FOOD CONSUMPTION BY PREDATORS IN A CCAMLR INTEGRATED STUDY REGION

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Abstract

A detailed description of the structure and mode of operation of a model for estimating food consumption of seabird predators is provided. This model is a development of earlier ones used in the South Georgia Integrated Study Region and incorporates new features, allowing for seasonal variation in predator weight (and hence energy requirements), diet composition and prey energy content. Specimen outputs are provided, illustrating the changes produced by using these new sub-models. Results of initial sensitivity analyses indicate particular sensitivity to estimation of metabolic energy requirements. The system is directly applicable also to fur seals and could be modified to incorporate phocid seal data, when available. Prey categories are readily modifiable to sub-divide krill into sexes and maturity stages. With existing empirical data on breeding population size, diet, activity-specific energy requirements and foraging ranges, it is possible to make realistic estimates of krill consumption of penguins and fur seals during their breeding seasons within specified areas.

Résumé

Sont décrits en détail la structure et le mode de fonctionnement d'un modèle destiné à évaluer la consommation de nourriture des oiseaux de mer prédateurs. Ce modèle a été élaboré sur des modèles antérieurs utilisés dans la zone d'étude intégrée de la Géorgie du Sud; de nouvelles caractéristiques qui tiennent compte de la variation saisonnière du poids des prédateurs (et donc des besoins en énergie), de la composition du régime alimentaire et de la teneur en énergie des proies, s'y trouvent incorporées. Les résultats fournis de l'étude des spécimens illustrent les changements produits par l'utilisation de ces nouveaux sous-modèles. Les résultats des premières analyses de sensibilité indiquent une sensibilité particulière à l'estimation des besoins en énergie métabolique. Ce système peut également être appliqué directement aux otaries et pourrait être modifié pour incorporer des données sur les phoques de la famille des Phocidae, lorsque cellesci sont disponibles. Les catégories de proies peuvent être modifiées à tout moment pour subdiviser le krill par sexe et stades de maturité. A partir des données empiriques sur la taille de la population reproductrice, le régime alimentaire, les besoins en énergie selon les activités et les secteurs d'alimentation, il est possible de faire des estimations réalistes de la consommation de krill par les manchots et les otaries au cours de leur saison de reproduction dans des régions précises.

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Резюме

В настоящей работе приводится подробное описание структуры и принципа работы модели оценки потребления пиши хищными морскими птицами. Данная модель является усовершенствованным вариантом моделей, Района применявшихся для комплексных ранее исследований на Южной Георгии, и включает новые учитывать характеристики. позволяющие сезонную изменчивость веса особей хищников (и следовательно потребностей), энергетических состав рациона И калорийность потребляемых видов. Приводятся данные по отдельным особям, иллюстрирующие изменения, вызванные использованием этих новых подмоделей. Результаты исходного анализа чувствительности свидетельствуют об особенной чувствительности модели K оценке энергетических потребностей, необходимых для метаболизма. Данная система непосредственно применима и для исследования морских котиков, а также может быть модифицирована с целью включения данных по настоящим тюленям по поступлении таких данных. Категории легко изменимы параметров потребляемых видов и позволяют классифицировать криль по половой принадлежности и стадиям половозрелости. На основании имеющихся эмпирических данных по размеру размножаэнергетическим ющейся части популяции, рациону, потребностям при различных типах активности И нагульным ареалам можно достоверно оценить потребление криля пингвинами и морскими котиками в течение периодов размножения в пределах отдельных районов.

Resumen

Se proporciona una descripción detallada de la estructura y modo de operación de un modelo diseñado para estimar el consumo de alimento de las aves depredadoras. Este modelo es una modificación de los previos modelos empleados en la Región de Estudio Integrado de Georgia del Sur e incorpora nuevas características, teniendo en cuenta la variación estacional en el peso del depredador (y por lo tanto el consumo de energía), la composición de la dieta y el contenido de energía de la especie presa. Se indican los resultados en los especímenes, que ilustran los cambios que se producen al emplear estos nuevos submodelos. Los resultados de los análisis iniciales de sensibilidad muestran una sensibilidad especial en la estimación de los requisitos de energía metabólicos. El sistema se puede aplicar directamente a los lobos finos antárticos y podría modificarse para incluir información sobre focas de la familia phocidae, cuando estuviese disponible. Las categorías de especies presa se pueden modificar facilmente para subdividir el krill por sexo y etapas de madurez. La información empírica actual sobre el tamaño de la población reproductora, dieta, el consumo de energía relacionado con actividades específicas y los rangos de alimentación, permite hacer estimaciones razonables sobre el consumo de krill de los pingüinos y los lobos finos antárticos durante sus temporadas de reproducción dentro de las áreas designadas.

1. INTRODUCTION

At SC-CAMLR-VIII requests by the Working Group for the CCAMLR Ecosystem Monitoring Program (WG-CEMP) for Members to synthesize data on predator population size, diet and energy budgets in order to provide estimates of krill requirements of predators in Integrated Study Regions, at least during their breeding seasons, were endorsed by the Scientific Committee (SC-CAMLR-VIII, paragraph 5.26).

The difficulties of doing these, however, were also recognized and discussion with Members and other appropriate specialists on how best to proceed towards this goal was advised (SC-CAMLR-VIII, paragraph 5.28).

This paper summarizes current progress towards these goals, in respect of the South Georgia Integrated Study Region, by the United Kingdom. This is a development of earlier work (Croxall *et al.*, 1984; Croxall and Prince, 1987), already made available to CCAMLR (SC-CAMLR-VIII/BG/12, SC-CAMLR-VIII/BG/15).

2. CONTENTS

The present paper comprises:

Part 1:

A description of the content, mode of operation and data input format of the current version of the system for estimating food consumption of breeding populations of South Georgia seabirds.

Part 2:

- (a) Some selected outputs obtained from using this system, chiefly featuring results of incorporating new sub-models allowing for seasonal variation in predator weight, diet composition and prey energy content.
- (b) Results of some initial sensitivity analyses.
- (c) Comments on the potential applicability of the system to other predators.
- (d) Comments on the potential application of the system to more detailed analyses of particular prey, e.g. krill.

PART 1: A COMPUTER PROGRAM FOR THE ASSESSMENT OF THE IMPACT OF SEABIRDS ON MARINE RESOURCES AROUND SOUTH GEORGIA

GUIDE TO THE SYSTEM

1. INTRODUCTION

The original version of this program was developed in 1982 and 1983 by Dr C. Ricketts at British Antarctic Survey (BAS), in conjunction with Dr J.P. Croxall and Mr P.A. Prince. The program was written in FORTRAN IV and implemented on the IBM 360 at Cambridge University. The program formed the basis of two papers, one referring solely to seabirds at South Georgia (Croxall *et al.*, 1984) and the other extending to seabirds and seals in the Scotia Sea (Croxall *et al.*, 1985). Unfortunately, the working version of the program was lost when BAS moved its computing away from Cambridge University. The lost program will be referred to as Version 1.0.

In 1990 there was a renewed interest in assessing the impact of seabirds on marine resources around South Georgia, partly driven by the needs of CCAMLR and partly by the Government of South Georgia and the South Sandwich Islands (GSGSSI) to develop a management and licensing strategy for finfish and krill in the South Georgia area. Version 1.0 of the program was restored to the BAS VAX computer and the PRIME computer at Polytechnic South West (PSW) from old printouts of the program source held by Dr C. Ricketts. During this process the program was updated to FORTRAN-77 and modified to include myctophids as a separate prey item and to allow the inclusion of non-breeding components of the population. The graphics output using the Cambridge University CAMPLOT routines were not implemented on the PRIME at PSW: this version of the program is referred to as Version 2.0. The graphics capability was transformed from the Cambridge University CAMPLOT system to the NERC GRAFIX system on the BAS VAX computer by Dr A.G. Wood. This version will be referred to as Version 2.10.

Subsequent developments have included:

- Version 3.10: The program can allow for seasonal variation in the calorific value of all prey items.
- Version 3.20 The program can allow for seasonal variation in the composition of the diet of predators.
- Version 3.30 The program can allow for seasonal variation in the body weight of predators; this is the current version.

The program will be enhanced by Dr A.G. Wood to use FORTRAN graphics from UNIRAS, probably late in 1990. This will be Version 3.40.

2. DATA PREPARATION

For all data input to the program the time-base used 1 September as day number 1.

The data preparation format for the predator data is given in Appendix 1. Note that provided that the relevant data can be manipulated into the correct form, the use of the program is not restricted to seabirds alone, but may include other predators such as seals.

The data which gives the seasonal variation in calorific value of the prey items must be held in separate files for each prey type as they are common to all predator species. The file names are prescribed and must be:

EUPHAUSI . CAL CEPHALOP . CAL MYCTOPHI . CAL OTHRFISH . CAL COPEPODS . CAL AMPHIPOD . CAL OTHRCUS . CAL ODDSNSOD . CAL

Any of these files may be included as necessary; if any file does not exist then the calorific value of that prey item will be assumed constant. Within each file the data is a series of day numbers and calorific values. Only one day and calorific value may be on any line, and its is sufficient to separate the calorific value from the day number by a space. The first day number must be 1 and the last must be 365; there must be at least three lines of data. The calorific value on each day will be calculated within the program by linear interpolation. An example is given in Appendix 2.

Note that although the names within the program refer to Euphausiids, Cephalopods, etc., the use of the program is not restricted to these prey items. The eight prey items could, for example, be different maturity stages of krill: the calculations would then be appropriate to these stages of krill - only the names would be wrong! Changing the headings for output is a fairly trivial task.

3. USING THE PROGRAM

The program is presently held on the VAX computer at BAS. Potential users should contact Dr A.G. Wood who will advise them on the correct way of starting the program.

The program asks the user for two file names, some dates (again day 1 is 1 September) and the type of graphical output required. Note that the data files may be held in any directory provided that the user gives the complete file name.

4. OUTPUT FROM THE PROGRAM

The program produces both printed output and graphs of the pattern of resource utilization in either space or time.

The printed output comprises a list of all prey consumed by each component (male, female, non-breeder) of each predator species together with a grand total for the whole community of predators. The output also includes the daily impact of the community on each prey category between the dates specified by the user (again day 1 is 1 September). Between these dates the program also produces a weekly distribution of foraging impact in relation to distance offshore for those birds rearing chicks.

The graphical output provides either the distribution of the predation on each day throughout the year, or distribution of the impact of predators rearing chicks by distance offshore, or both. Examples are given in Appendix 3.

5. METHODS OF CALCULATION

The methods of calculation used in Version 1.0 were described in Croxall *et al.* (1985). For the sake of completeness (and to correct a few typographical errors!) the details are repeated here, together with details of the enhancements made to the program.

To estimate the food consumption of a seabird community throughout the year requires knowledge of the population size, dietary composition and energy requirement on each day of the year for each species in the community. Because the sizes, activity patterns and hence energy requirements of males, females and non-breeders may differ, the food consumption of each component needs to be assessed separately. Moreover, although most species complete one breeding cycle in one year, wandering, grey-headed and light-mantled sooty albatrosses breed biennially (when successful in rearing a chick) and have cycles lasting two years. The king penguin typically has two breeding attempts in three years at South Georgia. Thus the estimation procedure is based on an activity cycle which can be one, two or three years long within which there may be two breeding attempts. Here we illustrate the estimation process for a species which breeds annually; the extension to more complicated activity cycles is straightforward.

5.1 Population Size

On each day throughout the year the breeding population is divided into active breeders and failed breeders. The total breeding population P is divided in P_1 (i) active breeders and P_2 (i) failed breeders on day i. The number of active breeders is calculated from the rate of egg loss between the laying date (day 1) and the hatching data (day h) and the rate of chick loss between hatching and fledging date (day f). Both egg loss and chick loss are assumed to be exponential at rates k_1 and k_2 respectively. Thus the populations on day i are given by:

| $P_1(i) = P$ | 1≤ i≤1 |
|--------------------------------------|---|
| $P_1(i) = P_1(l) \exp(-k(i-1))$ | 1 <i≤h< td=""></i≤h<> |
| P_1 (i) = P_1 (h) exp (-k (i-h)) | h <i≤f< td=""></i≤f<> |
| $P_1(i) = P$ | f <i≤365< td=""></i≤365<> |
| $P_2(i) = P - P_1(i)$ | 1≤i≤365 |
| | $P_{1}(i) = P$ $P_{1}(i) = P_{1}(l) \exp(-k(i-1))$ $P_{1}(i) = P_{1}(h) \exp(-k(i-h))$ $P_{1}(i) = P$ $P_{2}(i) = P-P_{1}(i)$ |

5.2 Dietary Composition and Energy Content

Here we specify the dietary composition of each species as the proportion by weight of each of eight different food types. These are krill, copepod, amphipod, other crustaceans, myctophid, other fish, squid and "other". Only free-living marine prey are considered; the carrion element, which is only important in the diets of giant petrels, is ignored.

We denote the proportion of the diet of food type \mathbf{k} on day \mathbf{i} by $\mathbf{d}(\mathbf{i},\mathbf{k})$. Dietary composition is assumed to change in a step-wise manner according to the data input. The dietary composition is also assumed to vary over a one-year period, irrespective of the number of years in the predator's activity cycle: diet is more likely to be determined by seasonal changes in prey availability than activity-dependent prey selection by the predator.

Default values for the energetic content of prey ($kJ g^{-1}$) are specified as constants in the program: krill and all other crustaceans, 4.35; myctophids, 10.0; fish, 3.97; and, squid, 3.47. Otherwise the seasonal pattern of energy content is interpolated from the values given in the appropriate calorific value file (see Part 2 and Appendix 2). The energy content of each food

type is assumed to be the same for each predator species. We denote the energy content of food type \mathbf{k} on day \mathbf{i} by $\mathbf{c}(\mathbf{i},\mathbf{k})$. The mean energy content of the diet on day \mathbf{i} is then

$$\Gamma_{i} = \sum_{k=1}^{8} c(i,k)d(i,k) \quad kJ g^{-1}$$

5.3 Activity Patterns

For simplicity, we assume that all members of each component of a species are performing the same activity on any one day and that they do it for the same (mean) length of time, while allowing for differences in activity between active breeders, failed breeders and non-breeders. Thus, changes from one activity to another are treated in a step-wise manner according to the data input. We have arbitrarily divided a bird's activity pattern into seven categories: absent from the population, attending at the nest site, incubating, brooding, feeding chick, foraging for self and moulting (penguins only). Failed breeders are assumed to forage for themselves only. Non-breeders may not incubate, brood nor feed chicks.

5.4 Energetic Costs

The energetic cost of each activity may be specified either as an equation of the form

$$\mathbf{E} = \mathbf{a}\mathbf{W}_{i}^{\mathsf{b}}$$

where W_i is the body weight on day i, or as a constant. The source of equation or constant is left to the user and may vary between species.

The energetic cost of foraging for a chick is calculated as the sum of the cost of foraging for self plus the energy content of the food delivered to the chick. Thus if g(c) is the daily energetic cost of feeding a chick, g(s) is the cost of foraging for self and M (grams) of food is delivered to the nest at frequency Φ (deliveries per adult per day) then

$$g(c) = g(s) + M\Gamma_i \Phi kJ d^{-1}$$

where Γ_i is the energetic content of the meal on day i.

5.5 Food Requirements

If the energy cost of the j-th activity is denoted by g(j), the total food required to fulfil activity j on day i is

$$F(j) = g(j)/\Gamma_i g d^{-1}$$

The total food requirements of the population performing activity **j** on day **i** is then

$$C(i) = P_1(i)F(j) + P_2(i)F(s) \text{ grams}$$

where F(s) is food required when foraging for self. The amount of food of type k required on day i is C(i)d(k).

The food required between days t_1 and t_2 is simply

$$\sum_{i=t_1}^{t_2} C(i), \text{ or, for food type } k \qquad \sum_{i=t_1}^{t_2} C(i)d(k).$$

5.6 Foraging Range

The potential mean maximum (i.e., greatest distance using mean values of parameters) foraging range of a species during the chick rearing period is calculated from the travel speed (corrected for indirect (zigzag) flight pattern), the time between feeds and proportion of that time spent on activities other than travelling (e.g., feeding or resting). If the travel speed is $\mathbf{v} \ \mathbf{m} \ \mathbf{s}^{-1}$ and proportion of the trip spent not travelling is τ then the maximum range is $86.4 \ v(1-\tau)/2\Phi$ where again Φ is the feeding frequency: the factor 86.4 converts travel speed from $\mathbf{m} \ \mathbf{s}^{-1}$ to $\mathbf{km} \ \mathbf{d}^{-1}$ and the factor 2 corrects for outward and return journeys. If \mathbf{z} is the correction factor for indirect flight, that is the distance flown to achieve a unit distance forward, then the corrected foraging range is

$$R = 86.4 v (1-\tau)/2z\Phi$$
 km.

5.7 Distribution of Foraging Effort and of Food Taken

For birds rearing chicks, the data on mean flight speeds, flight pattern and the time spent travelling between deliveries of food to the nest define a mean maximum foraging range.

We then classify each species as feeding primarily inshore, primarily offshore, or neither (and potentially intermediate). We assume that these intermediate species forage uniformly out to maximum range (R). For such species the proportion of foraging effort expended between r_1 and r_2 km offshore is then

| $f(r_1, r_2) = (r_2 - r_1)/R$ | $0 \le r_1 < r_2 \le R$ |
|-------------------------------|-------------------------|
| $f(r_1, r_2) = 0$ | $R \leq r_1 < r_2$ |

For species which forage primarily inshore we assume that the foraging effort at the inshore end of the range is 10 times that for uniform foragers and declines exponentially over the range so that the total foraging effort remains unity. The foraging effort between distances r_1 and r_2 offshore is then

| $f(r_1, r_2)$ | $= \int \mathbf{r}_2$ | |
|------------------------------------|-------------------------------------|-----------------------|
| | $(10/R) \exp(-10r/R) dr$ | |
| | J _{r1} | |
| | $= \exp(-10r_1/R) - \exp(-10r_2/R)$ | $0 \le r_1 < r_2 < R$ |
| f(r ₁ ,r ₂) | $= \exp(-10r_1/R)$ | $0 \le r_1 < r = R$ |
| $f(r_1,r_2)$ | = 0 | $R \leq r_1 < r_2$ |

This is based on the premise that inshore feeders attempt to satisfy their requirements as close to the breeding site as possible, only foraging further afield when unable to do so.

Species which forage primarily offshore are treated as the mirror image, over their range, of inshore feeders. We assume that offshore species usually travel to feeding grounds at or near their mean maximum range and only if they then fail to find food in this area do they forage closer to home.

Within the chick rearing period, that is from day **h** to day **f**, the amount of food taken on day **i** in the range \mathbf{r}_1 to \mathbf{r}_2 km offshore is

$$D(i,r_1,r_2) = C(i)f(r_1,r_2)$$

5.8 Community Food Requirements and Distribution

The food requirements of the multi-species seabird community on day i are calculated by summing the values of C(i) over all species. Similarly, the amount of food of type k taken on day i is the sum of the values of C(i)d(k) over all species. The distribution of the food taken by birds feeding chicks on day i, between r_1 and r_2 km offshore is the sum of the $D(i,r_1,r_2)$ over all species rearing chicks on that day.

REFERENCES

- CROXALL, J.P., P.A. PRINCE and C. RICKETTS. 1984. Impact of seabirds on marine resources, especially krill, of South Georgia waters. In: WHITTOW, G.C., and H. RAHN (Eds). Seabird Energetics. New York: Plenum. pp. 285-317.
- CROXALL, J.P., P.A. PRINCE and C. RICKETTS. 1985. Relationships between prey life cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea. In: SIEGFRIED, W.R., P.R. CONDY and R.M. LAWS (Eds). Antarctic Nutrient Cycles and Food Webs. Berlin and Heidelberg: Springer-Verlag. pp. 137-146.

SOUTH GEORGIA SEABIRD IMPACT ASSESSMENT DATA INPUT FORMAT

Each species is divided into two sexes whose data are entered separately to allow for sex differences in activity, diet and energy costs. Non-breeding populations can also be included. The various data types are entered on several different types of lines and allowance is made for future expansion. Although the output pertains only to one twelve-month period (starting 1 September) each species may have an activity cycle lasting up to three years, containing up to two breeding periods. Each data line is preceded by a line with a number typed in the first two columns indicating the type of data to follow. The data lines have columns 1 and 2 left blank. An example is follows.

Data Line 01

This contains the basic data for one component of one species: population size, length of activity cycle and number of breeding periods in that cycle.

| Columns | Content |
|---------|---|
| 1-2 | Blank |
| 3-6 | Species name (abbreviated to four letters). |
| 7 | Blank |
| 8 | Sex (M or F for breeders; any other character is assumed non-breeder). |
| 9 | Blank |
| 10 | Number of years to complete one activity cycle (e.g., 2 for wandering albatross). Must be 1 for non-breeders. |
| 11 | Blank |
| 12 | Number of breeding periods in one activity cycle. Must be 0 for non-breeders. |
| 13 | Blank |
| 14-21 | Total population size for this component. (For a population with a two-year activity cycle this population size will be divided by two within the program when their impact is assessed). |

Data Line 02

This line contains information on the weight of each species/sex and its changes throughout the season.

Weights are interpolated between the values given on successive lines.

Note that if more than one line is entered, the day number on the last card must be the last day of the activity cycle (365 for most species, 730 for species whose cycle lasts two years, and 1 095 for king penguins).

| Columns | Content |
|-----------------|--|
| 1-2 3-6 7 | Blank Day number (must be 0001 on first card). Blank |
| 8-12 | Weight (grams) |

Data Line 03

Reserved for future use.

Data Line 04

This card contains details of the dietary composition of a species/sex.

| Columns | Content |
|---------|---|
| 1-2 | Blank |
| 3-6 | Day number (must be 0001 on first card) |
| 7-9 | Percentage of diet Euphausiid |
| 10-12 | Percentage of diet Cephalopod |
| 13-15 | Percentage of diet Myctophid |
| 16-18 | Percentage of diet Other Fish |
| 19-21 | Percentage of diet Copepod |
| 22-24 | Percentage of diet Amphipod |
| 25-27 | Percentage of diet Other Crustacea |
| 28-30 | Percentage of diet Other (marine) |

Data Lines 05 and 06

These data give details of the daily energetic costs of each activity the bird undertakes. Currently these activities are:

- 0. absent from the sea
- 1. "standing around at nest site"
- 2. incubation
- 3. brooding
- 4. foraging for chick
- 5. foraging for self
- 6. moult.

Weight to energy relationships of the form $E=aW^b$ can be used. If b=0 then 'a' should be the energy consumption of a bird of average weight for that activity. The values of 'a' are given on line 05 and the values of 'b' on line 06. The values of a and b should be given for the weight in grams. Energetic costs should be calculated in kJ/d. Only activities 0, 1, 5 and 6 are used for non-breeders.

| Columns | Contents |
|---------|-----------------------|
| 1-2 | Blank |
| 3-7 | a or b for activity 1 |
| 8 | Blank |
| 9-13 | a or b for activity 2 |
| 14 | Blank |
| 15-19 | a or b for activity 3 |
| 20 | Blank |
| 21-25 | a or b for activity 4 |
| 26 | Blank |
| 27-31 | a or b for activity 5 |
| 32 | Blank |
| 33-37 | a or b for activity 6 |
| | |

Data Line 07 (omit for non-breeders)

These data relate to one breeding period. There should be one 07-type line for each breeding period within a complete activity cycle. All dates are referred to day 1 as the first day of the activity cycle (i.e., may go from 1 to 1 095).

| Contents |
|---|
| Blank |
| Laying date (number of days from start of activity cycle) |
| Blank |
| Egg loss rate (fraction per day) |
| Blank |
| Hatching data (as lay date) |
| Blank |
| Chick loss rate (fraction per day) |
| Blank |
| Fledging date (as lay date) |
| Blank |
| Feed size (grams delivered by one adult) |
| Blank |
| Feeding frequency (meals per <u>adult</u> per day) |
| |

Data Line 08

Lines of this type describe the activity budget of a bird throughout one activity cycle (which may include more than one breeding period and last for more than one twelve-month period). The activities are coded 1-6 or zero to indicate absence. Days are numbered from 1 September at the start of the activity cycle and may go up to 1 095 if the activity cycle covers three years. Non-breeders may only have activity codes 0, 1, 5 and 6.

As many cards as are necessary may be used but each card must be full before starting the next.

| Columns | Contents |
|---|---|
| 1-2 3-6 7 8-11 12 13-16 17 18-21 | Blank 0001 (day 1) activity on day 1 day start next activity activity day start next activity activity day start next activity |
| 68-71 72 73-80 | day start next activity activity blank |

Data Line 09 (omit for non-breeders)

These data describe the foraging range and pattern of the adults during the chick-rearing part of the activity cycle. There must be one card for each breeding period (e.g., two for king

penguins). A foraging trip is defined here as the time between feeds, and is calculated from the feeding frequency.

| Columns | Content |
|----------|--|
| 1-2 | Blank Flight group I (m/s) |
| 3-0 7 | Flight speed (m/s) Blank |
| 8-11 | Zigzag factor (distance flown to achieve unit distance forward) |
| 12 | Blank |
| 13-16 | Proportion not travelling (e.g., proportion of a foraging trip spent on water for flying birds, or on land for penguins) |
| 17 | Blank |
| 18 | Foraging type: $1 = uniform$, $2 = inshore$, $3 = offshore$ |

,

| Day No. | Calorific Value (kJ/g) |
|---------|------------------------|
| 001 | 3.84 |
| 091 | 3.84 |
| 154 | 5.45 |
| 197 | 2.79 |
| 213 | 3.84 |
| 365 | 3.84 |

(a) Data giving seasonal changes in calorific value of krill (from file name EUPHAUSI. CAL).

(b) Interpolated seasonal pattern.





APPENDIX 3

GRAPHICAL OUTPUT FROM THE PROGRAM (Produced by Dr A.G. Wood)

(a) Plot of daily food consumption throughout the year.



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PART 2: SELECTED OUTPUTS FROM SEABIRD IMPACT ASSESSMENT PROGRAM

This document contains outputs resulting from:

- 1. Running a new version of the original model incorporating the (few) changes to parameter values.
- 2. Running the new sub-models (for seasonal changes in predator weight, diet composition and prey energy content) and comparing these with the original version which lacks these.
- 3. Sensitivity analyses.
- 4. Comments on the potential applicability of the system to other predators and to more detailed analyses of prey such as krill.
- 1. Running Version 3.30 of the System

The changes to the data used in the original system are as follows:

- (a) Total population estimate for king penguins is now 188 000 pairs (Croxall *et al.*, 1988a).
- (b) Diet of king penguins is now 13% cephalopod, 86% myctophid, 1% other fish (Adams and Klages, 1987).
- (c) Diet of Wilson's storm petrel is now 35% krill, 2% cephalopod, 28% myctophid, 30% amphipod, 3% other crustacea, 2% other (Croxall *et al.*, 1988b).
- (d) fish prey of Antarctic (dove) prion, blue petrel, white-chinned petrel and black-bellied storm petrel is now all myctophid (Croxall and Prince, unpublished data).

The selected outputs are as follows:

- (a) Annual food consumption (tonnes) of seabirds breeding at South Georgia (Table 1). Note that this treats the sexes separately and does not incorporate the necessary correction for an assimilation efficiency coefficient of 75%.
- (b) Seasonal changes in food consumption by the combined breeding population of all South Georgia seabirds (Figure 1).
- (c) Food consumption, in terms of distance offshore, of the active breeding seabird population (i.e., all birds still engaged in rearing chicks) in mid-February (day 196) is shown in Figure 2. Note that all macaroni penguin chicks have fledged. The main peaks in Figure 2 correspond to:
 - (i) inshore-gentoo penguin, giant petrels, Wilson's storm petrel, Antarctic prion;
 - (ii) at 400 km black-browed albatross;
 - (iii) at 600 km grey-headed albatross; and

- (iv) at 1 000 km light mantled sooty albatross and white-chinned petrel (wandering albatrosses are incubating at this time).
- (d) food consumption, in terms of distance offshore, of the active breeding seabird population in mid-January (day 168) of gentoo penguin (small peak close inshore) and macaroni penguin only (Figure 3). Note the differences in both scales from Figure 2.
- 2. New Sub-Models
 - (a) Predator weight change

Figure 4a shows seasonal changes in food consumption by breeding macaroni penguins assuming constant weight. Figure 4b shows the effect of including seasonal changes in weight using data for macaroni penguins from Croxall (1984, Figure 25). Note particularly the new peak prior to the moult fast ashore.

(b) Diet composition change

Figure 5a shows seasonal changes in krill and fish consumption by breeding gentoo penguins, assuming constant diet composition (68% krill, 32% fish). Figure 5b shows the effect of varying the composition of the diet using also data from Williams (in press) for times of the year outside the chick-rearing period. Note the elevated consumption of krill, due to its high contribution in the winter diet. The 'step' changes in Figure 5a solely reflect changes in food consumption associated with different activities. The step changes which only occur in Figure 5b are those which reflect changes due to diet composition.

(c) Predator energy content change

Figure 6a shows seasonal changes in chinstrap penguin krill consumption, assuming that krill have constant energy content. Figure 6b incorporates the effect of varying krill energy content using data in Clarke (1980) as portrayed in Figure 6c.

(d) General

We have portrayed the effects of changes in each of these three parameters independently. In the system they can all be combined together, subject only to data availability.

3. Sensitivity Analyses

Analyses were conducted to compare the sensitivity of the model to specify changes in values for each of the key parameters. The results of one such analysis, using macaroni penguin data, are shown in Table 2. Note the overwhelming effect of changes in the exponent of the energetic equation.

Running the model using standard general equations for e.g., penguin incubation and moult energy costs, rather than empirical values for the species concerned, resulted in a 30% decrease in food consumption for male macaroni penguins. This reinforces the importance of obtaining accurate energetic data from field studies of Antarctic species.

We also examined the effect of the changes induced by the three new sub-models. Allowing for the changes in macaroni penguin weight produced a 12% decrease in food consumption compared with the assumption of constant weight.

Allowing for seasonal changes in gentoo penguin diet composition produced a 1.5% decrease in food consumption compared with extrapolating the diet in the chick-rearing period through the whole year.

Allowing for seasonal changes in krill energy content produced a 10% increase in food consumption by chinstrap penguins compared with the assumption that krill energy content remains constant year-round.

4. Application of System to Other Predators

Provided that the relevant data can be manipulated into the correct form, the use of the program and system is not restricted to seabirds alone, but may include other predators such as seals. In incorporating Antarctic fur seals into the system the following problems were encountered.

- (a) Values for daily energy consumption and mass of male seals exceeded the maximum currently allowed (five digits). This could be resolved by using kg and MJ and making concomitant changes.
- (b) It is necessary to equate pup birth date with chick hatching date and to insert dummy data for the pre-birth period (equivalent to the laying period in seabirds). Weaning equates to fledging.
- (c) Although determining feeding frequency in fur seals is straightforward (based on known foraging trip durations) estimation of meal size is currently difficult because it requires knowledge of the amount of milk transferred per attendance period and the conversion efficiency of krill into milk. Research is currently in progress to determine these.
- (d) Data line 09 would be completed using activity budget data from TDR studies, as in penguins.

The system might also be applied to other (e.g., phocid) seals but at present for most such species there are too many data deficiencies to make this feasible.

For southern elephant seals at South Georgia, however, recent studies on population size, diet, bioenergetics and diving activity patterns have provided most relevant data - including the ability to make rough estimates of energy costs of swimming.

This means that elephant seal activities could be regarded as belonging to one of two basic categories: ashore (i.e., breeding and moult period) and at-sea (rest of year). If periods ashore, when the animals are fasting, were regarded as involving no food consumption, the estimated at-sea daily energy costs could be assumed to include acquisition of any 'extra' food before and after the periods ashore. This would allow data lines 05, 06 and 08 to be completed and require 07 to be filled with dummy data. Data line 09 would be completed using data from TDR studies.

5. Application of System to Krill Prey Alone

The system and program currently allow analysis of up to eight prey categories, which are currently different species groups. However, these eight prey categories could easily be

different components of one prey species, e.g. sex and maturity stages/age classes of krill. All the calculations within the program would be appropriate; the names of the eight prey categories would simply need to be altered within the program.

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| Species | Sex | Weight | Population | Food Consumption (tonnes) | | | | | Total | | | |
|---|--|--|---|--|---|--|---|---|--|--|--|--|
| | | (kg) | (pairs) | Euphausids | Cephalopods | Myctophids | Fish | Copepods | Amphipods | Other Crustaceans | Oddsnsods | |
| -1- | -2- | -3- | -4- | -5- | -6- | -7- | -8- | -9- | -10- | -11- | -12- | -13- |
| -1- KINP GENP GENP CHP CHP MACP WALB WALB BBA BBA BBA GHA GHA LMS LMS SGP | -2- M F M F M F M F M F M F M F M F M F M | $\begin{array}{r} -3-\\ 13.450\\ 13.760\\ 5.890\\ 5.890\\ 4.000\\ 3.600\\ 5.000\\ 4.600\\ 10.580\\ 9.020\\ 3.922\\ 3.694\\ 3.751\\ 3.624\\ 2.840\\ 2.840\\ 5.035\end{array}$ | $\begin{array}{r} -4-\\ 188000\\ 188000\\ 100000\\ 100000\\ 4000\\ 4000\\ 5000000\\ 5000000\\ 4732\\ 4732\\ 4732\\ 60000\\ 60000\\ 60000\\ 60000\\ 60000\\ 8000\\ 8000\\ 8000\\ 8000\\ 5000\end{array}$ | $\begin{array}{r} -5-\\ 0\\ 0\\ 22902\\ 23032\\ 992\\ 914\\ 1480640\\ 1423880\\ 116\\ 105\\ 3183\\ 3013\\ 2369\\ 2350\\ 669\\ 680\\ 1083\end{array}$ | -6- 7727 7622 0 0 0 0 0 0 0 930 843 1759 1665 7741 7678 850 864 180 | -7- 51122 50427 0 0 0 0 0 0 0 0 0 0 0 0 0 | $\begin{array}{r} -8 \\ 594 \\ 586 \\ 10777 \\ 10838 \\ 0 \\ 0 \\ 30217 \\ 29058 \\ 116 \\ 105 \\ 3267 \\ 3092 \\ 5529 \\ 5484 \\ 217 \\ 220 \\ 90 \end{array}$ | -9- 0 0 0 0 0 0 0 0 0 0 0 0 83 79 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 | $ \begin{array}{r} -10-\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\$ | -11- 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 | $ \begin{array}{c} -12-\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\$ | -13- 59445 58636 33680 33871 992 914 1510857 1452939 1163 1054 8378 7930 15799 15671 1808 1838 1838 1354 |
| SGP | F | 3.798 | 5000 | 921 | 153 | Õ | 76 | Ō | 0 | 0 | 0 | 1152 |
| NGP | M | 4.902 | 3500 | 599 | 239 | 0 | 79 | 0 | 0 | 0 | 0 | 918 |
| NGP | F | 3.724 | 3500 | 537 | 214 | 0 | 71 | 0 | 0 | 0 | 0 | 824 |
| CAPE | М | 0.442 | 20000 | 1163 | 0 | 0 | 205 | 0 | 0 | 0 | 0 | 1368 |
| CAPE | F | 0.407 | 20000 | 1126 | 0 | 0 | 198 | 0 | 0 | 0 | 0 | 1325 |
| SNOW | M | 0.340 | 3000 | 144 | 18 | 0 | 18 | 0 | 0 | 0 | 0 | 180 |
| SNOW | F | 0.286 | 3000 | 135 | 16 | 0 | 16 | 0 | 0 | 0 | 0 | 169 |
| DOVE | М | 0.168 | 22000000 | 509935 | 8791 | 17583 | 0 | 272551 | 70335 | 0 | 0 | 879199 |
| DOVE | F | 0.168 | 22000000 | 472034 | 8138 | 16277 | 0 | 252294 | 65108 | 0 | 0 | 813851 |
| BLUE | M | 0.193 | 70000 | 2309 | 28 | 225 | 0 | 112 | 140 | U | 0 | 2816 |
| BLUE | F | 0.193 | 70000 | 2140 | 26 | 208 | 0 | 104 | 130 | U | U | 2009 |
| WCP WCP | M F | 1.368 1.368 | 2000000 2000000 | 56801 57755 | 98876 100537 | 50490 51338 | 0 | 0 | 2103 2139 | 0 | 0 | 208272 211771 |

Table 1:Total annual consumption of each category of prey by South Georgia breeding seabird populations.

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Table 1 (continued)

| -1- | -2- | -3- | -4- | -5- | -6- | -7- | -8- | -9- | -10- | -11- | -12- | -13- |
|------|-----|-------|---------|-------|-----|-----|--------|-------|-------|------|------|--------|
| WISP | м | 0.034 | 600000 | 1013 | 57 | 810 | 0 | 0 | 926 | 86 | 0 | 2895 |
| WISP | F | 0.034 | 600000 | 832 | 47 | 666 | ů 0 | ŏ | 761 | 71 | Ő | 2379 |
| BBSP | M | 0.053 | 10000 | 90 | 0 | 10 | 0 | 80 | 20 | 0 | 0 | 200 |
| BBSP | F | 0.053 | 10000 | 84 | 0 | 9 | 0 | 74 | 18 | 0 | 0 | 187 |
| CDP | M | 0.133 | 3800000 | 20778 | 0 | 0 | 0 | 94195 | 23548 | 0 | 0 | 138522 |
| CDP | F | 0.133 | 3800000 | 18800 | 0 | 0 | 0 | 85230 | 21307 | 0 | 0 | 125339 |
| SGDP | M | 0.107 | 2000000 | 49171 | 0 | 0 | 0 | 12939 | 2587 | 0 | 0 | 64699 |
| SGDP | F | 0.107 | 2000000 | 45005 | 0 | 0 | 0 | 11843 | 2368 | 0 | 0 | 59218 |
| BES | M | 2.867 | 7500 | 0 | 337 | 0 | 1179 | 0 | 0 | 168 | 0 | 1685 |
| BES | F | 2.473 | 7500 | 0 | 310 | 0 | 1085 | 0 | 0 | 155 | 0 | 1550 |
| ANTT | M | 0.151 | 2600 | 16 | 0 | 0 | 53 | 16 | 21 | 0 | 0 | 107 |
| ANTT | F | 0.151 | 2600 | 15 | 0 | 0 | 50 | 15 | 20 | 0 | 0 | 100 |

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| Parameter | Change in Food Consumption for: | | | | |
|---|---------------------------------|--------------|--|--|--|
| | 10% Decrease | 10% Increase | | | |
| | 2.01 | | | | |
| Weight | -1% | +6% | | | |
| Energy coefficient \mathbf{a} in $\mathbf{E} = \mathbf{a}\mathbf{W}^{\mathbf{b}}$ | -10% | +10% | | | |
| Energy exponent b in $\mathbf{E} = \mathbf{a}\mathbf{W}^{\mathbf{b}}$ | -43% | +76% | | | |
| Egg loss | +<1% | -<1% | | | |
| Chick loss | +<1% | -<1% | | | |
| Chick meal size | -<1% | +<1% | | | |
| Chick meal frequency | -<1% | +<1% | | | |

Table 2:The change in food consumption of male macaroni penguins induced by changes of
10% in each key parameter.







Week number 28

Figure 2: Distribution of food consumption (all seabirds), mid-February.

TONNES PER DAY

Figure 4: Food consumption in macaroni penguins without (Figure 4a) and with (Figure 4b) allowance for seasonal change in weight.

Figure 5: Food consumption in gentoo penguins without (Figure 5a) and with (Figure 5b) allowance for seasonal change in diet composition.

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