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Brood-guarding duration in black-browed albatrosses *Thalassarche melanophris*: temporal, geographical and individual variation

Paulo Catry, Richard A. Phillips, Isaac P. Forster, Rafael Matias, Miguel Lecoq, José P. Granadeiro and Ian J. Strange

P. Catry (paulo.catry@gmail.com), Eco-Ethology Research Unit, ISPA, Rua Jardim do Tabaco 34, PT–1149-041 Lisboa, Portugal. – R. A. Phillips and I. P. Forster, British Antarctic Survey, Natural Environment Research Council. High Cross, Madingley Road, Cambridge CB3 0ET, UK. – P. Catry, R. Matias, M. Lecoq and I. J. Strange, New Island Conservation Trust. New Island, Falkland Islands. – J. P. Granadeiro, CESAM, Museu Nacional de História Natural, Universidade de Lisboa, Lisboa, Portugal.

In birds, the period spent brooding or guarding young chicks is highly variable, but such variation has seldom been studied. Previous single-year studies of Antarctic petrels *Thalassoica antarctica* and grey-headed albatrosses *Thalassarche chrysostoma* revealed a pronounced seasonal decline in brood-guarding duration and gave rise to the 'synchronisation hypothesis', which suggests that some of the variation in the length of the brood-guarding stage is related to predictable seasonal changes in the risk of chick predation. We tested the predictions of this and three other hypotheses in a two-site, four-year study of the black-browed albatross *T. melanophris*. The existence of a pronounced seasonal decline in brood-guarding duration was apparent at both sites, and in years of contrasting food availability, providing further support for the 'synchronisation hypothesis'. Alternative explanations for this pattern are that short brood-guarding periods for late-hatched chicks result from a seasonal decline in food availability or from the fact that early nesting birds are of higher individual quality. However, these explanations are at odds with the absence of a seasonal decline in early chick growth or in probability of chick survival. Furthermore, adult quality (measured as past reproductive performance) had a weak and inconsistent effect on the duration of brood-guarding. Weather changes explained some of the variation in brood-guarding, but there were no differences between regions of contrasting climates. Individual pairs displayed a degree of inter-annual consistency in brood-guarding duration and, at least in some years, longer brood-guarding resulted in higher fledging probability. We speculate that a higher investment in brood-guarding increases the cost of reproduction, which counteracts other selective pressures that would otherwise lead to longer brood-guarding durations.

In virtually all birds, chicks are almost continuously attended by one parent during the first days of life (Düttman et al. 1998). Despite its universality, surprisingly little is known about the fine details of function and regulation of this behaviour. For example, although it is clear that brooding of the offspring provides obvious advantages to heterothermic young (Visser 1998), it is less clear whether the adult's attendance is also important for other reasons. Brooding can be an energy-saving mechanism for young chicks that, although potentially homoeothermic, can only maintain internal temperature through a substantial raise in metabolic rate (Pearson 1998, Schekkerman et al. 2003). However, continuous parental attendance may also be a strategy for the provision of frequent small meals to chicks with a very small stomach capacity, a defence against predators or aggressive neighbours, or a way to ensure that chicks can be protected to a large extent from the elements in case of a spell of bad weather (Weathers et al. 2000, Brodin et al. 2003, Lewis et al. 2004, Catry et al. 2009).

Because parents attending altricial chicks cannot forage, brood-guarding reduces the overall rate of acquisition of energy and nutrients, and probably affects the allocation of such resources between parents and offspring. The balance of the trade-offs mediating the conflict between foraging and brood-guarding shifts as offspring grow, as the chick capacity for effective thermoregulation and self-defence, as well as its nutritional needs, increase. Parents often lose mass during the brood-guarding stage (Tveraa et al. 1998, Weimerskirch and Lys 2000, Shaffer et al. 2003), which may also help tip the balance towards the decision to leave the offspring unattended. A large variability exists, both within species and between closely related taxa, in the duration of the brood-guarding stage of the nestling cycle (Ricklefs and Roby 1983, Hunter 1984, Varpe et al. 2004), yet very few studies have attempted to identify the primary mechanisms influencing the parental decision to terminate continuous guarding of the offspring (but see Tveraa et al. 1998, Brodin et al. 2003, Varpe et al. 2004, Catry et al. 2006, 2009).

In an experimental study of grey-headed albatrosses *Thalassarche chrysostoma* carried out in a single season, Catry et al. (2006) showed a marked seasonal decline in the duration of brood-guarding, i.e. late hatched chicks were left unattended at much younger ages than early hatched conspecifics. Contrary to expectations, there was no evidence that this seasonal pattern resulted from differences in the timing of breeding of high and low quality individuals, or from a seasonal decline in food availability. Similar patterns were found in a study with Antarctic petrels *Thalassoica antarctica* (Varpe and Tveraa 2005). The authors of these studies considered that the seasonal decline in brood-guarding could be attributed to the advantage to early breeding pairs in avoiding leaving their offspring unattended during the period when few other chicks were available to predators. Hence, the decline in brood-guarding would be a response to seasonal variation in predation risk, driven by predator-swamping effects (Ims 1990). Thus, Antarctic petrel and albatross parents behave in a way that results in greater synchrony at this critical breeding stage (chick parental emancipation) than at any other point during reproduction, including egg-laying (Varpe and Tveraa 2005, Catry et al. 2006). We will call this the 'synchronisation hypothesis', which predicts that, irrespective of temporal and spatial differences in food availability or weather conditions, there should always be a decline in brood-guarding duration in colonies where chicks are subjected to substantial predation pressure. It also predicts that a similar seasonal decline should not be found in species subjected to little or no predation at the end of brood-guarding, such as most burrow-nesting seabird species (Catry et al. 2009).

Alternative hypotheses exist, which are that shorter brood-guarding durations occur at times of the season when food is more scarce (which we term the 'food availability hypothesis'), or that high quality individuals (i.e. those with more experience or with better phenotypes) tend to nest earlier in the season and have a better capacity to sustain long periods of nest attendance, hence, brood-guarding durations decline as the season progresses (which we term the 'adult quality hypothesis'). Both the 'food availability' and the 'adult quality' hypotheses predict that if a seasonal decline in brood-guarding duration is found, other variables dependent on food allocation to offspring, such as chick growth/condition and chick survival probability should also display a seasonal decline. Furthermore, if the 'adult quality hypothesis' is correct, we might predict that a) brood-guarding duration should correlate with egg size (an indicator of female quality in albatrosses; Croxall et al. 1992, Sagar et al. 2005), b) brood-guarding duration should correlate with past breeding performance (another indicator of adult quality; Cobley et al. 1998) and that c) inexperienced birds should brood-guard chicks for shorter periods than more experienced individuals.

Finally, it is possible that the spatial and temporal variability in brood-guarding duration is related to prevailing weather conditions (which we term the 'cold protection hypothesis'). This would predict that chicks should be brood-guarded for longer periods in regions with a harsher climate and, moreover, that adults should respond to short-term variations in weather by prolonging brooding during spells of bad weather, and be more prone to terminate brooding under favourable (warm and dry) conditions.

The observations on grey-headed albatrosses that led to the formulation of the 'synchronization hypothesis' were carried out in a single year and location. In this paper, we test the applicability of this hypothesis and alternatives in another species, the black-browed albatross *Thalassarche melanophris*, in multiple breeding seasons and at two breeding colonies with contrasting climates. The implications of the results are discussed in the context of factors leading to the regulation of avian brood-guarding in general.

Methods

This study took place in the 2001/02, 2002/03, 2004/05 and 2005/06 (austral) summer seasons on Bird Island (BI), South Georgia (54°00′S, 38°03′W), and in the 2003/04, 2004/05, 2005/06 and 2006/07 summer seasons on New Island (NI), West Falkland (51°43′S, 61°18′W). Bird Island is ca 300 km south, and New Island is ca 600 km north of the Antarctic polar convergence, and consequently the two archipelagos have quite distinct climates. The West Falklands are generally sunny and enjoy relatively dry weather in summer, with variable winds, while Bird Island is almost permanently under cloud cover, with high precipitation and frequent moderate or strong winds (see results for details on wind and temperature).

Both islands hold several thousand pairs of black-browed albatrosses. In each study colony, all the nests in chosen plots were marked with numbered plastic tags for identification. At each nest, members of the breeding pair were identified by numbered darvic rings and/or marked on the breast by a small patch of paint (yellow or blue) for easy identification from a distance. Birds were never seen to preen the freshly painted feathers and paint never entered in contact with the bird's skin. Painting does not have any known effects on the behaviour or social interactions of the study birds.

All nests were visited daily (at ca 16.00 h) from 2 days before the hatching of the first egg until the end of brood-guarding; thereafter, nests were visited weekly until chicks were 70 days old. Nest contents were checked on each visit, allowing the determination of the exact hatching date and the date at which the chick was left alone for the first time, as well as its subsequent survival. No attempt was made to distinguish between brooding and guarding without brooding (the latter was rare, in any case).

In 2004/05 and 2005/06, the identity of the adult bird at the nest was recorded, allowing us to estimate the duration of foraging trips during brooding. The precision of such determination is low (±1 day), and foraging trips lasting less than 24 h could have been missed, although these are uncommon, particularly in chicks aged less than 13 days (Phillips et al. 2003). To dilute the influence of possible errors, we measured several trips for each pair and used mean values per nest when calculating the overall population mean. A random sample of eggs was measured with callipers on the first visit to each colony.

For the purpose of this study, chicks were considered to have fledged if they survived to the age of 70 days.

Normally, mortality after such age is very low, although in some years, at Bird Island, giant petrels *Macronectes* spp. can cause significant mortality among older chicks.

Brood-guarding duration was defined as the number of days the chick was attended until it was left alone for the first time. Sometimes, one parent resumed brood-guarding a chick that had been previously left unattended by the other member of the pair. Such events were not taken into account in this manuscript, as they could only be recorded when chicks were not immediately predated after being left alone, resulting in a (presumably) biased sample of surviving individuals.

Chick growth measurements

To have an indication of food availability during the brood-guarding phase and its seasonal variation, we weighed a sample of chicks when they were 14 days old (in 2004/05, 2005/06 and 2006/07 only).

Adult mass measurements

Adult mass was measured using different procedures in 2004/05 and in 2005/06. In the first year, we captured (by hand) a sample of adults (15–20) that had just finished a brood-guarding stint and were departing for the sea (i.e. walking away from the nest after being relieved by its partner). Birds were measured, weighed and immediately released. This technique proved extremely time-consuming and in the second year we weighed adults that were brooding their chicks using the technique described by Prince et al. (1981), with minor modifications (the technique was originally used on incubating birds). Briefly, the bird was encouraged to sit on a platform placed on the nest and then lifted and weighed using a spring balance. This did not require restraint, and hence, caused less disturbance than the first method. Adults were weighed on the second day of the brood-guarding stint. This standardisation ensured that parents had plenty of time to feed the chick before being weighed, which reduced (but obviously did not eliminate) variation in mass caused by differences in the volume of stomach contents. Albatrosses are extremely tame birds, and standard procedures such as ringing, egg measuring or even weighing of adults never resulted in nest desertion or in any obvious or measurable effects on the study birds or their breeding success.

Experiments to assess predation pressure

At the end of brood-guarding, the main albatross chick predators at our study sites were skuas *Stercorarius antarctica*. Giant petrels *Macronectes* spp. can also prey on small albatross chicks, but were never observed to attempt to do so during this study (although they did prey on almost fully grown chicks on Bird Island). On New Island, striated caracaras *Phalcoboenus australis* may also consume albatross chicks, but most of these they obtain by kleptoparasitism of skuas (pers. obs.). Predation rates can be both a cause and a consequence of the observed brood-guarding periods. We attempted to obtain an independent assessment of predation pressure as follows.

An experiment was conducted on two different dates in 2004/05 at each study site: a) four days after mean hatching date, when there were few or no unattended chicks at the colonies; b) four days after the day when 50% of the study chicks had been left unattended for the first time. Identical dummy young albatross chicks, made of pale grey socks with black eyes and bill, were used at both study sites. The size of the dummy was similar to a chick ca 15 days old. We chose 10 independent locations (10 different colonies) at each island, at sites where skuas had not had any previous experience of dummy prey. We chose an empty albatross nest with a clear view (not one surrounded by tussock or hidden by a rock) on which we placed the chick dummy. We then observed from a distance of 20 m (a distance that elicits no response by skuas when approached by humans in our study colonies) for a period of 15 min. We recorded skua attacks and also the number of skuas flying within 30 m of the dummy. No other predators, besides skuas, were observed approaching or attacking the dummies.

Previous breeding experience

Every year since the early 1990s at the study colony on BI, all new recruits are identified and ringed, which means that due to the high breeding site fidelity of albatrosses (Tickell 2000), unringed birds can be safely classified as inexperienced. On NI, procedures are similar, but as systematic ringing only started in the first study year (2003/04), we were less confident about the previous experience of the study birds.

Adult quality

In order to examine the relationship between brood-guarding duration and adult quality at Bird Island, we calculated for each pair of adults a quality index based on past reproductive performance (see Cobley et al. 1998 for detailed methodology and rationale). This index, for each individual, is given by the number of chicks successfully raised to fledging divided by the number of years since the bird bred for the first time (i.e. breeding failure was given the same weight as deferring breeding). In order for this index to be based on a minimum number of observations, we only included individuals for which at least 4 years had elapsed since the first breeding attempt. The quality of a breeding pair was given by the average of the quality indices of each pair member or, for just 20.3% of pairs, the index for the only pair member for which we had sufficient long-term data.

Weather conditions

From mean hatching date until two days after the end of the brood-guarding stage, we measured wind and temperature at the centre of our study colonies. Wind speed was measured during daily checks by holding an anemometer 150 cm above the ground for 2 min and reading the mean for that period. Maximum and minimum temperatures were obtained from a thermometer left in the shade, 20 cm above the ground, at the edge of the study colonies. Qualitative records of general weather (precipitation, cloud cover) were also kept.

Analyses

As we did not have data from both colonies in every year of the study, and there is in any case no evidence for any overlap in foraging areas of adults during brooding, rather than including year as a factor, we used the categorical variable COLYEAR (with a distinct value for each colony in each year of study) in logistic regressions and in linear models, unless stated otherwise. To address the occurrence of multiple observations on the same individuals and to avoid potential biases due to pseudo-replication, we used linear mixed models, and included the individuals as a random factor. We used the library nlme (Pinheiro et al. 2009), running in R (ver. 2.9.2, R Development Core Team 2009) to fit all models.

After examining the distribution of brood-guarding periods, we opted to eliminate apparent outliers (Fig. 1) from further analyses. Hence, measurements from nests where chicks were left alone alive after being guarded for less than 10 days were excluded. We regard those outliers as cases where reproduction failed before the end of the normal brood-guarding period (consult Catry et al. 2006 for a similar approach). Nests where chicks died while still under their parents were also excluded.

There were important inter-annual differences in brood-guarding duration (Results). To address the specific question of whether individual pairs were consistent in their relative duration of brood-guarding, despite these annual differences, we standardised this variable by subtracting the annual mean from each individual value. As body size of black-browed albatrosses in the Falklands and South Georgia is very similar (P. Catry and R. Phillips unpubl.), and egg sizes are also virtually identical, albeit with some annual variation, we made direct comparisons of adult and chick mass between NI and BI, without correcting for differences in body size.

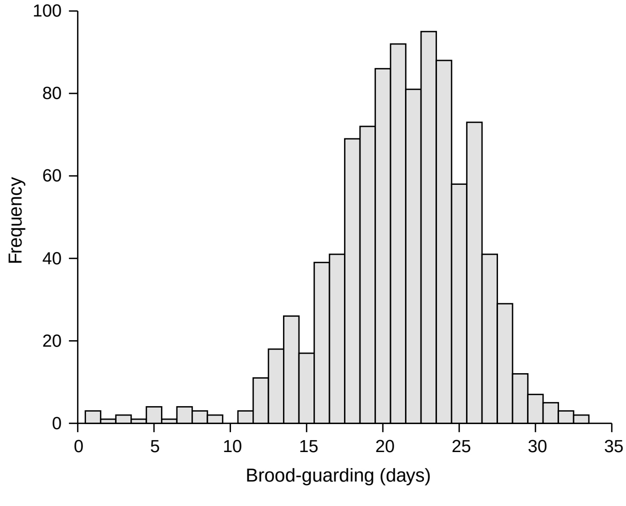

Figure 1. The duration of the brood-guarding period in 989 black-browed albatross nests. Data from 4 different years at New Island (Falkland Islands) and Bird Island (South Georgia) are pooled.

To assess the influence of daily weather variation on the decision of parents to terminate brooding, we correlated daily increments in wind chill index with relative daily increments in the number of brood-guarding terminations. Wind chill index (T_{wc}) was calculated, following Osczevski and Bluestein (2005), as:

$$T_{wc} = 13.12 + 0.6215\ T_a - 11.37\ V^{0.16} + 0.3965\ T_a\ V^{0.16}$$

where T_a is maximum air temperature (in Celsius degrees) and V is wind speed (in km h^{-1}). For wind speed values under 3 km h^{-1}, $T_{wc} = T_a$. Daily increment in wind chill (ΔT_{wc}) is the difference between T_{wc} of the focal day and T_{wc} of the previous day. Relative daily increments in the number of brood terminations (ΔB) are given by:

$$\Delta B = 2\ (B_i - B_{i-1})/(B_i + B_{i-1})$$

where Bi is the number of brood terminations on day i. This index was only calculated when $(B_i + B_{i-1}) > 4$, to avoid estimating ΔB on the basis of a very small number of individual decisions. We used contrasts between consecutive days to partially avoid the difficulties of estimating the number of chicks potentially available to be left alone on each date, a variable that undoubtedly can vary markedly in the course of a few days. If albatrosses respond to daily variations in weather when deciding to terminate brooding, we predicted a positive correlation between ΔT_{wc} and ΔB in each study colony and year. Unless stated otherwise, data are presented as means ± SD.

Results

Broad spatial and temporal patterns

Excluding 21 outliers (2.1% of the total) that left their chick to an inevitable death at a very early stage, pairs of black-browed albatross brood-guarded their chick for 11–33 days (Fig. 1). There were significant differences in brood duration among years ($F_{5,613} = 27.5$, $p < 0.001$) and between colonies in individual years ($F_{1,613} = 17.5$, $p < 0.001$), but no differences between study sites in overall mean brood-guarding duration ($F_{2,7} = 0.73$, $p = 0.4$, each site providing four annual mean values Table 1).

At each study site and year, there was a seasonal decline in the duration of brood-guarding, with hatching date explaining 5–20% of the variation (Table 1). This pattern of seasonal decline in brood guarding was similar in every year (interaction between COLYEAR and hatching date, individuals taken as random factor: $F_{7,613} = 0.90$, $p = 0.51$), despite the fact that mean brood-guarding duration varied substantially among years.

Individual consistency

Because pairs of albatrosses show a degree of consistency in the timing of breeding (authors unpubl.), and because hatching date influences brooding (above), we introduced hatching date as a covariate in the following general linear models. On NI, individual pairs ($n = 120$) were consistent in the duration of standardised brood-guarding

Table 1. The duration of brood-guarding at New Island (Falkland Islands) and Bird Island (South Georgia) in different years, and the relationships between brooding phase duration and hatching dates (modelled through liner regressions).

Colony	Year	Brood-guarding duration (days)	intercept	Slope	r^2	n	p
New Island	2003/04	19.4±3.1	148.2	−0.365	0.14	149	<0.001
	2004/05	19.6±3.2	173.3	−0.439	0.16	130	<0.001
	2005/06	20.1±3.2	112.6	−0.263	0.09	129	0.001
	2006/07	24.1±3.1	151.8	−0.397	0.20	124	<0.001
Bird Island	2001/02	22.9±4.1	186.1	−0.442	0.14	156	<0.001
	2002/03	21.9±4.1	107.6	−0.232	0.05	82	0.043
	2004/05	19.2±3.6	115.5	−0.261	0.11	79	0.003
	2005/06	24.6±3.9	143.6	−0.321	0.09	118	0.001

duration (repeatability = 0.42; pair effect: $F_{119,168} = 2.68$, $p < 0.001$) and the same was true, although with a much lower repeatability, on BI (for 121 pairs, repeatability = 0.11, pair effect: $F_{120,174} = 1.31$, $p = 0.051$).

Egg size

Egg size and brood-guarding duration were not related in any of the years and sites. Overall, the effect of egg volume, after controlling for the influence of year, site and individual female, was not significant ($\chi^2 = 0.03$, DF = 1, $p = 0.86$).

Effects of previous breeding experience

On BI, in 2001/02, the brood-guarding period of pairs of experienced breeders (22.8±4.2 days, n = 146) was not longer than that of pairs that included at least one first-time breeder (23.3±2.1 days, n = 10; $F_{1,154} = 0.13$, $p = 0.7$). Sample sizes were insufficient to test this hypothesis in other single years.

Adult quality

Adult quality (measured as past reproductive performance) had a weak and inconsistent effect on the duration of brood-guarding, with the (positive) relationship significant in two out of four years studied (Table 2).

Adult body mass

In 2004/05, body mass of departing adults after a brooding stint was lower on NI (3,021±333g, n = 20) than on BI (3,306±279g, n = 15; $F_{1,33} = 7.55$, $p = 0.01$). In 2005/06, the comparison was made between brooding adults on the second day of a brooding stint. The corresponding number of days since hatching was known for each measurement and entered as a covariate in the general linear models comparing colonies. There was no significant difference in the number of days since hatching when measurements were taken at each colony. Body mass was again considerably lower on NI (3,296±367g, n = 44) than on BI (3,635±256g, n = 40; $F_{1,83} = 24.0$, $p < 0.001$). There was a significant decline in adult mass as brooding progressed on NI ($r = -0.46$, n = 44, $p = 0.002$), but no such pattern was apparent in the BI data set ($r = 0.11$, n = 40, $p = 0.5$).

Table 2. Correlations between adult quality (measured by past reproductive breeding success) and the duration of brood-guarding in 4 years at Bird Island.

Year	r^2	n	p
2001/02	0.05	142	0.007
2002/03	0.00	77	0.93
2004/05	0.00	79	0.65
2005/06	0.04	116	0.035

Chick body mass

Chick mass at 14 days of age varied substantially between years (Table 3). At both NI and BI, the year with longest brood guarding (2006/07 and 2005/06, respectively) coincided with the highest recorded mean chick mass (Table 1, 3). A longer time-series would be needed to better assess this relationship, but the available data suggest that factors other than brood-guarding duration must also be important. For example, while chick-mass decreased significantly (by 18.3%) from 2004/05 to 2005/06 on New Island, mean brood-guarding duration showed a marginal, non significant, increase of 2.6% (Table 1, 3). Similarly, there was no direct relationship between length of brooding and chick mass at the individual level; in a model with COLYEAR as a factor and chick mass at 14 days as a covariate, mass was not related to brood-guarding duration ($F_{1,205} = 0.0$, $p = 1.0$).

Brood-guarding duration and fledging success

Longer brood-guarding periods improved the odds of successfully fledging a chick in some, but not all years (Table 4).

Table 3. Body mass (in grams) of albatross chicks aged 14 days at New Island (Falkland Islands) and Bird Island (South Georgia) in three contrasting years.

	New Island	n	Bird Island	n
2004/05	788±202	85	813±215	32
2005/06	644±185	69	1001±173	35
2006/07	902±140	76	N/A	

Table 4. The effect of brood-guarding duration on the probability of survival to 70 days of age at New Island (Falkland Islands) and Bird Island (South Georgia) in different years, assessed through logistic regressions. Significant p values are given in bold face.

Colony	Year	χ^2	β	n	p	Post-brood survival rate
New Island	2003/04	17.4	0.24 ± 0.06	149	< **0.001**	0.53
	2004/05	0.002	0.00 ± 0.05	130	0.96	0.68
	2005/06	1.45	0.07 ± 0.06	129	0.23	0.44
	2006/07	4.96	0.29 ± 0.13	124	**0.026**	0.70
Bird Island	2001/02	19.4	0.19 ± 0.05	156	< **0.001**	0.50
	2002/03	7.6	0.21 ± 0.09	82	**0.006**	0.45
	2004/05	1.3	0.07 ± 0.07	79	0.26	0.50
	2005/06	23.3	0.30 ± 0.07	118	< **0.001**	0.45

Foraging trip duration

In 2004/05, the mean foraging trip duration during the brood-guarding period was slightly longer on Bird Island (2.2 ± 0.4 days, n = 55 pairs) than on New Island (2.0 ± 0.3 days, n = 56; $F_{1,109} = 5.27$, p = 0.024), but the difference was small. In 2005/06 the opposite trend was found: Bird Island (2.0 ± 0.3 days, n = 30), New Island (2.3 ± 0.6 days, n = 30; $F_{1,59} = 9.6$, p = 0.003).

Seasonality in chick growth and survival

Early chick growth (measured by mass at 14 days) showed a weak linear relationship with hatching date on NI in 2005/06 (Pearson r = −0.26, n = 69, p = 0.03), but not in 2004/05 (r = −0.14, n = 85, p = 0.21), or at BI in either 2004/05 (r = −0.07, n = 32, p = 0.69) or 2005/06 (r = 0.10, n = 35, p = 0.57). In 2006/07 on NI, the relationship between hatching date and chick mass at 14 days was quadratic (chick mass = 574 − 48 (hatch. date) − 1.576 (hatch. date)^2, explained variance = 0.17, p = 0.001). Quadratic relationships were not significant in any other years. Additional data on chick growth (mass of chicks aged 19 days) were available for NI in 2003/04, and indicated, as above, no significant correlation between hatching date and chick mass (r = 0.12, n = 115, p = 0.19).

Fledging success and hatching date were only very weakly correlated. Hatching date influenced fledging success in only one site-year out of 7 possible cases: at BI in 2005/06, early hatched chicks had a significantly higher probability of fledging (logistic regression: β = −0.17 ± 0.06, n = 125, $\chi^2_1 = 8.1$, p = 0.005).

Predation experiment

Predation pressure on dummies was similar on NI and BI. During early brooding, at both sites, in 2 out of 10 (15 min) trials, the chick was attacked. Later in the season, there was an attack on the dummy chick in 2 out of 10 cases on BI, and in 3 out of 10 cases on NI. The number of skuas flying within 30 m of the dummy in the 15 min trials was also similar on both islands: First trial, NI 5.3 ± 4.0 skuas (n = 10 trials) and BI 6.0 ± 2.8 skuas (n = 10); second trial, NI 13.7 ± 14.4 skuas (n = 10) and BI 6.9 ± 3.8 skuas (n=10). The differences were not significant (all p > 0.05).

Prevailing weather patterns

During the brooding period, the weather on Bird Island was generally more severe than on New Island, with considerably lower maximum and minimum temperatures and higher wind speeds (Table 5). Although not quantified, our records also show that cloud cover and precipitation were higher on Bird Island.

There was no systematic trend in weather conditions that could potentially explain a seasonal decline in brood-guarding. During the period when chicks were being left alone, wind-chill index showed a negative correlation (indicating colder condition as days passed) on New Island in 2004/05 (r = −0.53, n = 22, p = 0.01), but not in 2005/06 (r = 0.07, n = 24, p = 0.73) nor on Bird Island in 2004/05 (r = 0.14, n = 22, p = 0.55) or in 2005/06 (r = −0.25, n = 23, p = 0.26).

Influence of weather on brood-guarding duration

Daily weather data were available only for 2 years in each colony, but in every case there were significant positive correlations between ΔT_{wc} and ΔB, indicating a relationship between daily increments in the wind chill index and the relative number of terminations of brooding (Fig. 2). This conformed to observations during fieldwork

Table 5. Temperature and wind speed at the study colonies on New Island (Falkland Islands) and Bird Island (South Georgia), measured during the brood-guarding stage.

Colony	Year	n (days of observation)	Temp. max. (°C)	Temp. min. (°C)	Wind (m s^{-1})
New Island	2004/05	33	17.5 ± 2.8	8.6 ± 2.1	1.86 ± 1.08
	2005/06	36	15.7 ± 4.0	7.0 ± 2.7	2.47 ± 1.61
Bird Island	2004/05	34	8.0 ± 2.4	3.3 ± 1.9	3.22 ± 2.36
	2005/06	35	6.7 ± 1.4	3.0 ± 1.5	3.64 ± 1.75

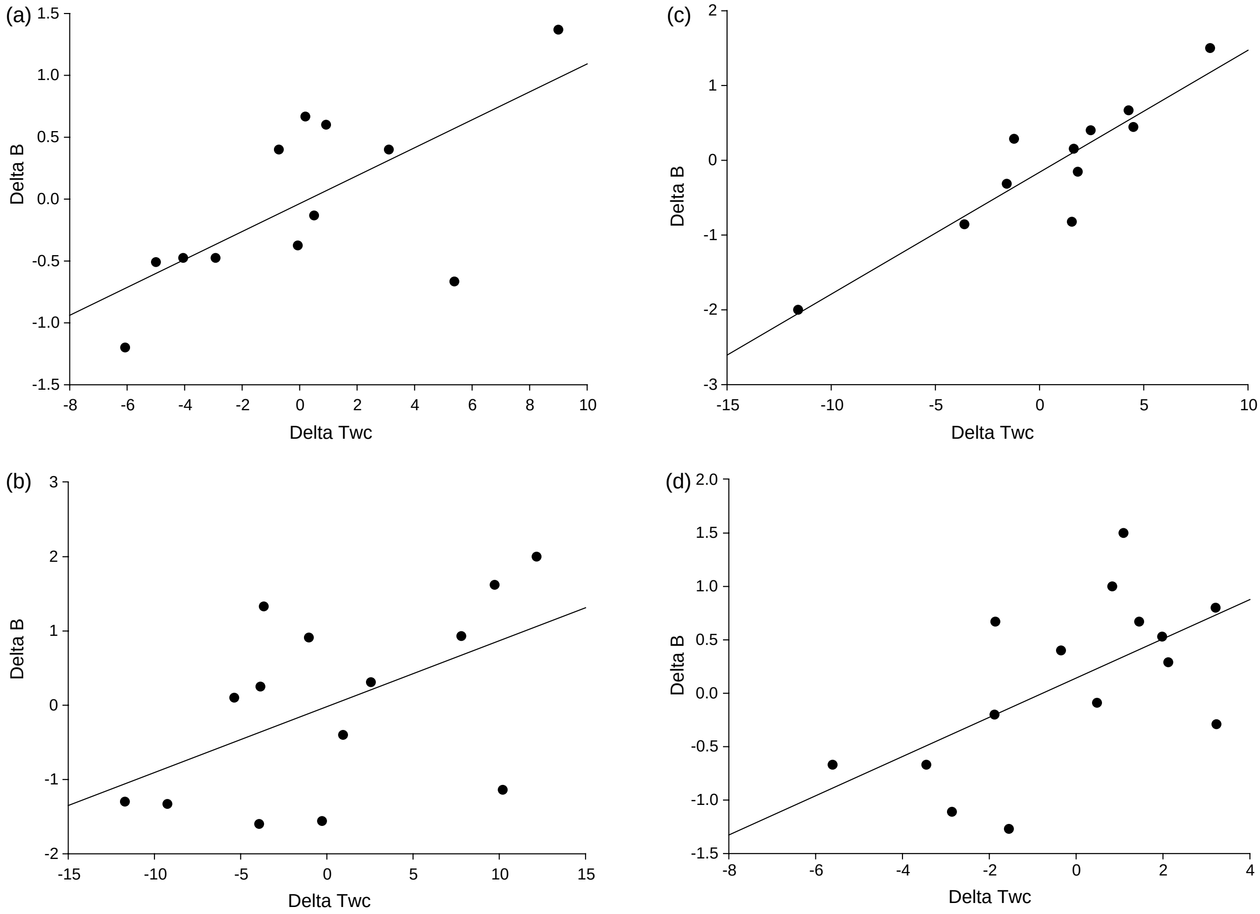

Figure 2. The relationship between daily increments in wind chill index (ΔT_{wc}) and increments of relative numbers of birds terminating brood-guarding (ΔB). The positive relationships indicate that more chicks are left alone for the first time on relatively warm days. Data for (a) New Island in 2004/05; $r_{12} = 0.71$, $p = 0.015$, (b) New Island in 2005/06; $r_{14} = 0.53$, $p = 0.053$, (c) Bird Island in 2004/05; $r_{11} = 0.91$, $p < 0.001$, and (d) Bird Island in 2005/06; $r_{15} = 0.59$, $p = 0.02$.

of an increase in the number of terminations of brood-guarding on warm sunny days.

Discussion

Our study suggests that a seasonal decline in brood-guarding may be the norm, at least amongst some albatross species. This study is also, to the best of our knowledge, the first to record consistent individual differences in brood-guarding duration, and important inter-annual variation in brood-guarding behaviour in birds.

The synchronisation hypothesis

We found strong support for the 'synchronization hypothesis', confirming that a marked decline in brood-guarding duration for late-hatched nests may be a rule in different petrel species and breeding sites where chicks are accessible to predators (Varpe and Tveraa 2005, Catry et al. 2006). Furthermore, the negative relationship between hatching date and brood-guarding duration was of a similar shape and slope in years and regions with contrasting seasonal trends in local food abundance or availability (as inferred from the substantial variation in early chick growth rates), and fledging success, as well as very different climates. Further supporting evidence was recently provided by a study on Cory's shearwaters *Calonectris diomedea*: in two colonies where this burrow-nesting species suffered from little or no predation, there was no seasonal decline in brood-guarding duration, which contrasts with patterns revealed by albatrosses and Antarctic petrels but is in line with the predictions of the 'synchronization hypothesis' (Catry et al. 2009).

The food availability and adult quality hypotheses

The present data also confirms earlier suggestions (Varpe and Tveraa 2005, Catry et al. 2006) that the seasonal decline in brood-guarding in albatrosses and petrels cannot be explained by a seasonal decline in food availability or by the early breeding of parents of higher individual quality. This contrasts sharply with the strong evidence for the importance of these factors in determining breeding performance and behaviour in many temperate-nesting birds (Daan et al. 1988, Catry et al. 1998).

The prediction that a seasonal decline in brood-guarding duration should co-occur with a seasonal decline in chick growth/condition was not upheld by the data. In only one year (out of 6 possible cases) did chick body mass show a slight decline in late- compared with early-hatched nestlings. Indeed, in grey-headed albatrosses, there was the opposite tendency, with late-hatched chicks having better growth-rate early in life (Catry et al. 2006).

Nor was the 'adult quality hypothesis' upheld. This postulates a relationship between brood-guarding duration and breeding experience or phenotypic quality and also a link between differential timing of breeding of individuals of different quality and a seasonal decline in breeding output. However, first-time breeders did not have significantly shorter brood-guarding periods than experienced individuals in our study, which again agrees with earlier evidence from grey-headed albatrosses (Catry et al. 2006). Furthermore, egg size (which may also convey information on parental quality) was not related to brood-guarding duration, and most importantly, early breeders did not, in most years, exhibit greater success than those hatching later in the season. Our data were insufficient to test whether adult body condition influenced the duration of brood-guarding, but comparisons between colonies revealed that while adults were in much better condition at Bird Island than on New Island in 2004/05, overall mean brood-guarding duration was similar at both colonies. Moreover, testing this issue at the individual level, Catry et al. (2006) did not find any relationship between adult condition and brood-guarding duration in grey-headed albatrosses (Varpe and Tveraa 2005).

Other results were more in line with the 'adult quality hypothesis'. In two out of four years at Bird Island, there was a significant positive relationship between adult quality (measured by past reproductive performance) and brood-guarding duration. However, the relationship was weak at best ($r^2 < 0.06$) compared with the seasonal decline in brood-guarding duration which was obvious in every year of study and explained a much greater proportion (up to 20%) of the variation. Nesting pairs showed a degree of inter-annual consistency in brood-guarding duration at both sites, although the effect was relatively weak at Bird Island. Furthermore, in 4 out of 7 study site-years, pairs with long brood-guarding periods were more likely to successfully raise their chick to fledging. However, alternative explanations for these patterns exist (below), and these results are therefore insufficient to salvage the 'adult quality hypothesis', given the challenges presented by the failure of some of its main predictions as discussed above.

The cold-protection hypothesis

One of the functions of brood-guarding is undoubtedly related to thermoregulation, at least for very young chicks (Visser 1998, Weathers et al. 2000). It naturally follows that brood-guarding should be longer in harsher climates. Our measurements at the study colonies confirm that climate is much more challenging at BI, at the northwest tip of South Georgia, than at NI, in the Falklands. Bad weather can be a problem for albatross chicks with limited thermoregulatory abilities, which is confirmed by the fact that we have seen, at both sites, young unattended black-browed albatrosses apparently dying of cold during spells of inclement weather. Hence, a longer duration of brood-guarding was predicted for BI. However, contrary to our initial expectation, comparing the behaviour of albatrosses at two colonies with markedly different climates did not reveal a clear response to this factor. On average, there was no difference between the duration of brood-guarding in South Georgia and the Falklands (4 years of data for each site). If climate influences brooding behaviour of black-browed albatrosses, the relationships is weak at best, and masked by other factors, despite the fact that short-term (daily) weather fluctuations had a clear influence on parental decisions to terminate brooding (below). It could be argued that the colder climate pressures adults to extend brood-guarding at BI, but that this is counter-balanced by a different factor or suite of factors promoting longer attendance at NI. However, in 2004/05, we measured other relevant variables besides weather. Predation pressure, early chick growth and foraging trip durations were broadly similar in the two areas, and so predators and food availability at the relevant time of the season did not seem to be counter-acting what were clearly substantial differences in weather. Adult masses were much higher at BI. Hence, it seems that there was nothing to prevent adult albatrosses brooding for longer on BI in response to the harsher weather conditions. That they did not do so challenges our understanding of this issue.

Short-term weather fluctuations (measured by the wind chill index) had a demonstrable effect on the decision by the parent to terminate brooding. Note that our tests probably are somewhat conservative, as we did not quantify solar radiation and precipitation, which would have made the relationship between weather and brooding behaviour even more apparent (for example, virtually no chicks were left on days with heavy rain). Although a direct response to the thermal environment in brooding behaviour is not surprising and has been shown in other birds (Krijgsveld et al. 2003), ours is the first study, to our knowledge, that has demonstrated its occurrence in a pelagic seabird that, once engaged in a foraging trip, cannot quickly resume brooding behaviour as a response to possible deterioration of the weather. Hence, the 'cold-protection hypothesis' received some support from our data. However, more work is needed to understand the response of parents and chicks to weather at appropriate spatio–temporal scales.

Finally, it is interesting to note that there was no seasonal trend in temperature and wind, as measured by the wind-chill index, that could explain a seasonal decline in brood-guarding duration. In fact, in only one out of four years there was a significant tendency for weather conditions to become worse.

Other influences on brood-guarding behaviour

Evidence from grey-headed albatrosses suggested that chicks in poor condition were brood-guarded for longer, which may be a strategy to allow underweight chicks to recover condition before being left to face one of the most critical periods of their life (Catry et al. 2006). In contrast, our study did not find a relationship between chick mass and brood-guarding duration in black-browed albatrosses. This may be because chicks were weighed a little too early (at 14 days), which is several days before they were usually left alone. On the other hand, there was a trend at the population level, for years with better chick growth to be the ones with longer brood-guarding. Hence, food availability may, like weather, influence parental attendance in complex ways that were not revealed by the present study.

Importance of individual variation

The exact duration of brood-guarding is influenced by the decisions and actions of two individuals, which, by itself, reduces the probability of obtaining high repeatability in measurements of this behaviour. Nevertheless, our data indicated that nesting pairs displayed a considerable degree of inter-annual consistency in the amount of time allocated to brood-guarding their offspring. This, and a correlation between past reproductive performance and the duration of the guarding period in some years, suggest a possible role for individual traits in the regulation of brood-guarding. Furthermore, it should be noted that in 5 of 8 possible year/sites, chicks brood-guarded for a longer periods had a higher survival to fledging. Hence, the time allocated to brood-guarding had important fitness implications for the offspring. These observations are somewhat difficult to reconcile with the above evidence for a weak and variable relationship between adult quality and brood-guarding duration (Catry et al. 2006). It is possible, however, that a trade-off exists between brood-guarding duration and chick survival, on the one hand, and adult condition and survival, on the other. Because albatrosses, as a result of constraints on time spent foraging and higher costs of foraging, generally lose mass while brood-guarding (Weimerskirch and Lys 2000, Shaffer et al. 2003, Catry et al. 2006, this study), it is reasonable to expect longer periods of nest attendance to result in a higher cost of reproduction for adults. Such trade-offs between investment in chick protection and adult condition and survival may vary with environmental conditions, which would contribute to maintenance of the variability we observed in the behavioural traits on which we focus in this paper.

Conclusions

This study highlights the complexity of the interaction between multiple factors and the variation in brood-guarding duration, a subject that has been somewhat overlooked by ornithologists. Several factors, such as predation pressure, parental characteristics, food availability and weather are likely to influence the decision on how much to invest in brood-guarding. The striking pattern of consistent seasonal decline in brood-guarding in albatrosses, which are open ground nesters, and the contrasting behaviour of Cory's shearwaters (Catry et al. 2009; above), seem to be best explained by predictable seasonal variation in predation risk. For further tests of the synchronization hypothesis, more studies focusing on species under little or no predation pressure are urgently required.

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