BEHAVIOR OF THE ADÉLIE PENGUIN CHICK

E. B. SPURR¹

Zoology Department University of Canterbury Christchurch, New Zealand

Previous studies have shown that chicks of the Adélie Penguin (Pygoscelis adeliae) are semialtricial when they hatch (Nice 1962, Reid 1965, Reid and Bailey 1966). At first they are unable to leave the nest and require a great deal of parental care. The chicks are covered in down at hatching, but their body temperature is not regulated completely until about 15 days of age (Sapin-Jaloustre and Bourliére 1951, Goldsmith and Sladen 1961). Their growth rate approximates a truncated normal curve (Sapin-Jaloustre and Bourliére 1951, Sapin-Jaloustre 1955, Sladen 1958, Taylor and Roberts 1962). For the first few days little or no weight may be gained; in fact, some chicks are not fed until 3 days old. With regular feeding, however, chicks show a rapid, steady increase in weight from about 90 to nearly 4000 g in about 6 weeks. In the week prior to departure for sea, the average weight of chicks decreases slightly, though weight may fluctuate markedly due to infrequent large feeds. Ainley and Schlatter (1972) showed that the weight of fledglings was correlated to the parents' ages.

Other studies have described changes in plumage of chicks (Taylor 1962) and aspects of parent-chick recognition (Sladen 1953, 1958, Penney 1968, Thompson and Emlen 1968).

The present paper describes the development of the behavior of the Adélie Penguin chick. Some aspects of chick behavior have been described previously (e.g., Sapin-Jaloustre and Bouliére 1951, 1952, Sladen 1953, 1958, Taylor 1962, Penney 1968), but here an attempt is made to provide a more complete account. Following the descriptions of behavior, the stages in development are compared with those determined for several species of birds by Nice (1962).

METHODS AND PROCEDURE

Observations were carried out over four summers as part of another study (Spurr 1972), at the University of Canterbury field station, Cape Bird, Ross Island, Antarctica (77°13'10" S, 166°28'30" E). Chicks were observed at marked nests from the time of hatching. In the first summer (1967–68), observations were made until the chicks departed for sea, but in subsequent summers observations were terminated just before chick departure. In the summer of 1968–69, individual chicks were observed for periods of 10 min at intervals of approximately 5 days. In 1969–70 and 1970–71, nests were checked daily but with no set observation period.

BACKGROUND AND DEFINITIONS

Most parents hatch two chicks about 1.4 days apart (Taylor 1962, Spurr 1972). The period during which parents care for their chicks can be divided into a guard stage and a crèche or post-guard stage. The term crèche is meant to imply simply a collection of young. There are no "guardians" of the crèche (Sladen 1958).

In the guard stage one of the parents guards and feeds the chicks while the other goes to sea to collect more food. At Cape Bird, the parents usually change duty every day or twice every 3 days (Spurr 1972). For about the first 5 days, chicks spend most of their time completely under the cover of the parent's brood patch. The parent lies over the chicks in a manner similar to the egg incubation posture (Spurr 1974). As the chicks grow, they become more exposed and can be brooded by their parents only partly. Until they are at least 10 days old, chicks usually have their heads under the brood patch with only the posterior part of the body sticking out. Between 11 and 15 days, the chicks simply may huddle against the parent (which may lean against the chicks). After about 15 days, by which time the chicks are completely homeothermic, most parents stand to one side of the nest, leaving the chicks lying or standing in it.

In the crèche or post-guard stage, the chicks are left unguarded by their parents for many hours of the day. Parents continue feeding their own chicks, but neither parent remains with the chicks very long after feeding. In the absence of their parents, the chicks may remain at the parental nest site or cluster with other unguarded chicks to form crèches.

The age at which chicks are first left unguarded varies slightly from colony to colony and from year to year. In 1969–70, the aver-

¹Present address: N.Z. Forest Service, P.O. Box 106, Rangiora, New Zealand.

age age was 19.2 days at one colony and 21.6 days at another. In 1970–71, the respective ages were 20.6 and 20.1 days. The youngest chick left unguarded was 14 days, and the oldest chick still being guarded was 30 days. At Cape Royds, Taylor (1962) recorded an average of 22.4 (R = 17-32) days. Sladen (1958) recorded an average of 30 (R = 28-32) days for six chicks at Hope Bay, and 19 (R = 17-28) days for ten chicks at Signy Island. However, he considered the Signy Island dates atypical and suggested that the average age of crèching was "about one month."

Taylor (1962)established that chicks hatched early in the season tend to be guarded longer than those hatched later. Also, parents at the periphery of a colony tend to guard their chicks longer than parents in the center of a colony. These same relationships were observed at Cape Bird. In addition, parents that hatched only one chick tended to guard their chicks longest. These parents need not supply as much food as parents with two chicks. Consequently, a returning parent may not feed its chick immediately upon arrival at the nest site, and the relieved parent may not leave for sea immediately.

Chicks are fed throughout the crèche stage, and probably do not go long without food before they depart for sea. However, for about two weeks before departure, they are fed progressively less by their parents, and their weight decreases slightly (Taylor and Roberts 1962).

RESULTS AND DISCUSSION

BEHAVIOR OF CHICKS

The behavior of chicks is described in its approximate order of appearance (table 1). References are made to adult behavior described elsewhere (Sladen 1958, Sapin-Jalous-tre 1960, Penney 1968, Spurr 1974).

Food begging. Food begging occurs on the day of hatching but at first is not essential to initiate feeding. A parent will bend over and place its bill beneath that of a newly hatched chick without any prior begging. Subsequent begging by the chick then stimulates the parent to regurgitate food into the chick's now open bill. As the chicks grow older, they initiate more feedings by begging from passive parents.

When begging for food, the chick reaches up with wobbly head movements and vibrates its bill at the base or tip of the parent's bill (fig. 1). The mandibles of the bill may be rubbed slightly against one another. Begging

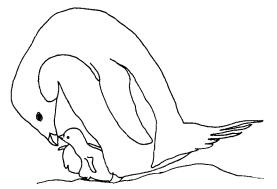


FIGURE 1. Chick begging for food from parent.

usually is accompanied by a single syllable call ("peep" of Sladen 1958). The white sclerae of the eyes may show slightly, apparently as a consequence of raising the head. The flippers may be held out for balance.

Chicks beg from parents at any time but do so especially when a parent just returns from sea. Older chicks may beg immediately following the Loud Mutual Display movements and vocalizations (see below), but begging and Mutual Display are separate movements (Sladen 1953, 1958).

Comfort activities. Comfort activities are among the first types of behavior recorded (table 1). Yawning, shaking (the whole body, head, or flippers), stretching (including stretching the flippers upwards), swallowing, scratching (with foot over flipper), and preening are all similar to adult activities. All occur in chicks less than 10 days old. Panting occurs from 7 or 8 days of age, although chicks are not completely homeothermic until about 15 days. Chicks commonly sleep lying flat on the ground, but as they grow older, they may also sleep while standing. After about 15 days, chicks may sleep with the bill tucked under the flipper, as do adults.

Chicks sometimes preen the breast feathers of their parents or the breasts of siblings. Such allo-preening does not occur in adult Adélie Penguins.

Gripping at nest stones. Chicks less than 5 days old may grip at nest stones with the bill. Between 6 and 10 days, chicks start reaching out and dragging in nest stones from the periphery of the nest (similar to the stone rearranging of adults during nest building). Small stones are sometimes swallowed.

Locomotion. Newly hatched Adélie Penguin chicks are unable to move out of the nest. However, in 6 to 10 days they may stand at the edge of the nest. Between 11 and 15 days, chicks start moving freely around the nesting territory. However, they seldom venture far

TABLE 1. Age of chick at which behavior patterns were first recorded.

Age (days)	Behavior recorded	Develop- mental stage ^a
0–5	Completely brooded by parent Beg with peeping call Some comfort movements (e.g., yawn)	I & II
6–10	Grip at nest stones Head under brood patch of stooping parent May stand at edge of nest Crouch in nest when disturbed or exposed	111
11–15	Comfort movements common (e.g., yawn, shake, stretch, scratch, preen) Pant on warm days Reach out and pull in stones; swallow small stones Head under brood patch, or lie in front of parent (who leans against chick) Move around nest freely when parent absent, as at nest change Loud Mutual Display with parents, especially at nest relief Avoidance reactions to disturbance by intruding adults, skuas, etc. Gape at one another, and	IV ,
16-20	peck at bills Lie in nest while parents stand beside	IV
21–25	Some left unguarded by parents Completely homeothermic Free movement around territory Quiet Mutual Display with parents when disturbed Peck and grip feathers on back of sibling and beat with flippers Most left unguarded by parents May venture alone outside colony React aggressively to adults or other chicks passing too close Feeding chases before and after feeding	V
	Start shedding down and acquiring juvenile plumage	

^a Stages in development corresponding to those determined for several species of birds by Nice (1962); see text for explanation.

from the nest until about 21 days. After this, chicks left unguarded by parents may move away from the nest to join with others in a crèche.

The ability to walk develops gradually. The first attempts around the nesting territory are very slow and are accompanied by frequent head-long falls. Even after chicks start moving farther away from the nest, they are prone to trip and fall. When trying to run, a chick may fall forwards and scramble along at times with its breast on the ground.

Loud Mutual Display. At about 11 days, chicks start performing an immature version

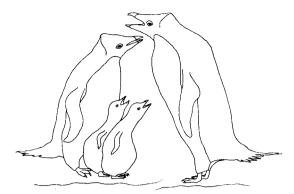


FIGURE 2. Chick Loud Mutual Display with parent.

of the adult Loud Mutual Display. This displaying occurs at reunion with parents, usually at the nest site (fig. 2). It is distinguished clearly from begging. The raised head is waved from side to side in a much more exaggerated manner than for begging; the bill is opened wide, and the accompanying call consists of several syllables ("tremulous" call of Sladen 1958). At first, the eyes may not be actively rolled downwards, but after about 16 days of age, the eyes usually are rolled strongly, exposing much white of the sclerae. Because of the covering of down, it often is difficult to determine if feathers are erected. However, when they do become visible, the crest feathers certainly are erect. Loud Mutual Display, begging, and feeding may follow in quick succession, but the three stages are separate.

Quiet Mutual Display. Chicks perform the Quiet Mutual Display with parents after both have been disturbed, for example, by an intruder. The head is raised and waved from side to side, but neither chick nor parent calls.

Escape behavior. Chicks show obvious escape reactions from about the time they can first stand at the nest. Stimuli that elicit escape reactions include intruding adults, predatory skuas (*Catharacta maccormicki*), and humans. When disturbed at the nest, a young guard-stage chick crouches low to the ground and huddles against its parent or sibling. When a parent has been drawn into a fight and the chicks are exposed at the nest site, young chicks usually remain crouched in the nest, keeping very still. Older chicks, however, often run away from these disturbances (see section on adult aggression toward chicks).

Unguarded chicks huddle together into crèches when disturbed. Chicks in these huddles characteristically face toward the source of disturbance. This is in contrast to undisturbed huddles in which they face inward, which may be either a response to temperature conditions or simply a propensity for company (Richdale 1951). In several species of penguin, the formation of crèches has been interpreted variously as a response to disturbance by predators and adverse weather (e.g., Roberts 1940, Stonehouse 1953, 1960, Pettingill 1960, Warham 1963, 1974). In the Adélie Penguin, however, probably most crèches are formed in response to aerial predators (Sladen 1958). Although chicks in the colonies have learned to respond to aerial predators, in the water there is at first an apparent lack of response to aquatic predators (see section on chick recognition of predators).

Aggressive behavior. Adélie Penguin chicks actively seek contact with other chicks. Sibling chicks frequently huddle together, side by side or one half on top of the other. As they get older, chicks from adjacent nests often huddle together into crèches without any signs of aggression.

The first indications of aggressive behavior occur ofter about 11 days, when sibling chicks occasionally gape and bill-grip with one another. From about 16 days of age, a chick may grip its sibling by the feathers of the back, and beat it with the flippers. Crèche chicks also gape and peck with the bill and beat one another with the flippers. However, these "aggressive" reactions probably are best termed play behavior because they lack any quality of "seriousness" (see Marler and Hamilton 1966). In these situations, the chicks do not compete with a rival for a possession (e.g., food, mate, or territory).

Serious aggressive behavior by chicks is observed only after about 21 days of age. This behavior is directed toward strange adult penquins or other chicks passing by the parental territory or coming too close to a crèche. Older crèche chicks also react aggressively to skuas. The change in response to skuas seems to occur when the chicks are large enough to defend themselves.

All aggressive reactions of chicks are similar to those of adults. Physical attack (with bill or flippers) is the most common form of aggression. However, charging forward, gaping, pointing the bill, waving the head from side to side, holding the head to one side, and rolling the head at the side of the body also occur. These correspond to the adult displays of Charge, Gape, Point, Alternate Stare, Sideways Stare, and Bill-to-Axilla (Spurr 1974). Until the down feathers start to molt, it is difficult to determine if the feathers are erected. However, the eyes are rolled to expose the white sclerae during threatening.

Feeding chase. Feeding chases become frequent when chicks are older than about 21 days and have joined a crèche. A parent who gives the Loud Mutual Display call on approaching the vicinity of its territory usually attracts only its own chick(s), although other chicks sometimes come out of the crèche. The parent then runs away from the area, often right out of the colony, and is pursued by the chicks. The chicks run along with flippers held up over the back, and open and close the bill to utter the *peep* call. Strange chicks ususally give up the chase very quickly. When there are two sibling chicks, one also eventually gives up the chase and walks back to the colony (usually to the vicinity of the parental territory). The other chick may be fed several times before it also loses contact with the parent. Contact is re-established when both parent and chicks return to the parental territory.

Sibling chicks do not fight one another for food. However, when two chicks are together, they both constantly reach up for food; this interferes with feeding and spills food. The feeding chase separates siblings, so that interference is reduced. It also may act as a selective mechanism if food is in short supply. However, by periodically returning to the nesting area, parents normally ensure that both chicks are fed.

Aark call. An immature aark call (Sladen 1958) is first heard among crèche chicks. It occurs when chicks are alarmed, for example, by the presence of skuas or humans. The calling becomes more frequent when the crèches start to disperse and the chicks move about outside the colonies, and is strongest when the chicks enter the water on departure for sea. Thus, in chicks it appears to be a response to a novel situation, whereas in adults it functions as a contact call. Ainley (1972) considered that the calling had little social significance for chicks because "they make no effort to catch up to or wait for each other" in the water. However, part of the explanation for this may be the small size of departing groups at Cape Crozier compared to Cape Bird (see section on chick departure). Cape Bird chicks which left in definite groups remained in groups although they were more dispersed than adult groups.

Play. Besides play-aggression, older crèche chicks perform play movements in which they run about, sometimes in semi-circles, waving their flippers in an irregular manner. Such running about occasionally leads to immature (play) flipper attacks when chicks collide. This running about does not appear to correspond to play-fleeing described by Nice (1962) for several bird species, and it occurs at a time when chicks already are showing escape reactions in response to skuas. Furthermore, adults have no natural terrestrial predators. Possibly it is important as "exercise" or "practice," aiding maturation of legs and especially flippers prior to departure for sea (see also Warham 1963). The behavior probably is best termed play-swimming (equivalent to flying in other species).

Ecstatic Display. An immature version of the adult Ecstatic (advertising) Display occurs in crèche chicks older than about 35 days. The head is raised vertically, the eyes rolled, and the flippers beat up and down. The bill is opened, and a shrill multiple-syllable call is uttered. The call resembles that of the Loud Mutual Display. Such an Ecstatic Display was given by a chick after losing its parent in a feeding chase. Another display was performed by a crèche chick standing at the colony periphery. The stimulus for these Ecstatic Displays of chicks may be separation from parents, while in adults the display seems to be stimulated by being alone and sexually receptive.

PARENT-CHICK RECOGNITION

Sladen (1953, 1958) was the first to show that Adélie Penguins feed only their own crèche chicks. This behavior implies that parents and chicks are able to recognize one another. Some aspects of this recognition can be determined from observations in both natural and experimental situations.

Crèche chicks clearly recognize their own parents. Many adults return with food to the vicinity of the crèche, but individual chicks usually respond only to the Loud Mutual Display call of their own parents. Occasionally, strange chicks initially will respond to an adult's call, but the response does not persist. Most crèche chicks ignore the calls of adults other than their parents. Penney (1968) provided experimental evidence of the importance of a parent's vocalizations in bringing parent and chick(s) together.

Parents also recognize their own chicks. This was demonstrated when, during a disturbance in the colony, a 14-day-old chick was displaced several meters from the nest. The parent apparently was unaware of its disappearance and remained guarding the sibling. The chick scrambled around between nearby

nests, occasionally calling loudly. Suddenly, the parent heard the calling, became restless, and started looking around. The parent then gave a Loud Mutual Display call. The chick seemed to recognize this call and ran a little closer, before pausing and calling again. The parent again replied with a Loud Mutual Display call. The chick soon found its way to the nest where it joined in a Loud Mutual Display with the parent. From cross-fostering experiments, Thompson and Emlen (1968) reported that parents begin to identify their own young between 8 and 17 days. This is also the period in which chicks start performing immature versions of the Loud Mutual Display.

Adults and chicks probably recognize one another visually also, using various features of appearance and behavior. However, rapid growth in size and changes in appearance of chicks require constant learning of visual cues. Vocalizations also change slightly as the chicks grow, but not so markedly as external appearance. The importance of auditory recognition is illustrated by its early appearance in the behavioral development of chicks. By the time chicks are first left unguarded, parents are able to recognize their own chicks, and chicks are able to recognize their own parents. This has also been reported for Little Blue Penguins (Eudyptula minor), Yellow-eyed Penguins (Megadyptes antipodes) (Richdale 1951), Rockhopper Penguins (Eudyptes chrysocome) (Pettingill 1960, Warham 1963), Royal Penguins (E. chrysolophus schlegeli) (Warham 1971), Chinstrap Penguins (Pygoscelis antarctica) (Sladen 1955), King Penguins (Aptenodytes patagonica) (Stonehouse 1960), and Emperor Penguins (A. forsteri) (Prevost 1955).

ADULT AGGRESSION TOWARD CHICKS

Chicks of any age wandering away from their natal territory are attacked by other territorial penguins as strongly as are intruding adults. This is especially evident before the breakdown of the territorial structure of colonies and the formation of crèches. Chicks of 16 to 20 days, with some degree of mobility but not yet crèched, may be pecked by neighbors if they take a few steps from the edge of the nest. Sometimes, instead of turning back to the parental nest, the chicks may run farther away, drawing threats and pecks from all territorial penguins in their path, and creating chaos in the colony. These wandering chicks usually run with the body almost horizontal and the head low to the ground. Younger chicks with little locomotor ability can be seriously injured and even killed by adults whose vicious pecks are usually directed at the head. The chicks' avoidance behavior clearly has survival value in that the chick is withdrawn as far as possible from adult attacks. However, it appears to have little appeasement value, as adults continue to attack wandering chicks so long as they remain within range. Wandering chicks often attempt to bury their heads into the brood patches of territorial adults. If they are successful, pecking may stop, at least briefly, especially when the adult has one or two chicks of its own.

Adult aggression to wandering chicks has marked survival value for their own chicks. Parents normally cannot rear more than two chicks. A few instances in which adults adopted a strange third chick all resulted in death by starvation of the smallest chick. This was usually the parents' own smallest chick because the adopted chick, already old enough to move about freely, was larger than the parents' own chicks.

Crèched chicks are sometimes molested by adult strangers. These adults are usually unsuccessful (probably young) breeders and nonbreeders (Sladen 1958). They may approach a crèche chick and attempt to mount it. When the chick tries to escape, it may be chased, severely pecked, and beaten with the flippers.

Parents show mild aggression toward their own chicks older than about 16 days when they persistently beg for food. Such aggression usually consists of mild snapping and jabbing the bill at the chick's bill, sometimes while backing away. This frequently occurs when the chicks approach a parent prior to, and during, feeding chases.

CHICK RECOGNITION OF NATAL TERRITORY

Even during the guard stage, chicks that are displaced or wander from the nest usually find their way back. However, they may be vigorously pecked by adults and wander aimlessly for some time before returning. As noted earlier, return to the nest may be aided by parental vocalizations.

Chicks that have entered crèches, however, are easily able to find their natal territory again. Before the return of the parent with food, chicks may leave the crèche (up to 10 m) and return on their own to the vacant natal territory. (The timing of this response possibly is based on the regularity of feeding and the amount of food in the chick's stomach.) Chicks that lose contact with a parent

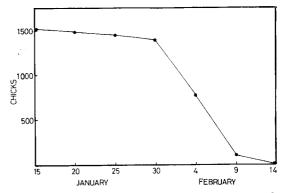


FIGURE 3. Number of chicks remaining in a sample of colonies at Cape Bird, Jan.–Feb. 1968.

during a feeding chase also may return to the natal territory, which may be up to 50 m away. Playbacks of parent Loud Mutual Display vocalizations from outside the colony by Penney (1968) also caused chicks to return to their natal territory.

The ability of chicks to return to their natal territory is very important for establishing contact with parents in a crowded colony. Nelson (1966) suggested that this ability may lead to philopatry, "the tendency for young adults to acquire nesting sites in the precise area of their birth." From a study of knownage birds, LeResche and Sladen (1970) demonstrated that philopatry exists in the Adélie Penguin.

CHICK RECOGNITION OF PREDATORS

Young guard-stage chicks at first appear not to recognize predators but must learn quickly from the crouching reactions of parents when predators approach. From the time when chicks are able to stand at the nest, they watch skuas flying high overhead and turn their heads to follow them as they fly farther away. When skuas approach, chicks dive head-first under a parent's brood patch. Unguarded chicks disturbed by skuas quickly form crèches and utter the *aark* call.

The responses to predators are learned individually for different types of predator. Chicks departing for sea have not previously encountered the Leopard Seal (*Hydrurga leptonyx*) and appear not to recognize it as a predator. Thus, chicks may enter the water and even swim toward seals that are attacking other chicks already in the water (see also Ainley 1972).

CHICK DEPARTURE FOR SEA

In the summer of 1967-68, chicks started to wander away from the confines of their col-

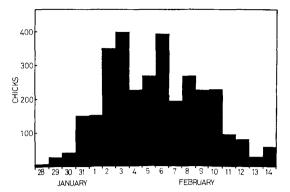


FIGURE 4. Number of chicks gathered on a section of shore at Cape Bird, Jan.-Feb. 1968.

onies from about 20 January. They began gathering on the beaches at the water's edge on 28 January. Most chicks had left their colonies by the end of the second week in February (fig. 3). Once they reached the beach, chicks usually did not remain ashore for long. The numbers gathered on the shore each day probably reflect the rate of departure quite closely (fig. 4). This pattern of departure is very similar to that recorded at Cape Royds by Taylor (1962) and Yeates (1968).

Chicks were first observed swimming out to sea, alone or in pairs, on 28 January, the same day they began gathering on the shore. Unfortunately, no chicks were marked the first summer, and it was not possible to make observations in subsequent summers. However, the maximum possible age of the chicks seen leaving in 1967–68 was 54 days. This is within the range of 41–56 days ($\bar{x} = 50.6$) recorded by Taylor (1962) for departing chicks at Cape Royds. Chicks that hatch later in the season tend to leave at a younger age than those that hatch earlier.

The chicks usually depart for sea in groups whose average size is 13 (R = 1-100). At Cape Royds, the departing groups never contain more than 12 chicks (Taylor 1962). However, the long sandy beaches at Cape Bird provide much wider access to the sea than the small rocky beach at Cape Royds. At Cape Crozier, where chicks must dive into the water, departing groups consist of only one or a few chicks (Ainley 1972).

Chicks often leave for sea when no adults are present. Nevertheless, departure of adults (usually not their parents) encourages chicks into the water. Once in the water, however, the adults soon leave the chicks behind. Chicks sometimes return to the shore after entering the water (Taylor 1962, Yeates 1968) or climb onto ice floes in the water. When the surf is heavy, chicks have difficulty getting to open water. Of a group that rushes toward the breakers, only a few get through. The rest are swept back up the beach. After regrouping, the sequence is repeated.

Once in the water, past the narrow line of breakers, the chicks splash around on the surface, with much loud calling (see *aark* call). They can swim under the water, but none was observed to "porpoise" as the adults do. After swimming several meters under water, the chicks stop and come to the surface. After splashing around on the surface for several seconds (sometimes minutes), they again dive under the water. By this slow alternation of of swimming and surfacing, the chicks gradually head away from the shore in a northerly direction.

STAGES OF DEVELOPMENT OF BEHAVIOR: A DISCUSSION

Nice (1962) recognized five stages in the development of avian behavior (table 1) and compared these in a number of species. The stages she recognized are:

I Post-embryonic: co-ordinations concerned mainly with nutrition.

II Preliminary: beginnings of comfort movements.

III Transition: maturation of comfort movements; escape reactions.

IV Locomotory: leaving nest; start of self-feeding.

V Socialization: aggression; perfection of locomotion.

The present study shows that Adélie Penguin chicks follow much the same pattern of development as the young of other birds. The first three stages of Nice (1962) are passed in about 10 days (table 1). During this period, activities are concerned mostly with feeding and comfort behavior. In the final two stages locomotory and social behavior are developed. Thus, after about 10 days, mutual recognition develops between chicks and parents. Locomotion becomes more evident along with escape reactions (from strange adults and predators). After about 21 days, serious aggressive behavior occurs. Isolated occurrences of the Ecstatic Display in older chicks may represent a precursor of adult sexual behavior. However, sexual behavior does not develop fully until the young penguins are more than two years old. First breeding does not occur until at least three years in females and four years in males (LeResche and Sladen 1970).

The first three stages in development of chick behavior represent a period of immobility; the fourth stage is a period of moderate mobility and the fifth stage is a period of full activity (Nice 1962). The period of immobility is characteristic of all altricial (and semi-altricial) species. The duration of each period, however, varies from species to species. Thus, the period of immobility lasts about 10 days in the altricial Song Sparrow (Melospiza melodia) (Nice 1962) compared to about 22 days in the altricial Shag (Phalacrocorax aristotelis) (Snow 1963). Even within one family, for example, the Spheniscidae, different species may have a chick period of different length. In the King Penguin, chicks are fed by their parents for about 10 months (Stonehouse 1960), and chick development is correspondingly drawn out compared to the Adélie Penguin.

The stage of development at which a particular behavior first appears is relatively constant in several different species (Nice 1962). Thus, of the 17 motor co-ordinations described by Nice (1962), most occur at a similar stage of development in all the species she analyzed, and also at a similar stage of development in Adélie Penguin chicks. However, exploratory pecking (at nest material) occurred very early, while bathing, swimming (the equivalent of flying), and feeding did not occur until chicks departed for sea at about 50 days. It is only when the chicks depart for sea that they become completely independent of parents. Swimming movements at first are not as efficient as those of adults and probably take time to perfect. "Play exercises" mentioned earlier possibly assist in this development. Observations are lacking on the development of self-feeding, but this must also improve with practice (see also Ainley and Schlatter 1972). As concluded by Kruijt (1964) for the Burmese Red Junglefowl (Gallus gallus spadiceus), various activities first develop in relative isolation of each other and only gradually become integrated into co-ordinated behavior patterns. Some examples in the behavior of Adélie Penguin chicks include exploratory handling of nest material, early escape reactions, play aggression, play swimming, and the immature Ecstatic Display. Thus, escape behavior first develops in response to external disturbances (such as intrusion of predators) and only later in response to aggression by other chicks and

adults. The integration of behavior is a continuing process, still occurring in juveniles and young birds who return to the colonies as "wanderers" (Sladen 1958, LeResche and Sladen 1970).

In the limited breeding season of the Antarctic summer, chicks hatched early in the season receive more care before being left unguarded and before departing to sea than chicks hatched late in the season. This suggests that they will be in better condition to face the northward migration to the wintering areas and will be better able to acquire the skills of swimming and feeding before the onset of adverse weather.

SUMMARY

Observations from time of hatching to time of fledging were made over four summers on Adélie Penguin chicks at marked nests. The chicks are semi-altricial at hatching, and require a great deal of parental care. Observations of known individuals show that feeding and comfort behavior develop first, followed by recognition of parents, locomotion, escape reactions, aggression, and finally sexual behavior. This follows closely the order determined by Nice (1962) for several species of birds.

Chicks become independent of parental protection from climate and aerial predators by about three weeks when they may be left unguarded for many hours of the day. Complete independence from the parents does not occur until the chicks depart for sea, at about seven weeks.

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LITERATURE CITED

- AINLEY, D. G. 1972. Flocking in Adélie Penguins. Ibis 114:388–390.
- AINLEY, D. G., AND R. P. SCHLATTER. 1972. Chick raising ability in Adélie Penguins. Auk 89:559– 566.
- GOLDSMITH, R., AND W. J. L. SLADEN. 1961. Temperature regulation of some antarctic penguins. J. Physiol., Lond. 157:251-262.

- KRUIJT, J. P. 1964. Ontogeny of social behaviour in Burmese Red Junglefowl (*Gallus gallus spadiceus*) Bonnaterre. Behaviour Suppl, 12:1-201.
- LERESCHE, R. E., AND W. J. L. SLADEN. 1970. Establishment of pair and breeding site bonds by young known-age Adélie Penguins (*Pygoscelis adeliae*). Anim. Behav. 18:517–526.
- MARLER, P., AND W. J. HAMILTON. 1966. Mechanisms of animal behavior. John Wiley & Sons, New York.
- NELSON, J. B. 1966. The behaviour of the young gannet. Brit. Birds 59:343-419.
- NICE, M. M. 1962. Development of behavior in precocial birds. Trans. Linnaean Soc. New York 8:1-211.
- PENNEY, R. L. 1968. Territorial and social behavior in the Adélie Penguin. Antarctic Res. Ser. 12: 83–131.
- PETTINGILL, O. S. 1960. Crèche behavior and individual recognition in a colony of Rockhopper Penguins. Wilson Bull. 72:213-221.
- PRÉVOST, J. 1955. Observations écologiques sur le Manchot Empereur (Aptenodytes forsteri). Acta XI Congr. Int. Ornithol.:248–251.
- REID, B. E. 1965. The Adélie Penguin (Pygoscelis adeliae) egg. N.Z. J. Sci. 8:503–514.
- REID, B. E., AND C. BAILEY. 1966. The value of the yolk reserve in Adélie Penguin chicks. Rec. Dom. Mus. 5:185–193.
- RICHDALE, L. E. 1951. Sexual behavior in penguins. Univ. Kansas Press, Lawrence.
- ROBERTS, B. 1940. The breeding behaviour of penguins with special reference to *Pygoscelis papua* (Forster). Brit. Graham Land Exped. 1934–37 Sci. Rep. 1:195–254.
- SAPIN-JALOUSTRE, J. 1955. Quelques aspects de la vie du Manchot Adélie en Terre Adélie. Acta XI Congr. Int. Ornithol.:231–240.
- SAPIN-JALOUSTRE, J. 1960. Écologie du Manchot Adélie. Hermann, Paris.
- SAPIN-JALOUSTRE, J., AND F. BOURLIÉRE. 1951. Incubation et développement du poussin chez le Manchot Adélie, Pygoscelis adeliae. Alauda 19: 65-83.
- SAPIN-JALOUSTRE, J., AND F. BOURLIÉRE. 1952. Parades et attitudes caracteristique de Pygoscelis adeliae. Alauda 20:39–53.

- SLADEN, W. J. L. 1953. The Adélie Penguin. Nature 171:952–955.
- SLADEN, W. J. L. 1955. Some aspects of the behaviour of Adélie and Chinstrap Penguins. Acta XI Congr. Int. Ornithol.:241-247.
- SLADEN, W. J. L. 1958. The Pygoscelid penguins. I. Methods of study. II. The Adélie Penguin Pygoscelis adeliae (Hombron & Jacquinot). Falkland Isl. Depend, Sur. Sci. Rep. 17:1-97.
- SNOW, B. K. 1963. The behaviour of the shag. Brit. Birds 56:77-103, 164-186.
- SPURR, E. B. 1972. Social organisation of the Adélie Penguin, Pygoscelis adeliae. Ph.D. Thesis, Univ. Canterbury, Christchurch, New Zealand.
- SPURR, E. B. 1974. Communication in the Adélie Penguin, p. 449–501. In B. Stonehouse [ed.], The biology of penguins. Macmillan, London.
- STONEHOUSE, B. 1953. The Emperor Penguin Aptenodytes forsteri Gray. I. Breeding behaviour and development, Falkland Isl. Depend. Sur. Sci. Rep. 6:1-33.
- STONEHOUSE, B. 1960. The King Penguin Aptenodytes patagonica of South Georgia. I. Breeding behaviour and development. Falkland Isl. Depend. Sur. Sci. Rep. 23:1–81.
- TAYLOR, R. H. 1962. The Adélie Penguin Pygoscelis adeliae at Cape Royds. Ibis 104:176-204.
- TAYLOR, R. H., AND H. S. ROBERTS. 1962. Growth of Adélie Penguin (*Pygoscelis adeliae* Hombron & Jacquinot) chicks. N. Z. J. Sci. 5:191–197.
- THOMPSON, D. H., AND J. T. EMLEN. 1968. Parentchick individual recognition in the Adelie Penguin. Antarctic J. U.S. 3:132.
- WARHAM, J. 1963. The Rockhopper Penguin, Eudyptes chrysocome, at Macquarie Island. Auk 80:229-256.
- WARHAM, J. 1971. Aspects of breeding behaviour in the Royal Penguin *Eudyptes chrysolophus schlegeli*. Notornis 18:91–115.
- WARHAM, J. 1974. The Fiordland Crested Penguin Eudyptes pachyrhynchus. Ibis 116:1–27.
- YEATES, G. W. 1968. Studies on the Adélie Penguin at Cape Royds 1964–65 and 1965–66. N. Z. J. Mar. Freshwater Res. 2:472–496.

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