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TEMPORAL VARIABILITY AND THE INTERRELATIONSHIPS BETWEEN CEMP PARAMETERS COLLECTED ON ADÉLIE PENGUINS AT BÉCHERVAISE ISLAND

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Abstract

Temporal variability in a series of CCAMLR Ecosystem Monitoring Program (CEMP) parameters and the interrelationships between these parameters were examined for Adélie penguins over a period of 12 years. Data were collected from 1990/91 to 2001/02 at Béchervaise Island, Eastern Antarctica. Parameters relating to chick survival (brooding nest counts, counts of chicks when two-thirds were crèched and fully crèched chick counts) display large temporal variability while other parameters, such as arrival counts and incubating nest counts, are more stable between years. The low degree of correlation between parameters collected before incubating nest counts with those collected after brooding nest counts reinforces the notion that events occurring during the hatching period are critical for chick survival. There was a strong negative correlation between female foraging trip duration during both the guard and the crèche period and breeding success, while the correlation between breeding success and foraging trip duration was low for males. Male foraging trips during the crèche period were, however, moderately correlated with fledgling mass.

Within-season penguin weights, the simplest output from the Automated Penguin Monitoring System (APMS), were also examined in terms of their correlation with breeding success. Results indicate that low weights of females at the time they depart after egg laying appears to be the first indication that a season may have low breeding success. The results obtained throughout these analyses indicate that knowledge of the sex of birds can be important for understanding breeding success and the interrelationships between CEMP parameters.

Résumé

La variabilité temporelle dans une série de paramètres du Programme de contrôle de l'écosystème de la CCAMLR (CEMP) et les interrelations de ces paramètres sont examinées chez les manchots Adélie sur une période de 12 ans. Les données ont été collectées de 1990/91 à 2001/02 à l'île Béchervaise, dans l'est de l'Antarctique. Les paramètres liés à la survie des jeunes (nombre de nids avec couvée en période d'élevage et nombre de jeunes lorsque deux tiers d'entre eux sont en crèche et lorsqu'ils sont tous en crèche) affichent une forte variabilité temporelle alors que d'autres, tels que le nombre d'individus arrivant et celui de nids avec couvée en période d'incubation, sont plus stables d'une année à l'autre. Le faible degré de corrélation entre les paramètres collectés avant les dénombrements des nids avec couvée en période d'incubation et ceux collectés après les dénombrements des nids avec couvée en période d'élevage renforce la notion selon laquelle la survie des jeunes dépend largement des événements se produisant pendant la période d'éclosion. La durée des sorties alimentaires des femelles tant durant la période de garde que celle de crèche affiche une forte corrélation négative avec la réussite de la reproduction, alors que chez les mâles, la corrélation est faible. Toutefois, entre les sorties alimentaires des mâles pendant la période de crèche et le poids à la première mue, la corrélation est modérée.

L'examen porte également sur la corrélation entre le poids des manchots au cours de la saison, fourni par les données les plus simples du Système de contrôle automatique des manchots (APMS), et la réussite de la reproduction. D'après les résultats, le premier signe d'une saison susceptible de connaître une faible réussite de la reproduction semble être le poids faible des femelles, au moment où elles quittent le nid après la ponte. Les résultats obtenus tout au long de ces analyses indiquent qu'il peut s'avérer important de connaître le sexe des oiseaux pour comprendre la réussite de la reproduction et les interrelations des paramètres du CEMP.

Резюме

Была проанализирована временная изменчивость ряда данных по параметрам Программы АНТКОМа по экосистемному мониторингу (CEMP) и взаимосвязь между этими параметрами для пингвинов Адели на протяжении 12-летнего периода. Данные собирались с 1990/91 по 2001/02 гг. на о-ве Бешервэз, восточная Антарктика. Параметры, относящиеся к выживанию птенцов (число гнезд с выводком, подсчет птенцов, когда 2/3 их вступило в ясельную стадию и при полном вступлении в ясельную стадию), отличаются большой временной изменчивостью, в то время как другие параметры, такие как численность по прибытии в колонию и число насиживаемых гнезд, более стабильны от года к году. Низкая степень корреляции между параметрами, собранными до подсчета насиживаемых гнезд, и параметрами, собранными после подсчета гнезд с выводком, подкрепляет тот взгляд, что события, происходящие во время периода выведения, являются решающими для выживания птенцов. Существовала сильная отрицательная корреляция между репродуктивным успехом и продолжительностью поиска пищи самкой во время охраны выводка и ясельного периода. В то же время для самцов корреляция между репродуктивным успехом и продолжительностью похода за пищей была низкой. Тем не менее, походы самцов за пищей во время ясельного периода были умеренно скоррелированы с массой птенцов при оперении.

Вес пингвинов в течение сезона – простейший выходной параметр Автоматизированной системы мониторинга пингвинов (APMS) – был также проанализирован с точки зрения его корреляции с репродуктивным успехом. Результаты говорят о том, что низкий вес самок, когда они отправляются на поиски пищи после кладки яиц, вероятно, является первым признаком того, что репродуктивный успех в этом сезоне может быть низким. Результаты проведенного анализа свидетельствуют о том, что для понимания репродуктивного успеха и взаимосвязей между параметрами CEMP может быть важно знать пол птиц.

Resumen

Se examinó la variabilidad temporal en una serie de parámetros del programa de seguimiento del ecosistema de la CCRVMA (CEMP), y las interrelaciones entre estos parámetros para los pingüinos adelia durante un período de 12 años. Los datos fueron recopilados desde 1990/91 hasta 2001/02 en isla Béchervaise, Antártida oriental. Los parámetros relacionados con la supervivencia de los polluelos (recuento de nidos con polluelos, recuento de polluelos cuando dos tercios están en guardería y cuando esta etapa ha terminado) muestran una elevada variabilidad temporal, mientras otros parámetros como el número de arribo a la colonia y el número de nidos con aves incubando son más estables de un año a otro. La baja correlación entre los parámetros recopilados antes del recuento de nidos con aves incubando y después del recuento de nidos con polluelos, reafirma la noción que los sucesos ocurridos durante la eclosión resultan críticos para la supervivencia de los polluelos. Se observó una fuerte correlación negativa entre la duración de los viajes de alimentación de las hembras durante los períodos de cría y guardería y el éxito reproductor, mientras que la correlación entre el éxito reproductor y la duración de los viajes de alimentación fue baja para los machos. Sin embargo, la correlación entre los viajes de alimentación de los machos durante el período de guardería con el peso del ave emplumada fue moderada.

También se examinó el peso de los pingüinos dentro de una temporada – el dato más simple obtenido por el sistema de seguimiento automático de pingüinos (APMS) – en términos de su correlación con el éxito reproductor. De los resultados se puede inferir que el bajo peso de las hembras al momento de partir al mar después de la puesta parece ser la primera indicación de que el éxito reproductor será bajo. Los resultados obtenidos a través de estos análisis indican que es importante conocer el sexo de las aves para entender el éxito reproductor y las interrelaciones entre los parámetros del CEMP.

Keywords: Adélie penguin, temporal variability, correlation, Antarctica, breeding success, CEMP, monitoring program, CCAMLR

INTRODUCTION

The CCAMLR Ecosystem Monitoring Program (CEMP) was established in 1985 to (i) detect and record significant changes in critical components of the ecosystem, so as to serve as a basis for the conservation of Antarctic marine living resources, and (ii) distinguish between changes due to harvesting of commercial species and changes due to environmental variability, both physical and biological (CCAMLR, 2003). CEMP comprises measurement of specified parameters using standard methods for selected indicator species at a number of sites in the CCAMLR Convention Area. At the inception of CEMP a suite of parameters were identified for measurement; the full suite has subsequently been measured at some of the sites, one of these being Béchervaise Island in eastern Antarctica.

CEMP is currently entering a review stage. The time series of CEMP data collected from Béchervaise Island can make a significant contribution to the review, as this is one of the sites where the parameters have been measured over a long time frame (12 years: 1990/91 to 2001/02). Recently, Clarke et al. (2002) analysed the relationships between a selection of CEMP parameters (population size, breeding success, foraging trip duration and diet) over eight successive seasons from 1990/91 to 1998/99. They found that breeding success was negatively correlated with female foraging trip duration during the guard phase. Their analysis is extended in this paper by including a wider range of CEMP parameters over a longer time frame (arrival weight, population size, breeding success, incubation shift duration, foraging trip duration during chick rearing and fledgling weight).

Additional data on Adélie penguin weight and direction of movement between the sea and the colony is obtained on Béchervaise Island from an Automated Penguin Monitoring System (APMS) (see Kerry et al. (1993) for details on the APMS). Penguin weights for the population at different periods within a season were examined with the notion that interannual differences between weights within a breeding season are likely to reflect some aspect of resource availability during that season. Irvine et al. (2000) reported that chick death during the guard stage was due to an inadequate rate of food delivery. It is suggested here that the latter would be reflected in the within-season penguin weights recorded by the APMS. If simple data from the APMS is successful in reflecting likely resource availability and subsequent breeding success, then it may provide a useful tool for increasing the number of field site locations within reasonable logistical limits.

The aim of this study was to examine the extent of temporal (between and within breeding season) variation of the CEMP parameters and the interrelationships between CEMP parameters over time. The degree of correlation between breeding success and parameters was of particular interest because it may directly indicate resource availability, such as within-season weights, incubation shift duration and foraging trip duration during chick rearing.

METHODS

General

Data collection for all parameters followed Standard Methods A1 to A9 prescribed by CCAMLR for CEMP data (CCAMLR, 2003). Within-season weights were recorded for birds tagged with implanted identification transponders as they crossed the APMS on their way into and out of the colony. The sex of tagged birds had previously been determined by cloacal examination. Ill effects of transponders were considered minimal (Clarke and Kerry, 1998); transponders were used instead of flipper bands to avoid any deleterious effects associated with banding (Ainley et al., 1983; Culik et al., 1993; Jackson and Wilson, 2002). Data included in the analyses presented in this paper are for Adélie penguins on Béchervaise Island (67º35'S 62º49'E), for the 1990/91 to 2001/02 seasons. There are approximately 2 000 breeding pairs of Adélie penguins on this island (Kerry et al., 2000). For consistency, a similar subset of years was examined in the correlation matrix analyses. This meant that some years were excluded from the analysis because a particular parameter had not been collected.

Data were analysed using a three-stage procedure to examine between-season variability of CEMP parameters and within- and between-season variability of APMS penguin weights. The first stage focused on data collected as whole-island counts (arrival, nest and chick counts). Additional parameters, namely foraging trip duration, penguin arrival weight and incubation shift duration, were included in the second stage of the analysis. The within-season weights recorded by the APMS were included in the third stage of the analysis. These within-season weights were correlated with breeding success and fledgling mass. In all cases, breeding success was defined as the number of chicks crèched per nest with eggs.

Annual Population Size, Nest Counts and Chick Counts

The initial analysis involved whole-island counts of population size (A3 and A9) and breeding success parameters (A6), including counts of arriving birds, the number of occupied nests, mid-incubation count of all nests with eggs, brooding nest count during early guard/late incubation, a chick count when two thirds of the chicks had crèched and the total number of crèched chicks. Data used in these analyses were from the 1991/92 to 2001/02 seasons. Data were analysed using a Friedman two-way analysis on ranks to determine whether parameters fluctuate similarly through time. A Spearman–Rank correlation matrix was constructed to determine the strength of pairwise correlations between parameters, in particular those represented by temporally adjacent data points. In all analyses, correlations with $r > 0.7$ were considered to be strong (Chatfield and Collins, 1980) rather than specifying statistical significance due to the large number of multiple comparisons being made. In this case, attention was specifically given to parameters which are most strongly correlated rather than to statistical significance. Presenting correlation strengths without attaching statistical significance is standard in population studies where multiple correlations are performed (e.g. Thomas, 1991).

Arrival Weights, Incubation Shifts, Foraging Trip Duration and Fledgling Mass

A Friedman two-way analysis on ranks was performed and a Spearman–Rank correlation matrix was constructed (as described in the previous section) on an additional series of CEMP parameters. These analyses were performed to investigate the temporal variability of CEMP parameters, including those collected on individuals within the population rather than just whole-island counts. The additional parameters include arrival weights (A1) for male and female penguins, foraging trip duration for each sex during the guard and crèche periods (A5), incubation shift duration (A2) and fledgling weights (A7). Where appropriate, the mean for each parameter for male and female birds was calculated and used in the Friedman analysis of ranks. Foraging trip duration data were initially $\log_e$ transformed because the data were highly skewed. Mean trip duration for each bird was calculated and a pooled mean across birds used in this analysis. A Spearman–Rank correlation matrix was constructed to determine which pairs of parameters were most highly correlated, both with each other and with breeding success. Once again, correlations within the correlation matrix with $r > 0.7$ were considered to be strong, but the P values for correlations with breeding success were also reported. The mean standard deviation (SD) and coefficient of variation (CV) were also calculated to determine which parameters displayed the most temporal variability.

Temporal Variation of Adult Penguin Weights measured by the APMS

The within- and between-season penguin weights were examined to determine whether penguin weight at different times within a season is correlated with breeding success, fledgling mass and incubation shift duration. Penguin weights for male and female tagged birds were obtained from APMS data or from manual weights when the APMS was not working during the arrival part of the breeding season. Weight data were extracted for periods within each breeding season related to season-specific chronological events (Table 1) to examine their correlation with breeding success. Data were collected from all tagged adult birds. These birds were likely to be breeding birds as their movements in and out of the colony reflected those of breeders and, furthermore, non-breeders generally arrive later in the season (Ainley et al., 1983; Kerry, unpublished data).

Three periods within the breeding season were used to compare between-season and within-season weights: female arrival, female departure after egg laying and female return after feeding at sea (after the first foraging trip – FFT) (Davis, 1988); male arrival, male departure after the females return, and male return after its departure to sea (after the second foraging trip – SFT) (Davis, 1988). Figure 1 shows weight data for penguins crossing the APMS for a typical breeding season, with periods of interest indicated. These periods were used because they represent penguin condition at the beginning of the year, the decline in condition of the females until egg laying, the decline in condition for males until they are relieved, and the ability of both sexes to regain weight during the FFT (females) and the SFT (males) after their partner has relieved them from nest duties. As such, penguin weights during these stages are likely to reflect resource availability to adults and fitness to raise their chicks.

Since chronological events varied between breeding seasons in terms of both timing and duration, data were extracted according to specific periods in the breeding cycle (Table 1 and Figure 1), namely (a) arrival: the 10 days following the first arrivals recorded for males and females, (b) female departure: 10 days prior to the last female departure to begin the FFT, (c) female return/male departure: 10 days after the return of the first female from the FFT, male departure indicates male beginning SFT, and (d) male return: 10 days after the return of the first male from the SFT. The first male returned relatively early in three of the seasons and the data collection period was increased to 20, 15 and

Table 1: Dates of chronological events within seasons of first arrival, first egg laid, first and last female departure for first foraging trip, first and last female return from first foraging trip, first male departure for second foraging trip, last male return from second foraging trip, and estimated first fledging for each season. The letters (a) to (d) correspond with similarly labelled events in Figure 1.

Season	First Arrival Date (a)	First Egg Laid	First Female Departs	Last Female Departs (b)	First Female Returns (c)	Last Female Returns	First Male Departs	First Male Returns (d)	First Fledgling
1	22/10/1990	14/11/1990	17/11/1990	30/11/1990	05/12/1990	20/12/1990	25/11/1990	18/12/1990	18/2/1991
2	25/10/1991	19/11/1991	22/11/1991	09/12/1991	08/12/1991	26/12/1991	8/12/1991	22/12/1991	20/2/1992
3	23/10/1992	16/11/1992	20/11/1992	04/12/1992	07/12/1992	30/12/1992	26/11/1992	8/12/1992	16/2/1993
4	18/10/1993	12/11/1993	16/11/1993	02/12/1993	01/12/1993	19/12/1993	30/11/1993	15/12/1993	12/2/1994
5	16/10/1994	13/11/1994	17/11/1994	30/11/1994	02/12/1994	18/12/1994	2/12/1994	6/12/1994	-
6	22/10/1995	16/11/1995	21/11/1995	09/12/1995	05/12/1995	24/12/1995	5/12/1995	18/12/1995	10/2/1996
7	16/10/1996	11/11/1996	13/11/1996	26/11/1996	30/11/1996	17/12/1996	29/11/1996	14/12/1996	12/2/1997
8	17/10/1997	14/11/1997	16/11/1997	30/11/1997	03/12/1997	20/12/1997	21/11/1997	20/12/1997	17/2/1998
9	18/10/1998	13/11/1998	15/11/1998	29/11/1998	03/12/1998	19/12/1998	26/11/1998	19/12/1998	15/2/1999
10	20/10/1999	13/11/1999	18/11/1999	02/12/1999	07/12/1999	21/12/1999	29/11/1999	19/12/1999	19/2/2000
11	18/10/2000	14/11/2000	17/11/2000	02/12/2000	04/12/2000	04/01/2001	30/11/2000	14/12/2000	13/2/2001
12	16/10/2001	11/11/2001	12/11/2001	01/12/2001	02/12/2001	16/12/2001	21/11/2001	12/12/2001	12/2/2002

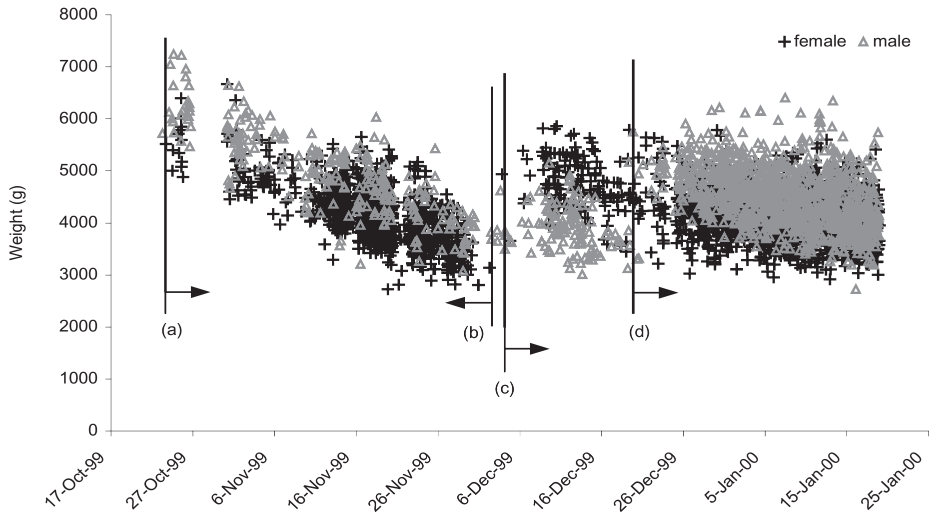

Figure 1: Automated penguin monitoring system weights of male and female crossings during the early part of the 1999/2000 breeding season. Vertical lines and arrows indicate period of data extraction for within-season weights during: (a) arrival, (b) female departure, (c) female return/male departure, and (d) male return.

25 days for seasons 1992/93, 1993/94 and 1994/95 respectively to ensure that a representative number of penguin weights were included in the analysis.

Within-season penguin weights recorded by the APMS were correlated with breeding success and fledgling mass. In addition, the relationship between within-season weights and incubation shift durations were examined by means of a correlation matrix. Once again, correlations where $r > 0.7$ were considered strong. These relationships provide information regarding the condition of penguins after the first and second incubation shifts and the duration of each shift.

RESULTS

Annual Population Size, Nest Counts and Chick Counts

There was a significant degree of temporal correlation between the whole-island count CEMP parameters (A3, A6, A9) (Friedman two-way analysis of ranks: $\chi^2 = 37.142$, $W = 0.619$, $n_{\text{variables}} = 6$, $n_{\text{years}} = 11$, $\chi^2\text{crit.}_{(0.05,10)} = 18.307$) (Figure 2). This result suggests that at least some of the parameters fluctuate similarly over time. The average correlation between parameters was reasonably high with $r_{\text{ave}} = 0.581$. The Spearman–Rank correlation matrix shows two groups of parameters which are correlated more strongly within the groups than between the groups (Table 2). The first group consists of the initial three parameters: arrival counts (A9), occupied nest counts and the number of incubating nests (A3), while the second group consists of the final three parameters: the number of nests with brooding chicks through to the number of fully crèched chicks (A6). In all cases, the correlations are positive, indicating that an increase in one parameter was reflected by an increase in the other. The correlation between the number of incubating nests and the number of nests in which adults were brooding chicks is the weakest between temporally adjacent counts throughout the season ($r = 0.62$) (Table 2). There was greater temporal variation in counts performed later in the season (brooding nest counts, counts of chicks when two-thirds were crèched and fully crèched chick counts: CV > 30%) (Figure 2 and Table 3) compared with counts near the beginning of the season (population size and the number of occupied and incubating nest counts: CV < 10%) (Figure 2 and Table 3).

Arrival Weights, Incubation Shifts, Foraging Trip Duration and Fledgling Mass

There was significant correlation between the CEMP parameters of incubation shift duration (A2), foraging trip duration (A5), arrival weights (A1) and fledgling mass (A7) as well as the whole-island counts (A3, A6, A9) listed in the previous section (Friedman two-way analysis of ranks: $\chi^2 = 29.33$, $W = 0.19$, $n_{\text{variables}} = 15$, $n_{\text{years}} = 10$, $\chi^2\text{crit.}_{(0.05,9)} = 16.919$; analysis not including breeding success). The average correlation between parameters was much lower than for the whole-island count data alone

Table 2: Spearman–Rank correlation matrix between pairs of CEMP parameters based on whole-island counts between 1991/92 and 2001/02. Parameters arranged in temporal order, from arrival counts occurring at the beginning of the breeding season through to fully crèched chick counts. Bold *r* values show correlations between temporally adjacent parameters, shaded squares represent correlations where $r > 0.7$.

		Arrival Counts (A9)	Occupied Nests	Incubating Nests	Brooding Nests	2/3 Crèched Chicks
A3	Occupied nests	**0.70**				
A3	Incubating nests	0.69	**0.93**			
A6	Brooding nests	0.22	0.58	**0.62**		
A6	Two-thirds crèched chicks	0.25	0.35	0.42	**0.86**	
A6	Fully crèched chicks	0.10	0.28	0.37	0.83	**0.96**

Table 3: Temporal mean, standard deviation (SD), sample size (*n*) and coefficient of variation (CV) for breeding success and population size parameters between 1990/91 and 2001/02. $n = 11$ indicates 1990/91 data not available. CVs above 30% are shown in bold.

	Mean	SD	*n*	CV (%)
Arrival counts	3839	341.43	12	8.89
Occupied nests	1925	150.2	12	7.80
Incubating nests	1936	168.5	12	9.18
Brooding nests	1276	436.8	11	**34.23**
Two-thirds crèched chicks	1297	597.5	12	**46.09**
Fully crèched chicks	1296	605.7	12	**46.75**

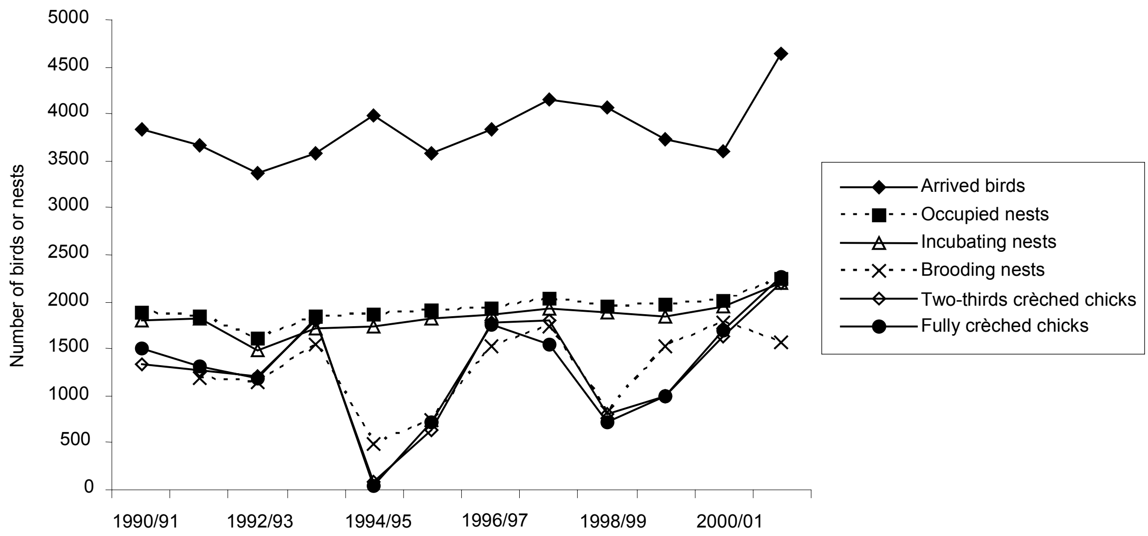

Figure 2: Temporal variation in CEMP whole-island count parameters. Parameters listed in order of timing throughout the breeding season starting from arrival counts through to fully crèched chick counts at the end of the season.

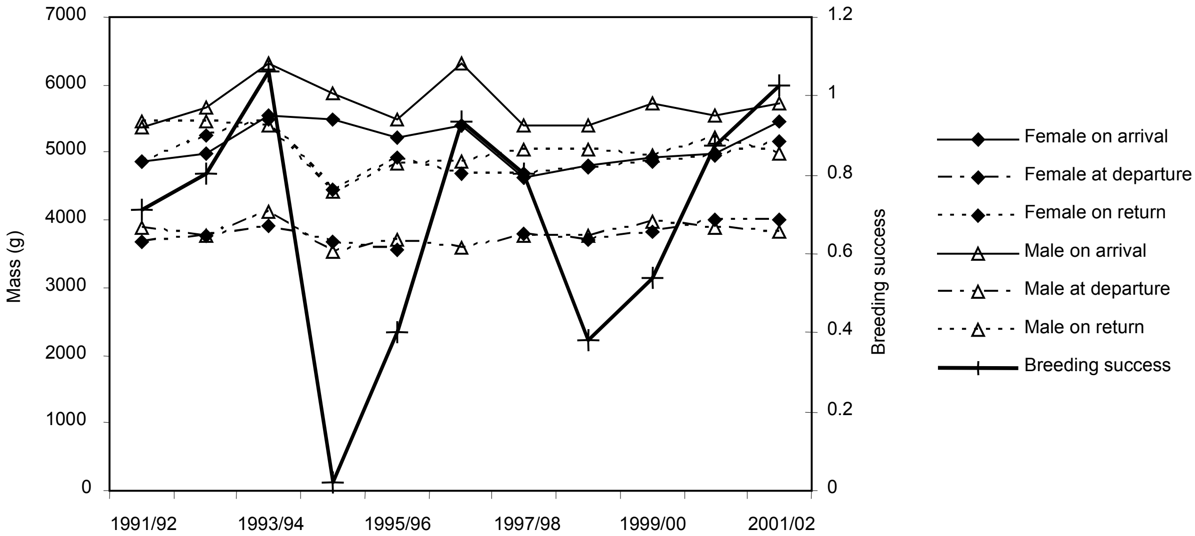

Figure 3: Average weight of male and female penguins at arrival, on departure for first and second foraging trips and on return from these foraging trips and the corresponding breeding success for the season.

with r_{ave} = 0.10. There were strong negative correlations between female guard foraging trip duration and breeding success and also between the second incubation shift duration and breeding success (Table 4). Male and female arrival weights were positively correlated (Spearman–Rank correlation: r = 0.80) indicating that between-year weight fluctuations at the beginning of the breeding season were reflected across the population. Most measures of foraging trip durations during chick rearing were strongly correlated (r > 0.7 for all but female guard and male crèche with r = 0.67) indicating that an increase in any particular component of foraging trip duration (e.g. female foraging trip duration during the crèche period) would correspond to an increase in the other measures. First and second incubation shifts were weakly correlated (r = 0.45). Fledgling mass was most strongly (and negatively) correlated with male crèche foraging trip duration (r = -0.64).

In general, the CVs for the additional CEMP parameters were low (<10%) (Table 5) except for breeding success (number of chicks per nest with eggs) and fledgling mass (CV = 43.98% and 34.31% respectively). In terms of penguin mass, the average male and female arrival weights varied between 5 377–6 321 g (males) and 4 634–5 535 g (females). Likewise, the between-year average fledgling mass varied between 3 012 and 3 944 g. The 1994/95 fledgling mass was given the lowest rank for data analysis as no chicks survived to fledge that year.

Temporal Variation of Adult Penguin Weights measured by the APMS

There was a decrease in the return weights of both female and male penguins after the FFT and SFT respectively during the 1994/95 incubation period when the breeding success for the population was very low (Figure 3). In contrast, the weight of birds returning after the FFT and SFT during the season of low breeding success of 1998/99 showed no decrease (Figure 3). Breeding success was strongly correlated with return weights of females after the FFT (Spearman–Rank correlation: $r = 0.72$, $P < 0.05$) (Table 6).

Of all the within-season weights examined, female departure weights for birds leaving for the FFT after egg laying were most strongly correlated with breeding success ($r = 0.76$) (Table 6). In contrast, breeding success was weakly correlated with male and female arrival weights at the beginning of the season (r < 0.24) (Table 6). Of all the within-season weights, fledgling mass was most strongly correlated with female return (after FFT) and male departure weights (r = 0.48 and 0.39 respectively) (Table 6).

The weight of females returning from the FFT was strongly and negatively correlated with the duration of the second incubation shift (r = -0.84) (Table 7). Therefore, if the females return heavy, their following incubation shift is likely to be shorter. In contrast, if they return light then their incubation shift is likely to be of a longer duration. The weight of females returning from the FFT

Table 4: Spearman–Rank r correlation matrix between pairwise combinations of parameters for foraging trip duration during chick rearing, incubation shift, arrival weights and breeding success (shown in bold). Lightly shaded squares represent positive correlations where $r > 0.7$, while heavily shaded squares indicate negative correlations where $r > 0.7$.

	CEMP Parameter	Arrival Weights (A1)		Incubation Shift		Guard Foraging Trip		Crèche Foraging Trip		Fledgling Mass
		Female	Male	First	Second	Female	Male	Female	Male	
A1	Arrival weights male (g)	0.80								
A2	First incubation shift (days)	-0.39	-0.29							
A5	Second incubation shift (days)	-0.33	-0.25	0.45						
A5	Female guard foraging trip (hours)	-0.20	-0.04	0.72	0.62					
A5	Male guard foraging trip (hours)	-0.43	-0.18	0.62	0.34	0.87				
A5	Female crèche foraging trip (hours)	-0.15	0.13	0.50	0.44	0.85	0.85			
A5	Male crèche foraging trip (hours)	-0.13	0.19	0.43	0.40	0.67	0.70	0.87		
A7	Fledgling mass (g)	0.24	0.03	-0.07	-0.45	-0.21	-0.14	-0.42	-0.64	
	Breeding success (chicks per nests with eggs)	**0.35**	**0.40**	**-0.30**	**-0.78**	**-0.72**	**-0.55**	**-0.60**	**-0.30**	**0.28**
	P value	0.30	0.23	0.37	0.01	0.03	0.11	0.07	0.41	0.40

Table 5: Temporal mean, minimum, maximum, standard deviation (SD), sample size (n) and coefficient of variation (CV) for each parameter from 1990/91 through to 2001/02 for $n = 12$. $n = 11$ indicates 1990/91 data absent, $n = 10$ indicates 2001/02 data absent. CVs above 30% are shown in bold. Note that foraging trip duration was $\log_e$ transformed prior to analysis.

	Mean	Minimum	Maximum	SD	n	CV (%)
Arrival weights female (g)	5119	4634.27	5534.57	312.9	11	6.11
Arrival weights male (g)	5713	5377.27	6321.20	338.1	11	5.92
First incubation shift (days)	17.36	16.20	18.40	0.6443	12	3.71
Second incubation shift (days)	14.25	12.60	15.60	0.9159	12	6.43
ln female guard foraging trip (hours)	3.651	3.39	4.15	0.2519	10	6.90
ln male guard foraging trip (hours)	3.257	3.00	3.53	0.1711	10	5.25
ln female crèche foraging trip (hours)	3.576	3.04	4.00	0.2662	10	7.44
ln male crèche foraging trip (hours)	3.4	3.05	4.00	0.2895	10	8.52
Fledgling mass (g)	3017	0.00	3944.00	1035	11	**34.31**
Breeding success (chicks per nests with eggs)	0.70	0.02	1.06	0.3077	12	**43.98**

Table 6: Spearman–Rank correlations and associated P values for correlations between within-season penguin weights and breeding success and fledgling mass. Shaded cells indicate statistically significant correlations. $n = 10$ in all cases, FFT – first foraging trip, SFT – second foraging trip.

	Male Arrival	Female Arrival	Female Departs on FFT	Female Returns from FFT	Male Departs on SFT	Male Returns from SFT
Breeding success	0.24	0.24	0.76	0.72	0.66	0.49
P value	0.514	0.514	0.015	0.023	0.044	0.166
Fledgling mass	0.13	0.33	0.25	0.48	0.39	0.22
P value	0.733	0.349	0.492	0.166	0.263	0.607

Table 7: Spearman–Rank r correlation matrix between pairwise combinations of parameters for within-season weights (g) and incubation shift duration (days). Lightly shaded squares indicate positive correlations where $r > 0.7$, while heavily shaded squares indicate negative correlations with $r > 0.7$. FFT – first foraging trip, SFT – second foraging trip.

	Arrival Weights		Female Departs on FFT	First Incubation Shift Duration	Female Returns from FFT	Male Departs on SFT	Second Incubation Shift Duration
	Female	Male					
Arrival weights male	0.78						
Female departs on FFT	0.20	0.43					
First incubation shift duration	-0.41	-0.16	-0.02				
Female returns from FFT	0.47	0.30	0.43	-0.67			
Male departs on SFT	0.02	0.20	0.66	-0.10	0.42		
Second incubation shift duration	-0.38	-0.30	-0.65	0.45	-0.84	-0.37	
Male returns from SFT	-0.26	-0.33	0.15	-0.50	0.52	0.43	-0.32

Table 8: Temporal mean, standard deviation (SD), sample size (n) and coefficient of variation (CV) of within-season weights at different times within the arrival and incubation periods of the breeding season. There were no weights recorded for female penguins during the departure period in the 1996/97 breeding season. All weight values measured in grams.

	Mean	Minimum	Maximum	SD	*n*	CV (%)
Male on arrival	5713	5377	6321	338.08	11	5.92
Female on arrival	5119	4634	5535	312.90	11	6.11
Female at departure for FFT	3785	3550	3995	146.16	10	3.86
Female on return from FFT	4916	4443	5474	287.69	11	5.85
Male at departure for SFT	3800	3526	4115	163.84	11	4.31
Male on return from SFT	4894	3903	5468	493.92	11	10.09

was also moderately negatively correlated with the duration of the first incubation shift (r = -0.67) (Table 7). This essentially suggests that the longer the females are away, the greater their weight gain. This study does not consider how an extended period away from the nest affects chick survival.

The within-season penguin weights all had coefficients of variation of less than 11% (Table 8). This is associated with a between-season difference of up to just over 1 kg in the average weights of penguins at any particular part of the breeding season (minimum and maximum average values shown in Table 8). The departure weights for birds leaving for the FFT and SFT showed the least temporal variation of all the within-season weights considered.

DISCUSSION

One of the most obvious results from these analyses is the lack of correlation between early season counts of population size and later measures of breeding success. These results are consistent with the findings of Trathan et al. (1996) who suggest that factors influencing breeding population size and condition are mostly independent of those influencing breeding success. This is primarily because breeding population size is affected by factors occurring between breeding seasons over a large area while factors affecting breeding success occur within the breeding season and are restricted to the area around the breeding colony. Events that occurred between the incubating nest counts (early December) and the brooding nest counts (early January) were critical for subsequent breeding success of Adélie penguins at Béchervaise Island. This corresponds to the time during the second half of incubation or shortly after hatching. Factors resulting in chick failure include a lack of coordination between partners in feeding chicks, failure of birds to return on time from the FFT or SFT, adults treading on chicks, parent foraging ability, and predation by skuas (Davis and McCaffrey, 1986). It is likely that new hatchlings which emerge between these counts are particularly vulnerable to limited food supply as only one parent forages while one is attending the nest (Irvine et al., 2000).

Clarke et al. (2002) report that breeding success was lower in years where the foraging trip durations of female birds during the guard period were long. This pattern persists when examining a longer time series. Clarke et al. explain this by the parents' increased time at sea resulting in a decreased chick feeding frequency and therefore a lower survival rate of chicks (Clarke et al., 1998, 2002; Irvine et al., 2000). Factors affecting foraging trip duration include food abundance, its availability at sea and the extent to which sea-ice cover reduces travelling efficiency to and from foraging grounds. The effects of sea-ice extent however, appear to be site-specific and are confounded by its variability through time and space (Fraser et al., 1992; Trathan et al., 1996; Kato et al., 2002). Essentially, a complex interaction of many factors affects the overall availability of food for chicks and, ultimately, breeding success. While the importance of the effects of sea-ice extent on penguin populations is well recognised, its relationship with breeding success at Béchervaise Island deserves further exploration.

Foraging trips earlier in the breeding season were more important for chick survival whereas later foraging trips were important for fledgling mass. This makes sense as foraging trips during the crèche period were the closest trip duration measure to the time of fledging, and resources available at that time are most likely to indicate resources available for final chick weight gain before fledging. Foraging trip durations during chick rearing were all strongly correlated irrespective of timing or sex of bird. If foraging trip duration does indeed reflect resource availability, then shortages which impact on breeding success appear to last throughout the guard and crèche stages rather than fluctuating strongly between those periods. These results suggest that foraging trip duration, particularly that of females during the guard stage, may be useful as an indicator of breeding success. However, the complex interaction between breeding success, foraging trip duration and environmental variables indicates that environmental variables should also be considered (Fraser et al., 1992).

Within- and Between-Season Differences in Adult Penguin Weight

Both within- and between-season variations in penguin weights are apparent and may be explained to some extent by resource availability. While the weight of penguins at certain stages within a breeding season is correlated well with breeding success, other parameters are not. For example, breeding success was not related to the arrival weights of penguins. This result implies that the availability of sufficient food for chicks during the breeding season was more important than the condition of parents when they arrive for the breeding season. However, penguin condition at arrival and the size of the breeding population may influence the total number of chicks that hatch. Both of these aspects of the breeding population are likely to depend on regional sea-ice conditions and food availability outside the breeding season

(Trathan et al., 1996). Unfortunately the information needed to explore this relationship for the Béchervaise Island Adélie penguin population is not available.

Breeding success was strongly correlated with both female and male departure weights at the beginning of the FFT and SFT respectively. Low departure weights for females may indicate a late breeding season which often equates to a subsequently low breeding success (Davis, 1982). The departure weight of females leaving for the FFT after egg laying was the first indication that breeding success for that season might be low. Birds with lower departure weights are likely to require longer foraging trips to regain condition. However, if the foraging trip duration is too long, egg failure may occur because the bird did not return in time to relieve its partner from nest duties.

Failure during the incubation period usually occurs during the first incubation shift when males lose condition and depart before the female partner returns (Davis, 1982). This was reflected in the data by the patterns of correlation between the weight of female penguins when they returned from the FFT and the duration of both the first and second incubation shift. Shorter incubation shifts for males were associated with heavier weights of females returning from the FFT. Additionally, if females returned in good condition, their following incubation shift (the second incubation shift) was typically shorter. These patterns can surely be explained by resource availability determining both the length of foraging trip duration during the incubation period and penguin weight on arrival at the breeding colony after foraging.

Although weight gains during foraging trips are likely to reflect resource availability, this simple relationship can be confounded by the amount of time spent away from the nest. Explanations for the lack of correlation between male return weights after the SFT and breeding success include: (i) data on weight derived from birds measured at breeding sites are biased by the tendency for only those birds who obtained sufficient food at foraging sites to return to their breeding sites, (ii) birds that do return with substantial meal sizes may do so after the partner has left and the egg has failed, which would not be reflected in the APMS weight records, or (iii) limited resource availability occurs in the post-hatch period rather than the earlier stages that are critical to chick survival. However, these possibilities can only be explored with detailed knowledge on individual penguins and are not as easy to obtain as population weights from the APMS. It might be more instructive to examine within-season weights after chick hatching rather than during the incubation period alone so that adult penguin weight gains could be related to food available to chicks. This may be problematic for population level APMS-collected data as nest duty shift changeovers are poorly defined in the post-hatch period.

CONCLUSIONS

Breeding success at Béchervaise Island was found to be strongly correlated with parent foraging trip duration, parent body mass at departure for the first and second incubation stage foraging trips, and the number of brooding nests in the colony. Foraging trip duration, return bird weights and environmental variables such as sea-ice extent may need to be considered simultaneously to obtain a better understanding of their relationship with breeding success. This may best be reflected in APMS data if considered at the level of an individual bird. Birds that do not return to the colony within the breeding season may fail to do so because of limited resources. If the non-returning birds are the key to explaining between-year breeding success, then interpreting weights at a population level as a monitoring parameter may be problematic.

The extent to which insights can be gained into the appropriateness of the current CEMP data is constrained by the absence of data on food abundance. Without such data we can merely observe how well various response parameters correlate with each other. As the data are derived from an observational study as opposed to a manipulative experiment, the frequency and magnitude of perturbations to the system were unable to be controlled. Given that within the 12 years of the study there has been only one major breeding failure, our ability to understand the interactions and relationships, which are likely to be complex, is limited. Much of the data examined in this paper was obtained from the APMS for sexed birds, and the results indicate that knowledge of the sex of birds contributes to the understanding of penguin breeding success. Additional field sites are required to examine the observed relationships and their generality over a broader spatial extent.

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