference is not further enhanced the longer the pair stay together. However for unsuccessful pairs the strategy of taking a new partner did not lead to any improved productivity compared with staying with the old one. Burrow changes are often associated with divorce, especially for the female, and may sometime confound the interpretation of changes in productivity.

Brood reduction and behaviour in Erect-crested penguins (*Eudyptes sclateri*).

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Obligate brood reduction in the crested penguins remains an enigma for biologists. Any satisfactory explanation must account for not only why they lay two eggs when they only fledge one chick, but also why it is that investment in the second egg is greater than in the first. Erect-crested penguins are the least-studied of all penguins. They exhibit extreme egg-size dimorphism and it has been suggested that they deliberately eject the first-laid egg from the nest. Amongst the many hypotheses proposed to explain brood reduction, the two that have gained most credence are that laying an extra egg provides options to adjust output to prevailing conditions or that the extra egg functions as insurance. Suggestions for why crested penguins should invest more in the second egg range from the greater likelihood of loss of the first egg due to high levels of fighting during the courtship period to a defence against sperm competition as a result of high levels of mate switching. We studied erect-crested penguins on Antipodes Island from 17 September to 2 November 1998. Levels of fighting and mate switching were low. Plasma levels of reproductive hormones were consistent with the observed patterns of behaviour and suggested differences compared to non-crested penguins. The first egg was typically lost on or before the day the second egg was laid, implying that it serves neither a bet hedging nor an insurance function. Eggs were not purposefully ejected from the nest but lost due to neglect or because the incubating bird was unable to adequately cope with the mechanical difficulties of manipulating two highly-dimorphic aspherical objects. The likelihood of loss was compounded by the lack of nesting material. However, an experiment to provide pairs with artificially secure nests delayed but did not prevent the ultimate loss of the first-laid eggs. In contrast to non-crested penguins, we suggest that female erect-crested penguins are being forced to produce a greater proportion of their eggs from endogenous energy reserves and that this process is facilitated by the increasing levels of social stimulation apparent in the colony as the long courtship period progresses. This would tend to give an advantage to the second egg. Given that the foraging distances of crested penguins make it unlikely that they could adequately provision two chicks, we contend that to explain why investment should have evolved to be greater in the second egg is to also explain why crested penguins are obligate brood reducers. To skew investment towards a second egg requires that there must be a first egg.

Magellanic Penguins and Marine Protection: Using Behavior and Ecology for Conservation.

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2. Department of Environmental Studies Magellanic Penguins and Marine Protection: Using Behavior and Ecology for Conservation. P. Dee Boersma,¹ and David L. Stokes²

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Increasing human numbers and rates of consumption underlie most conservation problems. To date, efforts to conserve biodiversity have focused on setting aside areas and/or managing human impacts. Often these efforts have fallen short of their goals, amounting to "too little, too late." in marine conservation, the problem is particularly acute. In contrast to terrestrial systems, there are far fewer marine reserves, and we know far less about the behavior and ecology of the [marine] species we wish to conserve. Magellanic Penguins are a case in point. Although land reserves exist at many of the main breeding sites for this species of penguins, corresponding protected areas in the marine environment do not exist. The conservation questions that we face then is: can species such as penguins that cross international boundaries and spend part of their lives in the open ocean be protected while at sea? Flexible behavior and variable environmental conditions make long-term protection for such species problematic. Moreover, oil pollution, fishing and global climate warming all negatively affect Magellanic Penguins. Conserving these penguins will depend [up]on learning more about how they use the environment and how environmental changes influence their population dynamics. Tools such as satellite telemetry are critical to this effort. They enable researchers to determine where penguins forage and how to make marine uses more compatible with wildlife protection. We report on variation in where magellanic penguins forage in the south atlantic at colonies at Punta Tombo, , Cabo dos Bahias, and Cabo Virgenes in Argentina and at New Island in the Falkland Islands. Results show long-distance movements, individual variation and effects of time of season and marine conditions. Marine zoning is likely to play a more critical role than marine reserves in conservation of some penguin species.

**Bias attributable to prey size in estimating diet
Of African Penguins by stomach flushing**

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Gales (1987) reported no bias in estimating the diet of penguins by means of stomach flushing, when 3-10 flushes were used, but suggested that single flushes would be biased in favour of smaller prey items. On account of obvious stress to African Penguins *Spheniscus demersus* that were flushed repeatedly, it was decided to use only one, or occasionally two, flushes in examining their diet. African Penguins feed mainly on shoaling epipelagic fish, notably Anchovy *Engraulis capensis* and Sardine *Sardinops sagax*. In the 1950s, when diet was estimated by shooting penguins, Sardine was an important component of the food. Recently, Sardine has been increasing rapidly off South Africa, but this is not reflected in the diet of penguins estimated by flushing. It was suspected that this was attributable to bias when using few flushes. To investigate this, African Penguins were starved for 24 hours and then fed Anchovy and Sardine of different sizes. After an interval of 90-120 minutes, they were flushed. Smaller prey was preferentially obtained and difficulty was experienced in obtaining prey > 9 cm. The proportion (P) of food recovered was inversely proportional to prey size and estimated by the equation $P = 0.46 - 0.019 * L$, where L is caudal length of prey in cm. The equation enables the relative contribution of different organisms to the diet to be calculated, provided the size structure of their populations is known and penguins do not select for certain size classes. If this is the case, it is estimated that 30% of Anchovy eaten by penguins will be recovered by stomach flushing, but only 20% of Sardine.



The effect of El Niño Southern Oscillation (ENSO) on foraging behaviour and breeding success of the Little Penguin *Eudyptula minor* on Bowen Island, Jervis Bay.

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The breeding success of the Little Penguin on the east coast of Australia was significantly higher in northern populations compared with documented southern colonies. Several southern colonies including Phillip Island in Victoria and colonies in Tasmania, have been characterised by poor breeding success, increasingly later commencement of breeding, and declining populations. This study examined the relationship between variability in breeding success, ocean currents and climate patterns, foraging behaviour and diet for a northern population. The foraging range of Bowen Island penguins was smaller than has previously been described. Little Penguins on Bowen Island had a heavy reliance on relatively shallow waters of the Bay, within 5 km of their breeding island. Daily foraging distances exceeding 20 km coincided with low breeding success, sometimes below that required for population replacement. The principal mechanism for nutrient enrichment of Jervis Bay waters was the East Australia Current. This is a large and powerful, warm water boundary current typically of 250 km diameter and 1000 feet depth, which promoted slope water intrusion and nutrient enrichment through upwelling along the New South Wales coast during the study, particularly during the penguin breeding season. The EAC effects northern colonies, but less so southern colonies. The Bowen Island colony was prone to periodic breeding failure, which was related to the El Niño Southern Oscillation (ENSO) phenomenon, indicated in Australia by the Southern Oscillation Index (SOI). ENSO warm events, corresponding with negative values of the SOI, depressed the EAC and caused downwelling, leading in some seasons to increased breeding failure. There was a correlation between both fledging success and adult mortality, and the SOI. The mean breeding success of the Bowen Island colony, at 1.46 chicks per pair over ten years, was the highest recorded for the Little Penguin, and the population was increasing. Greater daily foraging range during the breeding season in southern Victoria compared with northern colonies may explain in part why these populations are declining.

Stress responses to human disturbance in Magellanic Penguins under conditions of low vs. Moderate levels of visitation.

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Penguin and other seabird colonies have become important destinations for ecotourism during the past decade. Human disturbance can cause significant damage to reproduction in many seabird species, and has been demonstrated to elicit the typical vertebrate adrenocortical response to stress in penguins in some cases. However, in other cases where there has been a long history of high levels of tourism, penguins have been demonstrated to habituate to tourists and no longer show behavioral or adrenocortical responses to nest visitation. We studied behavioral and hormonal responses to, and recovery from simulated tourist visits at a colony that has been subjected to moderate amounts of tourism during 5-6 years prior to this study, compared to an island with little or no human visitation. Birds on both islands showed a clear adrenocortical response to visitation, but we found no evidence of a reduced reaction in the adrenocortical response of birds on the tourist island, although at the behavioral level the birds appeared less disturbed by human presence. The response to a single visit did not last long, and adrenocortical hormones returned to pre-disturbance levels within 2 hr of the initial disturbance. These results suggest that the birds may be in the process of becoming accustomed to human presence at the behavioral level, though not yet at the physiological level.

Seasonal and sex-based variation in the adrenocortical response to capture and handling in the Magellanic Penguin.

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Vertebrates respond to environmental stressors by secreting adrenocortical hormones (among other responses), but the magnitude of the adrenocortical response has been shown to vary on seasonal or habitat-related bases. We studied the adrenocortical response of Magellanic penguins to capture and handling stress during 3 nesting stages: the prelaying period, during incubation, and during egg-hatching. Penguins fast during the prelaying and incubation periods, but not during the hatching period. We predicted that basal corticosterone levels would be reduced during incubation, and that the stress response would be also be modulated downward in both sexes. Basal levels were significantly lower during incubation. Adrenocortical responses to capture and handling differed strongly between the sexes; males down-modulated the response during incubation, but females up-modulated. Pre-laying and hatching stage levels were similar within sex, but differed between sexes. Body weight varied significantly across nest stages, inversely to the modulation of stress-responses. The stress-response was significantly correlated with an index of body condition; fat birds responded much less strongly to capture and handling.

Preliminary findings of the intestinal parasite fauna of Gentoo penguin (*Pygoscelis papua*) at Waterboat Point, Paradise Bay, Antarctica.

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The study of pathogenic organisms on wild penguins is essential to discriminate between endemic and introduced diseases and risk analysis of potential introduction of diseases. This kind of information will contribute to the protection and conservation of penguins and other species of Antarctic seabirds. In addition, it is a good reason to monitor the parasite fauna of some wild Antarctic penguin populations. The parasite fauna may vary in composition, due to climatic conditions, human activities and the introduction of alien species and is related to food items consumed. The literature on wild penguin's populations is scant, in most cases the infection has been diagnosed *post mortem*. Many endoparasite studies specially those of the intestine are quite old. Taking into account the increase of visits to the Antarctic and the lack of recent studies we decided to obtain 100 faecal and tissue samples of Gentoo penguin breeding colony at Waterboat Point (64°49'S, 62°51'W), Paradise Bay. Our preliminary study indicates the presence of eggs and cysts of nematodes and cestodes belonging to intestinal parasites on both kinds of samples. Further analysis of our samples will enable us to identify the species of parasites and the frequency of infestation for each parasite.

Magellanic penguin mortality in a gillnet fishery of Southern Patagonia, Argentina

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Artisanal fishing along the Patagonian coast is carried out on a small scale by fishermen who use it as a means of small revenue and subsistence. The main fishing ground is located in the Río Gallegos estuary (51° 37' S 69° 13' W) where gillnets working with the high tide are employed. Target fish species are the Patagonian Blenni (*Eleginops maclovinus*), Parona Leatherjack (*Parona signata*) and the Fuegian Sprat (*Sprattus fuegensis*) which are Magellanic penguin prey at this latitude. Information was collected during 4 penguin breeding seasons (from September to April of 1995-1998). We analyzed the effect of the gillnet fishery on Magellanic penguins, evaluating the magnitude of incidental mortality. We characterized the gillnet fishery throughout a social survey and we interviewed 50 % of the fishermen operating in the study area. One of the authors is an artisanal fisherman in the area and he provided all the information about effective days of fishing, number of nets used, fishing effort (defined as the number of days each net was active) and the number of penguins caught each season. With this information we estimated the total fishing effort and the number of penguins killed per season. The incidental catch rate was variable among years. The annual mortality of penguins in nets was very high reaching several thousands of individuals per season. However, the incidental captures were not recorded homogeneously during the whole season. Incidental capture reached a maximum between January and March. This period coincides with the stage of high dispersion and the beginning of the migration of Magellanic penguins at this latitude. The impact of this fishery on the local population of penguins seems to have been important considering that the colony of penguins of Río Gallegos has suffered a decrease of almost 60% between 1986 and 1998 in the number of breeding pairs.

Digestive regulation and resource partitioning in penguins – implications for optimized foraging

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Penguins transport the food for their offspring inside the stomach on their way back to the colony. However, it still appeared mysterious, how the birds do achieve that gastric contents remain essentially undigested during the return journey and the subsequent period at the nest.

In earlier studies we could show that penguins are able to strongly regulate their digestion by altering gastric secretion and motility. Results on Gentoo penguins now show that there exists a strong relationship between the demands of the brood and the extent of this digestive arrest. Besides a principal function for food conservation, the ability to regulate the digestive activity, also in the short term, may further allow penguins to reduce their diving metabolic rate. Thus, the organization of foraging trips in single dive bouts appears to be in part the result of digestive phases at the surface. The interplay of this physiological and other behavioural traits are to be discussed in the light of a potential optimized behaviour.

Monitoring of seabird behaviour and physiology at the nest site using autonomous UHF-video-transmission.

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A novel low-cost video system is presented which allows penguins and other seabirds to be monitored at the nest site. The system is particularly useful in burrow-breeding species and species that attend the colony mainly during times of darkness (e.g. Certain penguins, puffins, petrels and shearwaters etc.).

Although use of telemetric devices, such as archival tags or radiotransmission- (vhf, satellite-ptt) tags, has allowed scientists to monitor a growing variety of parameters, there are some applications where it is still desirable to observe animals directly. This, either in order to attain information on events that cannot be easily monitored by using "on board"-devices (e.g. Chick-feeding behaviour, predation at the nest site, passage counts) or where certain behaviours need to be recorded in real-time and/or with high temporal resolution (e.g. Precise timing of nest attendance or activity patterns for the assessment of time-energy-budgets, detection of return for recapture of instrumented animals, etc.).

Therefore, we designed a video-monitoring and -transmission system with high versatility, where the signals of four miniature cameras with infrared-illumination are transmitted over distances of up to 25 km to a base station.

The advantages of the present design are (i) a very robust layout, allowing to set up this system in extreme environments, (ii) mains-independence of the camera- and transmission unit, (iii) a very high transmission range and (iv) a comparatively small size of the whole system providing high flexibility and low transport costs.

The system proved invaluable e.g. For the interpretation of physiological data from penguins equipped with archiving probes. Its use is particularly recommended for studies where handling of shy animals or endangered species needs to be avoided.

Parental investment in Humboldt penguins

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The Humboldt penguin (*Spheniscus humboldti*) is endemic to the cold, nutrient-rich Humboldt current along the west coast of South America. Due to its large distributional range of over 4500 km from Northern Peru to Southern Chile the Humboldt penguin is exposed to very different environmental conditions.

In a comparative field study we investigated the relationship between foraging ecology and reproductive success within the framework of different oceanographic conditions. At two ecologically distinct colonies 1500 km apart, Pan de Azúcar in Northern Chile and Puñihuil, the southernmost breeding colony of this species, we collected data on foraging behaviour and reproductive performance of chick rearing penguins, and on oceanographic conditions.

At Pan de Azúcar sea temperature was higher and marine productivity lower than at Puñihuil. Dive duration, dive depth and bottom time did not or only slightly differ between colonies whereas foraging trip duration and foraging range were significantly larger at Pan de Azúcar. Reproductive success was significantly lower at Pan de Azúcar.

The Humboldt penguin does not seem to be very flexible with respect to foraging components such as dive duration or dive depth. Instead the bird increases parental investment by expanding foraging trip duration and foraging range at low prey densities. However, this appears to be disadvantageous for chick survival because of e.g. negative effects on provisioning rates. Explanations for this at-sea-behaviour will be discussed in the presentation in the light of physiological and energetic constraints.

The impact of tourism on blue penguins

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In 1993, a community-based group started an eco-tourism venture in the Oamaru harbour based around the viewing of blue penguins (*Eudyptula minor*) as they return from the sea in the evening. Six years after opening to the public, more than 100,000 people have visited the site to watch the penguins arrive ashore and return to their burrows.

At the outset of the venture there was public concern about the impact of the tourism operation on the penguins. To observe any potential impacts, a monitoring program was established to compare the response of the project population with that of a nearby control population. The number of penguins coming ashore at the project site each evening was also counted.

Reproductive success at both sites has been high, but that of the project population has been consistently higher than that of the control, as has the number of chicks fledged per pair and average chick fledge weight. This success, combined with frequent double-brooding has contributed to the trebling in number of breeding pairs at the project site and a doubling in peak penguin numbers landing on the beach in the evening. There is no evidence to indicate that the controlled public viewing of blue penguins at the project site has provided any negative impact on either the breeding success or site fidelity of the project population.

The effects of pilchard mortalities on Little Penguins *Eudyptula minor*.

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There were widespread mortalities of adult pilchard *Sardinops sagax* across southern Australia in 1995 and 1998. Prior to 1995, pilchards were a major component of the diet of Little Penguins at Phillip Island (Victoria), Australia.

Following the 1995 mortality, which occurred after the annual moult, egg-laying was delayed and breeding success was substantially less (0.3 chicks fledged per pair) than the long-term mean of 1.0 chicks fledged per pair. Adult survival was significantly reduced in the following year also. The 1998 pilchard mortality occurred from December when penguins had small chicks and subsequent breeding success was not reduced and adult survival appeared not to be significantly affected.

The diet of penguins changed after 1995. In the 1980s, pilchards and anchovies comprised more than 50% of the diet. By the late 1990s, pilchards had virtually disappeared and anchovies decreased markedly in the diet of penguins. Instead, red cod *Pseudophycis bachus*, barracouta *Thyrsites atun* and warehou *Seriola lalandi* were major components of the diet. Some pilchard were consumed in October 1998 but disappeared from the diet again following the pilchard mortality in December 1998.

Adult survival and breeding success were substantially reduced in 1995 following the first pilchard mortality but it appears that the impact of the second pilchard mortality on the penguins was insignificant because they had a significantly different, and less pilchard-reliant, diet than at the time of the 1995 pilchard mortality.

Helminth fauna of Magellanic Penguins in a colony of Peninsula de Valdés, Chubut, Argentina.

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Studies linking the behaviour and feeding of Magellanic Penguins (*Spheniscus magellanicus*) were carried out at a colony in the north of Peninsula Valdés (42° S, 63° W). Moribund and recently-death specimens were examined to determine the taxonomic composition of the parasitic fauna harboured in these birds acting as the definitive host (HD). The digestive tracts of 15 penguins of different ages were analysed (8 adults, 2 juvenile immature and 5 chicks) collected during the reproductive season (November-April). The aim of this work was to evaluate the extent to which the dietary habits of the bird affects the structure of associated parasites. In particular, long-term resident parasites might allow speculation as to the feeding habits of the birds during the seasonal migrations. Viscera were conserved by freezing at -20°C. The digestive tract was separated into oesophagus, stomach and at least ten sections of intestine, each 20 cm. long. In adults, as well as in chicks, larvae and adult Nematodes *Contraecicum pelagicum* and *Cosmocephalus obvelatus*, were located in the oesophagus and stomach. Cestodes of the genus *Tetrabothrius* and Digenea of the genus *Cardiocephaloides* were found in the upper small intestine as were *Acantocephalans* of the genus *Corynosoma* although these parasites only occurred in 5 birds. In general, the mature host showed a parasitic load similar to that of the chicks, although the species diversity was lower. The results obtained allow us to hypothesize that Magellanic Penguins are primarily stenophagous during November-January (Scolaro et al. 1984). Stenophagy favours the decrease both of parasitic load and parasite species wealth, while euryphagy (February-March) results in an increase in these parameters.

Comparison of total mercury concentration in tissues of chick and adult *Pygoscelis adeliae* and *Pygoscelis papua* at Potter peninsula, South Shetland islands, Antarctica

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Seabirds are useful biomonitors for mercury pollution in the environment due to their wide distribution and high trophic level. The aim of this study is to provide information on the levels of total mercury in tissues of chick and adult Adélie (*Pygoscelis adeliae*) and Gentoo (*Pygoscelis papua*) penguins collected from the 1992/93 to the 1994/95 summer seasons at Potter Peninsula, South Shetland Islands, Antarctica. The mercury concentration in liver and muscle tissues were determined by the cold-vapour technique using a flameless atomic absorption spectrophotometer. For both species the levels of mercury were higher in liver than in muscle, being the differences statistically significant in adult Adélie penguins ($p < 0.0001$). The mercury levels found in liver of adult specimens (0.11 and 0.22 $\mu\text{g}\cdot\text{g}^{-1}$ wet weight for Adélie and Gentoo penguins respectively) were higher than those found in chicks (0.02 and 0.06 $\mu\text{g}\cdot\text{g}^{-1}$ wet weight respectively) being the differences statistically significant for Adélie penguins ($p < 0.01$). This suggests that mercury concentration in tissues of Antarctic penguins increase as birds grow older and that mercury was accumulated through food. The mercury levels in these two species were lower than the observed in other Antarctic seabirds breeding in the area (e.g. Antarctic shags, Brown skuas, South Polar skuas, Wilson's Storm petrels, Black-bellied Storm petrels). This could be explained by the feeding habits observed in the study area in *P. adeliae* and *P. papua* since they prey almost exclusively on krill which also present a low mercury concentration.

Cool chicks: the influence of thermoregulatory demand on contact creching behaviour in Adélie Penguin chicks

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The chicks of many penguin species characteristically aggregate together in groups referred to as crèches once they are no longer brooded by their parents. Adélie Penguin (*Pygoscelis adeliae*) chicks frequently form tight crèches in response to predators (Davis 1982). We hypothesized that contact creching in Adélie chicks is also influenced by thermoregulatory demand and therefore predicted that this behaviour is even more prevalent when heat losses are high. We also predicted that this effect is greater in early crèche (1kg) chicks than in late crèche (3kg) chicks due to their greater susceptibility to convective heat loss under similar micrometeorological conditions. This is a consequence of their smaller size (Buttemer 1985), poorer insulation (Janes 1997) and much higher (by 25-30°C) lower critical temperature (Chappell *et al.* 1989). Estimated thermoregulatory costs (% minimal metabolic rate) for early crèche stage chicks were much higher (13.4 to 121.0%) than for late crèche chicks (0 to 45.1%). The incidence of contact behaviour was high during early crèche, but uncommon during late crèche. Both the percentage of early crèche chicks forming contact groups and the mean number of chicks per group increased significantly as thermoregulatory demand increased. Thermoregulatory costs were significantly higher when late crèche chicks exhibited contact behaviour than when they did not. Predator presence was low throughout the study and did not appear to have any measurable association with contact behaviour.

We conclude that contact behaviour in Adélie Penguin chicks is multifunctional and, in addition to anti-predation benefits, confers important energy savings in terms of maintaining a favourable daily energy budget in early crèche chicks and maximum fasting duration in fledglings.

Avian malaria in some wild populations of penguins.

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Avian malaria has been responsible for dramatic changes in the avifauna of the Hawaiian Islands. In addition, it is an important disease of captive penguins and has caused considerable mortality. It may also be important in wild populations of some penguins because antibodies to avian malaria have been found in some wild penguins. Because of the potential threat of avian malaria to populations of wild populations, we tested three

species of *Spheniscus* penguins for malaria. We used an established two-step PCR method for detecting Plasmodium DNA in blood samples. We tested 109 Galapagos penguins, 20 Magellanic penguins and 15 Humboldt penguins for malaria. We found no malaria in any of the penguins though the control sample from a captive Humboldt Penguin consistently tested positive. Mosquitoes of the genus *Culex*, a known vector, live in all of the areas inhabited by these penguins. *Culex* mosquitoes in the Galapagos Islands, however, have only been reported since 1989 and only occur on Islas San Cristobal and Santa Cruz. Galapagos Penguins are probably not threatened by the presence of malaria yet, but because of their low population and restricted distribution, they may face a new danger if the mosquitoes spread through the islands.

Testing for some diseases in Penguins and Skuas.

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Penguins in the wild are susceptible to an array of infectious and parasitic diseases but clinical signs are rarely obvious. With the large number of people in Antarctica from national programs and the recent increase in the number of people traveling to Antarctica for tourism, it has become important that we develop ways to screen for a variety of diseases. We have used standard parasitological and PCR methods to screen Galapagos penguins, Adelic penguins and South Polar Skuas for Coccidia infections, Marek's disease and avian malaria (see related poster). We found a single infection of Coccidia in 140 fecal samples from skuas from Ross Island, Antarctica. We found no Coccidia infections in 44 Adelic penguin samples from Ross Island and none in 24 samples from Galapagos penguins. Similarly, we found no evidence of Marek's disease in 109 blood samples from Galapagos penguins and 29 Adelic penguins from the Antarctic Peninsula. Power analysis of sample sizes indicates that a good study will require 100-150 samples from a given population to be assured of finding a disease if infection rates are as low as 2%. Serological methods will continue to be the preferred method to look for some of the potential diseases, but PCR methods will be an effective method for some studies.

Genetic diversity of Galapagos Penguins (*Spheniscus mendiculus*).

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Because of their restricted mobility, compared with flying species, and their natal site fidelity, penguins should show distinct spatial patterns of genetic variability that will be useful for population studies. The Galapagos penguin is restricted to the Galapagos Islands where 1,700-8,500 individuals breed on 6 main islands and several other small islands. We used Randomly Amplified Polymorphic DNA (RAPDs) on a sample 109 individuals from 14 breeding sites to describe the genetic variability and spatial structuring of the world population of Galapagos Penguins. The distribution of haplotypes indicates that there is some isolation among the different breeding areas. Within the context of genetic variation, we will discuss possible conservation problems faced by the species.

A molecular phylogeny of penguins based on MTDNA *cytochrome-b* gene sequences

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Ambiguities exist in the phylogeny of the extant penguin species, and the fossil record does little to clarify these relationships. Currently, there are no molecular-based studies on the species level relationships among the penguins although such relationships using morphological characters have been attempted. It has been possible to differentiate the genera of penguins using morphology, but morphology only partially resolves the species relationships. In this study, we used sequences of the mitochondrial *cytochrome-b* gene for all three species of *Pygoscelis* penguins (*P. adeliae*, *P. papua*, and *P. antarctica*), three of the four *Spheniscus* penguins (*S. magellanicus*, *S. humboldti*, and *S. mendiculus*), both *Aptenodytes* penguins, (*A. forsteri* and *A.*

patagonicus), and three species of *Eudyptes* species (*E. schlegeli*, *E. chrysocome*, and *E. chrysotophus*). Partial *cytochrome-b* sequences (771bp) were obtained from multiple individuals from most species and published sequences were used for some. Alignments of the unique sequences were made with homologous sequences from other avian groups, and used to construct a phylogenetic relationship. The trees constructed from these analyses allow us to draw the following conclusions: First, the close relationship of penguins with loons (*Gaviidae*), cranes (*Gruidae*), and more distantly, the tube-nosed seabirds (*Procellariiformes*) is strongly supported. This result is congruent with published studies using DNA-DNA hybridization, morphological characters, and a nuclear gene sequence. Second, all the genera are strongly supported as separate genera. Third, a *cytochrome-b* based phylogeny was able to resolve the species relationships within genera, with each species forming distinct clades.

Correlations between body size, defensive behaviour and reproductive success in male little blue penguins *Eudyptula minor* : implications for female choice.

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Field studies were conducted on the relationships among body size, defensive behaviour and reproductive success in male little blue penguins (*Eudyptula minor*). In a range of species, large males are more successful during male-male competitions, court more frequently to promote early breeding, and acquire resources like food more efficiently making them superior parents. However, the ways in which male size might influence the reproductive success of female penguins have yet to be explored in any detail. Here we examined whether the male size influences: (1) nest defence, (2) the timing of reproduction, and (3) the quality of parental care. If sexual dimorphism in penguins is "driven" by a female preference for large males, it should be the male's size, not the female's size, that accounts for most size-success correlations. Therefore, we quantified the contribution that both male and female size made to the measures of success we recorded. Nests defended by large males produced eggs and chicks earlier in the breeding season, and contained chicks that grew at a faster rate than chicks in nests defended by small males. On the contrary, female body size did not affect the reproductive success. Therefore, male body size could be an important determinant of reproductive success. Female little blue penguins can improve their own reproductive potential by selecting large males as breeding partners.

Health state, condition, immunocompetence and reproductive performance in Magellanic penguins *Spheniscus magellanicus*

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Health status and immunocompetence have been proposed as important factors affecting individual variation in reproductive performance in birds. We studied individual variation in haematological variables indicating health status (haematocrit, 'buffy coat' layer, white blood cell count (WBC), heterophile/lymphocyte ratio) in breeding Magellanic penguins *Spheniscus magellanicus* and their association with reproductive variables like egg size, chick growth rate and fledging success. We sampled blood from both males and females shortly after hatching of their young to obtain haematological measures. We also measured the T-cell-mediated immune response as indicated by in vivo hypersensitivity response to an intradermal injection of a mitogen (Phytohemagglutinin) in the same individuals. Sex had a significant effect on WBC and immunocompetence, with males showing lower values. Females with more leucocytes in peripheral blood (sign of previous infection) laid smaller eggs and raised fewer chicks to fledging, and their chicks grew less rapidly with respect to foot length. Heavier females at laying raised chicks with a higher growth rate with respect to foot length. The only effect of male health status was a positive effect of H/L ratio (indication of stress) on culmen growth rate. Neither female nor male immunocompetence showed any trend with variables of reproductive

performance. The impact of parental health on variation in productivity in avian populations may be more important than has been usually contemplated.

Patterns of egg laying and breeding success in Humboldt Penguins (*Spheniscus humboldti*) at Punta San Juan, Peru.

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This study was undertaken between 1993 and 1997 at Punta San Juan, Peru. Humboldt penguins showed a consistent pattern of egg laying having two peaks in april and august/september. The extended breeding period of penguins was the result of their capacity to have a second clutch after having successfully raised chicks (double brooding) or failed their first breeding attempt (replacement brooding). About half of the females (n=182) laid two clutches per year, most of which were double-broods (73%). A high proportion of these penguins (58%) successfully reared two broods per year. The date of completion and outcome of reproduction, or whether a change of mates occurred from the previous year, did not affect the timing of egg laying. Most first clutches (62%) were laid in april each year. The timing of laying in april seems to be determined by the synchronous molt of adults, which occurs in january and february. Females that started laying eggs early in april had a higher breeding success than females that started in late april. Double brooders start to lay eggs earlier and had a higher breeding success than single brooders. Although replacement brooders were only as successful as single brooders, they started laying eggs earlier. Considering that a humboldt penguin breeding cycle (laying-fledging) lasts approximately 4 months, laying eggs early in april increases the chance of rearing two successful broods per year. Double brooding appears to be a strategy used by Humboldt Penguins in peru to maximize their lifetime reproductive success within a productive, but unpredictable environment.

Penguins of the Falkland Islands

By Mike Bingham

The Falkland Islands are an important breeding site for three species of penguin. During the 1980s and early 1990s these three penguin species all declined in the Falklands, with Rockhopper penguins declining by nearly 90% over a twelve year period. These declines were not occurring in South America. The most likely cause of the decline was over-fishing around the Falklands. In 1988 a 200 mile conservation zone was established by the Falkland Islands Government which limited fishing effort. Since then Rockhopper and Gentoos populations have ceased declining, and appear to have reached a new equilibrium, albeit at a much lower level than before fishing began. This has been matched by improved chick-rearing success and juvenile survival rates for these two species. Magellanic penguin populations continue to decline in the Falklands. In 1998 drilling began around the Falklands for oil, despite warnings that environmental protection was inadequate. Within a month the first of three separate oil spills occurred, killing and contaminating hundreds of penguins. The oil rig finally completed its drilling programme, and left the Falklands, since when no further spills have occurred. Despite the fact that all traces of oil had gone by the time egg-laying began, there was a noticeable reduction in breeding success for sites where penguins had previously been affected by oil. Ecotourism has increased rapidly over recent years in the Falklands, with penguins being the main attraction. Monitoring of the affects of tourism has concentrated on breeding success and population changes, and the results show no detrimental affects on penguin colonies.

Foraging strategies in Magellanic penguins (*Spheniscus magellanicus*): Habitat use and diving behaviour.

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We studied the foraging ecology of breeding Magellanic penguins (*Spheniscus magellanicus*) in two South Chilean colonies (Magdalena Island, Strait of Magellan, 52° 55' S, 70° 34' W and Otway Sound 52° 58' S, 71° 12' W) during three successive breeding seasons from 1996/97 (Radl A, Culik BM 1999, Mar Biol 133: 381-393) to 1998/99. We used time-depth-recorders to investigate diving behaviour, determined chick growth and breeding success and, in the last season only, equipped birds with satellite transmitters to observe their foraging routes. Results were compared between colonies and years. Fledging success (both colonies and years > 1.4) and chick growth (max. fledging weight regularly >3000 g) were exceptionally high compared to other breeding locations of Magellanic penguins. However, with regard to foraging effort penguins showed clear intercolonial as well as individual differences. Foraging trip durations were significantly longer through all seasons at Magdalena (means of 17.7, 25.2 and 38.2 h in '97, '98 and '99, respectively) than at Otway (9.2, 12.0 and 8.8 h, resp.). Consequently, penguins from both colonies had different chick feeding rhythms with shorter intervals at Otway. Foraging effort was also higher at Magdalena, as could be seen in deeper max. dive depths (17.0, 21.2 and 24.7 m, resp. at Magdalena compared to 15.4, 14.7 and 13.2 m at Otway), feeding depths (depths of the bottom phase during U-shaped foraging dives contrary to V-shaped searching dives 28.6, 31.0 and 46.4 m at Magdalena and 28.2, 24.8 and 25.4 m at Otway) and bottom phase durations (18.7, 21.4 and 19.5 s at Magdalena and 13.9, 16.4 and 14.9 s at Otway). Sprats (*Sprattus fuegensis*) were the dominant diet in both colonies, but other fish species such as silversides (*Odontesthes nigricans*) and cephalopods (*Loligo gahi*) were also found as prey items. Satellite tracking during foraging in the last season showed longer max. distances from the colony at Magdalena (55 km) as opposed to Otway (less than 20 km), and a strong individual behaviour regarding foraging direction at Magdalena, with individual birds travelling to north-eastern as well as to southern feeding grounds in the Strait of Magellan.

Underwater feeding behaviour study by multiple data recording on free-ranging Adélie penguins

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The underwater feeding behaviour of free-ranging Adélie penguins (*Pygoscelis adeliae*) during a single foraging trip was investigated by monitoring three parameters simultaneously at a frequency of 1Hz, these being: depth, swim speed and oesophagus temperature. Ingestion events were mathematically detected as abrupt drops in the oesophageal temperature. Although, a high percentage of oesophageal temperature loggers were rejected, one complete foraging trip was recorded for all the three parameters from one bird while 92 and 67% of the foraging trip was recorded for two other birds. 12.3% of the temperature drops occurred at surface but they were mainly small. All other drops were observed during dives deeper than 40 m and occurred mainly during an undulatory bottom phase of dives but were occasionally observed during the ascent part of dives. The mean swim speed during non-feeding shallow and V-shaped dives was relatively constant throughout the dive, whereas during W-shaped deep dives, swim speed during the undulatory phase was lower than during the descent and ascent and was characterized by a series of rapid accelerations and decelerations. 42.6% of these accelerations were followed by one or more ingestion events and birds swam upward in 60% of the accelerations. These features can help elucidate how the bird behaviour might enhance prey capture and minimize the energy or time expended for hunting.

Effects of nest group size and physical parameters on reproductive success of *Pygoscelis papua*, Ardley Island, South Shetland, Season 1997-98.

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Ardley Island is located at 62°13' S. and 58°54' W. and has a breeding colony of 3028 nests (November 18) of *Pygoscelis papua* (Gentoo Penguin), one of the largest of the S. Shetland. Using a topographic map and positions of all nesting groups, we recorded the reproductive success, (January 5) of 213 nesting groups belonging to seven different areas on the island. We analyzed the potential effects on reproductive success of the following parameters: number of nests, perimeter, distance to coastline, elevation, area and nest density. We used several statistics to estimate the influence of each parameter on reproductive success.

Our results show that overall reproductive success for *P. papua* for 97-98 season was 1.34 chick/nest. This is higher than published records for the species at other localities. The most frequent number of nests per group was 14 (S.D. 25), with range 2 - 285.

Reproductive success is lowest on the largest nesting group (area and total N° of nests). Statistical significant inverse correlations were found for area, density and perimeter. Elevation and distance to coast line do not have any correlation with reproductive success. These results show that group size has an inverse effect on reproductive success. This is more pronounced on groups smaller than 30 -35 nests.

Sex identification in the monomorphic Magellanic Penguin.

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Discriminant analysis was performed in order to identify the sexes of adult breeding Magellanic Penguins. Eleven morphometric measurements were recorded in samples of adult pairs (n=265) from five latitudinally-separated populations (from 42 to 52 S Latitude). Examinations were conducted on a colony basis as well as after mixing. Culmen length and beak depth (at the nostrils) showed the highest discriminant power by using the step-wise approach. There were minor variations in the percentage of cases correctly classified according to colony: Peninsula Valdes (97.9%), Punta Tombo (97%), Punta Lobería (95.5%), Monte Leon (95.8%) and Punta Dungeness (85%)(Chi Squared, p<0.001). The cases were also checked using a previous discriminant equation calculated for the P. Tombo population. We explore an unique classification function derived from all the cases treated together which reveals a high discriminatory ability (97.5%). Lines of probability of an individual being one determined sex, are also showed (Green and Theobald 1989). This method provides a simple and objective way of identifying the sex of the Magellanic Penguin by highlighting the most significant morphological differences.

Annual changes in the quality of semen in Humboldt penguin (*Spheniscus humboldti*)

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The aim of this study was to evaluate the annual changes in reproductive ability in male Humboldt penguin. We observed the behavior of Humboldt penguins kept in an open aquarium display and collected semen throughout the year (April 1998 - March 1999). For the study, I selected 10 pairs of propagative Humboldt penguins, which were kept in the Niigata city aquarium. Their ages were from 5 to 13 years. Semen was collected by abdominal massage. Volume and sperm concentration was measured. Humboldt penguins showed breeding activity throughout the year except for the period of molting (July to mid august). Semen volume showed no significant changes throughout this sampling period (0.026±0.009ml). Sperm concentration showed significant changes throughout this sampling period (ANOVA F(11, 55) = 2.9 P=0.05).

Sperm concentration decreased during the molting period, after the molting period, it began to increase from September and maintained high values between October and February. Maximum level was in November ($30.3 \pm 4.8 \cdot 10^8$ cell/ml). Sperm concentration of pre-incubation ($20.2 \pm 6.3 \cdot 10^8$ cell/ml $n=5$), incubation ($24.3 \pm 2.6 \cdot 10^8$ cell/ml $n=17$) and egg removed ($21.8 \pm 2.7 \cdot 10^8$ cell/ml $n=12$) in the male Humboldt penguin showed no significant changes throughout this breeding period. I conducted a reproductive study on captive male Humboldt penguins and obtain result indicating that there were changes in sperm concentration throughout the year. As a result of change of sperm concentration, it is thought that best reproductive period of captive male Humboldt penguins were indicated from late autumn to spring in the Northern hemisphere.

State-dependent decisions in long-term fasting king penguin during courtship and incubation

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Using an automatic identification and weighing setup, we have investigated the changes in adult body mass in relation to reproductive behaviour during courtship and incubation in free-living king penguins *Aptenodytes patagonicus*. Despite stressful nutritional conditions and variability of fast length, most pairs succeeded in incubation through an accumulation of large body reserves before fasting, which gave an important flexibility of fasting length capacity. Our data indicate the existence of body mass thresholds during fasting below which adults take a pause or stop breeding definitively: 1) the Courtship Threshold (CT) at 12 kg, interrupting courtship to replenish body reserves at sea before engaging again in breeding, 2) the Incubation Threshold (IT) at 9 kg during incubation, where a penguin deserts the egg. The behavioural decision to refeed at sea is not controlled by the time spent fasting, but by amount of body reserves. For those males that deserted, the depletion of body reserves during incubation before relief by the females was due to a lower energy stored (-2 kg) at the onset of courtship. These males began courtship at 12 kg, and consequently had no safety margin to allow them to wait for a late female's return. Compared to successful pairs, their female partner showed lower body mass gain at sea (-40 g day^{-1}) and a slightly longer foraging trip (+5 days). We suggest that the deserting males had taken the risk to start breeding at CT with the lowest fasting safety margin possible, rather than breeding later that year. However, in both sexes, most individuals deserted their egg at a body mass that did not affect their survival nor their refeeding capacity at sea, and which therefore did not compromise another breeding attempt during the next season.

Long-term study of a king penguin population using an automatic identification system

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Birds microtagged with transponders under the skin can be identified for life and detection antennas allow the automatic identification of the birds with minimal human disturbance and presence in the field. The king penguin cycle is unusual because it lasts more than one year and birds are not synchronised in their cycle. In addition, birds that failed in their reproduction still frequent the colony throughout the year. We have employed an automatic identification setup for the detection of the passage of free-living microtagged king penguins at Possession Island ($46^{\circ}25'S$, $51^{\circ}45'E$), Crozet Archipelago. A breeding area with about 10 000 pairs is connected to the sea by three pathways, where antennas for the identification of birds were installed. From February 1998, 500 breeding adults and 300 one-year old chicks were fitted with transponders without any external marks. In the future, cohorts of chicks will be implanted with transponders each year. The aim of this long-term population study is to determine the reproductive strategy of these long-lived birds (e.g. lifetime reproductive success, feeding frequency of chicks,...) and the effects of age and climatic changes on their breeding performance.



Parasitism of the King penguin by the tick *Ixodes uriae*: effects on breeding performance and relation with the breeding site in the colony

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The high densities of penguins, combined with the repeated use of traditional breeding sites year after year, increases the risk of development of parasite populations. We have therefore studied the effect of parasitism by the seabird tick *Ixodes uriae* on breeding performance of king penguins at Possession Island (46°25'S, 51°45'E), Crozet Archipelago. Although the King penguin colonies were occupied throughout the year, infestation was limited to the incubation and brooding period. The percentage of tick-infested adults differed significantly according to location in the colony, the highest density occurring on the upper slopes of the colony where the habitat on the ground was favourable for the ticks. Infested areas showed a lower breeding success. The adverse effects of ticks included the transmission of pathogens. Conversely to data on other seabirds, infestation of chicks was very low compared to that of adults.

Flexible diving behaviour, foraging effort and foraging success in Rockhopper Penguins (*Eudyptes chrysocome*) living in different marine environments

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To investigate the plasticity in feeding ecology of a diving marine predator, we studied the pattern and characteristics of foraging behaviour of female rockhopper penguins during the guard stage at three contrasted localities from the southern Indian Ocean: Amsterdam (AMS: oceanic subtropical waters), Kerguelen (KER: coastal subantarctic waters) and Crozet (CRO: neritic subantarctic waters). Females mostly performed daily foraging trips of similar durations at the three localities (about 11-13 hrs), but, owing to seasonal differences in phenology, birds from AMS stayed at sea a higher proportion of the daylight hours (93%) than those from KER (76%) and CRO (73%). Analysis of diving behaviour indicated different foraging strategies. Females from AMS and CRO did pelagic dives. AMS birds performed a higher number (on average 458 dives per foraging trips) of shallower dives (19 m) of shorter duration (65 s) at a higher rate (37 dives/hr) than those from CRO (299 dives/trip, 35 m, 89 s, 27 dives/hr). Penguins from KER had intermediate values (349 dives/trip, 25 m, 77 s, 30 dives/hr), but dive profiles indicated both pelagic and benthic dives, a new foraging behaviour in crested penguins. Both the absolute and relative values of time spent underwater per foraging trip did not differ between the three sites (about 7-8 hrs and 62-64%, respectively). The amount of food brought ashore and the chick growth rate followed the same pattern, being lower at AMS (107 g and 28 g/day, respectively), intermediate at CRO (151 g, 45 g/day) and higher at KER (215 g, 49 g/day). Consequently, catch-per-unit effort varied greatly among localities, being lower at AMS (8.6 g/hr at sea, 0.31 g/foraging dive), intermediate at CRO (12.4 g/hr at sea, 0.55 g/foraging dive) and higher at KER (18.0 g/hr at sea, 0.76 g/foraging dive). Some diving characteristics and indexes of foraging effort varied between localities and others not, suggesting fine adjustments of diving behaviour to the local marine environment. Dietary analysis together with foraging behaviour suggested that rockhopper penguins preyed upon dense and horizontally distributed epibenthic swarms of *Euphausia vallentini* at KER, and on dense but vertically distributed pelagic swarms of *E. vallentini* at CRO. In the poorer subtropical waters (AMS), birds preyed upon horizontal and much less dense pelagic swarms of *Thysanoessa gregaria*, but also on larger prey, mainly squids. Differences in prey predictability and density seem to be two crucial points in shaping foraging behaviour of air-breathing marine predators.



**The effects of human activity on the behavioural and hormonal stress response of Little penguins
(*Eudyptula minor*)**

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Little penguins on Phillip Island, Victoria are a popular tourist attraction. They are often exposed to visitors and are the subject of ongoing research. How does this human activity affect their stress response? What is a standard stress response in this species? Little penguins on Phillip Island were studied during the post-moult period from April 11 to 21, 2000 to determine how gender, time of day, and previous exposure to human activity affected their stress response. Stress response was measured according to behavioural and hormonal changes during controlled capture events. 104 penguins were sampled from visitor, research only, and control areas. Behavioural observations were conducted and blood samples were taken from individuals at four intervals following capture. Corticosterone and testosterone levels were evaluated using radioimmunoassay techniques. Preliminary analyses suggest that male penguins are more aggressive than females, particularly at night. Corticosterone levels range from 4.0ng/ml within 3 minutes of capture to 90.0ng/ml at 30 minutes post-capture. Initial testosterone levels of males range from 0.2ng/ml to 0.5ng/ml. Comparisons between males and females, day and night samples, and study areas are in progress. The final results and their implications for both tourism and research will be discussed.

Moult of Adelie Penguin Chicks.

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Chicks of Adelie penguins (*Pygoscelis adeliae*) must undergo a rapid intensive moult before they can fledge and go to sea to forage for themselves. Production of new adult feathers is energetically demanding and it also likely that during the period of moult the chicks must cope with increased thermal conductance. We hypothesized that chicks in good body condition should be able to complete the moult faster. As survival prospects of late-fledging chicks are likely to be reduced and, therefore, recruitment into the breeding population, there has been surprisingly little study of moult in penguin chicks. Here we provide the first quantitative description of moult in Adelie penguin chicks. We studied the chicks on Ardley Island, Antarctica, from 8 - 28 January 2000. Mass and other morphometric parameters were recorded in order to create an index of body condition. Feathers were measured to determine the rate and duration of primary moult. There was a significant effect of body condition on feather growth rates. Fat chicks do grow feathers faster. This could have important implications for any assessment of the costs and benefits of the timing of breeding and brood reduction in these penguins.

Efectos de El Niño en los Pingüinos De Galapagos y tendencia poblacional

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Estación Científica Charles Darwin

El monitoreo a largo plazo del pingüino de Galápagos (*Spheniscus mendiculus*) indica que la especie sufre fluctuaciones poblacionales severas, principalmente como resultado de los eventos de El Niño, los mismos que, en las últimas décadas, parecen estar aumentando tanto en frecuencia como en intensidad.

Desde 1970 a 1999, la Estación Científica Charles Darwin y el Servicio Parque Nacional Galápagos han desarrollado censos a lo largo de toda el área costera donde habita la especie. Estos conteos han servido para determinar la magnitud de los cambios poblacionales asociados a los eventos de El Niño, tanto leves como fuertes (e.g. 1982-83 y 1997-98)

En el censo anual de pingüinos, efectuado en 1998, durante el año de el niño, contamos 444 pingüinos. Esta cifra, comparada con la similar del censo 1997, significó una probable disminución poblacional en el orden del 65%. Las diferencias en los dos conteos realizados en el 97-98 sugieren que el niño 97-98 impactó a los

pingüinos con una intensidad, casi similar a la de el niño 82-83, cuando se registro una probable reducción poblacional de 77%. En estos dos periodos del niño fuertes, los pingüinos no se reprodujeron.

En el último censo de pingüinos llevado a cabo en Septiembre de 1999 contamos 683 pingüinos en el Archipiélago y encontramos nidos con huevos y pichones, más un alto porcentaje (25%) de juveniles

En función de los resultados de los censos en el periodo 1970-2000, la tendencia poblacional de los pingüinos muestra números altos de pingüinos a principios de los 70, seguido por una declinación en el Niño 82-83, una recuperación lenta hasta 1997, otra caída poblacional en 1998, para finalmente entrar otra vez en una aparente fase de recuperación. Esta tendencia a su vez indica que los pingüinos nunca lograron recuperar los números previos a El Niño 82-83 y que de mantenerse la misma frecuencia e intensidad de eventos de El Niño, los pingüinos podrían extinguirse en el futuro cercano.

En 1999, usando el método de captura y recaptura, estimamos una población total de 1200 (\pm 83SE) pingüinos en el Archipiélago. El estimativo de la población también sugiere que en cada censo anual contamos alrededor del 57% de la población total de pingüinos. Si aplicamos este estimativo al censo cuando se contó la mayor cantidad de individuos, que fue en 1971, significa que en ese año existieron alrededor de 3400 pingüinos en Galápagos, lo cual indica que la población actual sobreviviente (de 1200 individuos) representa sólo el 35% de la población original, previa a los años de El Niño. La estimación de la población efectuada en 1999 también sugiere que la población total de pingüinos es inferior a estimaciones anteriores.

La temperatura superficial del mar en las zonas costeras donde habitan los pingüinos mostro promedios de 19°C para los años pre-post niño (1996 y 1999 combinados) y 23°C para los años de el niño (1997-1998 combinados). Las diferencias de temperatura entre estos dos periodos fue significativa ($f = 2.87$, $g.l = 82$ y 60 , $p < 0.001$).

Penguins and People in Patagonia: An Example of Sustainable Nature Tourism

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Tourist visitation to the Magellanic Penguin (*Spheniscus magellanicus*) colony at Punta Tombo, Argentina, has existed for over 20 years, with current yearly tourist numbers reaching over 50,000 individuals. To determine if tourist interaction causes elevated stress in penguins, we compared a behavioral response (agonistic head movements) and circulating levels of the stress hormone corticosterone after exposing penguins to 15 minutes of human contact. Comparisons were made between naive birds (never previously exposed to tourists) and birds living directly in the area of tourist visitation. Tourist-exposed birds had significantly fewer agonistic head movements and significantly lower levels of corticosterone than naive birds, suggesting habituation to human contact. Studies of the rate of habituation in previously naive penguins showed decreases in both the behavioral and hormonal responses starting within 10 days of initial human contact. Finally, in both naive and tourist birds, levels of corticosterone after 15 minutes of tourist contact were significantly lower than for penguins subjected to an extreme stress event of capture, suggesting typical tourist/penguin interactions are not perceived as high stress events for either group of penguins. These results, coupled with previous studies of reproductive success, indicate that current levels of tourism at Punta Tombo, if well controlled, are sustainable and apparently not adversely affecting nesting Magellanic Penguins. Continued study of higher levels of human contact and the mechanism for this apparent adaptation are ongoing.

The ups and downs of diving in Magellanic Penguins: New angles on the effort of being at depth.

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During December 1999, loggers recording animal orientation and dive depth were deployed on Magellanic Penguins *Spheniscus magellanicus* breeding in Argentina. The units consisted of a back-mounted 3-dimensional compass, set to store information of penguin body orientation 30 times per second and a leg-mounted unit measuring depth once per second. Swimming movement caused minor fluctuations in body

orientation, even in birds that ostensibly maintained a constant heading, so that flipper beat frequency (FBF) could be determined. During movement FBF varied between 0 and 3.5 Hz but was dependent on dive depth (decreasing with increasing depth), body angle (increasing for increasing body angles between 0 and 90° with respect to the water surface) and swim speed (increasing with increasing swim speed), this latter being calculated using simple trigonometry on data on the rate of change of depth together with measured body angle. Consideration of FBF as a function of speed, together with previously-published data on swimming energetics of congeneric Humboldt Penguins *Spheniscus humboldti*, enabled us to propose a model of diving energetics so as to consider the relative importance of dives to particular depths in relation to the angles adopted by birds to reach these depths.

Heart rate as a measure of individual recognition in Little Blue Penguins (*Eudyptula minor*)

Winter, S. J. & Waas, J. R. (2000).

Social recognition by sound is common in birds, especially in those that breed in colonies where individuals are long-lived, give substantial parental care and have limited opportunities to use circumstantial cues to facilitate the recognition process. This paper describes an experiment designed to investigate the social recognition abilities of little blue penguins, a species that typically exhibits large inter-nest distances and may use nest-site location to aid in the recognition of individuals. The experiment involved exposing subjects to playback of low bray calls from mates, neighbours, and strangers. Breeding habitat and nocturnal habits of this species can make behavioural observations difficult, therefore social recognition was measured using heart rate. This study is the first to use heart rate to investigate social recognition in any bird species. Heart rate was recorded using a relatively non-invasive form of biotelemetry, an artificial egg based on a design described by Nimon *et al.*, (1996). Burrow-dwelling little blue penguins differentiated between the calls of mates, neighbours and strangers. The ability to recognise mates is common among monogamous colonial seabirds, whereas the ability to discriminate neighbours from strangers has been demonstrated in only the male Adélie penguin. Both male and female little blue penguins appeared capable of discriminating between different conspecifics. Little blue penguins exhibited a reduced heart rate in response to the playback calls of mates and neighbours in comparison to all other treatments and the pre-disturbance period. The decline in heart rate was thought to reflect a "relief response" by the incubating bird in response to calls of a familiar individual (as opposed to an intruder or predator).

Breeding success and productivity of rehabilitated African Penguins following the *Apollo Sea* oil spill

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The success of rehabilitation efforts with seabirds is often measured by the number of individuals which survive to return to their breeding colony. However, little is known about the effect of the oiling and subsequent rehabilitation on the breeding success of those birds which return to their breeding colony. At Dassen Island, in the south-western Cape, a monitoring study was initiated soon after the first rehabilitated African Penguins *Spheniscus demersus* were released following the *Apollo Sea* oil spill in June 1994 in which over 10 000 penguins were oiled. The study is still continuing and at the time of the conference would have been running for about six years. The main aim of the study is to determine the short-and medium-term (and ultimately long-term) effects of oiling on the breeding biology of African Penguins: The breeding and moult cycles of rehabilitated penguins, and how these differ to the cycles of penguins that were not affected by the oil spill, is investigated. The percentage of birds returning to the colony and attempting breeding is investigated, and the breeding success and quality of chicks produced by oiled and non-oiled birds is compared.

The breeding biology of the Humboldt penguin at Punta San Juan, Peru

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The breeding biology of the Humboldt Penguin (*Spheniscus humboldti*) was studied over a four-year period (1993-1996), at Punta San Juan, Peru. The number of active nests increased throughout the study period from around 520 to 1820 pairs. Egg-laying extended from 229 (1996) to 282 (1993) days, with peaks in april and august-september. The age at first breeding was 2.7 and 2.2 years for females and males, respectively. Adults bred more than once within a year, with 52%, 44% and 4% of females having single, double and triple clutches, respectively. Females invariably lay two eggs four days apart. One-egg clutches were uncommon and were laid mainly by young females. Mean volume index of eggs laid in april was similar among years. Incubation took between 40 and 45 days. Chicks hatched from the first week of may to late december. The mean duration of the chick guarding period varied among years from 45 to 54 days, but between 13% and 32% of pairs continued guarding the chicks until fledging. The mean fledging age ranged from 72 to 75 days. Mean fledging mass varied from 3335 g (1993) to 3550 g (1994). Egg mortality was high ranging from 31% to 55%, but chick mortality was lower than egg mortality, with less than 37% of the hatchlings dying before fledging. An extended laying period, high breeding frequency, premature maturity, inter-annual variability of the guarding period, fledging mass and breeding success may be adaptative strategies to face an unpredictable marine environment.

Foraging-area overlap among neighboring colonies of Adelie Penguins: Does competition play a role?

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We assessed the size and location of the foraging grounds among all (4) colonies of Adelie Penguins within one isolated colony-cluster in the southwestern Ross Sea. Colonies ranged three orders of magnitude in size from <5000 to >150,000 pairs. The study was conducted during the chick-provisioning period, when exploitation of food resources is deemed by theoreticians to be most intense, during 4-austral summers of dramatically varying sea-ice cover. The area exploited by each colony grew larger as the season progressed; maximum size of foraging grounds was proportional to colony size, but was affected, too, by the extent of fast ice. The degree of overlap of foraging grounds among colonies was affected by colony size (larger colony, less overlap) and the total amount of foraging area available (in turn a function of fast-ice cover; less total foraging area present, less overlap). These results are discussed in relation to possible interference competition.

Humboldt Penguin censuses in Chile

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Since 1981, we have made Humboldt Penguin censuses on the Chilean coast, from Iquique to Algarrobo. On the last time we also made a census on Puñihuil islets, but the number of penguins is very low, only 0,02% of the total population. Till 1996 the method used was counting the active nests during the Spring breeding peak, that is, during September and October.

In 1999 and 2000 we made the census in February, when the penguins were moulting, as was recommended at the CAMP meeting held in Cape Town in 1996.

In the February censuses the penguin count increased approximately threefold, compared with the censuses using the other method.

The main breeding colonies are Pan de Azúcar, Chañaral, Pájaros y Cachagua islands and former islet Pájaro Niño at Algarrobo.



Do nearby nursery areas for clupeoid fish dictate the breeding locations of Little Penguins *Eudyptula minor*

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Little Penguins *Eudyptula minor* appear to require an abundant and predictable supply of suitable food relatively close to their breeding colony, particularly when raising young. Individuals from Penguin Island, 50 km south of Perth, Western Australia, were radio-tracked at sea at different stages of their 1997 and 1998 annual cycles. Before laying, and even during incubation, Little Penguins were recorded 30-75 km from Penguin Island and ate a range of schooling clupeoid fish species. However, during chick rearing, most parents foraged within 20 km of Penguin Island and took mainly sandy sprats *Hyperlophus vittatus*. The seasonal predominance of Sandy Sprats in the dietary samples from the Little Penguins paralleled their presence in seine net samples from nearshore waters. Otolith microchemistry indicated that most sandy sprats taken came from the closest (8 km) of four distinctive local sprat populations. These results show many similarities to a study of Little Penguins from Phillip Island, Victoria, despite the wide separation and different geographical configurations of the two colonies. The apparent reliance of both populations on a single area of inshore water rich in clupeoid fish has important implications for the management of these, and possibly other, colonies of Little Penguins.

The effects of flipper bands on the survival of Little Penguins, *Eudyptula minor*.

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Flipper bands have been used extensively in penguin research for 50 years. Recent studies have indicated that banded penguins use more energy when swimming and may have higher predation rates than unbanded penguins. We examined the effects of flipper bands on the survival of Little Penguins at Phillip Island, Australia between 1994-2000 by comparing the return rates of 2490 adult penguins marked in one of three ways: with flipper bands, with injected transponders or with both.

Of the 4193 recaptures, significantly more birds marked with transponders were retrapped than birds with bands or with both bands and transponders. Banded birds survived equally well with and without transponders. The discrepancy in survival between banded and transpondered birds was actually greater than suggested by the recapture rates because transponders were more often overlooked or lost than were bands. Surprisingly, there was no significant difference in the mean body masses of the three groups. The implications of these results will be discussed.

Analysis of Molt Wing Swelling in a Captive Colony of African Penguins

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The African Penguin Banding Project is a study designed by penguin husbandry staff at the New England Aquarium to quantify the swelling of African penguin's wings during their annual molts. The goal of this project is to gather data that can be used to prototype wing bands that will adjust to this increase in wing size, since many bands currently used by field researchers may not accommodate this physiological change.

Reduced circulation caused by band restriction during molts can result in wing damage, which may cause direct mortality or increase the likelihood of predation.

The 13 African penguins that were used for gathering the data in this study were all born at the New England Aquarium and were partially hand raised by penguin husbandry staff and therefore were accustomed to being handled. Each penguin had its wings measured daily during the pre-molt and molt phase, which is the period during which the penguins' wings swell to their maximum size. Digital calipers were used to measure both wings from the frontal to distal edge and also from the dorsal to ventral surface. A measuring tape was used to determine the circumference of each wing. Quarterly measurements were also taken for a period of one year to determine average wing size while the penguins were not molting.

Our statistical analysis showed that wing circumference increased an average of 47%. The majority of wing swelling was from the dorsal to ventral surface of the wing, which increased by an average of 90%. The size of the wing from the frontal to distal edge increased by an average of 34.4%.

The use of heart rate to estimate field metabolism of king penguins

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Heart rate and oxygen consumption were measured in king penguins (*Aptenodytes patagonica*) while resting at different ambient temperatures and while exercising at different levels of activity on a treadmill. The experiments were carried out on Crozet Island (French sub-Antarctic Territories) over three summer seasons (1998-2000). 48 king penguins, at the beginning or at the end of a fasting period, were placed either in a thermostatic chamber or in a respirometer on a treadmill and equipped with externally mounted heart rate data loggers. Heart rate and oxygen consumption were simultaneously measured at a range of walking speeds (between 0.3 km.h⁻¹ and 3.0 km.h⁻¹) or ambient temperatures (between -10 C and -30 C). There was a good relationship between heart rate and oxygen consumption for each individual exposed to different environmental temperature ($r^2 > 0.7$), or different temperature ($r^2 > 0.8$). The fasting status of the bird had no influence on this relationship. Furthermore the level of activity (low or high walking speed) did not vary the slope of the relationship.

About 30 free-ranging breeding king penguins were implanted with heart rate and depth data loggers which were recovered at a high return rate (95%). Preliminary analysis showed that there was a good correlation between minimum diving heart rate and the dive duration. Ashore the mean heart rate decreased by 30% during the first 4 days of incubation. This reduction of heart rate at the onset of the fast is in agreement with the reduction of metabolism observed at the beginning of the fasting of king penguins.

Black-footed-penguins (*Spheniscus demersus*) in European zoos and the link to wildlife conservation.

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The European Endangered Species Programme (EEP) for the Black-footed penguin started in 1994. Now, six years later, there are about 900 penguins in 34 participating zoos and the demand for keeping this species is still growing.

The population consists of three main bloodlines, represented by Amsterdam, Baltimore and South-Africa animals. Their vitality is essential and can only be achieved through a close and intensive management of a core population. Therefore recommendations for breeding are made for the participating institutions by the programme coordinator.

Since the start of the breeding programme most surplus birds were donated to other participants. Because the captive birds are considered as the ambassadors for their wild counterparts, the establishment of a foundation is under consideration under the auspices of the Dutch Zoo Federation. The aim is that each participant, depending on the number of penguins in their collection, financially contributes to this foundation.

It is envisaged that with the contribution fees the foundation will assist rescue centres and wildlife conservation institutions in South-Africa, to rehabilitate oiled penguins in their care.

Behaviour and energetics of Macaroni Penguins (*Eudyptes chrysolophus*) at South Georgia

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Heart rate and oxygen consumption were measured simultaneously in 25 macaroni penguins (*Eudyptes chrysolophus*) at rest and while exercising at different levels on a variable speed treadmill. These penguins were divided into three groups: breeding males, breeding females and moulting females. A relationship between heart rate and oxygen consumption was calculated for each group. No significant difference was found in this relationship both within and between groups and hence a single equation linking oxygen consumption to heart rate for all macaroni penguins was calculated. During the 1997/98 and 1998/99 austral summers, 44 free-ranging breeding macaroni penguins were equipped with data loggers at Bird Island, South Georgia. These loggers recorded heart rate, abdominal temperature and in some cases diving depth, continuously for periods of 5-30 days. Large drops in abdominal temperature were observed during foraging trips and diving bouts. The equation obtained from the penguins on the treadmill was used to calculate energy expenditure for the free ranging penguins while ashore and foraging at sea.

Tracheal temperature changes associated with diving behaviour in free-ranging King Penguins

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While foraging at sea, King penguins can reach 300 m in a single-breath dive lasting 7 min. They alternate these long apnoeas with interdive periods of less than 2 min, during which they reconstitute their oxygen stores. However, virtually nothing is known about their breathing pattern. We therefore implanted a temperature sensor in the first 5 cm of the trachea of four King penguins before a foraging trip. This sensor was connected with a data logger which recorded temperature every second and the hydrostatic pressure every 4 s. For brooding shifts on shore and interdive periods at sea, the tracheal gas temperature (TGT) oscillated with an amplitude of 0.3-5°C and a frequency of 2-20 per min. These TGT oscillations clearly reflect breathing, i.e. the transient drops can be attributed to inhalations of surrounding air at 7°C and the rises to exhalations. The largest drops in TGT while surfacing were observed just prior to dives. Using these large drops as an index of the inhaled gas volume, we investigated their relationship with the duration and the maximum depth of the subsequent dive. In addition, during underwater apnoea, a rapid rewarming of tracheal gas occurred. Surprisingly, a single further oscillation of the TGT was observed during the ascending part of prolonged dives. This might be explained by body temperature changes during the dive, and/or exhalation of vitiated gas even before surfacing.

Penguin-Fishery Interactions off Punta San Juan, the main Humboldt Penguin colony in Peru

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The artisanal fisheries around Punta San Juan (PSJ, 15°22'S, 75°12'W) was studied between Nov. 1991 and Dec. 1998. Throughout this period 922 Humboldt penguins were landed. Most (81%) were caught in drift gillnets, within 40 km north of PSJ, probably while in transit to their foraging grounds. Most (77%) were caught between Sept. 1992 and Jan. 1994. At the time, the main target species, Cojinova or Palm Ruff (*Seriolaeta violacea*) moved to shallower waters and the fishermen switched from mostly using fixed gillnets to drift gillnets.

We performed a general linear model (GLM) analyses on the probability of catching a penguin in a trip, which is assumed to be a binomial process. The factors that were expected to influence the catch of penguins were fishing location, type of fishing gear used, fish species caught and date of the trip. The model showed that each were significant as main effects. The probabilities of penguin captures with fixed gillnets range from 0 to 3%, while capture probabilities with drift gillnets range up to 58%. Trips with a cojinova catch have higher penguin capture rates in the Pampa (open water area N of PSJ) in all years.

The number of dead penguins observed in this study represents 10-20% of the total Peruvian population at the time. The artisanal fisheries around PSJ are highly opportunistic and switch gears, fishing areas and target species unpredictably. Fortunately, most of the time the use of drift gillnets is limited and consequently, penguin capture rates are generally low. In order to reduce the probability of entanglement and to avoid another high mortality episode like the one reported in this study, it is necessary to ban the use of drift gillnets from areas around penguin rookeries.

Heart rate as a measure of social recognition: do little blue penguin chicks use unique vocal signatures to distinguish siblings from other chicks?

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Researchers investigating social recognition typically measure only behavioural responses during discrimination tests – physiological changes have been largely ignored. We examined whether little blue penguin (*Eudyptula minor*) chicks could distinguish siblings from other chicks using auditory cues, by measuring behavioural and heart rate changes during playback experiments. Chicks were exposed to five treatments, the begging calls of siblings, neighbouring chicks and unfamiliar chicks, and two controls (heterospecific begging calls and music). We also determined if chicks developed distinctive begging calls, by using F-values to quantify inter- versus intra-individual variability in a range of acoustic parameters, and applying a discriminant function analysis. Inter-individual variation was greater in pitch parameters than temporal or amplitude parameters, suggesting that call pitch may be important for individual recognition. The discriminant function analysis showed each chick's calls were distinctive and could act as a vocal signature. Treatments did not instigate different behavioural responses. However, chick heart rates during playback of sibling calls were significantly higher than those recorded during stranger, but not neighbour, playback. A simple recognition system based on familiarity may allow this plesiomorphic and loosely colonial penguin to gain at least some of the benefits associated with more advanced sibling recognition systems (some highly colonial seabirds discriminate siblings from neighbouring chicks). Heart rate can be a useful measure of social recognition abilities, particularly in species where changes in behaviour are not always evident or are difficult to observe.

Recent trends in diet composition and productivity of Gentoo, Magellanic and Rockhopper Penguins in the Falkland Islands.

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Over the past 14 years, data on diet composition and productivity of Gentoo Penguins (*Pygoscelis papua*), Magellanic Penguins (*Spheniscus magellanicus*) and Rockhopper Penguins (*Eudyptes c. chrysocome*) breeding in the Falkland Islands has been compiled as part of the Falkland Island Seabird Monitoring Programme (FISMP). This paper comprises a summary of the data obtained so far, in particular concentrating on inter-annual and inter-specific variation of productivity and general diet composition. Productivity of all three penguin species has improved or remained stable over the last few years. The highest average productivity of 0.95 (ranging from 0.41 to 1.51) chicks fledged per breeding pair was observed in Gentoo Penguins. Productivity of Rockhopper Penguins during the same period was on average 0.80 (ranging from 0.63 to 0.91), and the lowest productivity of 0.78 (ranging from 0.19 to 1.49) was observed in Magellanic Penguins. During the breeding season, all three penguin species preyed opportunistically on a mixture of fish, squid and crustaceans, with the general diet composition showing a high degree of spatial and temporal variation. The diet of all three penguin species did overlap with the commercial fishery with regard to the Patagonian squid *Loligo gahi*. There may also be some competition for Patagonian Toothfish (*Dissostichus eleginoides*), Hake (*Merluccius sp.*) and Southern Blue Whiting (*Micromesistius australis*), because the juveniles of these commercially-exploited species were found regularly in the penguin diet.



Winter foraging of King Penguins breeding in the Falkland Islands compared breeding sites elsewhere

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A small breeding colony of King Penguins has established in the Falkland Islands and breeding pair numbers have increased during the last 30 years to a current population of between 500 and 700 breeding pairs. This breeding site differs in many respects from the other breeding colonies of King Penguins, which are situated on subantarctic islands within the vicinity of the Antarctic Convergence. The Falkland Islands are the most temperate of the breeding sites, the furthest away from the Antarctic Convergence and part of the highly productive Patagonian Shelf. Different aspects of the foraging ecology of the King Penguins, such as winter migration, feeding behaviour and diving behaviour, have been studied in the Falkland Islands during the austral winter 1996 using sophisticated archival tags. The results of this study are presented with special focus on the adaptations to the particular environment by comparing the findings with those obtained in simultaneous studies on South Georgia and on the Crozet Islands.

Plasma chemistry changes of chicks and adults Gentoo Penguins (*Pygoscelis papua*).

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Blood chemistry can be influenced by various factors including age however the information about this variations in plasma of penguins is low. The aim of this investigation was obtained plasma concentrations of nine components in free - living Gentoo penguins (*Pygoscelis papua*).

This study was carried out on Munita peninsula (64° 49'S 62° 51'W), Paradise bay, Antarctica during between January and February of 1999.

We caught 67 clinical healthy Gentoo penguins: 21 guard phase chicks, 21 post - guard phase and 25 adults.

Blood samples were obtained from the brachial vein of the birds and placed in tubes with heparine. Plasma was separated by centrifugation and frozen for analysis in Santiago.

Adults Gentoo penguins had significantly ($p < 0,05$) higher total protein, globuline and urea than chicks. While Alkaline Phosphatase and uric acid were had significantly ($p < 0,05$) higher in guard phase chicks compared with post - guard phase and adults.

Albumin, calcium, sodium and chlorine values were not significantly different.

The variation with age of blood chemistry values were similar to the values for other groups of birds, with some differences.

Variability of foraging behaviour of King penguins at Macquarie Island

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The Australian Exclusive Economical Zone around Macquarie Island (54°30'S, 158°55'E) was declared a Marine Protected Area in 1999. The question of exclusion zones as foraging areas for top predators was raised in the light of a commercial fishing operation for Patagonian Toothfish *Dissotichus elliginoides*. King penguins *Aptenodytes patagonicus* are one of the major groups of top predators but their foraging areas and behaviour were yet unknown. With the simultaneous deployment of satellite trackers (PTT) and dive recorders (TDR) we attempted to determine the extent of their foraging area and their foraging behaviour. During incubation, 24 PTTs and 16 TDRs were deployed and diet samples were collected at a single occasion to determine diet composition. All King penguins travelled in a clockwise fashion leaving the island in an easterly direction. Foraging trips lasted from 12 to 21 days; total distances travelled ranged from 788 to 1604 km with maximal distances from the colony ranging from 312 to 623 km. Diving behaviour varied daily; most

noticeable were the increases in number of dives per day and dive depth once the penguins turned to come home. Dive depths rarely exceeded 200 m. The diet samples contained mainly *Electrona carlsbergi* and *Krefflichthys anderssoni*.

The fatter the better

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Emperor penguin *Aptenodytes forsteri* chicks are raised under the most severe weather conditions. The two most important issues for their survival are a) their energy expenditure and food ration during growth, and b) the energy cost of reaching open water after fledgling. Fat chicks have better chances to survive as body reserves buy them time to reach the ice-edge and survive the first few days at sea.

Recent trends in Adélie Penguin populations at Casey, East Antarctica

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Populations of Adélie Penguins have been surveyed at Whitney Point (SSSI 17) since 1959/60, and at Shirley Island since 1968/69. Both localities are within 4km of Australia's Casey station in East Antarctica. Studies commenced in 1989/90 to examine annual breeding success and population trends of colonies at these two locations. The Whitney Point population has increased from 1100 pairs in 14 colonies in 1959/60 to 5700 pairs in 35 colonies in 1999/00, at a mean annual rate in excess of 4%. The population on Shirley Island has increased from 7600 pairs in 45 colonies in 1968/69 to 9600 pairs in 52 colonies, at a mean annual rate of 0.6%. Breeding success for colonies on Shirley Island is 20% less than that for colonies at Whitney Point.

Increases in Adélie Penguin populations in the Australian Antarctic Territory

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Recent surveys of Adélie Penguin populations at Mawson, Casey and Cape Denison indicate that the breeding populations continue to increase. The population of Adélie Penguin in the Mawson region doubled between 1971/72 and 1993/94, with most of the increase occurring since 1988/89. The breeding population in the Casey region trebled between 1960/61 and 1989/90, with recent surveys (1990/91 and 1994/95) indicating that the increase continued during the 1990s. At Cape Denison, the population has more than trebled between the early 1980s and the late 1990s. These increases in breeding populations within the AAT are consistent with increases documented for Dumont d'Urville and adjacent localities within Terre Adélie by French researchers.

The Montana Report

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A Workshop held under the auspices of SCAR, CCAMLR & NSF in Montana in May 1999 examined statistically all available long-term population data for Southern Ocean seabirds. A total of 61 long-term data sets was examined, of which 31 were of Antarctic and Subantarctic penguins. For the Workshop, long-term was defined as either: i) continuous for more than 10 years, or ii) discontinuous for more than 10 years, but with more than 50% coverage. Here we report on the Workshop and present two sample data set with results of the statistical analyses undertaken. The Workshop attempted species and regional syntheses where data permitted.

Counting penguins

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The widespread monitoring of penguin populations around the Antarctic and on subantarctic islands is dependent on methods to determine annual population sizes (breeding pairs) with a high degree of precision. Typically, monitoring has relied on ground visits to colonies, and photographs of colonies, either oblique or aerial, from which birds were counted manually. These methods require considerable time and effort. Techniques that either increase the precision of individual counts or increase the number of counts for a given effort would improve our ability to identify statistically significant population changes. We demonstrate customised software that can quickly determine the numbers of penguins in aerial photographs with a high degree of precision. The software uses readily available hardware and is relatively cheap, both of which are prerequisites for broad scale adoption and application.

Thermoregulation of Humboldt Penguin chicks as related to the thermal characteristics of the nest-sites.

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Homeothermy necessitates that animals maintain body temperature within a very narrow range, a process that is facilitated when the animals live in a thermally-stable environment. This is particularly important in birds

where the ability of small chicks to thermoregulate is severely compromised. Birds compensate for environmental variability by brooding behaviour and construction of nests to temper the microclimate in which the chick lives. Humboldt Penguins *Spheniscus humboldti* breed in Peru and Chile and are subject to extremes in climatic conditions and ground temperatures may reach 60°C. To counteract this these birds build nests in burrows in the guano or in rock crevices or under bushes. We hypothesize that such behaviour results in minimal temperature fluctuations, bringing the temperature inside the nest as near as possible to the thermoneutral range of the brood. To test this we studied the thermal characteristics of Humboldt Penguin nests at Isla Pajaros, Northern Chile in relation to nest type and measured the metabolic rate of different size chicks exposed to different temperatures in the laboratory so as to determine the thermoneutral zone.

Analysis of breeding success fluctuation of Adelie Penguins in the Scotia Arc. Environmental warning or ENSO effect?

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During last years a calling attention has been done to environmental effect over Antarctic Ecosystem. Although links between physical processes and biological processes remain largely unknown nevertheless it is widely accepted that changes in population parameters of top predators reflect the direct, indirect and interlinked influences of biological and physical environmental variables (Croxall 1992).

However there is not agreement among authors about the main environmental forces that are actuating over the top predator parameters. Some work carried out in penguins make some connection between variation in population parameter on these species with the global warming (Fraser et al 1992, Taylor et al 1992) meanwhile work carried out in pinniped may attribute ENSO as the main environmental factor (Vergani & Stanganelli 1990, Testa et al 1990)

The balance between physic and biotic factor depends on the regions and components involved. In the present paper we are analysing population parameters on Adelie penguin taken in three different colonies from the Scotia Arc (King George, Antarctic Peninsula and Laurie Island) in a series of time (1987-1994) to make possible correlation between fluctuation on them and changes in environmental variables.

Foraging ecology of breeding Macaroni penguins at South Georgia. Are penguins in competition with seals?

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There are an estimated two to three million pairs of breeding Macaroni penguins *Eudyptes chrysolophus* at South Georgia. During the breeding season when provisioning offspring, Macaroni penguins are central-place foragers and are therefore limit in their foraging range. The Antarctic fur seal *Arctocephalus gazella* population at South Georgia is now more than three million and the major component in the diet of both these predators is Antarctic krill *Euphausia superba*. During the breeding season, female Antarctic fur seals are also central-place foragers. In the summer, therefore, these two species take similar size-classes of krill from largely overlapping areas of the ocean around South Georgia. It is a fundamental ecological principle that two species cannot coexist stably when in direct competition for a limiting resource. In this study we investigate whether the foraging ranges of these two breeding species overlap. We determine the foraging range of Macaroni penguins and Antarctic fur seals during the breeding seasons of 1999 and 2000 at Bird Island, South Georgia using satellite tracking. The density distributions of the two species are compared within each year and implications for the potential for competition between them are discussed.

Assessment of the initial impact of the Treasure oil spill on the African Penguin *Spheniscus demersus* off western South Africa

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The bulk ore carrier *Treasure* sank off western South Africa between Dassen and Robben Islands on 23 June 2000. These two islands support the largest and third largest colonies of African Penguins *Spheniscus demersus* respectively. Subsequently, over 19000 African Penguins were oiled, about twice the previous highest number of seabirds oiled during a single event in southern Africa. About 19000 oiled penguins were collected for cleaning and care; about 100 oiled adults died in the wild. More than 19000 clean penguins were caught at Dassen and Robben islands and relocated to Port Elizabeth, some 800 km to the east, to remove them from waters affected by the oil. Of all penguins caught, which amounted to 20% of the species population, only about 1500 died within the first month. This is considerably less than in the previous highest single oiling event when another bulk ore carrier, *Apollo Sea*, sank off Dassen Island in June 1994. In the latter incident, 10000 penguins were oiled, 5000 of which died. The lower incidence of mortality in the *Treasure* oil spill can be attributed to improved transport of penguins and the rapid arrival at rescue centres of experts able to administer emergency care. However, resources were severely extended and mortality would probably have been considerably higher had not large numbers of birds been removed from the area affected by the oil. Many relocated birds returned to their home islands within a month of being released. More than 3000 orphaned penguin chicks were collected for artificial rearing, but an estimated 4000 died at the islands before they could be rescued.

Phylogenical Analysis of Penguin (Spheniscidae) Based on genetic polymorphism in the MHC

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Penguins have been placed in the superfamily *Procellarioidae*, a penguin family consists of 6 genus 16 species. We are interested in identification of genetic variations and investigation of phylogenical relationship among all the species of penguin. We have initiated to determine systematically the nucleotide sequences of the Major Histocompatibility Complex (MHC) class II domain and class I domain regions. Which have been known to display a high degree of polymorphism in vertebrates. The *Mhc* genes provide excellent markers for studies on ecology and evolution, because of their extensive polymorphism. Our recent results suggest that species-specific variation in the nucleotide sequences of the *Mhc* genes are well correlated with each penguin's species.

The genus *Pygoscelis* forms a variegated group as its three species - Adeliè penguin (*Pygoscelis adeliae*), Chinstrap penguin (*Pygoscelis antarctica*) and Gentoo penguin (*Pygoscelis papua*). In this report we will describe the results obtained from the genus *Pygoscelis*

Management of the African Penguin colony at Robben Island, 1997-1999

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E. van der Merwe, M. Kroese and J. Kieser

African Penguins *Spheniscus demersus* recolonized Robben Island in 1983, after being absent from the island for about 180 years. The island now supports about 4000 pairs, making it the third largest breeding colony for this species. Robben Island Museum assumed control of the island on 1 January 1997. Subsequently, tourism to the penguin colony has grown rapidly and there is need to manage it in a sustainable manner. Penguins continue to be oiled at the island, necessitating rescue and cleaning. Attempts have also been made to rescue orphaned chicks, and to reduce mortality caused by a population of feral cats *Felis catus* at the island and by entanglement in discarded fishing gear. Future planning needs to take account of the need of shaded nest sites for penguins, and requirements to minimize the risk and impact of fire in the breeding area and mortality resulting from vehicular traffic. There must be adequate escapement of prey species from fisheries to ensure reproductive success sufficient to maintain penguin populations at present levels.

Entanglement of African Penguins at Dassen Island - How severe is the problem?

A.C. Wolfaardt, D.C. Nel and A.J. Williams

The African Penguin is facing many threats. The most important of these are competition with commercial fisheries and oiling. However, there are many other factors contributing towards the poor conservation status of this species. Entanglement of seabirds has recently received much attention. Most studies have focused on the interaction of pelagic birds and longline fisheries. This poster will present the results of six years of monitoring at Dassen Island in the south-western Cape. The frequency and type of entanglement as well as the kinds of items causing entanglement of African Penguins will be reported.

Whither the *Spheniscus* penguins - How many will be extant in the wild in 2100?

Ellis S., Lacy R., Crawford, R.J.M., Underhill, L.G., Whittington, P.A.

The four *Spheniscus* penguins have the most northerly distribution of the world's penguins, and as a result have had a longer history of interaction with man than other species. All are of conservation concern. The Galapagos penguin, most northern of the four, is rated by IUCN as Endangered, the Humboldt and African Penguins at intermediate latitudes as Vulnerable, and some populations of the more southern Magellanic Penguin as Near Threatened. For these four species demographic parameters, rates of decrease of regional populations, and factors causing these decreases are compared to indicate likely trends in the 21st century unless effective remedial measures are introduced.

The "Apollo Sea" revisited. The fortunes of victims from this and other oil spills.

Woolfaardt, A.C., Whittington, P.A., Nel, D.C. & Crawford, R.J.M.

In 1994, a bulk ore carrier, the "Apollo Sea" sank near Dassen Island on the west coast of South Africa, oiling 10 000 African Penguins. Over 4000 of these birds were cleaned, flipper-banded and released back to the wild. This paper reports on their progress six years after their release, and makes comparisons with results from cleaning penguins after other oil spills.



Staten Island, Tierra del Fuego: The unrevealed and largest breeding ground for Southern Rockhopper Penguins?

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This presentation provides new data on the location and size of Southern Rockhopper Penguin (*Eudyptes chrysocome chrysocome*) colonies at Staten Island, Tierra del Fuego, Argentina, and compares them with population sizes previously reported for all the subspecies.

Surveys were performed mainly during November-December 1998 and 1999. Nest density was extrapolated from mean nest density (estimated in circular plots of 100 m²) to the area occupied by nests assessed from aerial pictures and through ground controls. Nest density (\pm SD) was estimated at 102.5 (\pm 29.7) nests/100m².

Two localities, Cabo San Juan and Bahía Franklin, together held 173,793 nests (C.I. 95%, 156,688; 190,899). Bahía Franklin held 166,762 nests. Based on the reported world population data, the total population for Southern Rockhopper Penguins is likely to be close to 636,000 pairs, with Staten Island holding 27.3% and Bahía Franklin alone holding 26.2% of the world population. This relatively small locality would represent a very important breeding ground for this subspecies in the world. Moreover, the southern rockhopper penguin represents one of the more abundant breeding seabirds of the Southwestern Atlantic Ocean.

The Southern Rockhopper Penguins of Staten Island were almost undisturbed and unknown during the 20th century. The evidence presented here seems to indicate that the population at Staten Island is stable or increasing. The population importance of Bahía Franklin for the species was not previously recognized, but it should now occupy a central place of concern for the conservation of this species in view of the decreases reported in other localities of their distribution.

La dieta del pingüino Penacho Amarillo en el Mar Argentino Austral. Resultados preliminares.

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Presentamos los primeros datos sobre la dieta del pingüino penacho amarillo (*Eudyptes chrysocome chrysocome*) en aguas vecinas a la Isla de los Estados, Tierra del Fuego, durante el período posterior al nacimiento. Para ello colectamos 33 contenidos estomacales de adultos, mediante lavado estomacal, entre el 2 y el 12/12/1999, en la colonia de Bahía Franklin. El peso húmedo promedio de los contenidos superiores a los 50gr de peso (n=20), fue de 136,7 gr (rango 50,3-249,1 gr). La frecuencia de ocurrencia (FO%) de los grandes ítems fue de 100 % (cefalópodos), 95 % (peces, *Harpagifer hispidus* y *Sprattus fuegensis*) y 89% (crustáceos, principalmente eufáusidos y anfípodos). La identificación taxonómica de los cefalópodos se realizó en base a muestras comparativas y literatura. Se estableció sobre 27 contenidos la presencia de siete taxones. La FO% fue 50 % (*Moroteuthis ingens*), 35,7% (*Loligo gahi*), 85,7% (*Gonatus antarticus*), 3,6% (*Todarodes* sp.), 7,1% (*Sepiolidae*), 7,1 (cefalópodo oegópsido), 46,4% (Octopodidae). Los ítems más abundantes resultaron *G. antarticus* (456 picos inferiores) y el octopódido (695 picos inferiores). La distribución de tallas reveló el consumo de juveniles, con rangos en el largo rostral inferior del pico de 0,3-1,7 mm (*G. antarticus*) y rango de largo de capuchón inferior del pico de 0,3-0,8 mm (octopódidos). La dieta es muy similar a la determinada en las Islas Malvinas, destacándose la presencia de pequeños octópodos. Sugerimos la factibilidad de que este pingüino utilice tanto áreas de plataforma como del talud para alimentarse en este período.

The Otway Foundation: Ten years protecting penguins in Chile

Horst George
Fundación Otway, Puerto Mont Chile

In this contribution I will present the results we have obtained through ten years protecting penguins in Chile. The aims of this presentation will be: a) Governmental Services responsible for the application of the laws; b) The Chilean citizen and their behaviour regarding laws, authorities and governmental Services of control; c) How to convince people to involve in protecting the nature?; d) An Example: The Penguin Colony in Otway Bay, XII Region (Magellanic Penguin); e) Threatened Penguins; and f) The Campaign of the Ambrace of the Penguin.

Brood size determination in penguins¹

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Penguins are pelagic seabirds adapted to pursue prey underwater. In common with other pelagic seabirds, such as albatrosses and petrels, penguins have low reproductive rates. Effort is put into caring for a small number of offspring to maximise reproductive output over relatively long life spans. The maximum number of chicks that can be raised per breeding attempt is two, though actual brood size varies. The six genera of penguins may be distinguished by mechanisms for brood size determination. Aptenodytes (2 spp.) lay only a single egg, all other species lay two eggs but differ in degree of brood reduction. Megadyptes and Eudyptula (2 spp.) have synchronous hatching and frequently fledge twins. Pygoscelids (3 spp.) show slight hatching asynchrony and moderate sibling asymmetry. Spheniscids (4 spp.) show marked hatching asynchrony, facilitating sibling asymmetries and potential for brood reduction when food is limiting. Experimental studies have demonstrated advantages for asymmetric broods even when food is relatively plentiful. Crested penguins (Eudyptids; 6 spp.) show obligate brood reduction, facilitated by laying a small first egg. The degree to which penguin species exhibit potential for brood reduction is related to climatic conditions and food availability. The purpose of Eudyptid obligate brood reduction has eluded recent analyses, though several hypotheses have been proposed.

INTRODUCTION

Penguins evolved during the Cretaceous, some 65+ million years ago (MYA), from a common ancestor to the Procellariidae, Gaviidae and Fregatidae (Williams 1995). The proto-penguin probably lived in a temperate climate and cool waters, but although restricted to the southern hemisphere, no clear centre of origin is known. From 25 MYA, possibly in parallel with the development of circumpolar ocean currents (Fordyce and Jones 1990), the spheniscidae underwent rapid speciation, expanding to fill niches ranging from continental Antarctica to islands north of the equator. Ancestral adaptations for the pursuit of prey underwater, sometimes to great depth, have resulted in a common body form across the 17 species; adaptation to the great variety of environmental conditions however, have resulted in a diversity of reproductive and life history strategies. The defining feature shaping penguin reproductive strategies is the need to come ashore to lay eggs and raise chicks, thus increasing the distance to feeding grounds. Penguin breeding patterns are thus strongly influenced by conditions on land, access to feeding grounds and food availability.

Two of the 17 species of penguin lay a single-egg clutch; the 15 species of penguin that lay two eggs can be divided into two groups, brood maximisers (sensu Edge 1996) and brood reducers (sensu Lamey 1990).

¹ We acknowledge Philip Seddon for his kindly contribution to the Fourth International Penguin Conference.



depending on the potential for brood reduction that arises from three inter-linked factors: egg-size dimorphism, hatching asynchrony, and sibling size asymmetry.

Brood-reducers include penguins of the genera *Spheniscus* (4 species) and *Pygoscelis* (3 species), which show some degree of egg-size dimorphism, and generally commence incubation before the laying of the second egg, resulting in a mean hatching interval of 1-2 days (Williams 1995). Brood reduction theory (Lack 1947, 1954) suggests that in times of extreme food shortage, sibling size asymmetries established by hatching asynchrony may facilitate the rapid starvation of the smaller chick within a brood without endangering the survival of the larger chick, which will then, in the absence of competition for food, have a greater chance of fledging. A review by Timothy Lamey (1990), of the potential for adaptive brood reduction in penguins, lamented the lack of direct evidence available. His synthesis preceded a number of studies designed to examine brood reduction and sibling competition explicitly.

The six species in the genus *Eudyptes*, the crested penguins, exhibit varying degrees of obligate brood reduction (Lamey 1990), brought about through extreme egg-size dimorphism, large hatching intervals, reversed hatching asynchrony, and marked sibling-size asymmetry. The origins and adaptive significance of these patterns have been the subject of considerable speculation and study. In this review I examine the inter-specific variation in penguin brood size and consider some of the principal factors which influence the size of penguin broods. I start with a taxonomic summary, dividing species into those that lay one versus two eggs, and further dividing the two-egg species according to their potential for brood reduction. I consider two groups in detail: those with the apparent potential for adaptive brood reduction, and those which exhibit obligate brood reduction. In doing so I aim to revise the Lamey (1990) review, to see how understanding of these two groups has progressed in the intervening eight years.

1. One egg versus two: when one is enough.

Of the 17 species of penguin, only two lay a single egg, the other 15 lay two eggs. A single egg clutch is laid by penguins of the genus *Aptenodytes*, the Emperor *A. forsteri*, and the King *A. patagonicus*. Three factors are associated with a single egg clutch in these two species: a large egg, a long chick growth period, and the need to remain mobile during incubation. With adult male pre-breeding body masses of around 40 kg and 16 kg, respectively, the aptly named Emperor and King are the largest of the extant penguin species, and both incubate their single egg on top of their feet (Williams 1995). Large body mass requires a long chick growth period, longer than the period of peak food availability for both species; an apparent obstacle to successful reproduction that is overcome in two ways, both of which impose constraints that would make a two egg clutch impossible.

The breeding cycle of the Emperor takes nine months, excluding pre- and post breeding moult (Robertson 1995). If breeding commenced in the austral spring, chick rearing would have to extend into the Antarctic winter, and chick survival would probably be impossible due to reduced food availability to parents (Kooyman and Kooyman 1995; Robertson 1995), and the extreme cold. The Emperor Penguin therefore must undertake incubation during the austral winter in order to complete chick rearing during the improved feeding conditions in summer. Unlike all other penguin species therefore, the Emperor comes into reproductive condition in response to decreasing daylight (Groscolas et al. 1986). Adults arrive on breeding grounds on level areas of fast sea-ice in late March. After laying of the single egg in mid-May, the females depart for

the open sea leaving the males to perform winter incubation alone. This unusual breeding strategy of male-only incubation during winter is because extension of the sea ice would necessitate up to eight days travel one way between colony and open sea, and thus effectively prevents incubation changeovers (Kirkwood and Robertson 1997). The male therefore fasts for the pre-nuptial period and the entire 64 days of incubation, a total of four months (Williams 1995), and endures a loss of up to 40% in body mass (Prevost 1961).

Thermoregulation is a major concern for males, particularly during severe weather when temperatures may drop below -30°C (Jouventin et al. 1995; Kirkwood and Robertson 1997). Incubating Emperor Penguins may form huddles of 500 to 1000 birds (Le Maho 1977, Le Maho et al. 1976). These huddles move slowly in the direction of the prevailing wind as males on the outer edges move to the leeward side (Robertson 1990). The single egg is held on the top of the feet, beneath an overhanging brood pouch, enabling the penguins to adopt a slow shuffle. Hatching occurs in late winter, in mid-July, at which time the female returns to feed the chick and relieve the male for a 20 day feeding trip (Robertson 1995). Chick growth is constrained by low rates of food delivery and poor thermoregulation during the first third of the five month rearing period, apparently because parents experience difficulty obtaining enough food, due to low food availability, reduced daylight,

limited access to foraging waters and severe weather (Robertson 1995). Spring and summer conditions improve adult access to feeding grounds, while increased daylight and twilight allow increased frequency of feeding dives (Robertson 1995). Consequently chicks growth improves, allowing fledging by mid-December, when chicks depart for the ice edge. The Emperor Penguin is thus able to occupy its Antarctic niche and successfully rear a single large chick, to fledge in relatively mild conditions with good food availability, by beginning breeding in winter. The cost of winter breeding comes from the constraints imposed by reduced access to foraging waters, and are borne largely by the male, but may be additionally passed on to the chick in the form of delayed growth and chick mortality due to freezing after abandonment.

The King Penguin similarly incubates its single egg on top of the feet (Hazard 1894), but incubation takes place in the relatively kinder conditions of the sub-Antarctic spring. Access to offshore feeding grounds allows mates to share incubation duties. However, the long period of chick dependence and growth means that chicks are not yet fledged when winter conditions cause an apparent change in availability of myctophid fishes (Adams and Klages 1987; Cherel et al. 1987; Hindell 1988; Ridoux et al. 1988). Parents are unable to rear their single chick to sufficient size before the food supply declines (Stonehouse 1960), so between May and August/September, King Penguin parents largely stop feeding an almost fully grown chick (Stonehouse 1960; Barrat 1976; Cherel et al. 1987; van Heezik et al. 1993). The four-month fast may result in chick deaths due to starvation, or increased vulnerability to predation by Giant Petrels *Macronectes giganteus* (Hunter 1991; Weimerskirch et al. 1992). For those chicks that survive, feeding recommences in September-October with an apparent increase in food availability (Adams and Klages 1987) and chicks fledge from December, at 10-13 months of age (summary in Williams 1995). The breeding cycle of the King Penguin is therefore extended to 14 to 16 months, and pairs are unable to breed successfully in two consecutive years. Consequently, successful breeders cannot start a new attempt early in the season, and late attempts almost always fail; whereas failed breeders in one year can start a new attempt early and have increased likelihood of success (van Heezik et al. 1994). The ability to raise no more than one chick every two years results in a breeding strategy that has the appearance of being biennial (Barrat 1976). The King penguin is however, endocrinologically an annual breeder; the timing of annual cycles of LH and steroid hormones is probably in response to increasing photoperiod in spring (Mauget et al. 1994; Cherel et al. 1994; Jouventin and Mauget 1996). As a result there are two apparent paradoxes. The first is that successful breeders will start new breeding attempts late in the season, in the face of almost certain failure (van Heezik et al. 1994); resulting in an extended laying period and the overlap of several stages of breeding within one colony. Increased disturbance in breeding colonies caused by the overlap of stages may be responsible for adults that are incubating eggs or brooding young chicks having to spend almost 8% of their time in aggressive territorial defence, day and night (Challet et al. 1994). The second paradox lies in the ability of adults to sustain chick rearing behaviour over extended absences from the chick. This is due to sustained levels of prolactin (Cherel et al. 1994), maintained possibly by an endogenous rhythm as an adaptation to long parental care in the face of extended absences from the chick (Garcia et al. 1996). Prolactin secretion is sustained for a lesser period in failed breeders, preventing relaying (Jouventin and Mauget 1996), but, presumably in the absence of the stimulus of a chick subsequent to the completion of the endogenous cycle, failed breeders are able to make new attempts early in the following season. Annual periodicity in King penguins is therefore an artefact of low individual breeding success, so that the King penguin reproductive cycle only coincides with the annual rhythm of the environmental cycle when breeding fails (Jouventin and Mauget 1996). In captivity, without environmental constraints on chick feeding, parents are able to raise a chick within nine months (Gillespie 1932). Presumably in captivity therefore, prolactin secretion is triggered by laying/hatching, with the levels sustained endogenously during the shortened period of chick rearing possible with ad lib food, but with early chick independence the stimulus for sustained prolactin would be lost just when the endogenous cycle is ending (when birds in the wild are recommencing chick care after the winter fast), and annual breeding in captivity (or with abundant food) would be possible.

Therefore, as in Emperor Penguins, in King Penguins the long developmental stages needed to raise a large chick to fledging have become constrained by a winter decrease in food availability. Unlike Emperor Penguins however, winter conditions for King Penguins are more mild and the burden of an enforced fast is borne by the chicks, not by the adult males. Breeding has remained entrained by photoperiod so that hatching takes place in spring, and peak food availability allows chicks to gain sufficient fat reserves to survive the winter fast (van Heezik et al. 1993), regain lost weight at the end of winter, and fledge into the good feeding conditions of the following spring. It has been suggested that the King Penguin represents an intermediate evolutionary step towards cold adaptation (Le Maho 1977), with the Emperor being the furthest evolutionary stage (Jouventin 1971). However, it is likely that the divergent breeding strategies of

Aptenodytes have arisen from two different selection pressures. Evolutionarily, a declining availability of food during winter could have selected for King Penguin adults that had the endogenously sustained prolactin that allows extended chick rearing, but with a cut off point that required the active presence of a chick in order for prolactin to continue to be sustained, otherwise failed breeders would be unable to start new attempts early in the following season. For Emperor Penguins, increasing cold, and consequential decreasing accessibility to foraging waters, may have selected for birds that commenced breeding earlier in the season. To a large extent timing of breeding would be dictated proximately by the set and break-out of fast ice. Sustained selection for early breeding would have pushed the start of laying back to early winter, reversing the more usual response to decreasing photoperiod, since birds that could start laying then and which could complete a winter incubation successfully, would raise chicks to fledging in time for relatively mild austral summer conditions. In both species, long chick growth periods cannot be sustained in the face of seasonal declines in food availability; environmental constraints on the possible responses to this dilemma have given rise to two markedly different breeding strategies within the one genus. For Aptenodytes, as for the other penguin species, it should be remembered that observed breeding strategies are workable solutions to problems posed by environmental and physiological constraints, but are not necessarily the most parsimonious, elegant, or even the best.

2. Two-egg clutches and brood reduction

Adjustment of individual brood size may be related to a number of factors, including age (young breeders are more likely to lay or retain only a single egg), and nest site (nests on the periphery of large colonies, or in exposed settings, are most likely to lose eggs or chicks to disturbance, inclement weather, or predators). Apart from this brief mention, I will not discuss individual brood size adjustment further, but will consider in detail only generic patterns of brood size determination. Throughout the following discussions I use the designation A-(egg or chick) and B-(egg or chick) to refer to the first- and second-laid egg and their chick, respectively.

Brood maximising and the production of twins

The Yellow-eyed Penguin *Megadyptes antipodes* lays two similar-sized eggs (Richdale 1957), and delays the start of incubation (Seddon 1989), so that within a brood the hatching interval is often less than one day (Darby and Seddon 1990), and two same-sized siblings are produced (van Heezik and Davis 1990). Intra-brood aggression is rare or absent, and there is little sibling competition for the food regurgitated by either parent (Seddon 1990). Parents do not appear to favour one chick over its sibling, and as a consequence growth rates of siblings are similar (van Heezik 1990) and in most years a high percentage of breeding attempts will result in the fledging of two chicks (van Heezik and Davis 1990). In a recent study Keri-Anne Edge (1996) simulated a moderate degree of hatching asynchrony by the exchange of newly hatched Yellow-eyed Penguin chicks between nests. The resultant sibling asymmetries were unstable however, and no differences were recorded in subsequent chick survival, or age or weight at fledging, and there was no apparent effect on parental condition. It was therefore postulated that Yellow-eyed Penguins did not experience selection pressure for a certain degree of hatching asynchrony, and that hatching synchrony was the norm because neither are there selection pressures for early start of incubation. The low degree of hatching asynchrony may possibly be a derived trait due to environmental conditions which favour delayed incubation (Edge 1996), for example, a temperate climate, low risk of predation, and good food availability in most years.

Brood reduction and sibling asymmetries

The remaining 13 penguin species exhibit varying degrees of brood reduction. This ranges from the obligatory loss of one egg of the clutch, the obligatory loss of one chick before fledging, to the pre-established potential for loss of one chick only under certain conditions. A key question is whether this facultative brood reduction is of adaptive significance.

Do hatching asynchrony and sibling size asymmetry facilitate adaptive brood reduction in penguins?

Asynchronous hatching and subsequent disparities in chick size and competitive ability have been viewed as a means to facilitate brood reduction (reviewed in: Clark and Wilson 1981; Magrath 1990). The brood reduction hypothesis (Lack 1947, 1954, 1968; Ricklefs 1965; O'Connor 1978) postulates that sibling asymmetries set up by hatching asynchrony are an adaptive mechanism whereby parents can adjust brood size to match feeding conditions in an unpredictable environment. When food is plentiful, all chicks are able to receive enough food and can fledge. When food supplies fail during the breeding season, the starvation of the smaller chick is facilitated through the competitive advantage accrued to the larger sibling, thus avoiding

wasteful competition between equally matched siblings to the detriment of both. Broods adjusted by early loss of the weaker chick may be able to salvage at least one chick, rather than experience total failure.

Two genera of penguin, *Pygoscelids* and *Spheniscids*, appear to be suitable candidates for testing these ideas, to see whether the establishment of sibling asymmetries has an adaptive significance.

Pygoscelids and feeding chases

Egg-size dimorphism in the three species of *Pygoscelis* is slight, ranging from 4.4% in Chinstraps *P. antarctica* (Moreno et al. 1994) to 6.3% in Adelie *P. adeliae* (Lamey 1990), and is not believed to be the principal factor leading to the establishment of sibling size differences (Moreno et al. 1994). Hatching asynchrony is more marked, but also more variable, ranging from 1-4 days (mean 1 day between eggs) in Chinstraps (Moreno et al. 1994) to a mean of 1.4 days in Adelies and 1.6 days in Gentoos *P. papua* (Lamey 1990). The temporal advantage gained by the first-hatched (A) chick means that when the second (B) chick hatches there is a sibling mass asymmetry of 22.4% in Chinstraps (Moreno et al. 1994), and between 28% to 34.3% in Gentoos (Williams and Croxall 1991).

The establishment of a sibling size hierarchy provides a potential mechanism for classical brood reduction to take place when food is scarce. Whereas in most years Chinstrap parents are able to raise two chick broods to similar final masses as single chick broods (Moreno et al. 1998), food has been shown to be limiting in some years, and starvation of chicks has been recorded (Moreno et al. 1994). However, although when food is limiting the smaller chick in two-chick Chinstrap broods is most likely to succumb to starvation first, subsequent starvation of the surviving chick is not uncommon (Moreno et al. 1994). In addition, likelihood of brood reduction is not related to the degree of sibling asymmetry, and growth of surviving chicks is not markedly better, and may be worse than that of unreduced broods (Moreno et al. 1994). Why should this be so? *Pygoscelid* chicks compete for food, either through direct aggression or indirectly (Davis and McCaffrey 1989), suggesting that this initial size asymmetry could be maintained throughout the dependent period. However, there is evidence that this is not the case, that in Chinstraps and Gentoos at least, there is a tendency for sibling asymmetries to decrease over time, and that reversals in the size hierarchy are not uncommon (Moreno et al. 1994; Williams and Croxall 1991).

Apparently then, asynchronous hatching does not lead to stable hierarchies between siblings. One reason for this may be the way in which *Pygoscelid* chicks are fed during the creche phase. Feeding chases, whereby the feeding parent runs and is chased by begging chicks (Sladen 1958; Thompson and Emlen 1968; Thompson 1981), are a characteristic of all species of *Pygoscelid* (Gentoo: Pettingill 1964; Adelie: Thompson 1981; Chinstrap: Bustamante et al. 1992). Before the creche stage the chicks are fed on the nest site and apportionment of food is determined primarily by sibling competition (Davis and McCaffrey 1989). Feeding chases in the creche stage have been variously proposed as a mechanism for parents to separate their own chicks from a creche; for parents to regulate the distribution of food between the siblings in order to either promote brood reduction (summary in Bustamante et al. 1992), or to increase feeding efficiency by reducing scramble competition (Boersma and Davis 1997). Feeding chases are reduced or non-existent when only one chick is present (Thompson 1981; Bustamante et al. 1992; Moreno et al. 1996; Boersma and Davis 1997), suggesting that chases serve to increase feeding efficiency and/or reduce harassment to the parents (Bustamante et al. 1992). Dee Boersma and Lloyd Davis (1997) hypothesised that if feeding chases were a mechanism for facilitating brood reduction, then the larger chick of the brood should be able to monopolize access to the food delivered throughout a feeding session. This was not the case, rather the chick being fed appeared more likely to switch as a result of the chase. Chases are thereby apparently acting as a parental mechanism to ensure equitable food distribution, reduce direct competition and inefficient transfer of food, and actually act to prevent the development of overlarge asymmetries (Boersma and Davis 1997) that could result in wasteful brood reduction, even when food is plentiful.

Some other evidence further weakens any case for adaptive brood reduction in *Pygoscelids*. Chick starvation has been recorded in Adelies, but is due primarily to failed nest reliefs by parents, and in general food may not be limiting for Adelies (Boersma and Davis 1997). Nor too are other adaptive explanations for hatching asynchrony supported by the evidence. Synchronously hatching broods may comprise 22-31% of Chinstrap broods, and chicks in synchronous broods reach the same final mass as chicks in asynchronous broods, implying that sibling size asymmetries do not improve feeding efficiency in this species (Moreno et al. 1994).

Asynchronous hatching and subsequent sibling size differences may arise incidentally in *Pygoscelids* as a result of selection pressure for early commencement of incubation to avoid exposure of eggs to low ambient temperatures (Williams and Croxall 1991), and feeding chases may therefore be a parental mechanism for

ensuring that food allocation is equitable and that an overbalanced weight hierarchy does not develop from the incidental asymmetry caused by hatch order. There are three areas of interest for further investigation: (1) examination of post-fledging survival in relation to brood type (where symmetric and asymmetric broods either naturally occur or are created artificially), status of chicks within such broods, and fledging mass or timing; (2) the mechanics of sibling competition and food allocation in the absence of feeding chases (perhaps through erection of a barrier around the feeding group); (3) the proximate causes of intra-specific variation in the degree of hatching asynchrony.

Spheniscids and scramble feeding

In the four species of the genus *Spheniscus*, hatching asynchrony creates sibling size asymmetries that can lead to brood reduction (Lamey 1990; Boersma 1991; Boersma and Stokes 1995). Although slight egg-size dimorphism is common in these species, evidence suggests that its contribution to the establishment of sibling asymmetries may be negligible (Seddon and van Heezik 1991a).

The most detailed work has been done on Magellanic *S. magellanicus* and African *S. demersus* penguins. I assume that, because patterns of hatching asynchrony and sibling competition are similar amongst the four species, and seasonal variation in food availability is common (Boersma 1976, 1978, Boersma et al. 1990; Adams et al. 1992; Williams 1995), that the results from Magellanic and African penguins could be applied also to the Galapagos *S. mendiculus* and Humboldt *S. humboldti* penguins.

Magellanic penguins experience marked inter-annual variation in reproductive success, due primarily to variation in food availability (Boersma et al. 1990). Although symmetric broods do occur naturally, Magellanic chicks within a brood hatch on average two days apart, an interval that promotes the development of sibling size asymmetries (Boersma and Stokes 1995). Differential competitive ability means that starvation of the smaller, second-hatched (B) chick is not uncommon (Boersma and Stokes 1995). Observations indicate that the heavier chick (A) in a brood receives the most food, and that the difference in the amount of food obtained by the two chicks increases with increasing size asymmetry (Blanco et al. 1996). This differential feeding of the larger chick is believed to be due to the A-chick's greater mobility and strength (Blanco et al. 1996), but it is possible that parents may also treat one chick preferentially (Boersma 1991). Boersma and Stokes (1995) note that fledging success in Magellanic is not well correlated with the degree of hatching asynchrony, i.e., greater degrees of hatching asynchrony are not, on average, associated with greater numbers of chicks fledged per nest, suggesting that parental quality, the timing of the first feeds after hatching and other factors may strongly influence the degree of sibling asymmetry. The significance of this resulting asymmetry is uncertain, though there could be some relationship between broods with mean levels of asynchrony (1.9 days) and both their fledging success and fledging mass (Boersma and Stokes 1995).

African penguin siblings hatch a mean of 2.1 days apart (Williams and Cooper 1984), so that at hatching, the B-chick is on average only 59% of the mass of the A-chick (van Heezik and Seddon 1991). While B-chicks in normal asynchronous broods were more likely to die of starvation than their larger sibling, comparisons of fledging success and survival in normally asynchronous broods and experimentally created synchronous broods which contained two same-sized siblings did not support the predictions of the brood reduction hypothesis (Seddon and van Heezik 1991a,b). However, chicks in experimental synchronous broods had depressed growth rates (van Heezik and Seddon 1991), so that chicks in asynchronous broods fledged earlier and at greater body mass (Seddon and van Heezik 1991a). Observations indicated that A-chicks in normal asynchronous broods out-compete B-chicks, not through direct aggression, but through scramble competition (van Heezik and Seddon 1996), whereby the A-chick uses its superior weight, mobility and co-ordination to gain first access to food regurgitated by the parents (van Heezik and Seddon 1997). A-chicks gain most food during the first part of each feeding session, but following A-chick satiation, the B-chick is able to feed with few interruptions; in this way, in times of abundant food, the development of over-large asymmetries would be avoided, preventing wasteful loss of the B-chick (van Heezik and Seddon 1996).

The evidence to date for Spheniscid penguins, the prime candidates for adaptive brood reducers, suggests that the brood reduction hypothesis is not an adequate explanation for the presence of sibling asymmetries established by hatching asynchrony. A number of other hypotheses have been put forward to explain avian hatching asynchrony, the most applicable of these to *Spheniscus* penguins (Seddon and van Heezik 1991a) is the sibling rivalry reduction hypothesis SRRH (Hahn 1981), which postulates that sibling asymmetries result in a feeding hierarchy within which the older chick is able to dominate the younger, and wasteful competition between two evenly matched siblings is avoided; these advantages should be evident even in years of good food availability. The SRRH however, also makes predictions about differential fledging success between

synchronous and asynchronous broods, which are unsupported by the evidence from Magellanic and African penguins.

Seddon and van Heezik (1991a) proposed extensions to the BRH and the SRRH, whereby sibling asymmetries may result in better quality fledglings, with higher post-fledgling survival (see also Offspring Quality Assurance Hypothesis, Slagsvold et al. 1995). Results from the African penguin most strongly support such an extension to the SRRH, so that sibling asymmetries create a feeding hierarchy that allows efficient use of resources and result in heavier (better?, but see Williams and Croxall 1991) fledglings (Seddon and van Heezik 1991a; van Heezik and Seddon 1996).

Recent work (Mock and Lamey 1991; Forbes 1993; Ploger 1997) suggests that avian parents may deliver less food to reduced broods, and that under such conditions brood reduction should not increase the survival rate of the remaining sibling(s). Seddon and van Heezik (1991b) suggested that this parental matching of food delivery to brood size may explain the slightly lower likelihood of survival of surviving chicks in reduced broods. This could be an explanation for the same phenomenon recorded in Chinstrap penguins (Moreno et al. 1994). However, this may also be a reflection of poor parents or parental problems in delivering food. Closer examination is needed to determine if decreased food delivery also means a decrease in food biomass delivered to the surviving chick. In a review of siblicidal raptors Robert Simmons showed that while food delivery to broods may decrease when brood size decreases, food biomass per individual chick actually increased in all cases (Simmons, unpublished manuscript).

I suggest therefore, that rather than search for the adaptive significance of penguin hatching asynchrony as a means to promote brood reduction, we should perhaps consider that hatching asynchrony, in Spheniscids if not in other genera facing intermittent food limitation, serves to establish a sibling size asymmetry within a brood. Sibling size differences may result in a feeding hierarchy that prevents wasteful competition. More efficient use of resources, in asymmetric broods compared with symmetric ones, may be expressed as improved chick fledgling quality, therefore higher post-fledging survival and greater likelihood of recruitment into the breeding population. Considerations of offspring quality, as opposed to quantity, have been the basis for hypotheses concerning the adaptive significance of canism in some raptor species (Newton, 1979; Simmons 1988, 1989, 1997) - the terrestrial, ecological equivalent of long-lived seabirds. Shorter fledging periods may have benefits for parents also, and could improve lifetime reproductive fitness by improving survival and therefore reproductive output, in terms of both numbers of breeding attempts, and numbers of surviving fledglings. If the adaptive significance of hatching asynchrony is the establishment of a feeding hierarchy, then it would be expected that there would be mechanisms that (a) maintained the sibling asymmetry, at least through the period of peak chick growth, and (b) prevented the asymmetry from becoming too great and risking wasteful brood reduction even when food was plentiful.

Little Penguins *Eudyptula minor* do not fit readily into the breeding pattern of either Pygoscelids or Spheniscids. While they share with Spheniscids a marked inter-annual variation in the timing of breeding (Fortescue 1995) and breeding success (Dann and Cullen 1990) due to variation in oceanographic conditions (Mickelson et al. 1992), food abundance (Hobday 1992), and therefore in food availability, they do not as a group clearly exhibit features which would facilitate the formation of sibling asymmetries. Eggs within a clutch may be similar in size (Stahel and Gales 1987), or the second-laid egg may be lighter (Fortescue 1995). Hatching is mainly synchronous (Williams 1995), but a hatching interval of up to seven days has been recorded (Reilly and Balmford 1975). Sibling asymmetries, presumably established by greater degrees of hatching asynchrony, result in competitive disadvantage to the B-chick, longer B chick fledging periods (Williams 1995) and higher mortality (Gales 1987). The possible adaptive significance of Little Penguin sibling asymmetry has not been examined explicitly, and could lie in improved fledging success or greater fledging mass for chicks in more asymmetric broods. Variation in food availability, breeding success and the degree of hatching asynchrony make the Little Penguin suitable for addressing such questions.

Much work remains to be done concerning the adaptive significance of penguin sibling asymmetries. While the predictions of classical brood reduction theory should continue to be borne in mind, as should the possibility that hatching asynchrony is a non-adaptive consequence of other factors which promote early onset of incubation, greater attention could be given to sub-lethal advantages for the establishment of intra-brood feeding hierarchies, including fledging weight, fledging period, and the relationship between fledgling condition and survival until breeding age. Details of the mechanisms by which food is apportioned between siblings of different competitive abilities could be examined to determine if similar patterns are maintained by different species, or under different feeding conditions or degrees of asymmetry. Closer attention could be

paid to those species that show natural variation in the degree of brood reduction between pairs, between years or at different localities.

Crested penguins and obligate brood reduction

The adaptive significance of obligate brood reduction in the crested penguins is one of the more alluring of the penguin paradoxes (Croxall and Davis in press). Crested penguins have four traits that have largely defied a single adaptive explanation: (1) the first egg laid is markedly smaller than the second; (2) although two eggs are laid, two chicks are almost never fledged due to egg loss during laying, or to the starvation of the smaller sibling; (3) in instances when the first egg is retained throughout incubation, it hatches after the second-laid egg; (4) significant egg loss in at least two crested species may be due to the direct action of the attending adult (summaries in Williams 1995; St. Clair 1996).

In crested penguins the first-laid (A) egg is 15-45% smaller than, and is laid about four days before, the second-laid (B) egg (Warham 1975). If the A-egg is retained, as it may be in the Fiordland crested *Eudyptes pachyrhynchus* (Warham 1974a), Rockhopper *E. chrysocome* (Gwynn 1953, cited in Williams 1995) and Snares-crested *E. robustus* (Warham 1974b), it typically hatches after the B-egg. When two eggs hatch there is no overt sibling aggression, but the smaller chick from the A-egg virtually always starves to death (Lamey 1990). In the other three of the six *Eudyptes* species, the Macaroni *E. chrysolophus* (Gwynn 1953, cited in Williams 1995), the Erect-crested *E. sclateri* (Richdale 1941) and the Royal *E. schlegeli* (Carrick 1972, cited in Williams 1995), the smaller A-egg disappears from the nest by a few days after B egg laying.

The apparent viability of A-eggs has led to the suggestion that the smaller first egg may be an insurance against egg loss (Lack 1968; Warham 1975; review in Williams 1995), or a response to high losses of first eggs due to conspecific male aggression (Johnson et al. 1987). However, neither of these ideas have been fully supported by direct field tests (Williams 1989; St. Clair 1992; Lamey 1993; St. Clair and St. Clair 1996). The insurance value of the A-egg is limited where both eggs do not remain in the nest together long enough, and timing of A-egg loss is unrelated to levels of male aggression, which result in only minor egg loss (Williams 1995). Often A-eggs are lost in the last day of the laying interval (Williams 1990), and observations have shown that, in Royal and Erect crested penguins at least, the A-egg may be deliberately ejected from the nest, most commonly immediately before the second egg has been laid (St. Clair et al. 1995). Egg ejection, by parent or sibling, may also play a role in egg loss in Macaronis (Williams 1989), and possibly also in Rockhoppers, where peak loss of A-eggs also takes place during peak periods of B-egg laying and hatching (St. Clair and St. Clair 1996).

Explanations for the unusual breeding pattern in crested penguins must take into account reversed egg-size dimorphism, reversed hatching asynchrony, and deliberate and early egg loss. Below I summarise a scenario by which these patterns may have evolved.

Recent phylogenetic studies have confirmed the close relationship between the Yellow-eyed penguin and the crested penguins, and have been used to suggest that traits present in both genera represent common ancestral features (Edge 1996). The Yellow-eyed penguin is a brood maximiser (Edge 1996); same-sized eggs, delayed brood patch formation, delayed onset of incubation and subsequent synchronous hatching, results in two same-sized/aged siblings. Lack of competition during feeding, and adequate food availability means Yellow-eyed penguin parents can raise two chicks to fledging in most years. Edge (1996) postulated that delays in incubation and in brood patch formation have probably arisen independently of reduction in the size of the first egg in crested penguins. If *Eudyptid* penguins were once, or derived from, similar brood maximisers, and were faced with a decrease in food availability (possibly associated with a postulated change from inshore- to off-shore-foraging, Williams 1980) that meant that two chicks could not be raised to fledging in most seasons, then in many years low food availability would result in chick starvation. The absence of any differential in competitive ability between siblings, in accordance with the brood reduction or sibling rivalry reduction ideas, would be expected to result in low productivity in broods with two same-sized siblings, and total breeding failure might occur. There would therefore be selection pressure for the creation of some degree of competitive difference between siblings, so that either feeding efficiency could be improved, or brood reduction facilitated, in times of food shortage. Given the previous establishment of physiological and behavioural features that delay incubation, if selection favoured unequal investment in offspring, the evolution of egg-size dimorphism may be easier than a change to early brood patch formation (Edge 1996). Thus one way to create this differential would be through differential provisioning of eggs. Crested penguins could either make A-eggs or B-eggs smaller. But if B-eggs were smaller, yet delayed incubation was retained, what would be the outcome? Development in both eggs would start after laying of the smaller B-egg.

Hatching would be synchronous and the only differential between siblings would be that established through egg-size dimorphism. However, if the first laid egg were smaller, cooling during the laying period would be greater for the greater surface area to volume ratio (but see St. Clair 1996); incubation would begin with the laying of the B-egg, which would not have cooled, and may therefore get a head start in development through faster heating (e.g. Burger and Williams 1979) or other factors (e.g. St. Clair 1996). With egg-size dimorphism and delayed incubation both serving to disadvantage the A-egg, the B-egg would therefore hatch first, and produce a larger chick. This size differential could be further increased by early feeding of the B-chick before the smaller A-chick hatched, thus establishing a significant size hierarchy within the brood, and the potential for the benefits that may accrue from this, in times of food shortage.

So we have a facultative brood reducer with reversal of the usual egg-size dimorphism and hatching order. The move to offshore foraging may entail a decrease in the time available to feed two chicks, to the point where it becomes no longer possible to raise two chicks in any year (St. Clair pers. comm.). This would imply a selection pressure against the production of even a small egg/chick, unless there was some advantage in retaining the A-egg. It has been suggested that, since an A-egg may be relatively inexpensive to produce, there may be selective inertia against its elimination (Williams 1990), and even a weak secondary function during the laying period may be advantageous (St. Clair et al. 1995; St. Clair in press). There are four postulated secondary functions: (1) the A-egg is insurance against failure to produce a second egg (Williams 1989); (2) the A-egg is necessary to stimulate development of the brood patch in time for incubation to begin fully with the arrival of the B-egg (St. Clair 1992; but see St. Clair in press); (3) the presence of the A-egg ensures that the male will remain ashore, fasting with the female for long enough for the B-egg to develop and for full incubation to begin, i.e. to enhance mate fidelity (Williams 1995); (4) the A-egg may provide a signal to conspecifics that enhances synchrony between neighbouring pairs, and/or reduces contests for nesting space by signalling occupancy (Johnson et al. 1987).

If the value of the A-egg lies in its presence, for whatever reason, only until the B-egg arrives (or is about to arrive, an event that should be able to be predicted by the female as the egg moves down in the oviduct (St. Clair et al. 1995)), then its usefulness ends with the end of laying and the egg can be lost. The most efficient way to lose an unwanted egg is to eject it from the nest, and if this is done in response to the imminent arrival of the B-egg, the ejection would be expected to be done by the female before laying, as observed by Colleen Cassady St. Clair and her colleagues (1995), but possibly by either sex after laying. The observation that retained A-eggs are moved to an anterior position, where they are incubated less efficiently (Burger and Williams 1979; St. Clair 1992, 1996), hints that the action of egg ejection may derive as an extension, or exaggeration, of moving the smaller egg forward in the nest.

Given that an A-egg has been produced, and may be viable, why is this not retained throughout incubation and at least the first stages of chick rearing, for its insurance value? There would be selection to lose the A-egg before incubation if a two-egg clutch reduced B-egg survival, possibly via reduced efficiency of incubation resulting in longer incubation periods, or lower hatching success (St. Clair and St. Clair 1996). In such instances there would be pressure to lose the A-egg as soon as its usefulness during the laying period had been realised. Such factors may be important in Erect crested, Macaroni and Royal penguins, which lose the A-egg within 24 hours of laying of the B-egg. If, however, there was no disadvantage in retaining the A-egg during incubation, yet a possible advantage through its (even small) insurance value, the A-egg could hatch. But if the presence of an A-chick reduces the survival or quality of the B-chick, then there would be pressure for the A-chick to be lost as soon as its value during incubation had been realised. This occurs in Fiordland crested, Rockhopper and Snares crested penguins, where the A-chick is lost within a few days of hatching.

SUMMARY

Generic patterns of brood size determination in penguins have been shaped by conditions experienced on land, and by food availability to adults during breeding. The single-egg clutch of King and Emperor penguins appears to be a response to the severe constraints on breeding posed by a long period of chick-rearing in the face of marked seasonal variation in food availability. But whereas the Emperor Penguin has reversed the usual physiological response to photoperiod, and commences a breeding attempt when daylight is decreasing in order to complete chick rearing by the austral summer, the King Penguin extends the chick-rearing period by virtual cessation of chick feeding over winter. The variation between the two Aptenodytes species appears to be due to the inability of Emperor chicks to survive an Antarctic winter, the fasting period ashore being borne by Emperor Penguin adult males, but by King Penguin chicks in the relatively milder sub-Antarctic



conditions. The other 15 species of penguin lay two-egg clutches, but range from production of twins, through brood reduction under some conditions, to obligatory loss of one egg or chick. Brood reduction, whether facultative or obligatory, is facilitated by egg-size dimorphism and hatching asynchrony, and the resulting asymmetry between siblings. In potentially facultative brood-reducing genera such as *Pygoscelis* and *Spheniscus*, the adaptive significance of early onset of incubation and the establishment of sibling size asymmetries has been the subject of considerable study, although the results to date do not support the classical resource-tracking theories of brood reduction. Hatching asynchrony may result from pressure to protect eggs from predation, low ambient temperatures, or other factors, leading to the creation of non-adaptive sibling size differences. In *Pygoscelids*, feeding chases may serve to reduce the competitive disparity between two different-sized siblings to avoid loss of the less competitive smaller chick even when food is abundant. In *Spheniscids* it is possible that hatching asynchrony is adaptive, not in facilitating brood reduction, but in creating a feeding hierarchy within a brood which serves to reduce sibling competition, and may result in better quality fledglings, and perhaps also in greater lifetime reproductive success for adults. The significance of factors leading to obligate brood reduction in the *Eudyptids* eludes a single, parsimonious explanation. An evolutionary switch from inshore to offshore foraging may have reduced the ability of *Eudyptid* parents to raise two chicks, leading to selective pressure for the early elimination of one. The retention of a small, viable A-egg, in the face of almost certain loss, may be due to selective inertia for the elimination of an inexpensive egg with some secondary adaptive function. Hypotheses linking the retention of a small A-egg with secondary functions relating to physiological development, e.g. brood patch formation; social stimuli, or insurance value during the laying or early chick period, are currently the best candidates for a unifying theory.

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REFERENCES

- Adams, N.J. & Klages, N.T. 1987. Seasonal variation in the diet of the king penguin at sub-Antarctic Marion Island. *Journal of Zoology*, London 212: 303-324.
- Adams, N.J., Seddon, P.J. & van Heezik, Y. 1992. Monitoring of seabirds in the Benguela Upwelling System: can seabirds be used as indicators and predictors of change in the marine environment? In: Payne, A.I.L., Brink, K.H., Mann, K.H. & Hilborn, R. (Eds) *Benguela Trophic Functioning*. South African Journal of Marine Science 12:959-974.
- Barrat, A. 1976. Quelques aspects de la biologie et de l'ecologie du manchot Royal (*Aptenodytes patagonicus*) des Iles Crozet. *Comite National Francais de Recherches Antarctique* 40: 9-51.
- Blanco, D.E., Yorio, P. & Boersma, P.D. 1996. Feeding behavior, size asymmetry and food distribution in Magellanic Penguin chicks. *Auk* 113(2): 496-498.
- Boersma, P.D. 1976. An ecological and behavioural study of the Galapagos penguin. *Living Bird* 15: 43-93.
- Boersma, P.D. 1978. Breeding patterns of Galapagos penguins as an indicator of oceanic conditions. *Science* 200: 1481-1483.
- Boersma, P.D. 1991. Asynchronous hatching and food allocation in the Magellanic penguin *Spheniscus magellanicus*. *Acta Congressus Internationalis Ornithologici*, XX: 961-973.
- Boersma, P.D., Stokes, D.L. & Yorio, P.M. 1990. Reproductive variability and historical change of magellanic penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. Pp. 15-43. In: Davis, L. S. and Darby, J. T. (eds). *Penguin Biology*. Academic Press, San Diego.



- Boersma, P.D. & Stokes, D. L. 1995 Mortality, hatching asynchrony, and size asymmetry in Magellanic Penguin chicks. In: Dann, P., Norman, I. and Reilly, P. (eds). *The Penguins: ecology and management*. Surrey Beatty and Sons, Chipping Norton, Australia.
- Boersma, P.D. & Davis, L.S. 1997. Feeding chases and food allocation in Adelie penguins. *Anim. Behav.* 54: 1047-1052.
- Burger, A.E. & Williams, A.J. 1979. Egg temperatures of the rockhopper penguins and some other penguins. *Auk* 96: 100-105.
- Bustamante, J., Cuervo, J.J. & Moreno, J. 1992. The function of feeding chases in the chinstrap penguin. *Animal Behaviour* 44: 753-759.
- Carrick, R. 1972. Population ecology of the Australian black-backed magpie, royal penguin, and silver gull. Population ecology of migratorybirds, a symposium. U. S. Department of the Interior Wildlife Research Report 2: 41-98.
- Challet, E., Bost, C.A., Handrich, Y., Gendner, J. P. & Le Maho, Y. 1994. Behavioural time budget of breeding king penguins. *Journal of Zoology, London* 233: 669-681.
- Cherel, Y., Stahl, J-C. & Le Maho, Y. 1987. Ecology and physiology of fasting in king penguin chicks. *Auk* 104: 254-262.
- Cherel, Y., Mauget, R., Lacroix, A. & Gilles, J. 1994. Seasonal and fasting related changes in circulating gonadal steroids and prolactin in King Penguins. *Physiological Zoology* 67(5): 1154-1173.
- Clark, A. B. & Wilson, D. S. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction and nest failure. *Quarterly Review of Biology* 56: 253-277.
- Croxall, J.P. & Davis, L.S. in press. Penguins: paradoxes and patterns. *Marine Ornithology*.
- Dann, P. & Cullen, J.M. 1990. Survival, patterns of reproduction and lifetime reproductive output in little blue penguins (*Eudyptula minor*) on Phillip Island, Victoria, Australia. Pp. 63-84. In: Davis, L. S. and Darby, J. T. (eds). *Penguin Biology*. Academic Press, San Diego.
- Darby, J.T. & Seddon, P.J. 1990. Breeding biology of Yellow-eyed penguins (*Megadyptes antipodes*). Pp. 45-62. In: Davis, L. S. and Darby, J. T. (eds). *Penguin Biology*. Academic Press, San Diego, USA.
- Davis, L. S. & McCaffrey, F. T. 1989. Recognition and parental investment in Adelie penguins. *Emu*: 89: 155-158.
- Edge, K. A. 1996. Parental investment in penguins: a phylogenetic and experimental approach. PhD. Thesis. Department of Zoology, University of Otago, Dunedin, New Zealand.
- Forbes, L.S. 1993. Avian brood reduction and parent-offspring 'conflict'. *American Naturalist* 142: 82-117.
- Fordyce, R.E., & Jones, C.M. 1990. Penguin history and new fossil material from New Zealand. Pp. 419-446. In: Davis, L. S. and Darby, J. T. (eds). *Penguin Biology*. Academic Press, San Diego.
- Fortescue, M.E. 1995. Biology of the Little penguin *Eudyptula minor* on Bowen Island and at other Australian colonies. Pp. 364-392. In: Dann, P., Norman, I. and Reilly, P. (eds). *The Penguins: ecology and management*. Surrey Beatty and Sons, Chipping Norton, Australia.
- Gales, R. P. 1987. Growth strategies in blue penguins, *Eudyptula minor*. *Emu* 87: 212-219.
- Garcia, V., Jouventin, P. & Mauget, R. 1996. Parental care and the prolactin secretion pattern in the King Penguin: an endogenously timed mechanism? *Hormones and Behaviour* 30.
- Gillespie, T.H. 1932. *A Book of Penguins*. Herbert Jenkins Ltd., London.
- Groscolas, R., Jallageas, M., Goldsmith, A. & Assenmacher, I. 1986. The endocrine control of reproduction and moult in male and female Emperor (*Aptenodytes forsteri*) and Adelie (*Pygoscelis adeliae*) penguins. I. Annual changes in plasma levels of gonadal steroids and luteinizing hormone. *General and Comparative Endocrinology* 62: 43-53.
- Gwynn, A.M. 1953. The egg-laying and incubation periods of Rockhopper, Macaroni and Gentoo Penguins. *A.N.A.R.E. Report (Zoology)*. (B) 1: 1-29.

- Hazard, R.G. 1894. Breeding habits of the King Penguin (*Aptenodytes longirostris*). *Auk* 11: 28-282.
- Hahn, D.C. 1981. Asynchronous hatching in the laughing gull: cutting losses and reducing rivalry. *Animal Behaviour* 29: 421-427.
- Hindell, M.A. 1988. The diet of the King Penguin at Macquarie Island. *Ibis* 130: 193-203.
- Hobday, D.K. 1992. Abundance and distribution of pilchard and Australian anchovy as prey species for the Little Penguin *Eudyptula minor* at Phillip Island, Victoria. *Emu* 91: 342-354.
- Hunter, S. 1991. The impact of avian predator-scavengers on King Penguins *Aptenodytes patagonicus* chicks at Marion Island. *Ibis* 133: 343-350.
- Johnson, K., Bednez, J.C. & Zack, S. 1987. Crested Penguins: why are first eggs smaller? *Oikos* 49: 347-349.
- Jouventin, P. 1971. Comportement et structure sociale chez le Manchot empereur. *La Terre et la Vie* 25: 510-586.
- Jouventin, P., Barbraud, C. & Rubin, M. 1995. Adoption in the Emperor Penguin. *Animal Behaviour* 50: 1023-1029.
- Jouventin, P. & Mauget, R. 1996. The endocrine basis of the reproductive cycle in the King Penguin. *Journal of Zoology, London* 238: 665-678.
- Kirkwood, R. & Robertson, G. 1997. The foraging ecology of female Emperor Penguins in winter. *Ecological Monographs* 67(2): 155-176.
- Kooyman, G.L. & Kooyman, T.G. 1995. Diving behavior of Emperor Penguins nurturing chicks at Coulman Island, Antarctica. *Condor* 97: 536-549.
- Lack, D. 1947. The significance of clutch size. *Ibis* 89: 302-352.
- Lack, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, Oxford.
- Lack, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
- Lamey, T.C. 1990. Hatch asynchrony and brood reduction in penguins. Pp. 399-416 In: Davis, L. S. and Darby, J. T. (eds). *Penguin Biology*. Academic Press, San Diego.
- Lamey, T.C. 1993. Territorial aggression, timing of egg loss, and egg-size differences in Rockhopper Penguins, *Eudyptes chrysocome chrysocome*, on New Island, Falkland Islands. *Oikos* 66: 293-297.
- Le Maho, Y. 1977. The Emperor Penguin: a strategy to live and breed in the cold. *American Scientist* 65: 680-693.
- Le Maho, Y., Delelitte, P. & Chatonnet, J. 1976. Thermoregulation in fasting Emperor Penguins under natural conditions. *American Journal of Physiology* 231: 913-922.
- Magrath, R. D. 1990. Hatching asynchrony in altricial birds. *Biological Review* 65: 587-622.
- Mauget, R., Jouventin, P., Lacroix A & Ishii, S. 1994. Plasma LH and steroid hormones in King Penguin during the onset of the breeding cycle. *General and Comparative Endocrinology* 93: 36-43.
- Mickelson, M.J., Dann, P. & Cullen, J.M. 1992. Sea temperature in Bass Strait and breeding success of the Little penguin *Eudyptula minor* at Phillip Island, south-eastern Australia. *Emu* 91: 355-368.
- Mock, D.W. & Lamey, T.C. 1991. The role of brood size in regulating egret sibling aggression. *American Naturalist* 138: 1015-1026.
- Moreno, J., Carrascal, L.M., Sanz, J.J., Amat, J. A. & Cuervo, J.J. 1994. Hatching asynchrony, sibling hierarchies and brood reduction in the Chinstrap Penguin. *Polar Biology* 14: 21-30.
- Moreno, J., Carrascal, L.M. & Sanz, J.J. 1996. Parent-offspring interactions and feeding chases in the Chinstrap Penguin. *Bird Behavior* 11: 31-34.
- Moreno, J., Vinuela, J., Belliure, J. & Ferrer, M. 1998. Brood-size dependent growth in the Chinstrap Penguin: a field experiment. *Journal of Field Ornithology* 69: 269-275.
- Newton, I. 1979. *Population ecology of raptors*. T & AD Poyser, Berkhamsted, U.K. 399 pp.



- O'Connor, R.J. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? *Animal Behaviour* 26: 79-96.
- Pettingill, O.S. Jr. 1964. Penguins ashore at the Falkland Islands. *Living Bird* 3: 45-64.
- Ploger, B.J. 1997. Does brood reduction provide nestling survivors with a food bonus? *Animal Behaviour*. 54: 1063-1076.
- Prevost, J. 1961. *Ecologie du manchot empereur*. Hermann, Paris.
- Putz, K. & Bost, C.A. 1994. Feeding behaviour of free-ranging King Penguins. *Ecology* 75(2): 489-497.
- Reilly, P.N. & Balmford, P. 1975. A breeding study of the Little Penguin, *Eudyptula minor*, in Australia. Pp. 161-187. In: Stonehouse, B. (ed.). *The Biology of Penguins*. Macmillan, London.
- Richdale, L.E. 1941. The Erect-crested Penguin (*Eudyptes sclateri*). *Emu* 41: 25-53.
- Richdale, L.E. 1957. *A population study of penguins*. Oxford University Press, Oxford.
- Ricklefs, R.E. 1965. Brood reduction in the Curve-billed Thrasher. *Condor* 67: 505-510.
- Ridoux, V., Jouventin, P., Sahl, J-C. & Weimerskirch, H. 1988. Ecologie alimentaire comparee des manchots nicheurs aux Iles Crozet. *Revue Ecologie* 43: 345-355.
- Robertson, G. 1990. Huddles. *Australian Geographic* 20: 74-97.
- Robertson, G.G. 1995. The foraging ecology of Emperor Penguins (*Aptenodytes forsteri*) at two Mawson Coast colonies, Antarctica. A.N.A.R.E. Reports No. 138, 139 pp.
- Seddon, P.J. 1989. Patterns of nest relief during incubation and incubation period variability in the Yellow-eyed Penguin (*Megadyptes antipodes*). *New Zealand Journal of Zoology* 16: 393-400.
- Seddon, P.J. 1990. Behaviour of the Yellow-eyed Penguin chick. *Journal of Zoology*, London 220: 332-343.
- Seddon, P.J. & van Heezik, Y. 1991.a. Hatching asynchrony and brood reduction in the Jackass Penguin: an experimental study. *Animal Behaviour* 42: 347-356.
- Seddon, P.J. & van Heezik, Y. 1991.b. Effects of hatching order, sibling asymmetries, and nest site on survival analysis of Jackass Penguin chicks. *Auk* 108: 548-555.
- Simmons, R.E. 1988. Offspring quality and the evolution of cannibalism. *Ibis* 130: 339-357.
- Simmons, R.E. 1989. The Cain and Abel riddle in eagles and other birds. *African Wildlife* 43: 35-43.
- Simmons, R.E. 1997. Why don't all siblicidal eagles lay insurance eggs? The egg quality hypothesis. *Behavioural Ecology* 8: 544-550.
- Sladen, W.J.L. 1958. The *Pygoscelis* penguins. 1. Methods of study. 2. The Adelie penguin. *Falkland Islands Dependency Survey Science Report* 17: 1-97.
- Slagsvold, J., Amundsen, T. & Dale S. 1995. Costs and benefits of hatching asynchrony in Blue Tits *Parus caeruleus*. *Journal of Animal Ecology* 64: 563-578.
- St. Clair, C.C. 1992. Incubation behaviour, brood patch formation and obligate brood reduction in Fiordland crested penguins. *Behavioural Ecology and Sociobiology* 31: 409-416.
- St Clair, C.C. 1996. Multiple mechanisms of reversed hatching asynchrony in Rockhopper Penguins. *Journal of Animal Ecology* 65: 485-494.
- St. Clair, C.C., Waas, J.R., St. Clair, R.C. & Boag, P.T. 1995. Unfit mothers? Maternal infanticide in royal penguins. *Animal Behaviour* 50: 1177-1185.
- St Clair, C.C. & St. Clair, R. C. 1996. Causes and consequences of egg loss in Rockhopper Penguins. *Oikos* 77.
- St. Clair, C.C. in press. What is the function of the first eggs in Crested Penguins? *Auk*.
- Stahel, C. & Gales, R. 1987. *Little Penguin. Fairy penguins in Australia*, University of New South Wales Press.



- Stonehouse, B. 1960. The King Penguin *Aptenodytes patagonicus* of South Georgia. I. Breeding behaviour and development. Falkland Islands Dependencies Survey Scientific Report 6: 1-33.
- Thompson, D.H. 1981. Feeding chases in the Adelie Penguin. *Antarctic Research Series* 30: 105-122.
- Thompson, D.H. & Emlen, J.T. 1968. Parent-chick individual recognition in the Adelie Penguin. *Antarctic Journal of the United States* 3: 132.
- van Heezik, Y. 1990. Patterns and variability of growth in the Yellow-eyed Penguin. *Condor* 92: 904-912.
- van Heezik, Y. & Davis, L. 1990. Effects of food availability on growth rates, fledging sizes and reproductive success in the Yellow-eyed Penguin *Megadyptes antipodes*. *Ibis* 132: 354-365.
- van Heezik, Y. & Seddon, P.J. 1991. Influence of hatching order and brood size on growth in Jackass Penguins. *South African Journal of Zoology* 26(4): 199-203.
- van Heezik, Y., Seddon, P.J., du Plessis, C.J. & Adams, N.J. 1993. Differential growth of King Penguin chicks in relation to date of hatching. *Colonial Waterbirds* 16:71-76.
- van Heezik, Y., Seddon, P.J., Cooper, J. & Plos, A. 1994. Interrelationships between breeding frequency, timing and outcome in King Penguins *Aptenodytes patagonicus*: are King Penguins biennial breeders? *Ibis* 136: 279-284.
- van Heezik, Y. & Seddon, P.J. 1996. Scramble feeding in Jackass Penguins: within-brood food distribution and the maintenance of sibling asymmetries. *Animal Behaviour* 51: 1383-1390.
- van Heezik, Y. & Seddon, P.J. 1997. Penguins under the sun. *Natural History* 106: 30-35.
- Warham, J. 1974a. The Fiordland Crested Penguin *Eudyptes pachyrhynchus*. *Ibis* 116: 1-27.
- Warham, J. 1974b. The breeding biology and behaviour of the Snares Crested Penguin. *Journal of the Royal Society of New Zealand*, 4: 63-108.
- Warham, J. 1975. The Crested Penguins. Pp. 189-269. In: Stonehouse, B. (ed.). *The Biology of Penguins*. Macmillan, London.
- Weimerskirch, H., Stahl, J.C. & Jouventin, P. 1992. The breeding biology and population dynamics of King Penguins on the Crozet Islands. *Ibis* 134: 107-117.
- Williams, A.J. 1980. The breeding biology of *Eudyptes* penguins with particular reference to egg-size dimorphism. PhD. Thesis, University of Cape Town, South Africa.
- Williams, A.J. & Cooper, J. 1984. Aspects of the breeding biology of the jackass penguin, *Spheniscus demersus*. Pp. 841-853. *Proceedings of the Fifth Pan-African Ornithological Conference*.
- Williams, T.D. 1989. Aggression, incubation behaviour and egg loss in Macaroni Penguins, *Eudyptes chrysolophus*, at South Georgia. *Oikos* 55: 19-22.
- Williams, T.D. 1990. Growth and survival in Macaroni Penguin, *Eudyptes chrysolophus*, A- and B-chicks: do females maximise investment in the large B-egg? *Oikos* 59: 349-354.
- Williams, T.D. 1995. *The Penguins*. Oxford University Press, Oxford.
- Williams, T.D. & Croxall, J.P. 1991. Chick growth and survival in Gentoo Penguins (*Pygoscelis papua*): effect of hatching asynchrony and variation in food supply. *Polar Biology* 11: 197-202.



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