Dear Author:

Please find attached the final pdf file of your contribution, which can be viewed using the Acrobat Reader, version 3.0 or higher. We would kindly like to draw your attention to the fact that copyright law is also valid for electronic products. This means especially that:

- You may not alter the pdf file, as changes to the published contribution are prohibited by copyright law.

- You may print the file and distribute it amongst your colleagues in the scientific community for scientific and/or personal use.

- You may make your article published by Springer-Verlag available on your personal home page provided the source of the published article is cited and Springer-Verlag is mentioned as copyright holder. You are requested to create a link to the published article in Springer's internet service. The link must be accompanied by the following text: The original publication is available at http://link.springer.de or at http://link.springer-ny.com . Please use the appropriate URL and/or DOI for the article. Articles disseminated via SpringerLink are indexed, abstracted and referenced by many abstracting and information services, bibliographic networks, subscription agencies, library networks and consortia.

- Without having asked Springer-Verlag for a separate permission your institute/your company is not allowed to place this file on its homepage.

- Please address any queries to the production editor of the journal in question, giving your name, the journal title, volume and first page number.

Yours sincerely,

Springer-Verlag

Vincenzo Penteriani · Javier Viñuela · Josabel Belliure
Javier Bustamante · Miguel Ferrer

Causal and functional correlates of brood amalgamation in the chinstrap penguin *Pygoscelis antarctica*: parental decision and adult aggressiveness

Abstract Despite the high number of species in which crèching behaviour has been analysed, the factors determining brood desertion and chick aggregations remain relatively poorly understood. We analysed crèching behaviour of chinstrap penguins (*Pygoscelis antarctica*) to test whether: (1) timing of chick aggregations was mainly determined by the growth stage of chicks or by adult physiological constraints; (2) the crèche acts as a protective mechanism against predation or as a defence against conspecific adult aggressiveness. Our results show that chick desertion was not related to chick growth rate and was driven primarily by a parental decision, determined by adult physical constraints imposed by moulting needs and the short breeding season in Antarctica. With respect to the functional meaning of brood amalgamations, our results suggest that they are originated by the aggressive behaviour of adults, although the forces driving them could depend greatly on ecological conditions and vary among species and populations. Finally, because brood amalgamations can be determined by adult aggressiveness contrasting with the origin and typical definition of the term "crèche" (which implies the nursery concept), we propose the use of the term "brood amalgamation" for the penguin "crèches".

V. Penteriani (✉) · J. Bustamante · M. Ferrer
Department of Applied Biology,
Estación Biológica de Doñana, CSIC, Avda. María Luisa s/n,
Pabellón del Perú, 41013 Seville, Spain
E-mail: penteriani@ebd.csic.es

J. Viñuela
IREC, CSIC-UCLM-JCCLM, Ronda de Toledo s/n,
13005 Ciudad Real, Spain

J. Belliure
Departamento de Ecología, Facultad de Ciencias,
Universidad de Alcalá,
28803 Alcalá de Henares, Spain

Introduction

Chicks of chinstrap penguins (*Pygoscelis antarctica*), similarly to those of most penguin species, usually gather in more or less dense aggregations called crèches while waiting for the return of their parents from the sea to feed them (see review in Davis 1982). These chick gatherings are considered by various authors to have different functions, allowing the parents to leave the chicks unattended while they forage in the sea: (1) protection from predators (e.g. Pettingill 1960; Jouventin 1971; Besnard et al. 2002; see also review in Davis 1982), (2) protection from inclement weather (Yeates 1975; LeMaho 1977), and (3) social functions (Sladen 1958). However, a similar behaviour to crèching behaviour has also been described in all ground-nesting pelicans, and several species of gulls, terns, shags and cormorants, waterfowl, crows and parrots, and its functional and evolutionary significance is a matter of controversy (reviews in Carter and Hobson 1988; Wanker et al. 1996; Besnard et al. 2002).

At present, two groups of hypotheses have been proposed to explain why crèching behaviour occurs at a given chick age in penguins. In the first group, hypotheses are based on a "chick" perspective, and consider that the age at which chicks aggregate is determined by the moment at which the young are able to thermoregulate efficiently, recognise their parents and nests and/or increase their food requirements (see review in Lishman 1985; Young 1994). In the second and more recent group, hypotheses are based instead on a "parent" perspective, and consider brood desertion as a parental decision to favour adult survival (Williams 1990; Viñuela et al. 1996; Moreno et al. 1997). Actually, when the time available for breeding is limited, such as in polar climates, there is a crucial time during the breeding season at which brood desertion could become necessary for parents to initiate premoult resources storage. This view is also supported by findings about the crèching process in other species (e.g. goldeneye ducks, *Bucephala*

islandica), in which this social behaviour is driven primarily by parental investment decisions (Eadie and Lyon 1998).

In this study, we analyse two main elements of crèching behaviour that remain relatively poorly understood, despite the high number of species in which the crèching behaviour has been described and analysed: (1) what factor/s could determine the brood desertion by parents (i.e. leaving the chicks alone for extended periods) and, consequently, (2) what is/are the proximate causation/s determining chick aggregations.

If timing of incorporation to chick aggregations is mainly determined by the growth stage of chicks, we predict that brood desertion should correlate closely with the growth of the chicks (e.g. they are deserted by parents only when able to thermoregulate and becoming invulnerable to predators because of their relatively large size). In contrast, if brood desertion is mainly determined by the physiological constraints imposed on parents by the short austral summer (e.g. the premoult reserve storage needs) or poor individual physical condition, the age at which chicks enter crèches should be correlated with hatching date and/or parental condition, but not with chick growth.

Finally, if brood amalgamations primarily act as a defence against conspecific adult aggressiveness (Seddon and van Heezik 1993; De León et al. 2002), we predict that an increase in the proportion of adults per chick in the colony would cause an increase in the size of brood amalgamations.

Materials and methods

Study area

The study was conducted at the Vapour Col chinstrap rookery (approx. 20,000 breeding pairs) in Deception Island, South Shetlands (63°00′S, 60°40′W), during the austral summer of 1993/1994. Our main sample was part of a sub-colony of 150 pairs, and the nests we selected ($n=110$) occupied different locations with respect to the colony edge. As in preceding years (Viñuela et al. 1996), nests were marked with numbered sticks at the end of the incubation and adults were banded with metal flipper bands (standard 34×17 mm penguin bands, produced by Lambournes, Solihull, UK). To account for the impact of flipper bands on penguin body condition (see review in Jackson and Wilson 2002), blood samples were extracted before banding.

Brood desertion

We tried to visit the colony every day before hatching to obtain hatching dates, so as to be able to estimate the age at which the chicks were left alone by their parents. When chicks hatched between visits that were more than 1 day apart, we estimated the hatching date by a regression model of the flipper length (mm) on age (number of days after hatching): flipper $=30.3+3.9×$age, $r=0.999$ (Viñuela et al. 1996). We measured the body mass (with a spring balance), bill length (with a dial caliper) and flipper length (with a ruler) of the chicks at the ages of approx. 15 days (14–16 days, when chicks were banded with rubber bands), 25 days and 40–45 days (when chicks were in crèches and we marked them with flipper bands). No significant effects of our disturbance on

chick survival and the brood-desertion process were noted (Moreno et al. 1994; Viñuela et al. 1996). At that time, we evaluated a possible degree of weight and bill asymmetry in the nests with two chicks (M. Ferrer, unpublished data). Asymmetry was considered as [(difference between chick measurements/x̄)×100]. After chicks were 15 days old, we tried to visit the colony every day and recorded if chicks were accompanied by a parent (guard phase) or if they had been left alone (start of the brood-amalgamation phase). The 1st day on which chicks were seen alone was considered as the date on which they entered crèches, and the number of days elapsed between that date and hatching date as the age of crèche formation.

We extracted blood from a sample of adult penguins in the late guard stage (chicks 15–20 days old), 2–3 days after arriving from the sea to relieve their pairs from guarding duties. Blood was extracted from foot veins, collected in lithium heparin tubes, and maintained refrigerated. Blood centrifugation (10 min at 3,000 rpm) and separation of plasma were performed within 24 h after blood extraction. Blood analyses were carried out in a portable autoanalyser (Reflotron II, with the reagents recommended by Boehringer-Mannheim). As an indicator of body condition after fasting, we used plasma urea concentration (Alonso-Alvarez et al. 2003).

Brood amalgamation

To investigate the function of penguin crèches, we made 5-min focal observations of the behaviour of randomly chosen chicks ($n=40$) already left unguarded by their parents and within aggregations of different size, randomly selected at different parts of the rookery and during the whole crèching period. For each individual, we recorded the following information: (1) individual displacements (metres per minute). To compute this distance, we first counted the number of individual footsteps made by the chick and we successively multiplied them by the footstep length; (2) chick-chick interactions (e.g. aggregations); (3) adult-chick interactions (generally aggression by pecking). For each chick aggregation studied, we recorded the following additional information: (1) observation of the behaviour of the skuas *Catharacta skua*, the main potential predator of penguin chicks in the rookery, during the whole breeding cycle of the colony and for a duration of approx. 7 h/day; (2) size (number of chicks) of the brood amalgamations (a chick was considered to be part of a specific aggregation if the distance to its nearest neighbour chick was < 1 m); (3) number of adults present at the periphery of the chick aggregation (< 10 m from a chick); (4) evolution of the size of the brood amalgamations during the time of our behavioural observations. As the mean size of brood aggregations is correlated to the number of chicks present in the colony, we used the residuals of the regression of the number of chicks in the colony-mean size of brood aggregations to test our predictions.

Finally, we performed specific observations of the behaviour of skuas from vantage points near the colony over 26 h on 5 different days, continuously following each focal individual, and recording their feeding behaviour.

Results

Brood desertion

Hatching date ranged from 17 December to 11 January. Age of switching from the guard to the crèching phase ranged between 20 and 40 days (30.27 ± 3.45 days) within the period 16–31 January (24 January ±3 days; Viñuela et al. 1996). Age of crèching was negatively correlated with the hatching date ($F=113.6$, $P<0.001$, $R^2=51.5$, $n=109$), as also previously reported by Viñuela et al. (1996). A quadratic relationship was found between the age and the date on which chicks entered
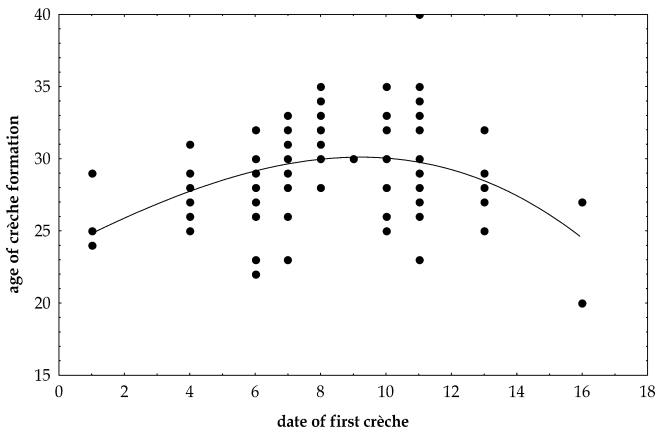
Fig. 1 Relationship between date and chick age at crèche formation ($n = 109$)

crèches ($F = 15.3$, $P < 0.001$, $n = 109$; partial F for date $= 10.1$, $P = 0.002$; partial F for date$^2 = 20.5$, $P < 0.001$; Fig. 1). That is, the end of the guard phase took place, on average, at a younger age for chicks hatched early and late in the colony. Urea concentration in the blood of parents (15.66 ± 5.73 mg/dl, $n = 39$) showed a negative correlation with the age when chicks entered crèches ($F = 5.8$, $P = 0.02$, $r = -0.37$, $n = 39$) and a positive correlation with hatching date ($F = 12.9$, $P < 0.001$, $r = 0.5$, $n = 39$). The first relationship suggests that parents in poor condition deserted their chicks at an earlier age, whereas the second relationship suggests that the adults laying eggs later in the breeding season were individuals in poor physiological condition.

No significant differences in the age of crèche formation between the nests with one or two chicks were found ($F = 0.6$, $P = 0.46$, ANOVA). However, analysing the residuals of the regression of age of crèche formation on hatching date, we found that the chicks from single broods started amalgamation later than chicks from double broods ($F = 13.2$, $P = 0.0004$).

Chick growth rates and asymmetry before the starting of crèches did not differ significantly between single and double broods (Table 1), and were not significantly correlated with either crèching age or the residuals of the crèching age on hatching date regression.

Our data on chick growth did not show any clear trend when correlated with the hatching date: after Bonferroni's correction, the only positive and significant correlation we detected was with bill length at the age of 15 days for the second chicks (Table 2).

Brood amalgamation

We observed the behaviour of chick and adult chinstraps, for a total of 1,226 min during the brood amalgamation phase.

The displacements of the chicks were negatively correlated with the size of the brood amalgamation ($F = 35.59$, $P < 0.001$, $r = -0.8$, $n = 22$). The mean distance moved per unit of time by lone chicks was 1.25 m/min, but they barely moved when the brood amalgamation included ten or more individuals (Fig. 2). Such movements were determined by the aggression of adults: the number of adult aggressions toward the chicks was inversely correlated with the size of the aggregations ($F = 64.06$, $P < 0.001$, $r = -0.87$, $n = 22$), and was directed more frequently toward the small groups (Fig. 3).

The number of chicks within the 40 chick aggregations we studied in Vapour Col varied between 14 and 242 individuals, and the number of adults ranged from 8 to 86. Figure 4 shows the positive relationship ($F = 10.98$, $P = 0.002$, $r = 0.47$, $n = 40$) between the ratio no. of adults/no. of chicks present at the chick gathering and the residuals of the regression chick number-mean size of the brood amalgamation. That is, chicks tended to aggregate in larger groups when the number of neighbouring adults increased. Actually, an increase in the proportion of adults close to the brood amalgamations determined: (1) an increase in the percentage of chicks of the colony that were included in the 2 largest aggregations ($F = 22.05$, $P < 0.001$, $r = 0.6$, $n = 40$; Fig. 5a); and (2) a reduction in the number of aggregations of < 5 chicks ($F = 7.52$, $P = 0.009$, $r = 0.2$, $n = 40$; Fig. 5b).

Table 1 Growth rate (measurements/age) of chicks at 15 and 25 days old approx. and within this period (growth/days) in single and double broods. As hatching is asynchronous (modal asynchrony = 1 day), we considered that the second chick was 1 day younger than the first chick. For double broods we calculated the mean of both the chicks. Comparisons are made with t-test. Body mass is in grams, bill and flipper length are in centimetres

		1 chick $\bar{x} \pm SD$ (n)	2 chicks $\bar{x} \pm SD$ (n)	t	P
15 days old	Body mass	67.10 ± 10.30 (25)	68.20 ± 8.40 (67)	-0.53	0.59
	Bill length	1.45 ± 0.13	1.43 ± 0.11	1.06	0.29
	Flipper	6.22 ± 0.77	6.21 ± 0.56	0.03	0.98
25 days old	Body mass	81.70 ± 11.10 (21)	80.10 ± 8.13 (59)	0.65	0.51
	Bill length	1.28 ± 0.12	1.26 ± 0.09	0.89	0.37
	Flipper	6.62 ± 0.43	6.48 ± 0.43	1.19	0.24
15–25 days	Body mass	105.90 ± 20.20 (18)	106.50 ± 16.03 (50)	-0.11	0.91
	Bill length	0.83 ± 0.24	0.80 ± 0.15	0.67	0.51
	Flipper	7.19 ± 0.86	6.91 ± 0.80	1.21	0.23

Table 2 Correlations between chick growth rates (measurements/ age, growth/days) and hatching date. Significance level = 0.0027 (after Bonferroni's correction). Body mass is in grams, bill and flipper length are in centimetres

		Younger/unique chick			Second chick		
		r	P	n	r	P	n
15 days old	Body mass	−0.08	0.44	93	−0.14	0.26	68
	Bill length	0.29	0.004	93	0.43	0.0002	68
	Flipper	−0.08	0.44	93	−0.08	0.50	68
25 days old	Body mass	−0.008	0.94	87	0.20	0.12	61
	Bill length	−0.02	0.85	87	0.12	0.37	61
	Flipper	−0.13	0.22	87	0.15	0.24	61
15–25 days	Body mass	0.001	0.99	68	0.24	0.09	50
	Bill length	−0.07	0.59	68	0.07	0.64	50
	Flipper	0.15	0.22	68	0.33	0.02	50

Fig. 4 Adult to chick aggressiveness: relationship between the residuals (increased to 10 to better represent them) of the regression chick number-mean size of brood amalgamation (n = 40)
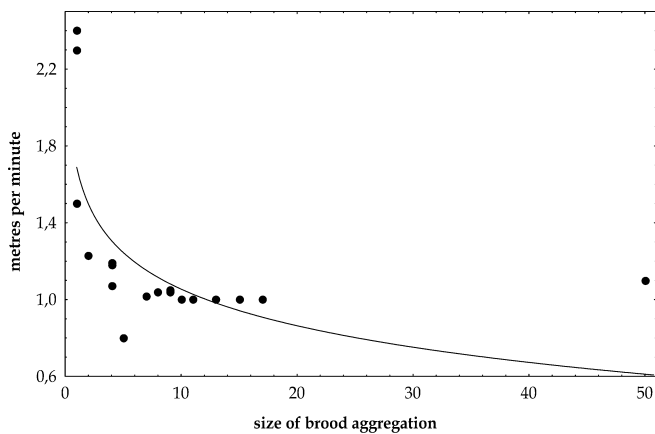

Fig. 2 Adult to chick aggressiveness: relationship between size of brood aggregation and chick displacement (n = 22)

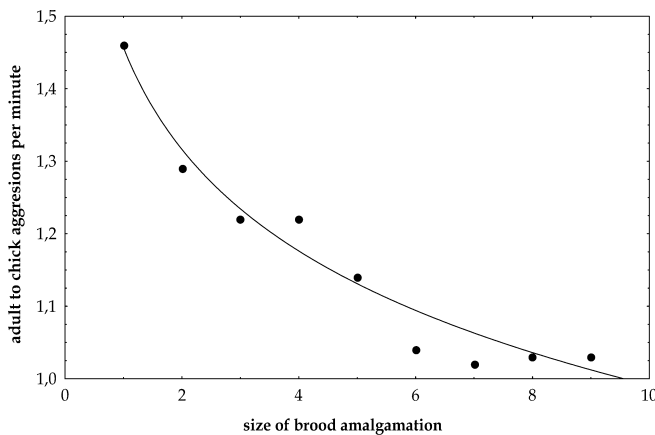**Fig. 3** Adult to chick aggressiveness in relation to size of brood aggregation (n = 22)

Fig. 5a, b Adult to chick aggressiveness: **a** increase in number of chicks in the two largest brood amalgamations due to the increase of the proportion of adults close to the aggregations (n = 40), and **b** decrease in number of brood amalgamations of < 5 chicks due to the increase in the proportion of adults close to the aggregations (n = 40)

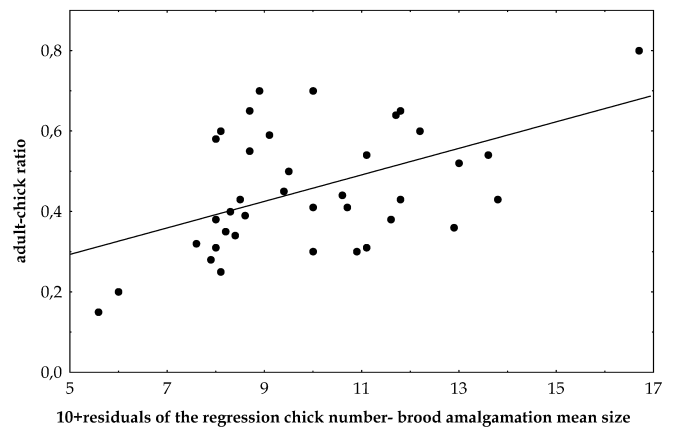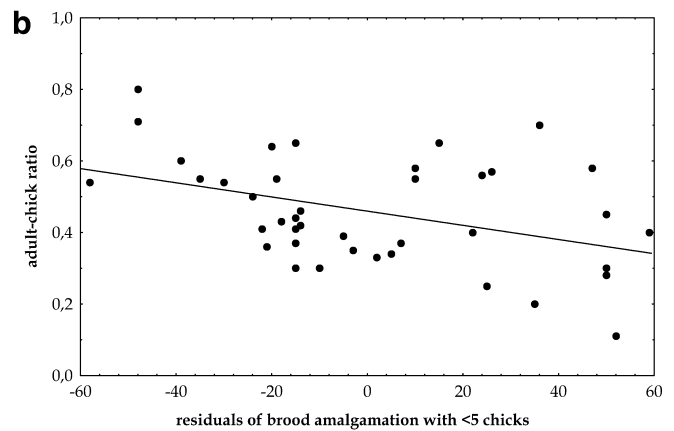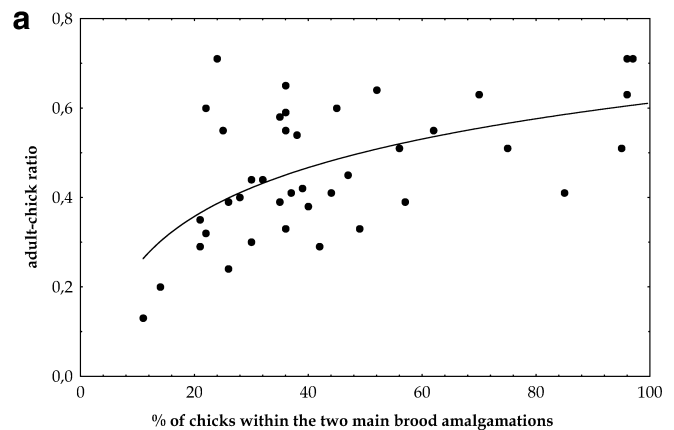During the observation of chicks' gatherings, we never observed any predation attempt by skuas on a chick in a group, regardless of its body size or the size of the aggregation. During the observations made on individual skuas (n = 15), we always observed this species feeding on carcasses of already-dead chicks or adults only.

Discussion

Brood desertion

We did not find any elements showing that brood desertion and, consequently, the formation of brood amalgamations were related to the growth rate of the chicks during the guard phase. Additionally, growth rate did not show any remarkable variation in relation to hatching date. Moreover, we found a negative correlation between: (1) the age of the chicks when they aggregate and the hatching date, a result reported previously for this species (Viñuela et al. 1996; Moreno et al. 1997), (2) the body condition of parents and the age of brood desertion, and (3) the body condition of parents and the hatching date. These relationships seem to indicate that adults that hatch their eggs later are forced to end the guard phase when their chicks are younger due to their relatively poor physical condition, although the pattern of parental investment in this species seems to be similar for early- and late-laying pairs (Viñuela et al. 1996). In fact, no differences in growth rates were found for early- and late-hatching chicks. Consequently, late-laying pairs may be performing similar investment efforts, but at a higher physiological cost, reflected in their poorer condition, because late breeders may be individuals of poorer quality, or because late breeders experience poorer conditions for breeding (see also Viñuela et al. 1996; Moreno et al. 1997). The short breeding season in Antarctica submits parents to conflicting pressures between guarding chicks and advancing the period of premoult reserve storage (adult penguins must moult before the arrival of the autumn), thereby determining a clear-cut limit (probably indicated by changes in day length) to the extent of the guard phase. An early shift from the guard to the brood-amalgamation phase, representing the moment at which the adults join their investment in the current brood with their energy need for moulting and their own survival (Bost and Jouventin 1991), must be especially important for chinstrap penguins, as they are the pygoscelid species with the latest laying dates (Trivelpiece et al. 1987). Actually, the moult of penguins requires fasting over long periods (13–34 days, depending on species), the energy reserves for which are accumulated throughout prolonged premoult periods requiring a foraging effort higher than the one of adult attending chicks (Adams and Brown 1990). This "parent" view of brood desertion in penguins and, consequently, of ages of crèche formation, agrees with the explanation proposed by Viñuela et al. (1996) and Moreno et al. (1997, 1998).

These results would explain the relatively young age at which late-hatched chicks enter crèches, but early-hatched chicks were also left unguarded when they were relatively young (Fig. 1). The fact that the first families to leave their chicks alone at the colony (when no brood amalgamation is possible) leave them at an age younger than the average, suggests that the earliest-laying adults are also forced to end the guard phase before their chicks reach the optimum age. In fact, the earliest chicks left unguarded in the colony may suffer high mortality due to aggressive behaviour by other brooding penguins in the colony (personal observation). The first pairs breeding in a given season may be exposed to particularly high costs, because weather or foraging conditions early in the season may be worse than later on (Viñuela et al. 1996 and references therein). Thus, these early pairs may be reaching a hypothetical threshold of poor condition induced by the high demands of the guarding phase (long periods without feeding at the nests and spending energy on incubation and brooding), at an earlier stage than later-laying pairs, thus explaining the relatively early end of the guarding phase in early-laying pairs (Taylor 1962). Unfortunately, blood samples from the very early breeding pairs could not be obtained due to logistic constraints and, thus, we cannot provide data about physiological condition of those adult birds, which presumably should be relatively poor, more similar to late breeders than to birds laying at central peak dates of the laying season.

It is well known that early grouping has additional costs for chicks in terms of persecution by adults (Penney 1968; Young 1994) and increased risk of predation (Davis 1982; Young 1994). As also suggested by Moreno et al. (1997) and Eadie and Lyon (1998), this seems to indicate that the adult decision to desert the chicks is driven primarily by a parental decision, because it is not profitable for them to continue guarding for longer. Brood amalgamation may therefore be best viewed as a consequence of the intergenerational conflict between adults and chicks (Pierotti 1991) and a secondary outcome of selection acting on deserted young (Eadie and Lyon 1998). Therefore, the decision to desert the chicks seems to be based on three factors that are not mutually exclusive: (1) the parent needs to divert resources to premoult reserve storage (Viñuela et al. 1996; Moreno et al. 1997); (2) the body condition of the parents (Williams 1990; Wanker et al. 1996; Moreno et al. 1997); and (3) the number of chicks the adults are raising (De León 2000). Our results fit the predictions of the energetic salvage strategy hypothesis (Eadie et al. 1988), which envisages that parents in poor body condition abandon their chicks to improve their own survival chances, also ensuring future breeding attempts in long-lived species (Maynard Smith 1977; Bustnes and Erikstad 1991). However, we cannot exclude the possibility that brood desertion could be, under several ecological conditions, a more flexible behaviour, the importance of adult decision varying among years, colonies and populations.

Brood amalgamation

The number of chick displacements and adult aggressions in relation to the size of brood amalgamation, the aggregation of chicks in larger groups when adults were

closer (the higher the number of adults near the chicks, the larger the brood amalgamation), and the absence of skua aggressions suggest that the possible origin of the observed brood amalgamation is the aggressive behaviour of adults. Actually, adults showed higher aggressiveness towards the chicks that were isolated or in small aggregations, forcing them to make frequent displacements until they reached a larger brood amalgamation. Such adults are mainly unrelated adults generally defending the area around their nest or, during feeding, preventing other young of the colony from taking the food they have brought to their chicks (De León et al. 2002). Furthermore, at this late stage of the breeding season, many subadult, non-breeding birds visit the colony before moulting, thus increasing the number of birds that may exhibit aggressive behaviour to chicks (personal observation). Intraspecific aggression towards wandering chicks has been frequently described in colonial species (Wittenberger and Hunt 1985) and Seddon and van Heezik (1993) have already explained the formation of brood amalgamations in the jackass penguin (*Spheniscus demersus*) as the result of aggression by adults towards chicks. This is the first time that adult aggression during the post-guard phase is described as the main proximate factor in the aggregation behaviour of the chinstrap penguin. For the greater flamingo, *Phoenicopterus ruber roseus*, Tourenq et al. (1995) showed that when a chick abandons the nest territory and starts to wander near other adults, it is attacked by other parents until it comes back to the nest or joins several other chicks of similar age at places with fewer, or no, aggressive adults. Nevertheless, in our opinion, the greater flamingo grouping behaviour has another and more important point in common with the brood amalgamation of the chinstrap penguin. In both species, the chick aggregations do not represent the classic example of the well-known crèching behaviour (see reviews in Riedman 1982; Eadie et al. 1988), in which young from different broods aggregate into a single group and subsequently receive care from alloparents (individuals other than the genetic parents that provide care for conspecific young, Wilson 1975). Our data on the brood amalgamations promoted by adult aggressiveness, as well as the results of Seddon and van Heezik (1993) and Tourenq et al. (1995), are opposite to the typical definition of the term crèche, which implies the nursery concept (brood aggregation cared for by adults). Despite this inconsistency, and especially for penguins in which the chick aggregations are not cared for by adults, flocking behaviour of chicks has always been defined as a crèching behaviour in the scientific literature, and all gatherings into a unique and dense aggregation have been called crèches. Now, in the light of what we observed (adult aggression on conspecific chicks) and the previous results of Seddon and van Heezik (1993) and Tourenq et al. (1995), we propose to review the use of the term crèche. For example, independently of the adaptive functions advanced for this behaviour, we consider it inaccurate to define indistinctly as crèching

behaviour such very different situations: (1) alloparents protect cubs from unrelated males trying to kill them, and allow them to gain access to their milk (e.g. African lion *Panthera leo*), (2) young are observed in aggregations with no guarding adults (e.g. Levy and Bernadsky 1991; Müller et al. 1995), (3) pairs, single parents or failed nesters attend to or care for chicks of other individuals (e.g. Pienkowski and Evans 1982; Schmutz et al. 1982; Bustnes and Erikstad 1991; Kilpi et al. 2001); (4) in species living in a complex social system throughout the year, offspring are guided by the parents to a crèche where there are ample opportunities for social interactions with similarly aged fledglings of other families (Wanker et al. 1996); or (5) chick grouping behaviour is determined by the aggressiveness of unrelated adults (Seddon and van Heezik 1993; Tourenq et al. 1995; this study). If we accept the original definition of crèche for birds (any group containing adult females and offspring, Bedard and Munro 1976), it is evident that this term cannot be applied to penguins, in which there is no particular care of the chicks by unrelated adults during the post-guard phase (De León et al. 2002), except when they thwart skua attacks (Davis 1982) or in the adoptions of emperor penguins *Aptenodytes forsteri* (Jouventin et al. 1995). Conversely, chicks are frequently attacked by adults (Seddon and van Heezik 1993; De León et al. 2002; this study). For this reason, we propose the use of the term brood amalgamation for penguin "crèches".

Several explanations have been suggested for the factors determining brood amalgamation. Our results have simultaneously shown that conspecific aggressiveness can explain aggregations and that predation by skuas, one of the main proximate causes of such a form of chick gathering (Davis 1982), had no influence at all on the aggregations we observed. Actually, the carcasses of chick and adult chinstraps, as well as abandoned eggs, were the main food of the skuas living close to the colony, due to their high frequency and the low deterioration rates (M. Ferrer, unpublished data). This kind of feeding behaviour, justified by the lower energy expenditure and easy gathering of carcasses, compared to more difficult, risky and energy-demanding active predation, seems to be relatively common in skuas (Pietz 1987; Norman et al. 1994; Young 1994). It is also true that Vapour Col rookery could represent a particular situation in Antarctica, because a relatively low number of skuas (estimated number of 6–7 pairs near the rookery, plus an unknown number of longer-distance breeding pairs visiting the rookery) inhabits a huge concentration of penguin pairs (ca. 20,000). Thus, easy food in the form of carrion may be plentiful, and this could explain the absence of predation attempts on chicks. All the above-cited elements could represent strong evidence that chick brood amalgamations in penguins originate from different but not mutually exclusive factors, depending on the local condition of the colony. However, it is not possible to discount the possibility that, when no negative factors influence the

544

behaviour of chicks, the amalgamations are the result of chick-chick conspecific attraction when temporary desertion by parents drives the lone chicks to aggregate. Moreover, chick aggregations could also be a function of the mean age of crèche formation and the size of the species, and could have different functions in the same species, given the changing ages and sizes of the chicks during the post-guard phase. In that case, a comparative study of the proximate factors causing brood amalgamation in penguins should be approached by combining body characteristics and behaviour, life histories and local conditions of the different penguin species.

References

Adams NJ, Brown CR (1990) Energetics of molt in penguins. In: Davis SL, Darby JT (eds) Penguin biology. Academic, San Diego, pp 297–315

Alonso-Alvarez C, Ferrer M, Viñuela J, Amat JA (2003) Plasma chemistry of chinstrap penguin *Pygoscelis antarctica* during fasting periods: a case of poor adaptation to food deprivation? Polar Biol 26:14–19

Bedard J, Munro J (1976) Brood and crèche stability in the common eider of the St. Lawrence estuary. Behaviour 20:221–236

Besnard A, Gimenez O, Lebreton J-D (2002) A model for the evolution of crèching behaviour in gulls. Evol Ecol 16:489–503

Bost CA, Jouventin P (1991) The breeding performance of the gentoo penguin *Pygoscelis papua* at the northern edge of its range. Ibis 133:14–25

Bustnes JO, Erikstad KE (1991) The role of failed nesters and brood abandoning females in the crèching system of the common eider *Somateria mollissima*. Ornis Scand 22:335–339

Carter HR, Hobson KA (1988) Crèching behavior of Brandt's cormorant chicks. Condor 90:395–400

Davis LS (1982) Crèching behaviour of Adélie penguin chicks. N Z J Zool 9:279–286

De León A (2000) Effect of brood size on crèching age in the chinstrap penguin. Waterbirds 23:117–120

De León A, Fargallo JA, Polo V, Potti J (2002) Adult aggression during the post-guard phase in the chinstrap penguin *Pygoscelis antarctica*. Polar Biol 25:355–359

Eadie JMcA, Lyon BE (1998) Cooperation, conflict and crèching behavior in goldeneye ducks. Am Nat 151:397–408

Eadie JMcA, Kehoe FP, Nudds TD (1988) Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. Can J Zool 66:1709–1721

Jackson S, Wilson RP (2002) The potential cost of flipper-bands to penguin. Funct Ecol 16:141–148

Jouventin P (1971) Comportement et structure sociale chez le Manchot empereur. Terre Vie 25:510–586

Jouventin P, Barbraud C, Rubin M (1995) Adoption in the emperor penguin *Aptenodytes forsteri*. Anim Behav 50:1023–1029

Kilpi M, Öst M, Lindstrom K, Hannu R (2001) Female characteristics and parental care mode in the crèching system of eiders, *Somateria mollissima*. Anim Behav 62:527–534

LeMaho Y (1977) The emperor penguin: a strategy to live and breed in the cold. Am Sci 65:680–693

Levy N, Bernadsky G (1991) Crèche behavior in the Nubian ibex *Capra ibex nubiana* in the Negev desert highlands, Israel. Isr J Zool 37:125–137

Lishman GS (1985) The comparative breeding biology of Adélie and chinstrap penguins *Pygoscelis adeliae* and *P. antarctica* at Signy Island, South Orkney Island. Ibis 127:84–99

Maynard Smith J (1977) Parental investment: a prospective analysis. Anim Behav 25:1–9

Moreno J, Carrascal LM, Sanz JJ, Amat JA, Cuervo JJ (1994) Hatching asynchrony, sibling hierarchies and brood reduction in the chinstrap penguin *Pygoscelis antarctica*. Polar Biol 14:21–30

Moreno J, Barbosa A, Potti J, Merino S (1997) The effects of hatching date and parental quality on chick growth and crèching age in the chinstrap penguin (*Pygoscelis antarctica*): a field experiment. Auk 114:47–54

Moreno J, Viñuela J, Belliure J, Ferrer M (1998) Effect of brood size on growth in the chinstrap penguin: a field experiment. J Field Ornithol 69:269–275

Müller DM, Kohlmann SG, Alkon PU (1995) A Nubian ibex nursery: crèche or natural trap? Isr J Zool 41:163–174

Norman FI, McFarlane RA, Ward SJ (1994) Carcasses of Adélie penguins as a food source for South Polar skuas: some preliminary observations. Wilson Bull 106:26–34

Penney RL (1968) Territorial and social behaviour in the Adélie penguin. Antarct Res Ser 12:83–131

Pettingill OS Jr (1960) Crèche behaviour and individual recognition in a colony of rockhopper penguins. Wilson Bull 72:213–221

Pienkowski MW, Evans PR (1982) Breeding behaviour, productivity and survival of colonial and non-colonial shelducks *Tadorna tadorna*. Ornis Scand 13:101–116

Pierotti R (1991) Infanticide versus adoption: an intergenerational conflict. Am Nat 138:1140–1158

Pietz PJ (1987) Feeding and nesting ecology of sympatric South Polar and brown skuas. Auk 104:617–627

Riedman ML (1982) The evolution of alloparents care and adoption in mammals and birds. Q Rev Biol 57:405–435

Schmutz JK, Robertson RJ, Cooke F (1982) Female sociality in the common eider duck during brood rearing. Can J Zool 60:3326–3331

Seddon PJ, Heezik Y van (1993) Chick crèching and intraspecific aggression in the jackass penguin. J Field Ornithol 64:90–95

Sladen WJL (1958) The pygoscelid penguins. Part 1 and 2. Falkland Isl Depend Surv Sci Rep 17:1–97

Taylor RH (1962) The Adélie penguin *Pygoscelis adeliae* at Cape Royds. Ibis 104:176–204

Tourenq C, Johnson AR, Gallo A (1995) Adult aggressiveness and crèching behavior in the greater flamingo, *Phoenicopterus ruber roseus*. Colon Waterbird 18:216–221

Trivelpiece WZ, Trivelpiece SG, Volkman NJ (1987) Ecological segregation of Adélie, gentoo and chinstrap penguins at King George Island, Antarctica. Ecology 68:351–361

Viñuela J, Moreno J, Carrascal LM, Sanz JJ, Amat JA, Ferrer M, Belliure J, Cuervo JJ (1996) The effect of hatching date on parental care, chick growth, and chick mortality in the chinstrap penguin *Pygoscelis antarctica*. J Zool 240:51–58

Wanker R, Bernate LC, Franck D (1996) Socialization of spectacled parrotlets *Forpus conspicillatus*: the role of parents, crèches and sibling groups in nature. J Ornithol 137:447–461

Williams TD (1990) Annual variation in breeding biology of gentoo penguins, *Pygoscelis papua*, at Bird Island, South Georgia. J Zool 222:247–258

Wilson EO (1975) Sociobiology. Belknap Press of Harvard University Press, Cambridge, Mass

Wittenberger JF, Hunt GL Jr (1985) The adaptive significance of coloniality in birds. In: Farner DS, King JR, Parker KC (eds) Avian biology, vol 8. Academic, Orlando, pp 1–78

Yeates GW (1975) Microclimate, climate and breeding success in Antarctic penguins. In: Stonehouse B (ed) The biology of penguins. University Park Press, London, pp 397–409

Young E (1994) Skua and penguin. Cambridge University Press, Cambridge