

Causes and Benefits of Chick Aggregations in Penguins

Author: Wilson, David

Source: The Auk, 126(3) : 688-693

Published By: American Ornithological Society

URL: <https://doi.org/10.1525/auk.2009.9709>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



The Auk 126(3):688–693, 2009
© The American Ornithologists' Union, 2009.
Printed in USA.

CAUSES AND BENEFITS OF CHICK AGGREGATIONS IN PENGUINS

DAVID WILSON¹

*Department of the Environment, Water, Heritage and the Arts, Australian Antarctic Division, 203 Channel Highway,
Kingston, 7050, Tasmania, Australia*

AGGREGATIONS OF PENGUIN chicks have been noted since the first scientific expeditions to penguin breeding colonies in the Antarctic and sub-Antarctic areas. Various authors have examined these aggregations in individual species and from limited perspectives. Chick aggregations are the result of a two-stage process; initially, chicks are abandoned by their parents, at which time they may choose to aggregate with other chicks. Here, I examine the causes and benefits of aggregations in all penguin species that display this phenomenon to identify any unifying evolutionary reasons for their formation. First, I consider the functional requirements of both parents and chicks before successful chick abandonment can occur and look at the motivations that may drive a parent or chick to leave the nest. Then I examine the evidence supporting the theories as to why a chick should join an aggregation. Finally, in light of this review, I discuss the appropriateness of applying the term “crèche” to penguin chick aggregations and offer some possible avenues of future research.

Chick aggregations have been reported in a variety of taxa, including the Anatidae (Eadie et al. 1988), Pelecaniformes (Johnsgard 1993, Velando 2001), Laridae (del Hoyo et al. 1996, Besnard et al. 2002), and Spheniscidae (present study). Ducks exhibit true crèche behavior—that is, young from different broods or families combine into a single group and subsequently receive care from parents other than their own (Eadie et al. 1988), which is significantly different from aggregations that occur in other species. In gulls, the evolution of chick aggregations has been linked to habitat instability leading to high levels of terrestrial predation, whereas low levels of aggression against predators may promote chick aggregation (Besnard et al. 2002). Chick aggregations are poorly understood in the Pelecaniformes; there is no evidence that aggregations reduce predation risk (Johnsgard 1993, Velando 2001) or reduce adult aggression (Velando 2001), but they may have thermoregulatory benefits (Carter and Hobson 1988).

Early reports applied the term “crèche” to groups of penguin chicks, assuming that the few adults present were caring for the aggregated chicks (e.g., Wilson 1907, Levick 1914). Although

this idea has subsequently been shown to be inaccurate (Williams 1995, and references therein), the term has persisted. Young (1994) highlighted that the term has been applied historically to two separate processes: a chick can crèche when its parent abandons it, and it can be part of a crèche when it is with other chicks. Here, I use the term “aggregation” to describe a group of chicks and “post-guard” to define the life-history stage once a chick has been abandoned.

Chick aggregations have been reported in 12 species of penguin: Emperor, King, Adélie, Chinstrap, Gentoo, African, Rockhopper, Macaroni, Fiordland, Erect Crested, Royal, and Snares penguins (scientific names are given in Table 1; Müller-Schwarze 1984, Seddon and van Heezik 1993a, Williams 1995). In 11 of these species, parents abandon their chicks, whereas in Rockhopper Penguins, chicks leave their parents and form aggregations (Pettingill 1960). The most recent penguin phylogeny (Baker et al. 2006) suggests that aggregation is the ancestral trait in the penguin family, being retained in the two most basal lineages (*Aptenodytes* and *Pygoscelis*) and in *Eudyptes*. Chick aggregation seems to have been lost in the genera *Spheniscus*, *Eudyptula*, and *Megadyptula* but has recently re-evolved in African Penguin, apparently in response to human disturbance (Cooper 1977).

Because penguins evolved in Antarctica (Baker et al. 2006), it is likely that chick aggregations initially arose as a way of reducing heat loss during extreme cold. For example, Emperor Penguins, which endure extreme conditions, are able to breed only because of the benefits gained by densely aggregating (Ancel et al. 1997). Penguins eventually expanded northward, to latitudes where reducing heat loss became less important (Table 1), and chick aggregations then evolved secondary functions such as avoidance of predators and of adult aggression. Once chicks are freed from thermoregulatory constraints, predator avoidance appears to be the main driver of aggregation. Penguin species in which chicks do not aggregate primarily nest in burrows or, if on the surface, in locations that protect them from aerial predators (Table 1; Seddon and Davis 1989, Stokes and Boersma 1998). The importance of

¹E-mail: david.wilson@aad.gov.au

TABLE 1. Latitudinal ranges and preferred nesting locations of penguin species (from Williams 1995) and the benefits of aggregating for chicks of those species (see text for discussion).

Species	Breeding latitudes	Preferred nest location	Role of chick aggregations
Fiordland Penguin (<i>Eudyptes pachyrhynchus</i>)	43–47°S	Surface	Poorly understood
Snares Penguin (<i>E. robustus</i>)	48°S	Surface	Poorly understood
Rockhopper Penguin (<i>E. chrysocome</i>)	37–53°S	Surface	Poorly understood
Macaroni Penguin (<i>E. chrysolophus</i>)	46–65°S	Surface	Poorly understood
Royal Penguin (<i>E. schlegeli</i>)	54°S	Surface	Poorly understood
Erect Crested Penguin (<i>E. sclateri</i>)	47–49°S	Surface	Poorly understood
Yellow-eyed Penguin (<i>Megadyptes antipodes</i>)	45–52°S	Surface	Not known to aggregate
African Penguin (<i>Spheniscus demersus</i>)	24–33°S	Burrow–surface	Reduces adult aggression (Seddon and van Heezik 1993a) and predation for small chicks (Seddon and van Heezik 1991)
Magellanic Penguin (<i>S. magellanicus</i>)	29–55°S	Burrow–surface	Not known to aggregate
Galapagos Penguin (<i>S. mendiculus</i>)	1°S	Burrow–surface	Not known to aggregate
Humboldt Penguin (<i>S. humboldti</i>)	5–42°S	Burrow	Not known to aggregate
Little Penguin (<i>Eudyptula minor</i>)	32–47°S	Burrow	Not known to aggregate
Chinstrap Penguin (<i>Pygoscelis antarcticus</i>)	54–64°S	Surface	Reduces adult aggression (Penteriani et al. 2003) but not important for thermoregulation (Martín et al. 2006)
Gentoo Penguin (<i>P. papua</i>)	46–65°S	Surface	Poorly understood
Adélie Penguin (<i>P. adeliae</i>)	54–77°S	Surface	Reduces thermoregulatory requirements, predation, and adult aggression (Penney 1968, Davis 1982, Lawless et al. 2001)
Emperor Penguin (<i>Aptenodytes forsteri</i>)	66–78°S	Surface	Presumably to reduce thermoregulatory requirements (Ancel et al. 1997)
King Penguin (<i>A. patagonicus</i>)	45–55°S	Surface	Reduces thermoregulatory requirements, adult aggression, and predation (Barré 1984, le Bohec et al. 2005)

predation is highlighted by re-evolution of chick aggregations in the African Penguin. This species is traditionally a burrow-nester, but guano mining has removed appropriate substrate for burrows and has forced some birds to nest on the surface (Frost et al. 1976). There is significantly less predation on chicks in burrows than on those in a nest on the surface (Frost et al. 1976), and predation is believed to have increased the prevalence of chick aggregations in this species (Cooper 1977).

PARENTAL CONSIDERATIONS THAT LEAD TO CHICK ABANDONMENT

Parental condition.—Penguins with a constrained breeding season face two potentially conflicting interests: the need to successfully raise the current breeding season's chicks to fledging, and the need to maintain enough energy reserves to survive to the next breeding season. In this sense, adults make a tradeoff between the short-term benefits of producing chicks in a specific year and their potential lifetime reproductive effort (Maynard Smith 1977). There is a large body of evidence that this is a critical decision for parents. During the incubation and guard periods, parents rely on stored energy reserves and may lose considerable body weight (e.g., Tremblay and Cherel 2003, Clarke et al. 2006, Green et al. 2007). These reserves need to be regained before the pre-winter molting period, when birds cannot feed (Adams and Brown 1990). It has been suggested that parents have a physiological “trigger” that alerts them when their own reserves are dangerously low (e.g., Olsson 1997) and that this may lead to chick abandonment.

This suggests two predictable outcomes: that adults in poorer condition will abandon their chicks earlier than adults in

better condition (Penteriani et al. 2003), whereas parents with two chicks will abandon them earlier than parents with only one chick. In both cases, parents should “recognize” that they require more time to regain energy reserves and feed chicks than birds that are in better condition or have only one chick. For instance, Chinstrap Penguin pairs with lower energy reserves breed later and abandon chicks at an earlier age (Viñuela et al. 1996). Presumably, this allows them to forage longer before the winter. In years with decreased food availability, Adélie Penguin chicks are abandoned earlier than average, as adults reach their threshold body condition earlier than in years with high food abundance (Ainley 2002). In both Adélie and Chinstrap penguins, two-chick broods are abandoned earlier than one-chick broods (Davis 1982, Lishman 1985). The timing of abandonment may also depend on the age or breeding experience of the individual, in that more experienced individuals may be better foragers; however, Moreno et al. (1997) found that age at abandonment was not related to differences in parental quality.

The timing of parental abandonment of chicks should be related to the energetic requirements of the offspring in addition to their own requirements. In Southern Rockhopper Penguins (*E. c. chrysocome*), Eastern Rockhopper Penguins (*E. c. filholi*), and Adélie Penguins, parents forage for the same length of time and bring the same weight of food to chicks at both the guard and post-guard stages (Chappell et al. 1993, Hull et al. 2004, Rey et al. 2007), despite the much higher energy requirements of older chicks. There may be physiological limits to chick-provisioning rates, controlled by the stomach size of the parents. Modeling of the energetic requirements of Adélie Penguin chicks has shown that they could not survive to fledging on the food brought back by

one parent alone (Salihoglu et al. 2001). Thus, parents must abandon their chicks to ensure that the chicks' food requirements are met, even though individual parents may not increase their food-delivery rates. In Macaroni Penguins (in which only the female forages during the guard stage), a chick's peak food requirement is ~ 400 g day⁻¹. However, adult females can bring in only ~ 290 g day⁻¹ (Green et al. 2007). Thus, in this species, both parents must forage simultaneously to satisfy the food requirements of chicks during peak demand.

Constraints on chick-abandonment age.—Although a parent can abandon a breeding attempt at any stage, for chicks to survive the initial abandonment, two requirements must be met. First, the parent–chick bond must be sufficiently developed for both to recognize each other among hundreds or potentially thousands of individuals. Second, the chick must be able to regulate its own body temperature, because it may not aggregate with other chicks. In African Penguins, parent–chick bonds were absent in chicks <16 days old but fully developed by 21 days (Seddon and van Heezik 1993b). Similarly, in Adélie Penguins, the parent–offspring bond was complete by day 17 (Thompson and Emlen 1968). Interestingly, Davis and McCaffrey (1989) presented evidence that Adélie Penguin chicks can recognize their parents as early as day 12, almost a week earlier than adults can identify their chicks.

Newly hatched chicks rely on a brooding parent for warmth because they are unable to produce sufficient heat to maintain their body temperature (Taylor 1985). As chicks age, their capacity to produce heat increases, and then their ability to retain it through better insulation increases until they become thermally independent (Duchamp et al. 2002) and are able to be successfully abandoned by their parents. In Gentoo and Chinstrap penguins, chicks reach thermal independence after 15 days (Taylor 1985), whereas in King Penguins, a similar state is reached in two to three weeks (Duchamp et al. 2002). In the pygoscelid penguins, the earliest age of abandonment and subsequent aggregation is 16 days for Adélie, 20 days for Gentoo, and 23 days for Chinstrap penguins (Ainley 2002). Thus, 15–16 days after hatching appears to be a critical period: chicks abandoned before then have little chance of survival, but those abandoned when >16 days old are likely to survive, especially if they can aggregate with other chicks.

CHICKS' DECISIONS ONCE ABANDONED

Once abandoned by its parents, a chick can remain by itself or aggregate with other chicks. This decision must be made in light of any potential benefits gained by aggregating and may be mediated by a chick's age or health status at abandonment (e.g., Martín et al. 2006). Traditionally, four reasons have been proffered to explain chick aggregation behavior in penguins, some of which may act in unison. Various authors have suggested that aggregations provide increased protection from predation (Pettingill 1960, Davis 1982) or from aggression by unrelated adults (Seddon and van Heezik 1993a, Penteriani et al. 2003), reduce the energy requirements of individual chicks for thermoregulation (Le Maho 1977, Davis 1982), or have some social function (Sladen 1958). Each of these potential benefits is examined in light of our current knowledge of penguin ecology.

Reduced risk of predation.—One of the functions of gregarious behavior is to reduce predation risk to the individual, for

two reasons. First, a group is likely to detect a potential predator sooner and, second, each individual in the group has a smaller chance of being the one attacked (Hamilton 1971, Pulliam 1973). Chicks in larger aggregations should be exposed to less successful predation. For most penguin species, skuas (*Catharactes* spp.), gulls (*Larus* spp.), and giant-petrels (*Macronectes* spp.) are the main terrestrial predators (Young 1994, Stokes and Boersma 1998, Le Bohec et al. 2005). These species can subdue chicks only up to a certain size, so aggregations should be more prevalent in smaller chicks. In Adélie Penguins, skuas have only been recorded killing chicks that were ≤ 30 days old, and especially chicks that were isolated by feeding chases or at the edge of an aggregation (Davis 1982). Larger aggregations also lost proportionally fewer chicks to skuas than small ones (Davis 1982). In African Penguins, chicks of all ages aggregated, even though only the smallest chicks could be taken by natural predators at the site (Seddon and van Heezik 1991); hence, predator avoidance is not the only reason for aggregation in this species. In Rockhopper Penguins, only lone chicks were taken by skuas, whereas individuals in an aggregation were never preyed upon (Pettingill 1960). Similarly, in Chinstrap Penguins, skuas were never observed attempting to take chicks from within an aggregation, regardless of the size of that aggregation (Penteriani et al. 2003). In general, aggregations appear to confer substantial predator-avoidance benefits to chicks.

To avoid adult aggression.—Initially, abandoned chicks remain at their nest but may move for a variety of reasons. Once a chick leaves the nest, it can be subject to aggression from both adjacent nest owners and subadult or "floater" individuals (Seddon and van Heezik 1993a, de León et al. 2002), as has been commonly described for many colonial-nesting species (Wittenberger and Hunt 1985). This adult aggression has been suggested as a proximate factor underlying the formation of chick aggregations (Tourenq et al. 1995). To avoid these attacks, chicks choose, or are forced, to move away from brooding nests—either to the edge of the colony or to free space within the colony. Because all chicks are responding to the same stimuli, they may be directed to the same areas. In this case, chick aggregations could be argued to be purely a result, but not the intent, of chicks trying to avoid adult aggression. However, evidence suggests that chicks move toward aggregations when attacked. In African Penguins, abandoned individual chicks were attacked by unrelated adults at a much higher rate than either chicks in an aggregation or guarded chicks. They also suffered more attacks than guarded chicks of the same age (Seddon and van Heezik 1993a). When attacked, unguarded chicks preferentially moved toward other chicks (74% of the time) rather than toward unrelated adults or clear areas in the colony (Seddon and van Heezik 1993a). In Chinstrap Penguins, adult aggression is suggested as the proximate cause of chick aggregations, given that lone chicks were attacked more and fled farther than those within an aggregation (Penteriani et al. 2003). Importantly, lone chicks were often pursued until they reached an aggregation, at which point the aggression ceased (Penteriani et al. 2003). Interestingly, when guard-stage Rockhopper Penguin chicks were attacked by unrelated adults, they preferentially left their parents to join a chick aggregation (Pettingill 1960), whereas lone Adélie Penguin chicks that were attacked by adults also joined aggregations (Penney 1968).

More favorable thermal environment.—Huddling in groups is an important method of saving energy by conserving heat, and this behavior may be especially important under environmentally harsh conditions (Barré 1984, Ancel et al. 1997). This energy saving may increase the survival of chicks while they are waiting for parents to return from foraging trips. If aggregation confers thermal benefits, both the percentage of chicks within a colony and contact with aggregations should increase as conditions become more harsh. However, thermoregulatory costs decrease with chick age (Lawless et al. 2001), so chick aggregations should be more prevalent among younger chicks. In Adélie Penguins, the proportion of young chicks aggregating increased as thermoregulatory demand increased. At the same time, older chicks aggregated only in severe weather events (Lawless et al. 2001), when thermoregulatory costs were presumably high. In King Penguins, during harsh conditions, chicks formed fewer but larger aggregations, and individuals were more closely packed within each aggregation (Le Bohec et al. 2005). By contrast, in African Penguins, chick aggregations were formed even in warm weather and even thermally mature chicks joined them (Seddon and van Heezik 1993a), which suggests that thermoregulation is less important in this species.

Their gregarious nature.—Sladen (1958:62) has suggested that chick aggregations are partially a result of the “gregarious nature of penguins”; however, there is no evidence that this is the case in penguins or in any other species in which chicks aggregate. Colonial breeding is widespread in avian species (Lack 1968), and its social benefits include enhanced food finding through information sharing and prospecting for future mates (e.g., Wagner and Danchin 2003, Wright et al. 2003). Although these may be important factors in coloniality in penguins, chick aggregations do not appear to confer any extra benefits over coloniality, unless physical contact between chicks is important. These functions could all be achieved more easily by single chicks moving through a colony than by aggregation. There may be a social basis of aggregation if aggregations comprise related individuals rather than a random group of chicks; however this has yet to be tested.

A REVIEW OF THE TERM CRÈCHE

Thus far, I have purposely avoided using the term “crèche,” because the behavior of penguin chicks is not crèching *sensu stricto* and because the use of this term in the literature has been ambiguous and inconsistent. Traditionally, crèche refers to a group of offspring adopted and raised by unrelated adults, and this definition is applicable in some avian systems. For instance, adults of some Anatidae adopt, raise, and protect unrelated chicks (e.g., Gorman and Milne 1972, Kehoe 1989, Eadie and Lyon 1998). However, this is not the case in penguins. Even though penguin chicks aggregate, parents feed only their own offspring (Thompson 1974), and adults at the edge of chick aggregations defend their own nest site or chicks from predators, rather than protecting the crèche *per se* (Sladen 1958, de León et al. 2002). Thus, although the term crèche is legitimately applied to some species, it is biologically misleading to describe penguin behavior in this way.

Traditionally, development of penguin chicks has been separated into guard and crèche stages, the latter defined as starting when chicks are independent of the nest (Richdale 1957,

Sladen 1958, Ainley 2002). However, Adélie Penguin chicks may be abandoned some days before they leave the nest site (D. Wilson pers. obs.), and this may occur in other species, but has perhaps been masked by the definition of “crèched chicks.” Thus, there is the confusing possibility that chicks are neither in the guard phase (because parents have left) nor in the crèche phase (because they are still alone on the nest). There is also the confusion that chicks have crèched but are not in a crèche (i.e., they have left the nest but have not united with other chicks). Young (1994) has suggested that the stages of chick development be designated “guard” and “post-guard” to resolve these potential confusions. These two phases are easy to differentiate: chicks in the guard phase have a parent present, whereas chicks in the post-guard phase do not. Chicks in the post-guard phase can either be alone or aggregate with other post-guard chicks. These terms can be applied to all penguin species, not just those with chicks that aggregate.

Young’s (1994) definition of chick stages also avoids the difficulties faced by other authors as to when a group of chicks constitutes a crèche. For example, a crèche has been defined as “a minimum of three chicks in close association, where the distance between individuals was less than half the mean distance between nests” (Davis 1982:279); as “more than a normal brood of two chicks gathered together in a group, which were normally unguarded by adults” (Ainley et al. 1983:18); as “two or more chicks in close proximity . . . where individuals are less than two chick wing lengths apart” (Le Bohec et al. 2005:528); and as “a cluster of three or more chicks” (Seddon and van Heezik 1993a:91). This variation makes comparisons between studies extremely difficult.

As this review has shown, chick aggregations can be fluid in time and are a response to a variety of stimuli. It appears that aggregation is an ancestral trait in the penguin group and probably arose in Antarctica as, initially, a way of conserving heat (and therefore energy) in extreme cold. As penguins expanded northward, aggregations evolved alternate roles as a method of increased predator avoidance and to avoid adult aggression. The importance of each benefit on chick aggregation varies between species and will also vary across breeding sites and will change as chicks mature.

There are several areas for potential future research, at both the species and individual levels. Effort should be directed to species for which there is little information on chick aggregations (Table 1), primarily *Eudyptes*. This group could be specially interesting, given the observation that Rockhopper Penguin chicks on the Falkland Islands (Islas Malvinas) left their nests to aggregate with other chicks “even while parents were brooding them” (Pettingill 1960:217). Species with a large latitudinal range (Table 1) would be ideal candidates for testing the influence of temperature on aggregation formation, and experimental removal of predators at some colonies could be used to test the importance of predation pressure on the formation of chick aggregations. Studies should also focus on the influences that cause an individual chick to join an aggregation. It seems counterintuitive that when some chicks aggregate, others of the same size remain alone even if the benefits of joining an aggregation are small. It may be that aggregating chicks are more closely related than chicks that remain alone. This would be a fascinating social benefit of the formation of aggregations through kin selection.

ACKNOWLEDGMENTS

Discussions with L. Emmerson, C. Southwell, M. Weber, P. Seddon, and one anonymous reviewer greatly improved earlier versions of the manuscript.

LITERATURE CITED

- ADAMS, N. J., AND C. R. BROWN. 1990. Energetics of molt in penguins. Page 297–315 in *Penguin Biology* (L. S. Davis and J. T. Darby, Eds.). Academic Press, San Diego, California.
- AINLEY, D. G. 2002. *The Adélie Penguin: Bellwether of Climate Change*. Columbia University Press, New York.
- AINLEY, D. G., R. E. LERESCHE, AND W. J. L. SLADEN. 1983. *Breeding Biology of the Adélie Penguin*. University of California Press, Berkeley.
- ANCEL, A., H. VISSER, Y. HANDRICH, D. MASMAN, AND Y. LE MAHO. 1997. Energy saving in huddling penguins. *Nature* 385:304–305.
- BAKER, A. J., S. L. PEREIRA, O. P. HADDRATH, AND K.-A. EDGE. 2006. Multiple gene evidence for expansion of extant penguins out of Antarctica due to global cooling. *Proceedings of the Royal Society of London, Series B* 273:11–17.
- BARRÉ, H. 1984. Metabolic and insulative changes in winter- and summer-acclimatized King Penguin chicks. *Journal of Comparative Physiology B* 154:317–324.
- BESNARD, A., O. GIMENEZ, AND J.-D. LEBRETON. 2002. A model for the evolution of crèching behaviour in gulls. *Evolutionary Ecology* 16:489–503.
- CARTER, H. R., AND K. A. HOBSON. 1988. Creching behavior of Brandt's Cormorant chicks. *Condor* 90:395–400.
- CHAPPELL, M. A., V. H. SHOEMAKER, D. N. JANES, S. K. MALONEY, AND T. L. BUCHER. 1993. Energetics of foraging in breeding Adélie Penguins. *Ecology* 74:2450–2461.
- CLARKE, J., L. M. EMMERSON, AND P. OTAHAL. 2006. Environmental conditions and life history constraints determine foraging range in breeding Adélie Penguins. *Marine Ecology Progress Series* 310:247–261.
- COOPER, J. 1977. Energetic requirements for growth of the Jackass Penguin. *Zoologica Africana* 12:201–213.
- DAVIS, L. S. 1982. Creching behaviour of Adélie Penguin chicks (*Pygoscelis adeliae*). *New Zealand Journal of Zoology* 9:279–286.
- DAVIS, L. S., AND F. T. MCCAFFREY. 1989. Recognition and parental investment in Adélie Penguins. *Emu* 89:155–158.
- DEL HOYO, J., A. ELLIOTT, AND J. SARGATAL, Eds. 1996. *Handbook of the Birds of the World, vol. 1: Ostrich to Ducks*. Lynx Edicions, Barcelona, Spain.
- DE LEÓN, A., J. A. FARGALLO, V. POLO, AND J. POTTI. 2002. Adult aggression during the post-guard phase in the Chinstrap Penguin *Pygoscelis antarctica*. *Polar Biology* 25:355–359.
- DUCHAMP, C., J.-L. ROUANET, AND H. BARRÉ. 2002. Ontogeny of thermoregulatory mechanisms in King Penguin chicks (*Aptenodytes patagonicus*). *Comparative Biochemistry and Physiology A* 131:765–773.
- EADIE, J. MCA., F. P. KEHOE, AND T. D. NUDDS. 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: A review of hypotheses. *Canadian Journal of Zoology* 66:1709–1721.
- EADIE, J. MCA., AND B. E. LYON. 1998. Cooperation, conflict, and crèching behavior in goldeneye ducks. *American Naturalist* 151:397–408.
- FROST, P. G. H., W. R. SIEGFRIED, AND J. COOPER. 1976. Conservation of the Jackass Penguin (*Spheniscus demersus* (L.)). *Biological Conservation* 9:79–99.
- GORMAN, M. L., AND H. MILNE. 1972. Creche behaviour in the Common Eider, *Somateria m. mollissima* L. *Ornis Scandinavica* 3:21–26.
- GREEN, J. A., I. L. BOYD, A. J. WOAKES, C. J. GREEN, AND P. J. BUTLER. 2007. Feeding, fasting and foraging success during chick rearing in Macaroni Penguins. *Marine Ecology Progress Series* 346:299–312.
- HAMILTON, W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31:295–311.
- HULL, C. L., M. HINDELL, K. LE MAR, P. SCOFIELD, J. WILSON, AND M.-A. LEA. 2004. The breeding biology and factors affecting reproductive success in Rockhopper Penguins *Eudyptes chrysocome* at Macquarie Island. *Polar Biology* 27:711–720.
- JOHNSGARD, P. A. 1993. *Cormorants, Darters, and Pelicans of the World*. Smithsonian Institution Press, Washington, D.C.
- KEHOE, F. P. 1989. The adaptive significance of crèching behavior in the White-winged Scoter (*Melanitta fusca deglandi*). *Canadian Journal of Zoology* 67:406–411.
- LACK, D. 1968. *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- LAWLESS, R. M., W. A. BUTTEMER, L. B. ASTHEIMER, AND K. R. KERRY. 2001. The influence of thermoregulatory demand on contact crèching behaviour in Adélie Penguin chicks. *Journal of Thermal Biology* 26:555–562.
- LE BOHEC, C., M. GAUTHIER-CLERC, AND Y. LE MAHO. 2005. The adaptive significance of crèches in the King Penguin. *Animal Behaviour* 70:527–538.
- LE MAHO, Y. 1977. The Emperor Penguin: A strategy to live and breed in the cold. *American Scientist* 65:680–693.
- LEVICK, G. M. 1914. *Antarctic Penguins: A Study of Their Social Habits*. Heinemann, London.
- LISHMAN, G. S. 1985. The comparative breeding biology of Adélie and Chinstrap penguins *Pygoscelis adeliae* and *P. antarctica* at Signy Island, South Orkney Islands. *Ibis* 127:84–99.
- MARTÍN, J., L. DE NEVE, V. POLO, J. A. FARGALLO, AND M. SOLER. 2006. Health-dependent vulnerability to predation affects escape responses of unguarded Chinstrap Penguin chicks. *Behavioral Ecology and Sociobiology* 60:778–784.
- MAYNARD SMITH, J. 1977. Parental investment: A prospective analysis. *Animal Behaviour* 25:1–9.
- MORENO, J., A. BARBOSA, J. POTTI, AND S. MERINO. 1997. The effects of hatching date and parental quality on chick growth and creching age in the Chinstrap Penguin (*Pygoscelis antarctica*): A field experiment. *Auk* 114:47–54.
- MÜLLER-SCHWARZE, D. 1984. *The Behavior of Penguins: Adapted to Ice and Tropics*. State University of New York Press, Albany.
- OLSSON, O. 1997. Clutch abandonment: A state-dependent decision in King Penguins. *Journal of Avian Biology* 28:264–267.
- PENNEY, R. L. 1968. Territorial and social behavior in the Adélie Penguin. *Antarctic Research Series* 12:83–131.
- PENTERIANI, V., J. VIÑUELA, J. BELLUERE, J. BUSTAMANTE, AND M. FERRER. 2003. Causal and functional correlates of brood

- amalgamation in the Chinstrap Penguin *Pygoscelis antarctica*: Parental decision and adult aggressiveness. *Polar Biology* 26:538–544.
- PETTINGILL, O. S., JR. 1960. Crèche behavior and individual recognition in a colony of Rockhopper Penguins. *Wilson Bulletin* 72:213–221.
- PULLIAM, H. R. 1973. On the advantages of flocking. *Journal of Theoretical Biology* 38:419–422.
- REY, A. R., P. TRATHAN, AND A. SCHIAVINI. 2007. Inter-annual variation in provisioning behaviour of Southern Rockhopper Penguins *Eudyptes chrysocome chrysocome* at Staten Island, Argentina. *Ibis* 149:826–835.
- RICHDALE, L. E. 1957. *A Population Study of Penguins*. Oxford University Press, Oxford, United Kingdom.
- SALIHOGU, B., W. R. FRASER, AND E. E. HOFMANN. 2001. Factors affecting fledging weight of Adélie Penguin (*Pygoscelis adeliae*) chicks: A modeling study. *Polar Biology* 24:328–337.
- SEDDON, P. J., AND L. S. DAVIS. 1989. Nest-site selection by Yellow-eyed Penguins. *Condor* 91:653–659.
- SEDDON, P. J., AND Y. VAN HEEZIK. 1991. Effects of hatching order, sibling asymmetries, and nest site on survival analysis of Jackass Penguin chicks. *Auk* 108:548–555.
- SEDDON, P. J., AND Y. VAN HEEZIK. 1993a. Chick creching and intraspecific aggression in the Jackass Penguin. *Journal of Field Ornithology* 64:90–95.
- SEDDON, P. J., AND Y. VAN HEEZIK. 1993b. Parent–offspring recognition in the Jackass Penguin. *Journal of Field Ornithology* 64:27–31.
- SLADEN, W. J. L. 1958. The pygoscelid penguins. I. Methods of study. II. The Adélie penguin, *Pygoscelis adeliae* (Hombron & Jacquinot). Falkland Islands Dependencies Survey, Scientific Reports, no. 17.
- STOKES, D. L., AND P. D. BOERSMA. 1998. Nest-site characteristics and reproductive success in Magellanic Penguins (*Spheniscus magellanicus*). *Auk* 115:34–49.
- TAYLOR, J. R. E. 1985. Ontogeny of thermoregulation and energy metabolism in pygoscelid penguin chicks. *Journal of Comparative Physiology B* 155:615–627.
- THOMPSON, D. H. 1974. Mechanisms limiting food delivery by Adélie Penguin parents exclusively to their genetic offspring. Ph.D. dissertation, University of Wisconsin, Madison.
- THOMPSON, D. H., AND J. T. EMLÉN. 1968. Parent–chick individual recognition in the Adélie Penguin. *Antarctic Journal of the United States* 3:132.
- TOURENQ, C., A. R. JOHNSON, AND A. GALLO. 1995. Adult aggressiveness and crèching behavior in the Greater Flamingo, *Phoenicopterus ruber roseus*. *Colonial Waterbirds* 18:216–221.
- TREMBLAY, Y., AND Y. CHEREL. 2003. Geographic variation in the foraging behaviour, diet and chick growth of Rockhopper Penguins. *Marine Ecology Progress Series* 251:279–297.
- VELANDO, A. 2001. Postfledging crèche behavior in the European Shag. *Journal of Ethology* 19:121–127.
- VIÑUELA, J., J. MORENO, L. M. CARRASCAL, J. J. SANZ, J. A. AMAT, M. FERRER, J. BELLUERE, AND J. J. CUERVO. 1996. The effect of hatching date on parental care, chick growth and chick mortality in the Chinstrap Penguin *Pygoscelis antarctica*. *Journal of Zoology* 240:51–58.
- WAGNER, R. H., AND E. DANCHIN. 2003. Conspecific copying: A general mechanism of social aggregation. *Animal Behaviour* 65:405–408.
- WILLIAMS, T. D. 1995. *The Penguins*. Oxford University Press, Oxford, United Kingdom.
- WILSON, E. A. 1907. Aves. In *British National Antarctic Expedition 1901–1904*, vol. 2: Zoology. British Museum (Natural History), London.
- WITTENBERGER, J. F., AND G. L. HUNT, JR. 1985. The adaptive significance of coloniality in birds. Pages 1–78 in *Avian Biology*, vol. 8 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). Academic Press, New York.
- WRIGHT, J., R. E. STONE, AND N. BROWN. 2003. Communal roosts as structured information centres in the raven, *Corvus corax*. *Journal of Animal Ecology* 72:1003–1014.
- YOUNG, E. 1994. *Skua and Penguin: Predator and Prey*. Cambridge University Press, Cambridge, United Kingdom.

Received 2 September 2008, accepted 18 March 2009

Associate Editor: D. C. Dearborn