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WEIGHT LOSS IN INCUBATING ALBATROSSES AND ITS IMPLICATIONS FOR THEIR ENERGY AND FOOD REQUIREMENTS

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ABSTRACT.—The weight loss of incubating Black-browed Albatrosses (*Diomedea melanophris*) and Grey-headed Albatrosses (*D. chrysostoma*) was measured at Bird Island, South Georgia. The rate of weight loss did not differ significantly either between the sexes or between the species. The results suggest that these two species have the same metabolic requirements. The difference in the quality of their diet leads to estimates of daily food intake considerably higher for the Grey-headed than for the Black-browed albatross. This may have been a factor in the evolution of biennial breeding in the Grey-headed Albatross.

The Black-browed Albatross (*Diomedea melanophris*) and Grey-headed Albatross (*D. chrysostoma*) are widely distributed in the subantarctic zone. Their breeding biology (Tickell and Pinder 1975) and food and feeding ecology (Prince 1980) have been extensively studied at South Georgia. The timing and duration of events in their breeding cycle are similar although Grey-headed Albatrosses take approximately six weeks longer to complete the cycle. The chicks of the two species grow at different rates (Ricketts and Prince, in press), possibly as a result of difference in diet. The Black-browed Albatross feeds mainly on krill and fish whereas the Grey-headed Albatross feeds principally on squid; krill have a higher energy content (Grantham 1977) than squid (Voss 1973).

The basic energy requirements of birds are closely related to their weight. Black-browed and Grey-headed albatrosses are similar in size and weight but the different energy content of their food suggests that they may have different energy requirements. We therefore studied the rate of weight loss in incubating birds to assess whether there is any indication of a metabolic difference between these two species.

METHODS

The weights of 31 pairs of Grey-headed Albatross and 30 pairs of Black-browed Albatross from two separate colonies at Bird Island, South Georgia (54°00′S, 38°03′W) were measured every two days during the incubation period, starting in late October 1978 and continuing until hatching. The technique employed to weigh each incubating albatross involved one person lifting the bird by hand a few inches above its egg and nest while a hoop of wire covered with nylon netting was placed over the egg and nest. The albatross was then lowered onto its egg and, after it had settled, lengths of nylon line were attached to the wire hoop, drawn upwards above the bird and attached to a 5-kg Pesola balance. The incubating albatross was then gently lifted from its egg until clear of the nest and its weight recorded. The bird was not restrained and if it became agitated it was quickly lowered onto the nest. Eighteen of the Grey-headed and 20 of the Black-browed albatrosses were each recaptured once and weighed immediately after feeding their chick.

The sexes of either species are indistinguishable in the field. We could not be present before egg-laying so each bird's sex was determined from the incubation routine and behavioral characteristics. The first incubation shift is by the female and is significantly shorter than the next shift, by the male, which lasts for up to 25 days (Tickell and Pinder 1975). The laying date was calculated from the observed hatching date and known incubation period for each species. The bird taking the first long shift after the laying date was assumed to be the male. When the incubation routine of any pair did not follow the established pattern the birds were excluded from the study.

Incubation shifts with less than four weighings were not analyzed. Weight loss during each shift could be described as an exponential function of time, $W_t = W_0 e^{-kt}$, where W_t is the weight t days from the start of the shift, W_0 is the weight at the start of the shift and k is the proportion of the bird's weight lost each day. For every incubation shift the bird's initial weight, W_0, and the rate of loss, k, were estimated by regression of the logarithm of weight against time. The slopes of the individual regressions for birds of each sex in each species were compared by standard techniques. The common slopes for these four groups of birds were similarly compared.

RESULTS

WEIGHT LOSS DURING AN INCUBATION SHIFT

The rate of weight loss ranged from 0.5 to 3.5%/d over the 83 incubation shifts analyzed. Individuals of each sex and species

TABLE 1. Rate of weight loss in incubating albatrosses calculated from the regression of the logarithm of weight against time for 83 incubation shifts.

Species	Sex	No. of shifts	No. of weighings	Range of rates	Pooled rate	F	
Grey-headed Albatross	F	19	98	.005–.025	0.012	0.01	$P > 0.10$
	M	22	118	.008–.023	0.010	0.01	$P > 0.10$
Black-browed Albatross	F	19	88	.007–.035	0.011	0.01	$P > 0.10$
	M	23	125	.008–.029	0.013	0.02	$P > 0.10$

showed a similar degree of variation but did not differ significantly from the pooled slope for their group (Table 1). Moreover, the pooled slope for each sex and species group did not differ from the slope (0.012) common to all the four groups. Thus, both sexes of the two species lost, on average, the same proportion (1.2%) of their body weight each day while incubating (Fig. 1).

WEIGHT CHANGES DURING THE INCUBATION PERIOD

Despite the considerable weight losses incurred during each incubation shift, neither species showed any decline in weight over the whole incubation period (Table 2). In addition, the males of both species were significantly heavier than the females at the beginning and end of shifts.

DISCUSSION

WEIGHT LOSS AND ENERGY REQUIREMENTS

Both Grey-headed and Black-browed albatrosses of both sexes lose the same proportion of their body weight each day during incubation. Because males and females of both species are of different weights they will lose different absolute amounts of weight each day. The loss of weight represents, at least in part, the utilization of stored energy. This energy utilization is the field equivalent of the existence energy requirement (EER) defined by Kendeigh (1970) or the resting metabolic rate (RMR) which Baudinette and Schmidt-Nielsen (1974) suggested was 1.7 times the standard metabolic rate (SMR).

Although the observed weight loss cannot be precisely partitioned into fat, water and protein loss, these measurements do allow calculation of upper and lower limits for the resting metabolisms of these two species. A possible lower limit can be calculated assuming that the weight loss comprised 45% fat, 45% water and 10% protein. These figures are derived from two studies of penguins (Groscolas and Clement 1976, Williams et al. 1977). The upper limit can be calculated assuming that all weight loss represents utilization of fat reserves. Utilization of fat and protein are assumed to liberate 39.7 and 16.7 kJg^{-1} respectively (Petrusewicz and Macfayden 1970). These derived limits are shown in Table 3 together with theoretical calculations of standard metabolic rate (Lasiewski and Dawson 1967) and existence energy requirements for non-passerines at 0°C (Kendeigh 1970). The calculated lower limit for energy requirement is similar to the estimated standard metabolic rate and it therefore seems likely that fat utilization comprised considerably more than 45% of the weight loss. The calculated upper limit is somewhat higher than the estimated existence energy requirement of birds of this size. However, incubation is unlikely to demand much more energy than inactive existence and this suggests that the weight loss is less than 100% fat utilization.

FOOD REQUIREMENTS

Although these two mollymauks appear to have similar metabolic costs, and also wing areas and wing loading (Warham 1977; Pennycuick, unpubl.) and therefore perhaps similar flight costs, this does not imply that the cost of obtaining energy is the same for both species. They take different prey as the major component of their diets: the Grey-headed Albatross takes mainly squid and the Black-browed Albatross takes krill and fish (Prince 1980).

While fish and krill have similar caloric values (4.6 kJg^{-1} wet weight; Grantham 1977) that of squid is probably only 3.3 kJg^{-1} wet weight (Voss 1973). Indeed, assuming that albatrosses mainly glide, the gliding flight consumes about twice the energy used while resting (Bernstein et al. 1973, Tucker 1973, Baudinette and Schmidt-Nielsen 1974) and that the assimilation efficiency from food is 75%, then maintaining energy balance would require 750 g of fish or krill but 1,100 g of squid to be taken each day. In addition, breeding birds during the incubation period have to replenish the reserves consumed during each incubation shift and this will require a similarly greater weight of squid, rather than fish or krill, to be caught.

FIG. 1 A

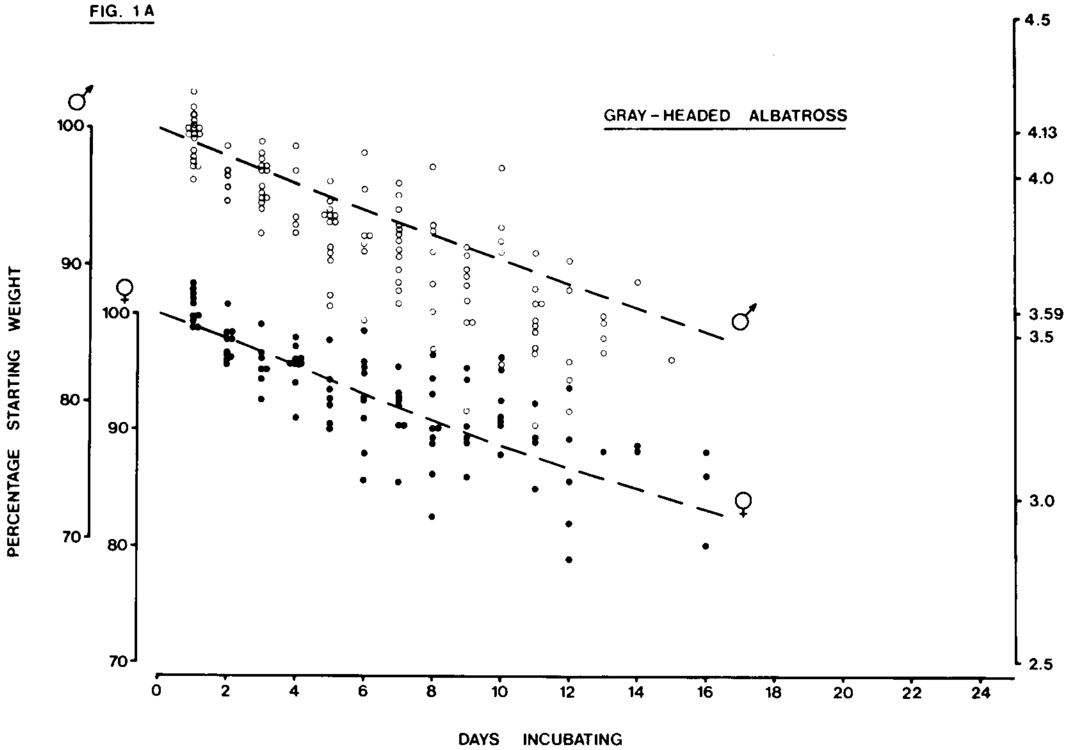

FIG. 1 B

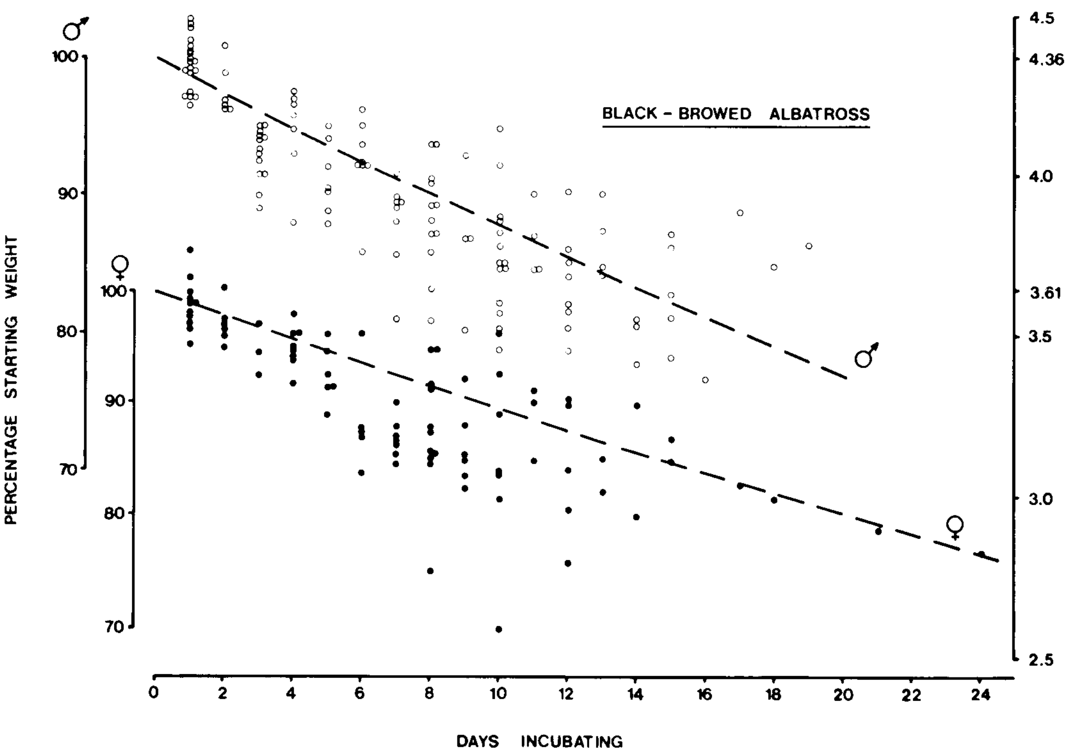

FIGURE 1. Weight loss in male (open circles) and female (closed circles) Grey-headed Albatrosses (A) and Black-browed Albatrosses (B). The data points for each shift are expressed as a percentage of the initial weight (W_0) at the start of that shift estimated from the regression of the logarithm of weight against time. The data from all incubation shifts are plotted together but the dashed lines show the line of pooled slope for all individual shifts. The scale for females is aligned with the scale for males by expressing the mean female starting weight as a percentage of the mean male starting weight. A weight scale is given for comparison on the right of the graph.

TABLE 2. Albatross weights (g) at beginning and end of incubation shifts and the mean duration of each shift.

	Grey-headed Albatross				Black-browed Albatross			
	Female		Male		Female		Male	
Shift	n	Mean SD	n	Mean SD	n	Mean SD	n	Mean SD
1	—	—			—	—		
2			5	4,130 ± 239 3,468 ± 295 13 days			3	4,308 ± 92.3 3,441 ± 240 16 days
3	11	3,565 ± 173 3,107 ± 215 12 days			6	3,532 ± 207 2,866 ± 153 16 days		
4			10	3,991 ± 307 3,470 ± 250 12 days			11	4,289 ± 298 3,623 ± 240 14 days
5	8	3,612 ± 194 3,147 ± 296 12 days			9	3,622 ± 259 3,051 ± 231 12 days		
6			7	4,298 ± 379 3,613 ± 288 10 days			9	4,474 ± 272 3,640 ± 206 11 days
7					4	3,689 ± 165 3,082 ± 136 9 days		

WEIGHT AND BREEDING ABILITY

Body weight is widely recognized to be an important index of condition and breeding ability. The pattern of weight change throughout the breeding season derived from this study and using data for immature and pre-laying birds from Tickell and Pinder (1975) is summarized in Table 4. Because of the small sample sizes in some cases we have not attempted any statistical analysis but merely present our interpretation of the data. Immature birds are lighter than breeding birds: this is consistent with the suggestion of Fisher (1967), Carrick (1972) and Brooke (1978), from work on Laysan Albatrosses (*Diomedea immutabilis*), Royal Penguins (*Eudyptes schlegeli*) and Manx Shearwaters (*Puffinus puffinus*), respectively, that immature birds increase in weight with age and that the onset of breeding is determined, at least in part, by weight.

When breeding birds of both species are attending the nest at the start of the breeding season, they are heavier than during incubation or when rearing the chick. To be able to breed in the next season the birds must reattain their pre-laying weight. After their chicks leave the nest towards the end of April, Black-browed Albatrosses move northwards in South African waters (Tickell 1967), probably because krill are no longer so readily available around South Georgia, but return to breed each year. Grey-headed Albatross chicks grow more slowly (Ricketts and Prince, in press) and they fledge about 30 days later. The adults remain in higher latitudes throughout the winter, probably feeding on squid, which also support the winter-breeding Wandering Albatrosses (*Diomedea exulans*). Grey-headed Albatrosses that are successful in rearing a chick one year do not breed in the following season whereas nearly all the birds that lose

TABLE 3. Calculated and theoretical values for energy consumption in albatrosses.

				Energy consumption (kJ d^{-1})			
				Calculated			
		Average weight (g)	Weight loss (g/day)	Lower limit	Upper limit	Theoretical SMR	Theoretical EER
Grey-headed Albatross							
Adult mid-incubation	M	3,751	45	879	1,791	854	1,423
Adult mid-incubation	F	3,624	43	849	1,724	828	1,393
Black-browed Albatross							
Adult mid-incubation	M	3,922	47	920	1,870	879	1,456
Adult mid-incubation	F	3,694	44	866	1,761	841	1,410

TABLE 4. Weights (g) of immature and breeding albatrosses.

	Male		Female	
	n	Mean	n	Mean
Grey-headed Albatross				
Pre-laying	5	4,100	4	4,061
Incubation period	133	3,751	95	3,264
Chick rearing period	6	3,624	12	3,206
Immature	5	3,166	2	2,854
Black-browed Albatross				
Pre-laying	2	4,488	1	3,806
Incubation period	132	3,922	94	3,206
Chick rearing period	9	3,694	11	3,336
Immature	5	3,470	8	3,166

eggs or young chicks do breed the following year. The longer breeding schedule and lower quality diet of the Grey-headed Albatross may limit its ability to reattain breeding condition outside the breeding season.

Body size and duration of the period of parental care of the chick may be important in determining whether breeding in albatrosses occurs annually or biennially. Fisher (1976) emphasized the similarities between the Laysan and Grey-headed albatrosses but noted that the Laysan Albatross usually breeds each year. However, there are marked differences between these two species. Firstly, although the Laysan Albatross is believed to feed on squid there are no data on the proportion of squid in its diet. Without a detailed analysis of its diet it is easy to underestimate the importance of the more easily digested components such as fish. Secondly, and more important, are the probable differences in the food available to these two species between breeding seasons. The Laysan Albatross inhabits a less seasonal environment than the Grey-headed Albatross and seems to move to areas of high food availability outside the breeding period (Fisher and Fisher 1972). In this latter respect it resembles the annually-breeding Black-browed Albatross. The Grey-headed Albatross, in contrast, inhabits an intensively seasonal environment throughout the year and the Antarctic winter is a period of markedly reduced food availability. It therefore seems likely that a major determinant of breeding frequency is food availability during the non-breeding part of the year.

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