J Ornithol (2009) 150:103–108
DOI 10.1007/s10336-008-0322-x

ORIGINAL ARTICLE

Brood-guarding behaviour in Cory's Shearwaters *Calonectris diomedea*

Paulo Catry · Rafael Matias · Luís Vicente · José Pedro Granadeiro

Received: 3 January 2008 / Revised: 15 April 2008 / Accepted: 13 May 2008 / Published online: 13 June 2008

Abstract Brood-guarding (or the continual attendance at the nest by one parent) has been relatively little studied in altricial birds. Parental investment in brood-guarding is often highly variable within a species, and the study of such variability may contribute to the understanding of the functions and regulation of this behaviour and of the trade-offs involved in the choice between attending the nest and leaving to forage. In some colonial birds, it has been found that early nesting pairs attend their chick for longer than later nesting counterparts, giving rise to the *synchronisation hypothesis* that suggests that early pairs prolong brood-guarding in order to reduce the probability of nest predation by a dilution effect. In this paper, for the first time we test the prediction that burrow-nesting colonial birds subject to little predation pressure should not display a seasonal decline in brood-guarding duration. The *growth assistance hypothesis* suggests that brood-guarding may allow the provision of frequent small meals and the efficient use of energy by chicks with poor homeothermic capabilities, resulting in improved early chick-growth. Finally, the *chick-protection hypothesis* predicts that chicks in more exposed nests should be brood-guarded for longer. Data collected at two Cory's Shearwater *Calonectris diomedea* colonies situated in contrasting environments supported the synchronisation hypothesis, as there was no seasonal trend in brood-guarding duration. Contrary to the growth assistance hypothesis, chicks brood-guarded for longer periods did not have an improved growth (in one colony there was even a negative effect of brood-guarding on early chick development). Finally, we found no difference in brood-guarding between nests with contrasting levels of exposure to potential predators and weather. Despite confirming the prediction of the synchronisation hypothesis, more research is needed to identify the main factors underlying the variability of brood-guarding observed in this and other studies.

Keywords Brooding · Parental care · synchronisation hypothesis

Communicated by P.H. Becker.

P. Catry (✉) · R. Matias · L. Vicente
Unidade de Investigação em Eco-Etologia,
Instituto Superior de Psicologia Aplicada,
Rua Jardim do Tabaco 34, 1149-041 Lisbon, Portugal
e-mail: paulo.catry@gmail.com

J. P. Granadeiro
Centro de Biologia Ambiental,
Museu Nacional de História Natural,
Rua da Escola Politécnica, 58, 1299-102 Lisbon, Portugal

Introduction

In most bird species, recently hatched chicks are almost continuously attended at the nest by one parent (Düttman et al. 1998), during a phase of the nesting cycle here called brood-guarding. Brood-guarding involves a permanent trade-off between the benefits of attending the offspring and the benefits of foraging. Generally, the overall rate of energy acquisition of a couple of parent birds cannot be maximised if only one individual can forage at a time. Such a trade-off is likely to be particularly acute in birds which use distant foraging grounds, such as pelagic seabirds, because in this case foraging cannot be accomplished during relatively short absences from the nest. Such a limitation in the rate of energy acquisition often results in a decline in parental body mass during the brood-guarding stage (e.g. Wendeln and Becker 1996; Catry et al. 2006a).

Brood-guarding has been relatively little studied in altricial birds and its functions and regulation are poorly understood (but see, for example, Tveraa et al. 1998; Tveraa and Christensen 2002; Brodin et al. 2003; Varpe et al. 2004).

Studies with albatrosses have shown that there is usually a seasonal decline in the duration of brood-guarding, with late-hatched chicks being attended for shorter periods (Catry et al. 2006a, and unpublished data). Such a pattern does not seem to be related to seasonal variation in food supplies or to the later nesting of low-quality or inexperienced individuals (Catry et al. 2006a). These observations make us propose the *synchronisation hypothesis*, which suggests that prolonged brood-guarding of early breeders observed in some colonial seabirds results from early breeders attempting to achieve greater synchronisation with later breeders when making the dangerous transition from continuous attendance to chick partial emancipation. Higher synchronisation would reinforce predator-swamping mechanisms and increase the survival probability of young (Ims 1990). The synchronisation hypothesis predicts that, in burrow-nesting colonial species with few or no nest predators, a seasonal decline in brood-guarding duration should not be apparent (unless other relevant factors, such as food availability, also vary seasonally).

In birds, the need for brooding chicks that have not developed homeothermic competence is obvious (Visser 1998). However, in many taxa, chicks can be brood-guarded beyond the onset of homeothermy (Warham 1990), and brooding could be an energy-saving mechanism when chick homeothermy can only be achieved by a raise in metabolic rate, with a greater expense of energy (Ricklefs and Roby 1983; Weathers et al. 2000). Continuous attendance of offspring may also allow the provision of regular small meals for very young chicks with limited gut capacity and rapid digestion times. If these factors are of paramount importance, the *growth assistance hypothesis* predicts that chicks brood-guarded for longer periods should grow faster and attain larger body mass than conspecifics of the same age that were left at a younger age.

Even for chicks that no longer require homeothermic assistance under normal conditions, continual attendance at the nest may allow parents to readily resume brooding during spells of inclement weather (Weathers et al. 2000). Brood-guarding may also serve as a protection against predators (Warham 1990). The *chick-protection hypothesis* predicts that, in a colony where different pairs use nesting sites of contrasting characteristics (such as burrows vs open sites), chicks in exposed places should be brood-guarded for longer periods.

Intra-specific variation in brood-guarding is considerable and its study may contribute to understand the functions and regulation of this behaviour. In this paper, we present results from a study with a (mostly burrow-nesting) pelagic seabird, the Cory's Shearwater *Calonectris diomedea*, conducted at two widely separated colonies. We make a general quantification of the parental investment in brood-guarding, compare colonies in two distinctive environments, and test the three non-mutually exclusive hypotheses detailed above.

Methods

This study was carried out at Selvagem Grande (30°09′N, 15°52′W) and at Berlenga (39°24′N, 9°30′W) in 2006. Selvagem Grande is located in deep oceanic waters, south of Madeira, while Berlenga is on the continental shelf, just off the Portuguese mainland.

During early incubation, a sample of accessible nests was selected and numbered at each colony. Measurements of eggs were taken with callipers (to the nearest 0.1 mm). Egg volume (cm^3) was calculated as 0.551 × egg length × egg breadth (Warham 1990).

On Selvagem Grande, two contrasting types of nests were selected. Sheltered nests were in deep burrows in stone walls (see Catry et al. 2006b). Nest contents were inaccessible to Yellow-legged Gulls *Larus michahellis* (the only potential aerial predators) and completely sheltered from wind or sunshine. Exposed nests were usually protected by a rock or a slight overhang, but they were easily accessible to gulls (which often eat abandoned eggs in this type of nests) and exposed to wind and, at certain times of the day, to direct sunshine. All study nests at Berlenga were in deep burrows or in caves, inaccessible to gulls, but potentially accessible to Black Rats *Rattus rattus*.

At each study nest, each member of the pair was captured during early to mid-incubation and painted (breast and tail) with a different colour spray paint, to allow rapid identification of incubating or brooding individuals without disturbance. From 22 June (mid-incubation) to 8 August (the end of brood-guarding), nests were checked daily and the identity of the bird incubating the egg or brood-guarding the chick was recorded. These checks also allowed the determination of hatching date. Nest checks were always carried out in the morning, when no adult arrivals or departures were recorded.

Chick mass (to the nearest 10 g) at each study nest was measured with a spring balance when the chick was 10 days old (variable Mass10), after brood-guarding had completely ceased. Subsequently, mass measurements were only taken on 20 and 25 September, when chicks were, on average, ca. 60 days old and almost reaching peak mass (Granadeiro 1991). Because individual chicks differed in their ages on each particular September date, such measurements were only used to make broad comparisons between colonies (a valid comparison, since mean hatching

Table 1 Comparison of brood-guarding, chick growth parameters and fledging success in sheltered and exposed nests of Cory's Shearwater *Calonectris diomedea* on Selvagem Grande (sample sizes in parentheses)

Nest type	Brood-guarding	Brood10	Mass 10 days	Mass 20 September	Fledging success
Exposed	2.8 ± 1.1 (22)	4.5 ± 1.2 (21)	277 ± 63 (21)	1059 ± 113 (17)	0.75 (24)
Sheltered	3.1 ± 1.5 (38)	5.1 ± 1.5 (38)	247 ± 58 (34)	1012 ± 113 (37)	0.95 (40)
Statistical comparison	$F_{1,59} = 0.75$, $P = 0.39$	$F_{1,59} = 2.01$, $P = 0.16$	$F_{1,54} = 3.27$, $P = 0.08$	$F_{1,53} = 2.04$, $P = 0.16$	Fisher test, $P = 0.044$

date was the same at Berlenga and Selvagem; see "Results").

Definitions and statistical analyses

Foraging trip duration during incubation was given by the number of consecutive days an individual was absent from its nest, as assessed by daily checks. To compare trip durations between localities, only one randomly selected trip per individual bird was considered. Mean starting date of the trips studied was the same in Berlenga and Selvagem.

Throughout this paper, the duration of brood-guarding (variable Brood-guarding) is defined as the number of days the chick was seen attended by one parent until the first day it was left alone. Parents sometimes resume brooding at a later date (but only exceptionally after the chick is 10 days old); Variable Brood10 was defined as the number of days the chick was diurnally attended by a parent in the first 10 days of life.

Fledging success was given by the proportion of chicks hatched that survived until 25 September (the time of our last visit to the study sites). Cory's Shearwater chicks do not fledge until late October, but mortality in the last month of pre-fledging life is usually negligible (own observations at the study sites).

Results

Duration of brood-guarding

Brood-guarding duration in the study nests varied from 0 (parent absent on the first day the chick was seen out of the egg) to 8 days. Brood10 varied from 1 to 9 days. Cory's Shearwaters brood-guarded their chick for longer periods on Berlenga (4.3 ± 2.1 days, $n = 32$) than on Selvagem (3.0 ± 1.3 days, $n = 60$; $F_{1,91} = 17.9$, $P < 0.001$). There was no seasonal decline in the duration of brood-guarding either at Berlenga ($R = -0.10$, $n = 32$, $P = 0.57$) or at Selvagem ($r = 0.02$, $n = 60$, $P = 0.90$). At this last colony, separate tests of exposed ($r = -0.21$, $n = 22$, $P = 0.35$) and sheltered nests ($r = 0.08$, $n = 38$, $P = 0.64$) yielded similar, non-significant, results.

There were no differences in the brood-guarding behaviour of parent Cory's Shearwaters attending nests in exposed and in sheltered situations on Selvagem Grande (see Table 1). Chick growth was similar in these two habitats, but there was a higher post-brooding chick mortality in exposed nests.

Consequences of brood-guarding for the chicks

At Berlenga, chicks more frequently attended by their parents had a lower mass at 10 days of age (correlating Brood10 and Mass10, $r = -0.48$, $n = 28$, $P = 0.009$; Fig. 1). Controlling for egg volume in a partial correlation did not change this result. The relationship at Selvagem was non-existent ($r = -0.03$, $n = 55$, $P = 0.82$). These relationships are similar when substituting Brood10 by Brood-guarding. At Berlenga, the number of recorded shifts during the first 10 days was also negatively correlated with Mass10 ($r = -0.45$, $n = 28$, $P = 0.017$), but the same did not apply at Selvagem ($r = 0.06$, $n = 55$, $P = 0.69$). There was no evidence for a seasonal variation in early-chick growth, as hatching date did not correlate

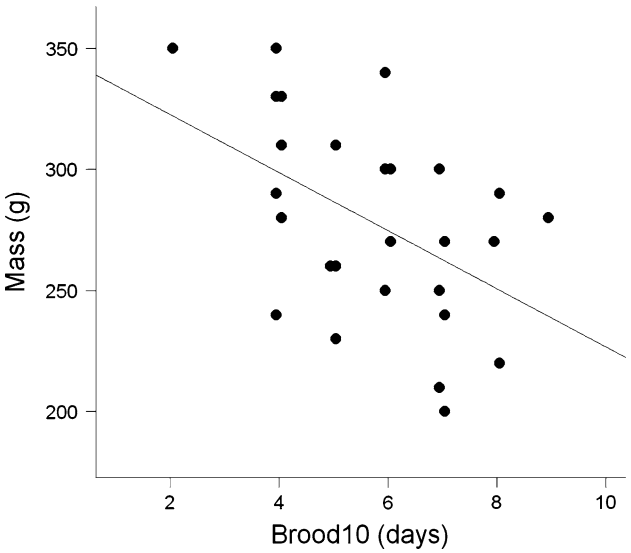

Fig. 1 The relationship between number of days with adult diurnal attendance in the first 10 days of life (Brood10) and chick mass of Cory's Shearwater *Calonectris diomedea* when 10 days old at Berlenga. The relationship is significant (see text for statistics)

with chick mass at 10 days either at Berlenga ($r = 0.24$, $n = 28$, $P = 0.22$) or at Selvagem ($r = 0.20$, $n = 55$, $P = 0.14$).

No chicks were recorded disappearing from the nests in the first 12 days of life. The only cases of predation happened on Selvagem and involved two chicks (one in an exposed nest and one in a sheltered nest) that were eaten, on the spot, by lizards *Teira dugesii*. These chicks were killed by the lizards during or immediately after hatching, when their plumage was still wet.

There was no detectable effect of the duration of brood-guarding on the probability of fledging in either Berlenga (logistic regression: $\beta = 0.46$, $n = 32$, $G_1^2 = 1.3$, $P = 0.26$) or Selvagem ($\beta = 0.01$, $n = 60$, $G_1^2 = 0.0$, $P = 0.99$).

Other comparisons between Berlenga and Selvagem

Foraging trips during incubation were longer on Selvagem (6.3 ± 3.3 days, $n = 56$) than on Berlenga (4.6 ± 2.8, $n = 71$; $F_{1,126} = 10.5$, $P = 0.002$). Egg volume did not differ between Berlenga and Selvagem ($F_{1,125} = 0.86$, $P = 0.35$). Mean hatching date did not differ between colonies ($F_{1,96} = 10.5$, $P = 0.5$), the overall average being 25 July. The shorter foraging trips at Berlenga allowed a better synchronisation between hatching and the arrival of one parent from the sea. At this island, 66% ($n = 32$) of the nests saw a change-over between the parents within 24 h of hatching, while the corresponding figure for Selvagem was only 20% ($n = 61$; Fisher's exact test, $P < 0.001$). Chick body mass at day ten was 278 ± 41 g ($n = 28$) on Berlenga and 258 ± 61 g ($n = 55$) on Selvagem ($F_{1,82} = 2.5$, $P = 0.12$). On 20 September, chick mass was 1,049 ± 150 g ($n = 35$) on Berlenga and 1,012 ± 113 g ($n = 83$) on Selvagem ($F_{1,117} = 2.2$, $P = 0.14$). Mass measurements taken on 25 September gave similar results, with no differences between colonies. Fledging success was similar at both colonies, with 0.88 fledglings per chick hatched ($n = 34$) on Berlenga and 0.88 ($n = 64$) on Selvagem.

Discussion

The duration of the brood-guarding stage in Cory's Shearwaters is highly variable. Our study shows that chicks can be left on their own in the first 24 h of life and still survive to fledging, which suggests they can maintain body temperature (almost) from hatching. Yet, some chicks are diurnally brood-guarded for much longer periods (up to 9 of the 10 first days of life).

Nests on Berlenga are inaccessible to gulls and Cory's Shearwater chicks suffered no predation, despite the presence of Black Rats. It could be argued that the presence of potential predators on this island make our test of the synchronisation hypothesis invalid, as it could be conditioning parental behaviour. However, we find this unlikely. Cory's Shearwaters seem unable to respond to rat presence when selecting nest sites (Igual et al. 2006), which is in line with the well-known general inability of pelagic seabirds to adequately respond to the presence of introduced terrestrial predators. On Selvagem, gulls have access to exposed nests, but we recorded no cases of gull predation. In any case, we also tested the synchronisation hypothesis for a sub-sample of nests that were inaccessible to gulls on this island. Predation rates were very low at Selvagem Grande, where 2 chicks (out of 64) apparently died from the attacks of small lizards. One of these was still being attended by its parent who did not attempt or did not succeed in defending it. Lizards are extremely abundant on Selvagem and it is unlikely that they could be "swamped" by a greater synchronisation of nesting. Furthermore, our observations (unpublished data) indicate that, on Selvagem, chicks are taken by lizards only on the day of hatching, when their plumage is still wet ($n = 40$ observations). Given that virtually all the variation in brood-guarding behaviour of Cory's Shearwaters takes place after the day of hatching (only 1% of the chicks were left on their own on the day of hatching), it does not seem to be reasonable to assume that lizards could be a factor responsible for such variation.

The synchronisation hypothesis states that early-nesting pairs of colonial birds should brood-guard offspring for longer periods than late-nesting counterparts, when unattended young chicks face a significant risk of predation. This hypothesis has received empirical support from studies with albatrosses, where predation rates of young chicks are typically high and where there is a clear seasonal decline in brood-guarding duration (Catry et al. 2006a, and own unpublished data). The present study is the first to test the synchronisation hypothesis in a species and/or situation where unattended chicks face little or no predation. As predicted by this hypothesis, there was no seasonal decline in brood-guarding duration in Cory's Shearwaters nesting in a variety of environments. The fact that early and late hatched chicks had a similar early-growth rate suggests that no seasonal trend in food availability was present that could confound this interpretation. More research focussing on a diverse array of species is needed to further confirm or reject the above ideas.

The growth assistance hypothesis predicts that chicks benefiting from longer parental attendance will gain from assistance in thermoregulation and/or from being provisioned with frequent small meals, and hence achieve higher mass growth rates early in life. This prediction was not upheld by the data from either Berlenga or Selvagem. In fact, at Berlenga there was a *negative* significant

correlation between chick mass at 10 days and the total parental investment in diurnal brood-guarding. This indicates that, at least under certain conditions, such as the ones verified at Berlenga in 2006, parents investing more on brood-guarding (and hence less on foraging) trade-off physical presence at the nest for chick condition. Still, the slower growth of chicks guarded for longer periods did not have a measurable impact on their survival to fledging, although it might have consequences later in life (e.g. Ludwigs and Becker 2006).

Exposed nests are potentially more susceptible to predation by gulls and to factors that can cause thermoregulatory stress, such as direct sunshine, wind and rain. Hence, according to the chick-protection hypothesis, longer brood-guarding was predicted to occur in exposed situations. This prediction was clearly not upheld by the data, with (non-significantly) longer brood-guarding occurring in the sheltered nests. It could be argued that birds nesting on sheltered spots are of higher quality and, as a result, able to attend their nest for longer, counteracting any tendency for a relative higher investment in brooding at exposed sites. This view is supported by the finding that there was a lower chick mortality in sheltered nests (see also Mougin et al. 1987). On the other hand, chick mass was not lower in exposed nests. Furthermore, when we compare brood-guarding using only successful nests (in an attempt to exclude possible low-quality individuals that subsequently failed reproduction at the exposed sites), there is still no difference in brood-guarding behaviour at sheltered and exposed nests. Hence, we conclude that Cory's Shearwaters do not display a behavioural response in brood-guarding in relation to variation in nest-site characteristics.

Harris (1969), studying Audubon's Shearwater *Puffinus lherminieri*, reported that when feeding conditions were poor, chicks were brood-guarded for shorter periods. The inter-colony comparison made in this study also suggests that in situations with low food availability or accessibility, Cory's Shearwaters may brood-guard offspring for shorter periods. Selvagem is located in a deep and presumably less productive ocean area, and many off-duty birds during incubation move to the distant upwellings of the NW African coast to forage (own unpublished data). This results in longer foraging trips than the ones made by the Berlenga birds, which have ready access to the productive waters of the Portuguese continental shelf. Berlenga birds synchronise their nest change-overs better with hatching, which may enhance early chick growth. There were no significant differences in chick body mass between Selvagem and Berlenga, with a slight tendency for heavier weights at the latter site. This may be indicative of a better growth in Berlenga, given that adult Cory's Shearwater linear measurements are, on average, ca. 4% larger at Selvagem (Granadeiro 1993). It should be noted, however, that there are alternative explanations for a longer brood-guarding at Berlenga than at Selvagem. For example, differences in nest micro-climate and a cooler environment at the northernmost site (Berlenga) may also have contributed to inter-site differences. Only by studying a larger number of sites and years can the effects of food availability and climate be properly assessed.

Zusammenfassung

Brutbewachungsverhalten bei
Gelbschnabelsturmtauchern *Calonectris diomedea*

Brutbewachung (die fortwährende Anwesenheit eines Elters am Nest) ist bei nesthockenden Vögeln bislang nur relativ wenig untersucht worden. Die elterliche Investition in Brutbewachung ist oftmals stark variabel innerhalb einer Art, und die Untersuchung solcher Variabilität könnte dazu beitragen, die Funktionen und die Steuerung dieses Verhaltens sowie die trade-offs, die bei der Wahl zwischen Bewachen und Verlassen des Nests zwecks Nahrungssuche eine Rolle spielen, zu verstehen. Bei einigen koloniebrütenden Vögeln wurde beobachtet, dass sich früh brütende Paare länger um ihr Küken kümmern als später brütende, was zur Formulierung der „Synchronisationshypothese" führte, die davon ausgeht, dass früh brütende Paare die Brutbewachung verlängern, um die Wahrscheinlichkeit von Nestprädation durch einen Verteilungseffekt zu verringern. In dieser Studie testen wir zum ersten Mal die Vorhersage, dass in Bruthöhlen nistende koloniebrütende Vögel, die nur geringem Prädationsdruck ausgesetzt sind, keine saisonale Abnahme in der Dauer der Brutbewachung zeigen sollten. Die „Wachstumshilfehypothese" besagt, dass Brutbewachung die Versorgung der Küken mit kleinen Futterportionen in kurzen Abständen und daher die effiziente Nutzung von Energie durch Küken mit schlechten thermoregulatorischen Fähigkeiten erlauben könnte, was zu verbessertem Wachstum der Küken in der frühen Entwicklungsphase führen könnte. Die „Kükenschutzhypothese" schließlich sagt vorher, dass Küken in stärker exponierten Nestern länger bewacht werden sollten. Daten, die in zwei in unterschiedlichen Umwelten gelegenen Kolonien von Gelbschnabelsturmtauchern *Calonectris diomedea* gesammelt wurden, stützten die „Synchronisationshypothese", da es keinen saisonalen Trend in der Dauer der Brutbewachung gab. Entgegen der „Wachstumshilfehypothese" wiesen länger bewachte Küken kein verbessertes Wachstum auf (in einer Kolonie gab es sogar einen negativen Effekt der Brutbewachung auf die frühe Kükenentwicklung). Schließlich fanden wir keinen Unterschied in der Brutbewachung zwischen Nestern, die

potentiellen Prädatoren und Wetter unterschiedlich stark ausgesetzt waren. Obwohl die Vorhersage der „Synchronisationshypothese" bestätigt wurde, ist weitere Forschung notwendig, um die Hauptfaktoren zu identifizieren, die zu der in dieser und anderen Studien beobachteten Variabilität in der Brutbewachung führen.

Acknowledgments Paulo Oliveira, Dília Menezes and António Teixeira provided permissions to carry out the work and, together with the wardens at the two Nature Reserves where this study took place, gave important logistical support. This study is an output from a project on the ecology of Cory's Shearwaters (PDCT/MAR/58778/2004) supported by Fundação para a Ciência e a Tecnologia (FCT–Portugal). P. Catry benefited from postdoctoral fellowships from FCT (BPD/11631/02 and SFRH/BPD/30031/2006) and further support was received through Programa Plurianual (UI&D 331/94).

References

Brodin A, Jönsson I, Holmgren N (2003) Optimal energy allocation and behavior in female raptorial birds during the nestling period. Ecoscience 10:140–150

Catry P, Phillips RA, Forcada J, Croxall JP (2006a) Factors affecting the solution of a parental dilemma in albatrosses: at what age should chicks be left unattended? Anim Behav 72:383–391

Catry P, Granadeiro JP, Oliveira P (2006b) Do Cory's shearwaters *Calonectris diomedea* synchronize laying among close neighbourhoods? A reappraisal using data from artificial nest sites. Acta Ethol 9:87–90

Düttman H, Bergmann H-H, Engländer W (1998) Development of behavior. In: Starck JM, Ricklefs RE (eds) Avian growth and development. Oxford University Press, Oxford

Granadeiro JP (1991) The breeding biology of Cory's shearwater *Calonectris diomedea borealis* at Berlenga Island, Portugal. Seabird 13:30–39

Granadeiro JP (1993) Variation in measurements of Cory's shearwaters between populations and sexing by discriminant analysis. Ring Migr 14:103–112

Harris MP (1969) Food as a factor controlling the breeding of *Puffinus lherminieri*. Ibis 111:139–156

Igual JM, Forero MG, Gomez T, Orueta JG, Oro D (2006) Rat control and breeding performance of Cory's shearwaters: effects of poisoning effort and habitat features. Anim Conserv 9:59–65

Ims RA (1990) On the adaptive value of reproductive synchrony as a predator-swamping strategy. Am Nat 136:485–498

Ludwigs J, Becker PH (2006) Individual quality and recruitment in the common tern *Sterna hirundo*. Acta Zool Sinica 52(Suppl):96–100

Mougin J-L, Jouanin C, Roux F (1987) Les paramètres contrôlant la réussite de l'incubation chez le puffin cendré Calonectris diomedea borealis de l'ile Selvagem Grande (30°09′N, 15°52′W). Bocagiana 112:1–11

Ricklefs RE, Roby DD (1983) Development of homeothermy in the diving petrels *Pelecanoides urinatrix exul* and *P. georgicus*, and the Antarctic Prion *Pachyptila desolata*. Comp Biochem Physiol A 75:307–311

Tveraa T, Christensen GN (2002) Body condition and parental decisions in the snow petrel (*Pagodroma nivea*). Auk 119:266–270

Tveraa T, Sæther B-E, Aanes R, Erikstad KE (1998) Body mass and parental decisions in the Antarctic Petrel *Thalassoica antarctica*: how long should the parents guard the chick? Behav Ecol Sociobiol 43:73–79

Varpe Ø, Tveraa T, Folstad I (2004) State-dependent parental care in Antarctic petrel: responses to manipulated chick age during early chick rearing. Oikos 106:479–488

Visser GH (1998) Development of temperature regulation. In: Starck JM, Ricklefs RE (eds) Avian growth and development. Oxford University Press, Oxford

Warham J (1990) The petrels their ecology and breeding systems. Academic Press, London

Weathers WW, Gerhart KL, Hodum PJ (2000) Thermoregulation in Antarctic fulmarine petrels. J Comp Physiol B 170:561–572

Wendeln H, Becker PH (1996) Body mass change in breeding common terns (*Sterna hirundo*). Bird Study 43:85–95