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THE ONTOGENY AND ORGANIZATION OF COMFORT BEHAVIOR IN ADÉLIE PENGUINS

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Comfort behavior, which has been analyzed in detail in a variety of bird species (Kortlandt 1940; van Iersel and Bol 1958; McKinney 1965; Delius 1969; Ainley 1970, 1974; Borchelt 1975; van Rhijn 1977), serves an important function in maintenance of the body surface. Although many other aspects of avian behaviorial ontogeny have been studied extensively (e.g., prenatal motility, imprinting, song, caregiver–young interactions) much less is known about the development of comfort activities (Bekoff 1978). We studied the comfort behavior of Adélie Penguins (*Pygoscelis adéliae*) in order to answer, with a quantitative base, the following questions. (1) At what ages do various comfort movements first appear? (2) How do these behaviors become organized into sequences during ontogeny and later life? (3) In what ways (frequency, distribution, serial order) is the behavior of chicks different from the behavior of adults? Specifically, we were interested in analyzing processes of development to study the continuity of change from early ontogeny to adulthood. Comfort activities are a good behavioral phenotype for this kind of analysis because they appear early in life, are readily identified as individual acts that change little (if at all) in appearance during ontogeny (Thompson 1974, Spurr 1975, this study), and are repeated often. Adélie Penguins were particularly suitable for such a study because, while there is little known about the development of behavior in this species other than some general descriptions provided by Taylor (1962), Penney (1968), Thompson (1974) and Spurr (1975), the chicks are easily observable at all stages due to the simple ground nests built by the adults (Fig. 1a).

METHODS

Penguin chicks of known age (dye-marked offspring of banded adults) and adults (over 2 years of age) were studied at Cape Crozier, Ross Island, Antarctica, during the austral summer, 1974–75. Chicks were observed from hatching until the last week of January, shortly before fledging. Observations were made directly at close range or with the aid of binoculars. Behavioral sequences and a time indication (every 15 sec) were read directly into a cassette tape recorder and later transcribed. Since wind conditions may affect the performance of some comfort movements (Ainley 1974), all observations were made when winds were light.

We observed behavior sequences in the following 6 different groups of dry birds which had been out of the water at least 1–2 h prior to observation: (1) adults non-oiling (bill contact with the uropygial, or oil, gland was not made); (2) adults dry-oiling (contact

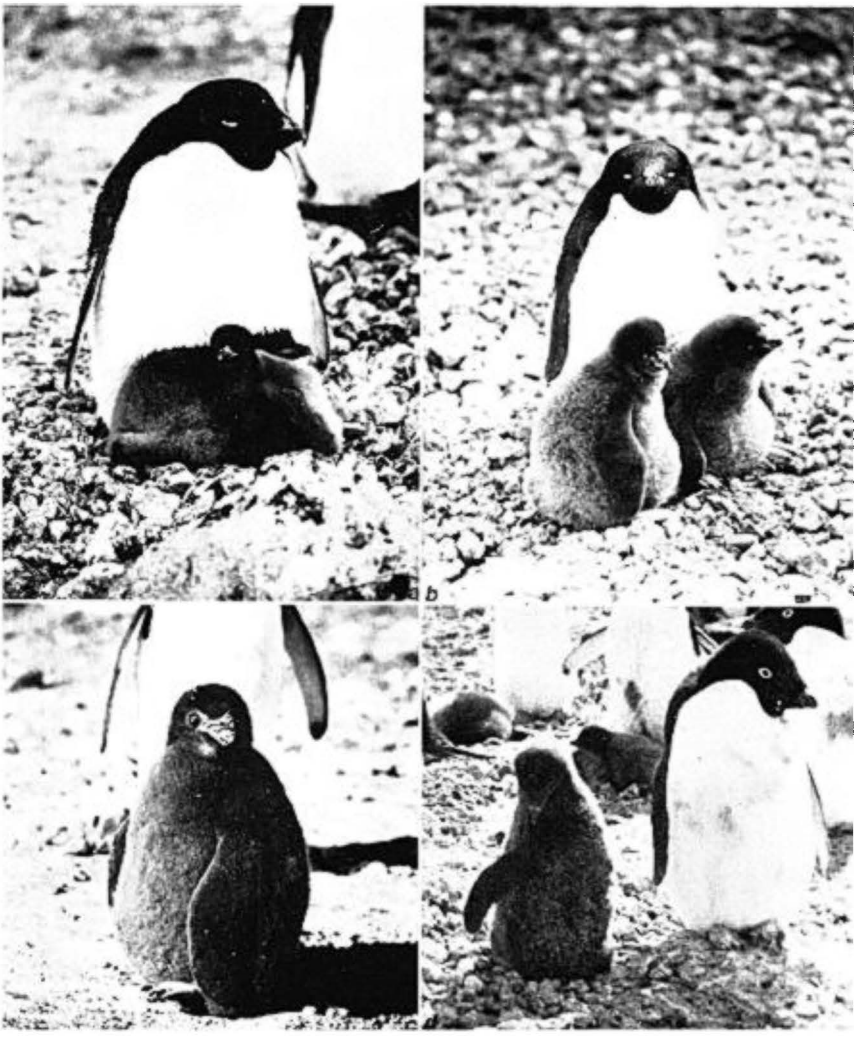

FIG. 1. (a) One-week-old chicks. Note the simple nest made of pebbles that surrounds the chicks and parent. (b) Two-week-old chicks. (c) Three- to 4-week-old chick. (d) Four- to 5-week-old chick preening its shoulder.

with the uropygial gland was made and oil was distributed over the dry plumage); (3) chicks aged 7–13 days (Fig. 1b) (4) 14–20 days (Fig. 1c), and (5) 21–28 days (Figs. 1d and 2a) non-oiling; and (6) chicks aged 35–43 days (Fig. 2c) dry-oiling (no dry-oiling was observed prior to 35 days of age).

Due to a number of factors (e.g., mortality, inactivity, weather conditions), it was not

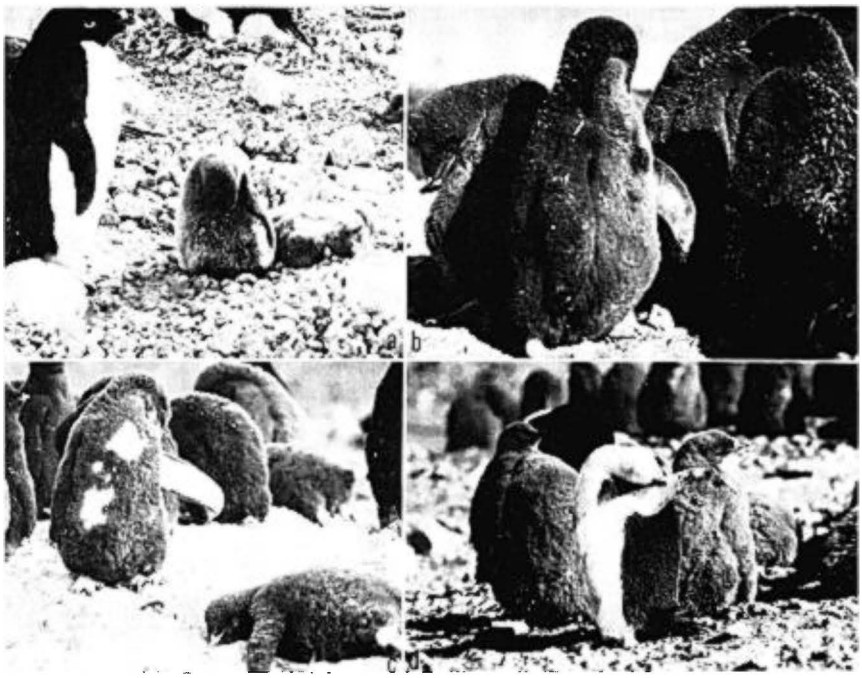

FIG. 2. (a) Four- to 5-week-old chick back preening. Note the loose down. (b) Five-week-old chick preening its shoulder. (c) Six-week-old chick preening its shoulder. Note the patches of contour feathers on the breast, belly and wing. (d) Seven-week-old chick performing bill-to-wing-edge, during which the bird grasps the top edge of the wing between its mandibles and draws the bill along the wing's edge toward its body. This is the first step in the transfer of oil to the head.

possible to observe the same chicks or adults throughout the duration of the study so for analysis we assumed that the samples were independent.

Sequence analysis.—In order to compare series of comfort movements that differed greatly in duration, we used Ainley's (1974: 18–19) method to study behavioral sequences and temporal distribution of individual movements. To analyze 2-act transitions, data for some of the comfort movements were cast into 15 × 15 contingency tables (see Ainley 1974, Table 2 for the way in which comfort movements were combined). Z scores were calculated to determine whether the 2-act transition in each cell was significant (i.e., not random). This method has been used by several workers (Ainley 1974; Poole and Fish 1975, 1976; Stevenson and Poole 1976). In our analyses, we considered transitions between an act and itself (separated by a brief pause during which the bird lifted its head away from the body surface), although some workers have excluded them (e.g., Fentress 1972). We included these because they occur with a high frequency and simply are representative of what the animals did.

Actions observed.—The actions observed are listed in Table 1. Terminology and detailed

TABLE 1

LIST OF ACTIONS (AND CODE) OBSERVED AND DAY OF FIRST OCCURRENCE

Action*	Day	Action*	Day
Yawn (Y)	1	Rapid-wing-flap leading to Phase II wing-stretch	14
Head-shake (HS)	2	Wing-shake (WSh) (L,R,B)	15
Leg stretch (LS) (L,R,B)	6	Bill-to-wing-edge (BW) (L,R)	16
Rapid/slow-wing-flap (RWF, SWF)** (L,R,B)	6	Shoulder-rub (SR) (L,R)	33
Sneeze (SN)	6	Oil (L,R)	35
Wing-extend (WE) (L,R,B)	7	Preening (L,R):	
Nibble-preen of various body regions	7	Breast (BR)	7
Wing rub (WR) (L,R)	7	Belly	7
Phase II wing-stretch (PII)	9	Back	9
Tail-wag (TW)	9	Side	10
Ruffle-shake (RS)	9	Wing	12
Bite-wing (BWg) (L,R)	9	Shoulder (SH)	13
Foot-shake (FS)	10	Leg	14
Wing-stretch with yawn (WSY)*** (L,R,B)	12	Cloaca (CL)	15
Wing-stretch (both with body shake) (WSBS)	13	Flank	15
Head-scratch (HSC) (L,R)	14	Tail-base (TB)	21

* For full descriptions see Ainley (1974) and text. L = left, R = right, B = both left and right. The following actions were not observed in chicks: body-shake (BS), neck-stretch (NS), ruffle-feathers only (RF).

** The mean rate of rapid-wing-flapping for adults ($N = 27$) was 5.5 cycles/sec and that for chicks ($N = 18$) was 3.7 cycles/sec (determined by movie analysis, $t = 2.12$, $df = 43$, $P < 0.05$).

*** Can occur without yawn.

descriptions provided by Ainley (1970, 1974) are used throughout. See Figs. 1, 2 and 3 for photographs of chicks of different ages and an adult performing some of the common comfort actions.

RESULTS

Age at first performance of comfort movements.—Prior to day 7 when 4 new actions were recorded, 5 actions had been observed (Table 1). By day 21, all actions except "shoulder-rub" (SR) and "oil" had been observed. Our data on the first occurrence of preening directed to various parts of the body surface agree with those of Spurr (1975, pers. comm.).

No oiling was observed prior to 35 days. We noted that chicks began to exude oil from the uropygial gland between 30–33 days of age: none of the 8 chicks checked were secreting oil prior to day 30. After day 33, all of the 11 chicks checked were secreting oil. The feather tuft extending out of

FIG. 3. Wing-rubbing by an adult. This is the action used to transfer oil from the wing edge (Fig. 2d) to the head. Note the feather tuft surrounding the uropygial gland at the base of the tail.

the gland (Fig. 3) did not reach full length until days 34–38. When oiling, the penguins contact this tuft with the bill.

The growth of contour feathers may have a great deal to do with the appearance of several behavior patterns (see Discussion). By day 17, feather sheaths were visible amidst the down and there was a lot of loose down. By day 20, small contour feathers were observable on most chicks. Taylor (1962) and Spurr (1975) also observed that loss of down began at approximately 3 weeks of age.

TABLE 2

A. THE MEAN DURATION (MIN) AND B. THE MEAN RATE (ACTS PER MIN) FOR NON-OILING AND DRY-OILING SEQUENCES BY CHICKS AND ADULTS

Non-oil sequences				Dry-oil sequences	
Chicks			Adults	Chicks	Adults
Group: 1 7–13 days	2 14–20 days	3 21–28 days	4	5 35–43 days	6
A. Mean duration[1]					
0.6 (N = 12) (SD = 1.7)	6.3 (N = 15) (2.7)	8.4 (N = 7) (3.5)	7.1 (N = 26) (4.6)	16.5 (N = 6) (8.1)	9.4 (N = 1) (8.7)
B. Mean number of acts/min[2]					
3.3 (0.9)	4.5 (1.2)	4.7 (1.4)	6.2 (2.1)	6.9 (1.6)	8.5 (2.5)

[1] When all 6 groups were compared (one way analysis of variance: $F = 4.69$, $df_1 = 5$, $df_2 = 76$, $P < 0.001$) only 7–13-day chick non-oiling sequences (group 1) and chick dry-oiling sequences (group 5) differed in mean duration (Duncan's Multiple Range Test). (When the largest variance was more than 1.5 times greater than the smallest variance, a log transform was used.)

[2] When all 6 groups were compared ($F = 6.32$, $df_1 = 5$, $df_2 = 76$, $P < 0.001$), it was found that group 2 did not differ significantly from group 3 and group 4 did not differ from group 5.

Comfort sequence analyses

The mean duration (min) of comfort sequences is presented in Table 2a. The duration of non-oiling sequences did not differ when 14–20-day chicks, 21–28-day chicks and adults were compared. However, 7–13-day chicks performed significantly shorter non-oiling sequences than those of older chicks and adults and the first dry-oiling sequences by chicks 35–43 days of age were significantly longer than those of adults.

The mean number of acts performed per min (rate) is presented in Table 2b. Adults performed comfort behavior actions at significantly higher rates than did chicks when the same types of comfort sequences were compared. Since the durations of non-oiling sequences in chicks were about the same as (14–20 days; 21–28 days) or shorter than (7–13 days) in adults and the rate was lower in chicks, fewer acts were performed per non-oiling sequence in chicks. However, we observed a gradual increase with age in the mean number of acts performed per non-oiling sequence. The mean number of times oiling was performed in dry-oiling sequences also increased from 4.7 in 35–43-day chicks to 6.2 in adults.

Distribution of comfort movements

Frequency of occurrence.—The frequency with which 10 comfort actions occurred was compared for chicks and adults. These frequencies were

TABLE 3

THE DISTRIBUTION IN TERMS OF RELATIVE % OF OCCURRENCE OF 10 COMFORT ACTIVITIES DURING NON-OILING AND DRY-OILING SEQUENCES BY CHICKS AND ADULTS[1]

	Non-oiling sequences				Dry-oiling sequences		
	Chicks			Adults	Chicks	Adults	
Behavior	Group: 1 7–13 days	2 14–20 days	3 21–28 days	4	5 35–43 days	6	Proportions[2] test
Oil	–	–	–	–	3.7	9.1	
Bill-to-wing-edge	–	1.0	0.8	4.8	2.6	5.0	$2 = 3, 4 = 6$
Wing-rub	8.2	4.9	3.7	13.8	4.8	14.3	$2 = 3, 2 = 5, 3 = 5$
Shoulder-rub	–	–	–	11.4	12.9	9.8	$4 = 6$
Preen breast	30.0	21.6	24.8	15.9	12.0	13.6	$2 = 3, 4 = 6, 5 = 6$
Preen back	12.2	9.8	5.4	5.8	16.0	5.2	$3 = 4, 3 = 6, 4 = 6$
Preen side/flank	6.1	9.4	8.6	13.6	12.1	14.7	$2 = 3, 4 = 5$
Preen leg	1.7	3.6	8.8	1.5	6.1	2.2	$1 = 4, 1 = 6, 4 = 6$
Preen belly	11.7	7.2	7.4	3.6	5.6	4.8	$2 = 3, 4 = 6, 5 = 6$
Ruffle-shake	1.7	1.2	2.8	0.9	–	0.5	$1 = 2, 4 = 6$

[1] See Table 2 for sample sizes.
[2] Results of a proportions test. An "=" sign means the groups did not significantly differ from one another ($Z < \pm 1.96$, $P > 0.05$).

expressed as a percentage derived from the number of times a particular act occurred out of the total number of acts performed in a sequence (Table 3). Several differences and trends were identified. (1) The most frequently observed comfort act in chicks was breast preening, as was also true of the tern (*Sterna* spp.) chicks observed by van Iersel and Bol (1958). (2) There was a general trend toward a decrease in breast preening with increasing age (except at 21–28 days) during non-oiling. However, there was no difference in the relative frequency of breast preening when dry-oiling by chicks (35–43 days) and adults were compared. (3) Back preening (Fig. 2a) during non-oiling generally declined as the chicks grew older until, by 21–28 days, the same relative frequency as in adults was seen. The highest relative frequency of back preening was seen in 35–43-day chicks during dry-oiling. (4) Belly preening occurred more frequently in chicks than in adults during non-oiling, but at similar frequencies during dry-oiling. (5) While breast, back and belly preening tended to decrease with age, side and flank preening during non-oiling increased. Side and flank preening also occurred more frequently during dry-oiling by adults than chicks. (6) During dry-oiling, chicks performed oiling, bill-to-wing-edge (Fig. 2d) and wing-rub (Fig. 3), 3 behaviors which are important in the distribution

TABLE 4

FREQUENCY DISTRIBUTIONS OF NON-RANDOMLY OCCURRING ACTS DURING DRY-OILING BY ADULTS AND CHICKS[1]

	Action unit												
Adults[2]	1	2	3	4	5	6	7	8	9	10	Total	χ^2	P
Oil	24	20	15	11	12	6	9	5	6	3	111	36.95	0.001
Bill-to-wing-edge	12	6	13	9	8	4	3	1	2	3	61	26.34	0.005
Chicks[3]													
Oil	8	1	0	5	3	2	5	3	0	1	28	21.90	0.01
Bill-to-wing-edge	0	1	2	1	6	0	2	3	4	1	20	16.02	NS
Preen back	4	12	15	19	10	22	13	11	7	7	120	23.16	0.01

[1] The number of times each movement was performed in each action unit is shown. The distribution of all acts listed in Table 1 was random for non-oil sequences by chicks aged 14–20 and 21–28 days and for adults. For chicks aged 7–13 days, only the distribution of breast preening was non-random ($\chi^2 = 33.57$, $df = 9$, $P < 0.001$), with the highest frequencies occurring in the first 2 action units. An action unit equals 1/10th of a sequence (see Ainley 1974).

[2, 3] The distribution of all other acts listed in Table 1 was random. Bill-to-wing-edge for chicks was included because the distribution approached non-randomness (required χ^2 value for $P < 0.05$ is 16.9).

of oil, significantly fewer times than did adults. (7) As far as the other comfort movements are concerned, chicks and adults rarely showed the same relative frequencies, especially during non-oiling. For example, during non-oiling sequences, chicks showed higher relative frequencies of head-shaking, ruffle-shaking, yawning and rapid-wing-flapping than adults.

Temporal distribution patterns.—For analyzing the distribution of comfort movements within a sequence, each sequence was divided into 10 equal parts, called action units (see Methods). While most comfort movements were found to be distributed randomly throughout a sequence, a few occurred non-randomly (Table 4). Oiling, for example, occurred most frequently in the first 3 action units in dry-oiling sequences of both chicks and adults. Bill-to-wing-edge followed a distribution pattern similar to that of oiling in adults. That both oiling and bill-to-wing-edge followed the same distribution pattern in adults is not surprising, since oiling is frequently followed by bill-to-wing-edge in adult dry-oiling sequences (see below).

In chicks the distribution of bill-to-wing-edge approached non-randomness, but it occurred most frequently during the fifth action unit and thus did not immediately follow oiling. Back preening was the only other comfort movement distributed non-randomly during dry-oiling by chicks. It occurred most frequently in action units 2–8.

The continuity of comfort movements.—Adult penguins tend to treat 1

TABLE 5

THE CONTINUITY OF COMFORT MOVEMENTS BY CHICKS AND ADULTS ACCORDING TO SIDE OF BODY AND AREA DURING 2-ACT TRANSITIONS

	Non-oil sequences				Dry-oil sequences	
	Chicks			Adults	Chicks	Adults
Movements remaining on:	Group: 1 7–13 days	2 14–20 days	3 21–28 days	4	5 35–43 days	6
Same side[1]	65.5% (38/58)	75.3% (204/271)	77.6% (104/134)	70.0% (389/556)	83.7% (461/551)	83.3% (685/822)
Same area[2]	48.3 (28/58)	27.6 (75/272)	21.3 (29/136)	14.1 (79/562)	12.8 (75/586)	8.8 (75/855)
Same side and area[3]	25.9 (15/58)	18.1 (49/271)	12.7 (17/134)	13.5 (75/556)	10.3 (57/551)	7.7 (63/822)

[1] Result of proportions test: $1 = 2, 3, 4; 2 = 3, 4; 3 = 4, 5, 6; 5 = 6$ ($Z < 1.96$, $P > 0.05$).
[2] Result of proportions test: $2 = 3; 4 = 5$ ($Z < 1.96$, $P > 0.05$).
[3] Result of proportions test: $1 = 2; 2 = 3, 4; 3 = 4, 5, 6; 4 = 5; 5 = 6$ ($Z < 1.96$, $P > 0.05$).

side of the body for some time before switching to the other (Ainley 1974). To determine whether this tendency develops gradually during ontogeny, we compared the various groups (Table 5). During non-oil sequences, chicks switched sides more often than adults during transition from 1 act to another. There was a steady increase with age, from 7–28 days, in the tendency of chicks to remain on the same side of the body. By 21–28 days, there was no significant difference between chicks and adults during non-oiling. During dry-oiling, however, chicks remained on the same side of the body less than adults. Nevertheless, in dry-oiling sequences performed by both chicks and adults, there was a strong, significant tendency for acts leading to, and following, oiling to occur on the same side of the body to which the head was turned when gathering oil in the bill from the uropygial gland (greater than 75% for chicks and 85% for adults).

While chicks tended to remain on the same side less often than adults, they remained in the same area (regardless of side) during the transition from 1 act to another, more frequently than adults. Furthermore, in those cases of which the younger chicks (7–20 days of age) remained on the same side of the body, they also tended to stay in the same area of the body. This was also true for both non-oil and dry-oil sequences. Thus, chicks appear to be less effective than adults in distributing the oil to all parts of the body during dry-oiling.

TABLE 6

A COMPILATION OF SELECTED 2-ACT TRANSITIONS FOR DRY-OILING BY CHICKS AND ADULTS FOR WHICH $P < 0.001$ ($Z > 3.29$)

2-Act transition[1]	Chicks		Adults	
	Conditional probability	Z value	Conditional probability	Z value
Oil/BW	–	–	0.40	12.60
Oil/BR[2]	0.24	2.89	–	–
BW/WR[2]	0.81	11.65	0.71	19.32
WR/BR[2]	0.36	5.38	0.14	3.50
SH/side	0.44	14.28	0.32	4.21
BR/belly[2]	0.41	11.80	0.23	5.61
BR/BR	0.22	5.13	–	–
Belly/BR	0.29	5.11	–	–
Side/WR	–	–	0.17	4.80
Side/SR	–	–	0.14	3.18

[1] See Table 1 for code.
[2] Same transitions found during wet-oiling by adults (see Ainley 1974, p. 33).

Two-act transitions

To understand in greater detail the way in which comfort sequences develop and become organized, analyses were performed on transitions between an act and the one immediately following.

Significant transitions.—In all groups, a few instances occurred in which there was a significant transition between a behavior and itself (Tables 6 and 7). That is, the individual performed an action, paused and lifted its head from the body surface, and then immediately performed the same action again. Of the 3 significant transitions within non-oiling sequences in chicks aged 7–13 days, 2 represented a transition between an act and itself. Only this group of chicks differed significantly from all other groups in the proportion of times a transition occurred between an act and itself (proportion test $Z > 1.96$, $P < 0.05$). Data for selected 2-act transitions are presented in Tables 6 (dry-oiling) and 7 (non-oiling), and may be summarized as follows. (1) When chicks aged 7–13 days were included, no 2-act transitions were common to all 6 groups. However, when this youngest group of chicks was excluded, breast/belly and shoulder/side were shared by the remaining 5 groups. (2) Breast/breast, breast/belly and belly/breast were observed in all groups of chicks, during both types of sequences. During non-oiling, 6 of the 8 significant transitions involved the breast area. (3) Bill-to-wing-edge/wing-rub, wing-rub/breast, shoulder/side, breast/belly and cloaca/breast were common to dry-oil sequences by both chicks and

TABLE 7

A COMPILATION OF SELECTED 2-ACT TRANSITIONS FOR NON-OILING BY CHICKS AND ADULTS FOR WHICH $P < 0.001$ ($Z > 3.29$) IN AT LEAST 1 GROUP OF BIRDS[1]

2-Act transition[2]	Chicks				Adults	
	14–20 days		21–28 days			
	CP[3]	Z value	CP	Z value	CP	Z value
BW/WR	–	–	–	–	0.23	3.95
SH/BR	0.24	2.68[a]	0.40	5.00	–	–
SH/side	0.41	5.53	0.27	2.98[a]	0.18	2.25[b]
BR/BR	0.44	14.53	0.30	6.12	0.15	2.32[b]
BR/belly	0.27	7.79	0.23	4.41	0.18	3.31
Back/BR	0.44	5.76	0.30	2.84	–	–
Belly/BR	0.30	5.54	0.40	4.07	–	–
Side/BR	0.32	6.21	0.35	5.24	–	–
Side/WR	–	–	–	–	0.15	3.35
Side/SR	–	–	–	–	0.15	3.35
Leg/leg	0.35	4.91	0.29	3.18[a]	–	–

[1] For chicks aged 7–13 days, there were only 3 significant 2-act transitions: Belly/belly ($P < 0.001$, $Z = 6.62$), BR/BR ($P < 0.001$, $Z = 8.06$), and Belly/BR ($P < 0.05$, $Z = 2.27$).
[2] See Table 1 for code.
[3] CP = conditional probability.
[a] $P < 0.01$.
[b] $P < 0.05$.

adults. (4) When significant 2-act transitions between movements performed on the same side of the body were considered in adult dry-oil sequences, oil/bill-to-wing-edge occurred on the same side of the body 35/37 (95%) times, bill-to-wing-edge/wing-rub occurred on the same side of the body 42/42 times, and wing-rub/shoulder-rub occurred on the same side of the body 10/10 times. (5) During dry-oiling by chicks, the shoulder appeared to be a "pivot" for crossing from 1 side of the body to another. For example, for transitions involving the shoulder (excluding shoulder/shoulder), the chicks remained on the same side of the body only 8/115 (7%) times. In contrast, during dry-oiling by adults and non-oiling by chicks, when transitions involved the shoulder, the birds tended to remain on the same side of the body 10/10 and 41/44 (93%) times, respectively.

DISCUSSION

Age at first appearance of movements.—Adélie Penguins are semi-altricial birds (Nice 1962). Most of the different comfort movements appeared in chicks after 7–9 days of age, in contrast to precocial fowl, ducks and geese, in which many comfort (and other) behaviors are performed within a few days of, or even during, hatching (Nice 1962, McKinney 1965, Dawson

and Siegel 1967, Brown et al. 1976). The earliest comfort movements performed were directed to body areas (breast, belly) comprising a major portion of the bird's surface area. In addition, it is these areas of the body that make the most contact with the ground and thus tend to get soiled when the young chick lies down. Later, when the chick begins to stand upright for a greater period of time and beings to walk around, dirt collects on other body areas as well. These changes in posture and activity may then play a role in the change in relative distribution of comfort behaviors during early ontogeny.

The last comfort activities to emerge ontogenetically were shoulder-rubbing (day 33) and oiling (day 35), just after the uropygial gland became functional (days 30–33) and just prior to fledging (going out to sea for the first time; approximately 6–8 weeks of age). That both oiling and shoulder-rubbing appear at approximately the same time is perhaps not surprising since shoulder-rubbing is the specific behavior used to distribute oil from the head to the shoulder, after the oil has been transferred to the head by wing-rubbing (Ainley 1974). A similar relationship was noted by Kruijt (1964) for Burmese Junglefowl (*Gallus gallus spadiceus*) in which head-rubbing, an action used to release oil from the oil gland, appeared simultaneously (day 11) with the development of function of the gland. Wing-rubbing, on the other hand, a behavior that is used in other contexts as well, first appeared in the penguins very much earlier, on day 7.

The appearance of several other comfort movements in Adélie chicks coincided with growth of contour feathers. At approximately 20 days of age, contour feathers began to emerge (Taylor 1962, Spurr 1975, this study). This corresponded to a marked increase in the number of acts per sequence during non-oiling. The oldest chicks still performed fewer acts than adults during non-oiling. The highest rate (8.4 acts/min) and highest number of acts per sequence (63.6) were performed during dry-oiling by adults. Overall, penguin chicks performed more acts per sequence than the terns studied by van Iersel and Bol (1958). Van Iersel and Bol reported that young terns (age not given) performed an average of 4.2 acts in succession, and never more than 6.

A change in the distribution of preening effort also occurred during the fourth week, apparently related to feather growth. For example, down is lost from the legs at about 25 days of age (Taylor 1962); correspondingly, the proportion of leg preening increased from 3.6% in chicks 14–20 days of age to 8.8% in those 21–28 days old. Mergler (pers. comm.) observed a similar trend towards increased preening in areas where down was being lost in Greylag Geese (*Anser anser*).

Dry-oiling compared to wet-oiling.—The mean duration of dry-oiling by

adult Adélies (9.4 ± 6.7 min, range 2–24 min) was less than that recorded for wet-oiling. Ainley (1974) reported a range of 2–40 min with an average of approximately 12–15 min for wet-oil sequences. However, the durations of both wet- and dry-oil sequences by the Adélie Penguins were longer than wet-oil sequences recorded either for Mallards (*Anas platyrhynchos*) or White-fronted Geese (*Anser albifrons*) for which the duration of oiling sequences was usually less than 5 min (McKinney 1965). Furthermore, during dry-oiling by young and adult penguins, oiling occurred in a sequence an average of 4.7 and 6.2 times, respectively, compared to 9.0 times per wet-oiling sequence by adults (Ainley 1970). McKinney (1965) reported that Mallard Ducks and White-fronted Geese may oil from 1 to 7 times during an individual oil-preening session, but in the vast majority of sessions the oil gland is used 3–5 times.

The sequence oil/bill-to-wing-edge, the major initial route by which oil is transferred from the oil gland to other body areas, did not occur during dry-oiling by chicks, but did occur during both dry- and wet-oiling by adults (Ainley 1974). In addition, during wet-oiling by adults, wing-rubbing, the action that is used to carry oil to the head, occurred significantly more frequently than during dry-oiling (Ainley 1974:41, Table 6). Wet adults seem more "concerned" with distributing oil around their bodies than are dry adults, and both these groups make more effective attempts to distribute oil than do chicks.

Two-act transitions and the organization of sequences.—In order to gain a more complete understanding of the ontogeny of comfort behavior and the way individual actions become organized into sequences, 2-act transitions were analyzed. There were few highly significant ($P < 0.001$) 2-act transitions common to groups of penguins performing similar types of comfort sequences. The present results combined with those presented by Bekoff (1978) on behavioral variability suggest that although behaviors associated with the gathering and distribution of oil (and some other acts, as well) may be tightly linked in sequence, it is not possible to decipher a "typical" stereotyped comfort movement sequence for each age group. The possibility remains that individuals may show some degree of stereotypy.

Most significant 2-act transitions involved the breast area. For example, of the 5 two-act transitions common to dry-oiling by both adults and chicks, 3 involved the breast. Similarly, of the 8 two-act transitions that were common to non-oil sequences performed by chicks aged 7–13 and 21–28 days, 6 involved the breast area. Van Iersel and Bol (1958) considered breast-preening to be a low-threshold act. Since the breast occupies the largest surface area of any body section in adult Adélies (Ainley 1974) and this also appears to be true in chicks, it it not surprising that it is involved in a

large number of 2-act transitions, both those that are common to a number of groups and those that occur only in 1 group.

In addition to extensive preening of the breast by adults and chicks, the shoulder also took on special significance among dry-oiling chicks. During dry-oiling by chicks, the shoulder appeared to be a "pivot" point from which the birds would cross from 1 side of the body to the other. In transitions involving the shoulder (excluding shoulder/shoulder movements), the chicks changed sides 93% of the time. In contrast, in the other groups of penguins, over 90% of the transitions involving the shoulder were on the same side of the body. There is no obvious reason for these differences. During dry-oiling by chicks, shoulder preening did not occur at a specific point in the ongoing sequence, and the posture that the chicks assumed while preening their shoulders during dry-oiling did not appear to differ from the posture that the non-oiling chicks assumed when they preened their shoulders. Possibly a more subtle factor was involved. Perhaps the dry-oiling chicks were trying to make the transition from shoulder preening to gathering oil and in doing so began to lose their balance. The best way to regain balance would be to shift their weight to the other side of the midline. After this shift they might simply continue preening. The fact that the shoulder did not seem to be a pivot point in the younger chicks in which the oil gland was not functional makes this suggestion plausible. In any case, the large difference between the groups seems worthy of further study.

Our data also showed major differences between dry-oiling and non-oiling sequences of comfort movements in adult Adélie Penguins. Furthermore, our developmental data showed a gradual refinement in the organization of non-oil sequences performed by the chicks so that by the time they were 21–28 days of age they resembled adults in a number of ways. Dry-oiling by chicks also shared many common characteristics with dry-oiling by adults. Unfortunately, Adélie Penguin chicks are inaccessible to study soon after they reach 6–8 weeks of age when they fledge and go out to sea, usually for a period of 2–3 years (LeResche 1971). Consequently, behavioral development during this period cannot be studied.

SUMMARY

The development of comfort behaviors in Adélie Penguins and the organization of comfort activities in adults, were studied at Cape Crozier, Ross Island, Antarctica. Non-oiling and dry-oiling (feathers not wet) comfort sequences were compared to one another; these results were then compared to data collected by Ainley (1974) on wet-oiling by adults immediately after they emerged from the sea. For purposes of analyzing the ontogeny of non-oiling comfort activities, chicks were grouped into 3 groups: 7–13, 14–20 and 21–28 days of age. Dry-oiling was observed in chicks 35–43 days of age. Our

results were as follows. (1) Only yawning occurred on the day after hatching. The earliest preening movements appeared on day 7 (breast and belly preening). Oil distribution behaviors appeared between days 30–33, the same period during which the oil gland became functional. The first dry-oiling sequence was observed on day 35. (2) There was no difference in the duration of non-oil comfort sequences between chicks over 13 days of age and adults. Chicks performed fewer acts per min than did adults and therefore the mean number of acts per sequence was lower in chicks. (3) In general, behaviors were randomly distributed throughout comfort sequences. Exceptions include oiling by adults and chicks, bill-to-wing-edge by adults, and back preening by chicks. (4) During transitions from 1 act to another, chicks aged 21–28 days remained on the same side of the body and in the same area with the same relative frequency as non-oiling adults. (5) Dry-oiling by chicks and adults shared many common characteristics: (i) oiling occurred non-randomly in the beginning of the sequences, (ii) the relative frequency of occurrence of breast and belly preening was the same, (iii) during transitions from 1 act to another, the groups did not differ with respect to remaining on the same side of the body and in the same body area, (iv) actions leading to and immediately following oiling occurred very frequently ($> 78\%$) on the same side of the body to which the head was turned when gathering oil in the bill.

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