Reviews

MARINE MAMMALS: ADVANCES IN BEHAVIOURAL AND POPULATION BIOLOGY. I.L. Boyd (Editor). 1993. Oxford: Clarendon Press for the Zoological Society of London. xix + 404 pp, illustrated, hard cover. ISBN 0-19-854069-8. £55.00.

Ian Boyd's edited volume was compiled from a symposium held at the Zoological Society of London in April 1992. The papers are divided into three sections: genetic identity of stocks and influences on gene flow; foraging ecology of marine mammals; and physiology and bioenergetics. The majority of chapters concern pinnipeds rather than cetaceans, since it has generally been easier to apply recent technological advances to seals than to whales and dolphins. This will present an exciting challenge for future research, as these state-of-the-art techniques and processes are developed to apply to cetaceans.

The genetics section includes seven papers on a variety of topics ranging from the social organisation of humpback whales in the North Atlantic to DNA fingerprinting in pilot whales, northern elephant seals, and harbour seals. The methodology used is carefully described in papers by A.R. Hoelzel and Bill Amos, while the benefits of the practical applications of the techniques are discussed in contributions by D.J. Boness and others (mating systems and reproduction strategies of pinnipeds), Fritz Trillmich (pinniped social structure and population dynamics), and N.J. Lunn and Boyd (reproduction in the Antarctic fur seal). The methodologies outlined in this section include some of the most recently developed methods in the rapidly expanding field of genetics, and the immense potential for future research in these areas is very apparent.

The second section, foraging ecology of marine mammals, contains eight papers on subjects as diverse as the use of satellite telemetry to record the movements and behaviour of belugas in the high Arctic, and recent developments in the dietary analysis of marine mammals. Papers by J. Le Boeuf and others, and P.S. Hammond and others, describe in detail information recently gathered on the movements at sea of northern elephant seals and grey seals, respectively. Le Boeuf and others analyse data generated from microcomputer time–depth recorders attached to free-ranging northern elephant seals, and relate them to differences in feeding strategies between the sexes. Although it is widely acknowledged that the extreme sexual dimorphism in elephant seals may result in a dissimilarity in diet, this had not yet been tested in relation to differences in dive patterns between males and females. Three principal dive types and variants were identified by Le Boeuf and his associates, which were then related to prey species likely to be found at these specific depths and locations. One observation of particular importance was that differences in the type of dives between sexes began to occur when the seals were as young as 18 months old, suggesting that 'a different foraging strategy of males is important for attaining as well as maintaining large size' (page 149).

In a chapter entitled 'Recent advances in diet analysis of marine mammals,' G.J. Pierce and others describe an alternative, or perhaps complementary, method for the identification of piscivorous hard tissues in scat and stomach contents by analysis of fish muscle proteins using isoelectric focusing or liquid chromatography. Some proteins survive fairly long periods before the mammalian digestive process destroys them. Pierce and his associates raised antisera to salmon proteins, and found that they could be used effectively to recognise salmonid fish residues; antisera for gadids were less successful. It is noted that the main disadvantages with using this method are that it is expensive and time-consuming to produce antisera; that separate antisera are necessary for each species that the researcher requires to identify; and that the proteins can be difficult to identify due to degradation during digestion, or because the species-specific banding patterns are almost impossible to identify when an animal has been feeding on several species simultaneously. This needs to be weighed against the disadvantages of traditional hard tissue identification from scats and stomach contents — namely, that not all prey species have otoliths that appear in the samples, and that degradation of at least some hard tissues occurs during the digestive process (for example, in the case of seals eating salmon, the otolith recovery rate in faecal samples may be as low as 2%, even in optimum conditions). Despite its problems, there is considerable potential for this technique to be developed, for example, using proteins present in the durable eye lenses of fish, which frequently survive the digestive process.

Daniel P. Costa's paper on reproductive and foraging energetics explores the way in which otariids and phocids have evolved solutions to trade-offs between maternal investment in their young and the need to maximise energy acquisition at sea. Phocids, with relatively short weaning periods, tend to store the energy necessary for lactation so that the need to feed is less immediate; otariids, with a much longer lactation period, need to feed. These strategies have necessitated the evolution of differences in metabolic rate, energy and oxygen storage capacity, and body size. These factors affect the ability to make long dives, lactation duration, fasting ability, the degree of maternal investment, and 'prey energy acquisition.' It is suggested that the otariid pattern is probably more closely related to its terrestrial ancestry.

The final section contains five papers on physiology and bioenergetics. Topics covered are the extent to which

heart rate can be used as an indicator of metabolic rate in marine mammals, behavioural and physiological options in diving seals, the behavioural implications of diving physiology, plasma and tissue lipids of the harbour seal, and the aerobic costs of diving and swimming in bottlenose dolphins.

This book is an excellent compilation of some of the most recent developments in behavioural and physiological research in marine mammals by some of the world's foremost authorities. It has a good balance of general information and original data, all presented in a comprehensive manner, and it is a book for the serious researcher rather than the general reader. It will be of interest to researchers in most fields of marine mammal studies and is highly recommended as a valuable addition to any library or collection. (E. Cruwys, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ.)

SKUA AND PENGUIN: PREDATOR AND PREY. Euan Young. 1994. Cambridge: Cambridge University Press. xvi + 452 pp, illustrated, hard cover. ISBN 0-521-32251-0. £65.00/US$99.95.

From the earliest days of Antarctic exploration, the skua achieved notoriety as a cruel and relentless predator of penguins, and this reputation has remained to the present. I am particularly fond of the cult film *Mr Forbush and the penguins*, which gives a recent expression of this view. In the film, a socially privileged Cambridge graduate goes off to study penguin–skua interactions living alone in a hut on Antarctica. He develops too strong bonds with his 'brave little penguins' and becomes increasingly unhinged at the activities of the murdering skuas, eventually building a medieval seige cannon to try to drive the skuas away (without success). However, this stereotyped image of skuas is misleading. Euan Young discovered in the 1960s that many skuas (*Catharacta maccormicki*: South Polar, Antarctic, or McCormick's skua) nesting near penguin rookeries (*Pygoscelis adeliae*: Adélie penguin) feed predominantly on the Antarctic silverfish *Pleuragramma antarcticum*, which they catch at sea. Only a few specialists kill penguin chicks, and even they feed extensively on fish much of the time.

This book provides a detailed account of that research, including quantitative analyses of the numbers and biomass of penguins available to skuas, the behaviour of penguins and skuas, skua diets and feeding, and the impact of penguins. These data are then used to model the energetics of skua foraging and food gain at sea and at the penguin colony, making use of recent developments providing information on BMR of skuas and energy costs of flight. The entire text is illustrated by sketches, graphs, and superb black-and-white photographs, including many remarkable shots of skua–penguin interactions.

Although the title may suggest that this book is a study in co-evolution, the author does not use that as a central theme. Rather he points out that the nesting association of the two species may be largely due to their need for a particular habitat in short supply. Nevertheless, the colonial nesting of the penguin is clearly an adaptation reducing their vulnerability to skua attacks. Not only are central penguins less at risk than peripheral ones, but the highly territorial behaviour of breeding skuas leads to penguins nesting within a skua territory being protected from attack by other skuas. One could view this as a skua 'protection racket,' except that while some specialise on penguins, many skuas 'protecting' groups of penguins feed entirely at sea. The skua territory is clearly defended as a space for breeding and chick-rearing and not predominantly as a defended source of food. Using exclosures to stop skua access to areas of penguin colonies, Young found that the impact of skuas on penguin breeding success was generally trivial. Many penguin eggs eaten by skuas were scavenged. Indeed, penguins had a greater impact on the hatching success of skuas by trampling their eggs (by accident), perhaps further evidence that skuas only nest beside penguins because of a shortage of nesting habitat.

So why do so few skuas feed predominantly on the abundant penguins? Apparently skuas are not strong enough or well enough equipped with predatory weapons to kill adult penguins without risking serious injury to themselves. Attacking penguin chicks carries a real risk of injury to the skuas, from large penguin chicks or from the defence put up by adults. Even stealing penguin eggs is risky. Only a few skuas become skilled at these hazardous feeding techniques and many wimps opt for the easier life of catching fish at sea. This can lead to the apparently bizarre situation of skuas being unable to provision their chicks because they cannot get enough food, especially when ice at sea means long foraging flights. Most skuas lay two eggs, but the second hatched chick normally dies because there is not enough food for two. The loss of the second chick occurs as a result of sibling aggression, the older and stronger chick dominating and killing its sibling. The inability of skuas to rear two chicks despite the abundance of penguins in many territories is most easily explained by the weak link between predator and prey. This is further emphasised by the timing of breeding of the species. The skua breeding season is later than that of the penguin, leaving the skuas to feed their growing chick at a time when virtually no food remains available for skuas in the penguin colony. Feeding at sea then becomes essential rather than an option.

These arguments are put forward carefully by Young, with a most interesting estimation of the energy gains for birds feeding at the penguin colony or at sea. The evolutionary question remains unanswered. Do birds that feed on penguins do better or worse than those that feed only at sea? Apparently the two strategies lead to similar breeding success, but it would require some years of study of survival rates to determine whether birds that specialise on penguins are the 'best' birds or whether these individuals pay a cost in a higher mortality rate as a result of accumulated injuries. While reading this book I recognised many parallel features of skua–seabird interactions in the North Atlantic, and I suspect that similar generalisations apply to