THE USE OF ANALYSIS OF PENGUIN STOMACH CONTENTS IN SIMULTANEOUS STUDY OF PREY AND PREDATOR PARAMETERS

E. Marschoff and B. González

Abstract

Size selectivity of krill by penguins is shown to be highly sensitive to the statistical assumptions made during the analysis of data. The nested ANOVA method is proposed as being the correct approach for analysis because lack of independence between krill specimens found in the stomach of a given penguin prevents the pooling of krill lengths from different samples. Samples taken in Bahía Esperanza were used to illustrate the different approaches to this analysis. A highly significant linear regression between krill size and time of sampling was found.

Full use of information obtained from analysis of penguin stomach contents requires block sampling designs. Replicating samples from the same penguin or studying portions of stomach samples at different stages of digestion are proposed as alternative methods.

Résumé

La sélectivité de la taille de krill par les manchots est démontrée comme étant très sensible aux hypothèses statistiques sur lesquelles l'analyse des données est fondée. Il est proposé de considérer que la méthode correcte est celle des modèles ANOVA à emboîtements, étant donné que le manque d'indépendance entre les spécimens de krill trouvés dans l'estomac d'un manchot donné empêche de regrouper les longueurs du krill provenant d'échantillons différents. Les échantillons prélevés dans la Bahía Esperanza sont utilisés pour expliquer les différentes approches à cette analyse. Une régression linéaire très significative entre la taille du krill et l'époque d'échantillonnage a été observée.

L'utilisation intégrale des informations provenant de l'analyse des contenus stomacaux des manchots nécessite l'emploi de modèles d'échantillonnage en bloc. La reproduction des échantillons provenant du même manchot ou l'étude de portions du contenu stomacal à différents stades de digestion est proposée comme autre méthode possible.

Резюме

Селективность пингвинов в отношении размера потребляемого ими криля проявляет высокую чувствительность к статистическим допущениям, сделанным при анализе данных. В качестве верного подхода предлагается гнездовой метод анализа (ANOVA), поскольку данные по длине криля, полученные по отдельным пробам, невоможно свести воедино в связи с тем, что в желудке пингвина криль в значительной степени перемешан. Пробы, взятые в районе залива Эсперанза, используются в качестве иллюстрации различных подходов к такому анализу. Была выявлена важная линейная регрессивная зависимость между размером криля и временем сбора проб.

Для извлечения максимального количества информации при исследовании содержимого желудков пингвинов необходимы схемы проведения групповой выборки. В качестве альтернативных методов предлагаются многократные пробы содержимого желудка одного и того же пингвина и изучение фрагментов содержимого желудка различной степени переваренности.

Resumen

La selectividad del tamaño del krill hecha por los pingüinos demuestra ser sumamente sensible a las suposiciones estadísticas hechas en el análisis de datos. El método inclusivo ANOVA se propone como el correcto enfoque para análisis, porque la falta de separación entre los especímenes de krill que se encuentran en el estómago de un cierto pingüino evita hacer un agrupamiento de datos sobre medidas del krill de diferentes muestras. Muestras tomadas en la Bahía Esperanza se utilizan para ilustrar los diferentes aproches a este análisi. Se encontró una regresión linear sumamente significante entre el tamaño del krill y tiempo.

Se necesita un conjunto de diseños de muestreo para lograr la utilización completa de la información obtenida de los contenidos estomacales. Se proponen como métodos alternativos, la reproducción de muestras de un mismo pingüino o estudiando porciones del contenido estomacal que presenten diferentes niveles de digestión.

A study of penguin diet conducted simultaneously with monitoring prey parameters would be clearly advantageous. It would enable interpretation of changes observed in predator parameters by taking into account changes in monitored prey parameters. It would also allow prediction of possible consequences for predators of changes in prey parameters. Such a simultaneous approach is fundamental to the CCAMLR Ecosystem Monitoring Program.

It would be difficult to design an experiment which combines simultaneous measurement of prey and predator parameters (e.g. measurement of krill size distribution and abundance within the foraging range of a monitored colony of predators during their breeding season). Sampling of krill introduces the problem of net selectivity which, together with krill swarming behaviour, makes it extremely difficult to ensure that the area of sampling coincides accurately with the foraging range of penguins.

A study of krill length frequency distribution in samples taken from penguin stomachs provides a great deal of important information on prey and predators. If designed properly, a study of this type may be used for evaluating the variability of some prey parameters.

The value of this study would depend on selectivity properties of penguins as krill samplers; whether or not a length frequency distribution of krill in their stomachs reflects changes in food availability. If penguins do have selectivity properties, would it be possible to define which characteristics of penguins (e.g. sex, age, etc.) may be considered as representative selection factors and also, would it be possible to define groups of penguins lacking selectivity?

Some published studies on size selectivity of krill describe penguins as highly selective predators. A statistically significant difference was found in length distribution of krill in samples taken from penguins of different sex and size. In these studies, all krill taken from stomachs of a particular group of penguins were pooled together in order to estimate the mean size of krill which in turn, was tested against the variance of the pooled samples. These analyses imply that an individual krill was independent from the remaining krill in the same penguin stomach. This assumed independence does not take note of krill swarming behaviour and is therefore incorrect.

In our study we made comparative analyses of 41 stomach samples of penguins from Bahía Esperanza, randomly divided into two groups (Table 1). Obviously, the highly significant F-statistic means only that the assumption of independence is incorrect, and demonstrates that differences between groups of penguins cannot be tested against the "krill in penguins variance" because such tests will yield misleading results.

The nested ANOVA method is the correct statistical procedure for this type of analysis. This method of analysis demonstrated that there was an insignificant F-statistic for the random groups, but a highly significant F-statistic for penguins within the random groups (Table 2).

At this stage it seems reasonable to assume that the question of size selectivity of krill by penguins is at least open to question.

Results shown in Table 3 are much more interesting. When samples were grouped according to their collection dates, the resultant statistics were insignificant both for the dates and "penguin within dates" groups. It is now evident that individual penguins feed on krill of different sizes; but krill size is also affected by the date of collection.

The "penguin within dates" component is, at least partially, a consequence of patch distribution of krill. A fraction of this component might reflect particular characteristics of penguins (e.g. sex, age, etc.), which may be responsible for their preference for krill of a particular size.

It should be stressed that unless any grouping by date is tested against the appropriate variance (between dates), erroneous results will be obtained. One example is shown in Table 5: samples from penguins have been classified in accordance with the day of the week of collection (e.g. Monday, Tuesday, etc.). The resulting nested ANOVA does not take into account "between dates" variability and shows a significant result. Obviously, penguins do not observe religious fasts stipulating that only smaller krill be eaten on Wednesdays and Fridays. This result illustrates that penguins included in any weekday group are not independent but related through sampling dates, and this dependence should be reflected in the analysis.

The regression analysis demonstrates a positive trend in mean sizes of krill with time (Table 4 and Figure 1). In view of this significant regression, it is reasonable to assume that the variance component due to date is the result of differences in krill population parameters during the sampling period. It may be argued that some pertinent component may result from the changing preferences of penguins (e.g. due to their varying needs throughout the creche period). The complex nature of these possible changes prevents the comparison of colonies to test the existence of more general trends.

The important point here is that data as currently collected will not contribute towards resolving this difference. A random block design is needed to separate penguin dependent sources of variation from those depending on krill availability, and increasing a number of samples in order to include adults is desirable.

Blocks might be defined in different ways, but the most interesting would be a swarm of krill. Unfortunately it would be technically very difficult, if not impossible, to identify the swarm on which individual penguins feed. Another useful set of blocks would be obtained by replicating samples from the same individual. This procedure would provide the "within blocks" degree of freedom needed for the independent testing of hypotheses about selectivity and prey parameters and can be obtained simply by replication of samples from the same individual, by comparison of differently digested portions of the same sample or by a combination of both methods.

Other definitions of blocks based on penguin characteristics (sex, age, beak size, reproductive condition, etc.) can be used, but results would be difficult to interpret because the distribution of penguins at sea is basically non-random.

The proposed methodology would also be useful for krill studies. When preferences of penguins are evaluated and discounted, the remaining effects of variations in prey parameters will provide valuable information about krill populations. Krill length distributions might be considered as resulting from environmental conditions within the area continuously sampled by penguins in the foraging range of a colony, thus opening the possibility for combining ship and land-based studies using powerful and well designed dynamic models.

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Table 1: One factor ANOVA for two random groups of penguins. See text for discussion.

Analysis of Variance					
Source of Variation	DF	Sum of Squares	Mean Square	F_s	Probability
Random groups	1	611.46	611.46	8.01	0.004772
Krill (within group)	2238	170824.75	76.33		

Table 2: Nested ANOVA for two random groups of penguins. See text for discussion.

Analysis of Variance					
Source of Variation	DF	Sum of Squares	Mean Square	F_s	Probability
Random groups	1	611.46	611.46	0.32	0.57913
Penguins in groups	39	73702.28	1889.80	42.79	0.0
Krill (within group)	2199	97122.39	44.17		

Components of Variance	
Source of Variation	Percentage
Random groups	0.0
Penguins in groups	45.07
Krill (within group)	54.93

Table 3: Nested ANOVA for groups of penguins sampled on the same day. See text for discussion.

Analysis of Variance					
Source of Variation	DF	Sum of Squares	Mean Square	F_s	Probability
Dates	9	56052.57	6220.06	10.57	0.0
Penguins in dates	31	18261.16	589.07	13.34	0.0
Krill (within group)	2199	97122.39	44.17		

Components of Variance	
Source of Variation	Percentage
Dates	37.50
Penguins in dates	11.82
Krill (within group)	50.68

Table 4: Regression of krill mean size consumed by penguins as a function of collection date.

Source of Variation	DF	Sum of Squares	Mean Square	F_s	Probability
Between dates	15	1043.63	69.58	4.43	0.00055
Linear regression	1	908.46	908.46	57.81	0.0
Constant regression	1	52911.36	52911.36	3367.10	0.0
Deviation from regression	14	135.17	9.66	0.61	0.82842
Error within groups	25	392.86	15.71		
Total sum of squares	40	1436.49			
Uncorrected total	41	54347.84			

Table 5: Nested ANOVA for groups of penguins sampled on the same weekday. See text for discussion.

Source of Variation	DF	Sum of Squares	Mean Square	F	Probability
Between days of the week	5	39299.13	7859.83	7.86	0.000055
Penguins in weekday	35	35014.61	1000.42	22.65	0.0
Krill (within group)	2199	97122.39	44.17		

Components of Variance

Source of Variation	Percentage
Between days of the week	26.84
Penguins in groups	21.70
Krill (within group)	51.46

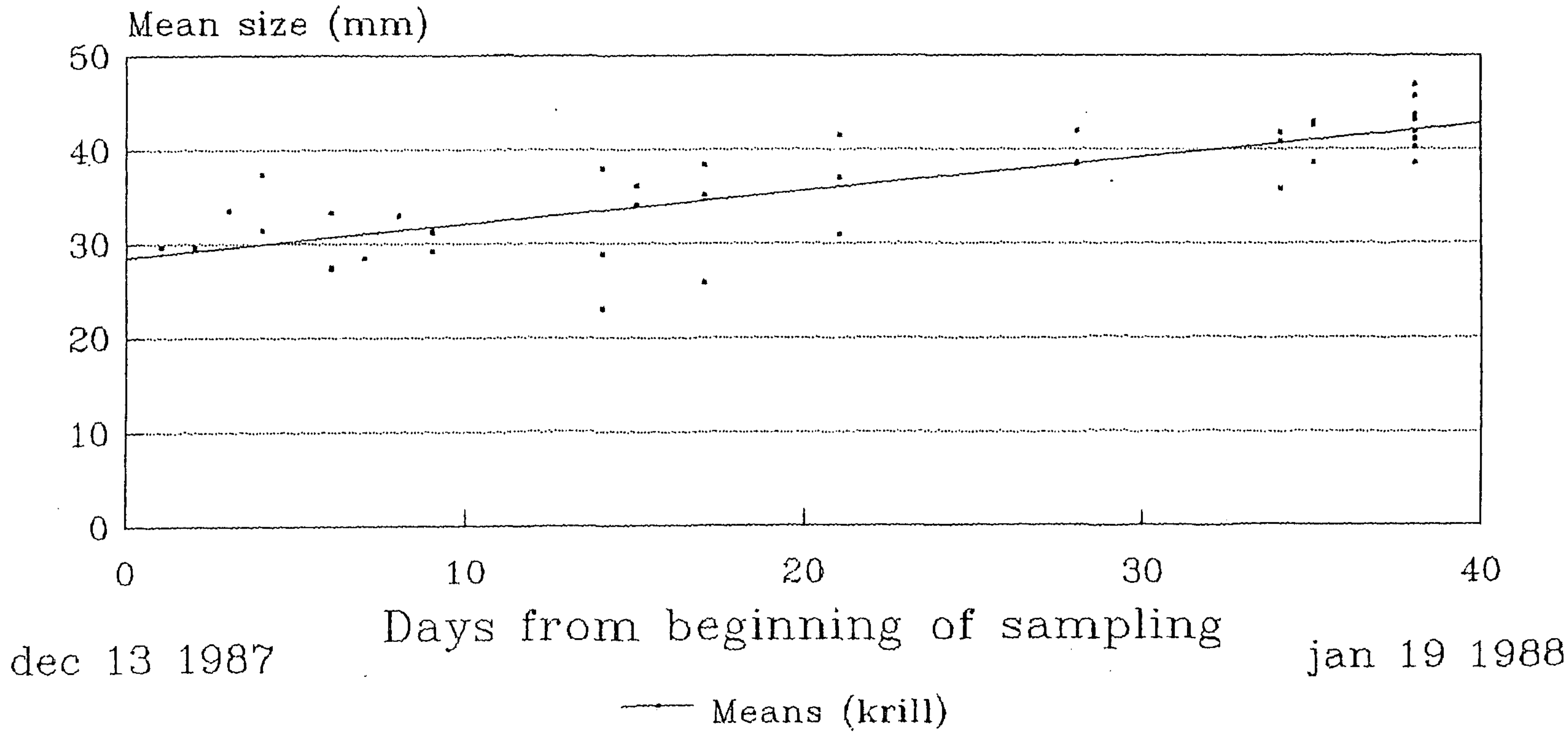

Figure 1: Krill size as a function of time of sampling. Krill consumed by penguins in Bahía Esperanza. Observed trend in the size of krill consumed by penguins. See Table 4 for statistical analysis.

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