Condor, 80:138–146

ACTIVITY PATTERNS AND SOCIAL BEHAVIOR OF NON-BREEDING ADÉLIE PENGUINS

DAVID G. AINLEY

This paper completes a three-part study of non-breeding individuals in the nesting population of the Adélie Penguin (*Pygoscelis adeliae*) at Cape Crozier, Ross Island, Antarctica, where many banded, known-age individuals are present. LeResche and Sladen (1970) and LeResche (1971), who also worked with these birds, found that they first visit the breeding rookery as two-year-olds and first breed when three (female) or four (male). Moreover, many do not breed until five to seven years old. These findings suggest that the rates and processes of physiological, morphological, and behavioral maturation related to reproduction may account for non-breeding individuals.

Initially, I compared degree of maturity of the reproductive systems of penguins of various ages. I found that males and most females less than four years old are physiologically or morphologically incapable of breeding (Ainley 1974a). This discovery made it even more intriguing that so many four- and five-year-olds, particularly males, failed to breed. I therefore turned my attention to these birds. A preliminary analysis showed their reproductive behavior to be immature in several respects; hence, they failed to pair and to breed (Ainley 1974b). Four years later I was able to renew work at Cape Crozier. Upon returning, I was amazed to find non-breeding penguins even as old as 13 years. Questioning why they failed to breed led to the present study which compares the activity patterns and social interactions of non-breeding and breeding birds, mainly those 5 to 13 years of age. I also present remarks on the behavior of younger birds where new data, added to those in Ainley (1974b), help to understand non-breeding in older individuals. Finally, this paper compares breeding and non-breeding Adélie Penguins in the way they budget their time during pair formation.

METHODS

Observations were made at Cape Crozier, Ross Island, Antarctica, site of one of the largest Adélie Penguin breeding populations. During 1962 to 1970, 2,500 to 5,000 chicks were banded yearly by the USARP Bird-banding Program. I was able to identify and observe these birds without disturbance as band numbers could be read with 8× binoculars from a distance of 5–12 m.

Most data were gathered during the 1974–75 and 1975–76 austral summers; other observations were made in 1969–70. Other projects and the large number of banded birds (Table 1) limited my observations on individual birds to every other day. Upon finding a banded bird, I noted its behavior, concentrating on the activities of non-breeders in 1974–75 and of breeders in 1975–76. Observation of an individual lasted less than a minute. I also noted the quality of its nest on a four-point scale—0: a scoop with no stones, 1: a scoop with a few scattered stones, 2: a scoop with many loosely arranged stones, and 3: a scoop with stones neatly arranged into a bowl. Only nests in the same colonies were compared, as recommended by LeResche (1971) because stones were not equally available in all colonies.

In one manipulative experiment I recorded the behavior of lone males when a dead penguin, frozen into the position assumed by females during copulation (Fig. 1), was placed in each one's nest. After positioning the model, which required about 5 sec and often drove the male 3 to 10 m away, I started a stopwatch and quickly retreated 12 m. The male was then allowed 5 min to return and respond. Each one usually expressed the entire range of his "feelings" within a minute. Observations on younger birds, which were made in 1969–70 and reported in Ainley (1974b), were combined with results from the 1974–75 and 1975–76 experiments.

Interpretations and nomenclature are similar to those presented in Ainley (1974b); only birds of known sex are included. A bird's sex was determined by examination of its cloaca (Sladen and LeResche 1970, Ainley 1974a) or that of its mate, or by noting the following: (1) pairings with banded mate(s) of known sex, (2) position during an observed copulation, (3) clear tread marks on its or its mate's back (left by a male's muddy feet during copulation) *in conjunction with* a normal incubation routine (see Ainley and LeResche 1973), and (4) prolonged presence alone on the same territory (1–3 weeks) and observation of Ecstatic Vocalization (Ainley 1974b) during that time (= a male).

PATTERNS OF ROOKERY VISITATION BY BREEDERS AND YOUNG NON-BREEDERS

To supply a context for this paper, I describe here the normal patterns of rookery visits by breeding adults. This information was gathered by Sladen (1958), Taylor (1962), Penney (1968) for adults, and by LeResche (1971) and Ainley (unpubl. data) for young non-breeders.

The pattern for breeders is as follows: After a courtship period of 7–12 days, a female lays her eggs (ca. 15 Nov.) and then departs to feed at sea, leaving her mate to incubate for about two weeks. This first incubation duty

comes after the male has normally been present one to three weeks. Upon return, the female incubates for about 10 days, followed by a few more days of incubation by the male. When she returns again (ca. 20 Dec.), the eggs usually hatch. Parents then alternate between guarding chicks and feeding at sea, with nest relief every 3–4 days, until the chicks are about three weeks old and large enough to remain unattended. Chicks then enter the crèche and are fed by the parents, each of whom visits every 2–3 days. This schedule continues until the chick fledges, whereupon the parents cease visting the rookery (ca. 5 Feb.).

Young non-breeders, however, spend more time in the rookery and visit more often as they get older. Almost all two-year-olds and most three-year-olds visit once for a few days late in the breeding season (15 Dec.–15 Jan.). By four years of age, 75% make two visits, one during late egg laying (late Nov.) and the other when chicks are hatching and being guarded (late Dec.). During the first visit, non-breeding, four-year-old males and females spend 10 and 4 days and during the second visit, 14 and 4 days, respectively.

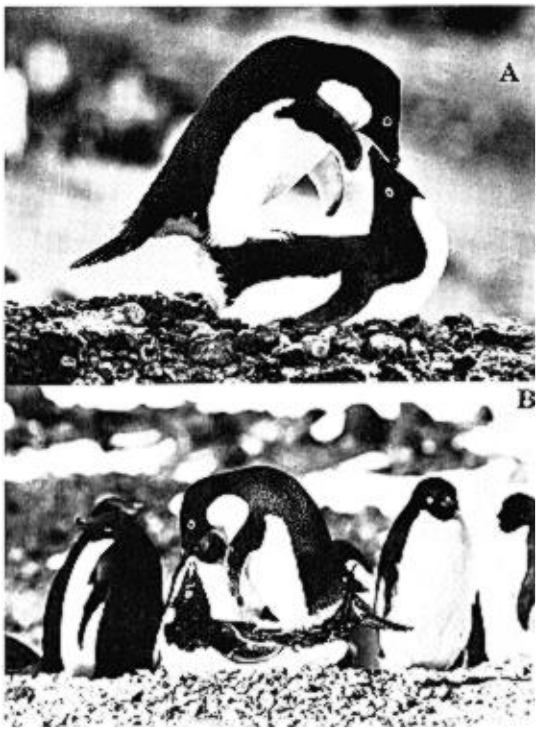

FIGURE 1. (A) Copulation in Adélie Penguins; (B) a male Adélie copulating with the model.

RESULTS

SPRING ARRIVAL

Non-breeding males aged 5 to 11 years arrived later on the average than males of similar age that eventually bred ($P < 0.05$, t-test; Table 2). This same trend was evident among females ($P < 0.05$). It is important to note here that many non-breeding males arrived as early as eventual breeders and thus had the opportunity to secure central territories. On the other hand, all non-breeding females arrived later than females who eventually bred.

TABLE 1. Proportion of non-breeders among age groups of Adélie Penguins at Cape Crozier.

	MALES		FEMALES		UNSEXED BIRDS			TOTAL[b]	
Age	Number	% Not breeding	Number	% Not breeding	Number	% Not breeding	% Status unknown	Number	% Not breeding
1	—	100	—	100	—	—	—	—	100
2	230	100	196	100	357	100	0	783	100
3	148	100	161	82	277	100	0	586	95
4	173	87	159	54	164	96	1	496	80
5	209	43	164	15	74	31	45	447	40
6	256	29	239	13	43	5	74	538	21
7	245	22	205	5	38	5	76	488	14
8	152	13	110	9	25	0	72	287	11
9	71	15	43	5	12	0	67	126	11
10	60	10	35	9	14	0	43	109	9
11	45	13	29	3	14	0	71	88	9
12	35	9	25	0	7	0	71	67	4
13	17	6	8	13	2	0	100	27	7
14	4	0	1	0	0	0	0	5	0
TOTAL	1645	48[c]	1375	36[c]	1027			4047	54

[a] Data for birds less than five years old are from 1968–69 and 1969–70; the remainder are from 1974–75 and 1975–76. Included are birds banded in USARP Bird-banding Program areas B and C, except for birds 11 to 14 years old where those banded in area E also were included.

[b] That portion of birds of unknown sex and breeding status was divided among breeders and non-breeders based on the proportion of non-breeding males and females of known sex combined for each age group.

[c] For males and females five years of age and older, the percentages are 24% and 10%, respectively.

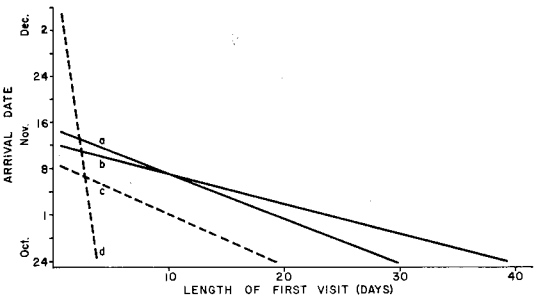

FIGURE 2. Correlations between arrival date and length of first visit during the courtship and egg laying period for four groups of birds: (a) non-breeding males ($m = -1.5$, $r = -0.8477$, $n = 99$, $P < 0.05$), (b) breeding males ($m = -2.1$, $r = -0.7844$, $n = 328$, $P < 0.05$), (c) breeding females ($m = -1.2$, $r = 0.7418$, $n = 171$, $P < 0.05$), (d) non-breeding females ($m = -0.15$, $r = -0.2824$, $n = 12$, $P > 0.05$).

LENGTH AND NUMBER OF VISITS

Once at the rookery, the length of time a non-breeder remained during its first visit was related to its arrival date. This was also true for breeders (Ainley 1974a). Earliest arriving birds stayed longer during their first visit than later arriving ones, a correlation that was linear ($P < 0.05$; Fig. 2). Also, birds that eventually bred stayed longer than non-breeders ($P < 0.05$, t-test; Table 3). However, many male non-breeders remained at their territories for as long as many breeders, but many failed to pair even for short periods. Among females, breeders also remained longer than non-breeders, a difference that was statistically significant ($P < 0.05$, t-test; Table 3). Unlike other birds, non-breeding females did not remain long enough for their arrival date to be correlated with the length of their stay (see Fig. 2).

Most non-breeders five years old and older visited the rookery twice. Males remained about 23.4 days (SD = 5.0, range 17–40 days) at sea between visits, their average date of return being 23–24 December (SD = 4.4, range 17 Dec.–2 Jan., $n = 54$) or after most chicks had hatched. They then remained in the rookery for about three weeks ($\bar{x} = 22.9$ days, SD = 4.7, range 6–32 days). I could detect no linear or other correlation between the lengths of their first visit and the absence between visits ($r = 0.0837$), nor between the lengths of the first and second visits ($r = 0.2770$). Including both visits, non-breeding males 5 to 11 years old spent, on the average, 39.7 days (SD = 9.8, range 17–65 days) in the rookery. This compared to 56.2 days (SD = 6.8, range 51–73; Taylor 1962) for breeders. Thus, some non-breeders were present for as long as breeders but made only two visits versus 35–45 visits for the breeders. Non-breeding females of the same ages also visited twice. They were absent between visits for an average 26.8 days (SD = 6.4, range 17–35 days) similar to males ($P > 0.05$, t-test), and also returned about 23 December (SD = 6.0, range 13 Dec.–7 Jan.). They remained about three weeks ($\bar{x} = 18.2$ days, SD = 5.3, range 8–30 days) during their second visit, a period slightly less than that of males ($P < 0.05$, t-test).

ACTIVITY PATTERNS

How Adélie Penguins of different breeding status occupied themselves during the period when pair formation occurred provided clues to why some did not breed. First, I determined the behavioral time budgets during periods progressively closer to pairing of lone males who eventually bred. Observations were analyzed at two-day intervals working backward from the date of pairing (Fig. 3); intervals 4 and 5 and 6 through 10 were combined to increase respective sample sizes. Some trends were obvious. Twelve or more days (intervals 6 through 10) before pairing, males were often lying inactive or standing quietly in their nests and were engaged in little nest building or social interaction, i.e. displaying, defending their territory, etc. By contrast, two days before pairing 22% fewer were lying down ($P < 0.05$). I interpret this to mean that as males became more active, both individually and socially, they were more likely to pair. Also, it seems that standing in the nest, although relatively inactive, signified that a bird was ready for whatever social situation developed.

Next, I compared behavior during the spring of male non-breeders and those who eventually bred. Observations were combined into six-day periods beginning 29 October and continuing through egg-laying to 5 Decem-

TABLE 2. Date of first arrival of penguins 5–11 years old during 1974.

Penguin	Mean	SD	Range	N
Breeding male	5.8 Nov	6.7	24 Oct–24 Nov	328
Non-breeding male	11.5 Nov	4.4	24 Oct–26 Nov	99
Breeding female	0.6 Nov	2.6	28 Oct–16 Nov	171
Non-breeding female	19.7 Nov	3.5	14 Nov–27 Nov	12

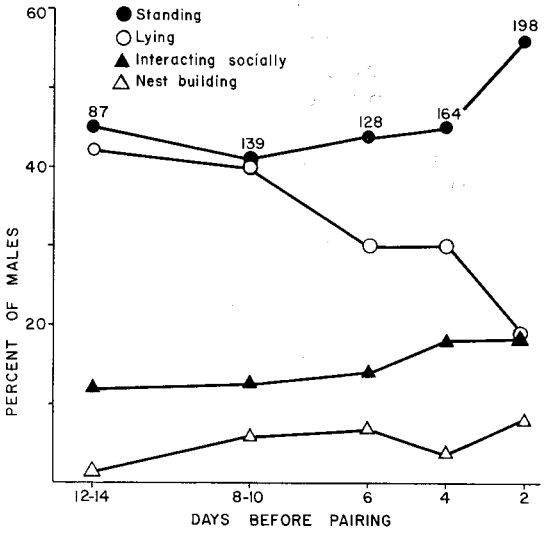

FIGURE 3. Behavior of lone males observed at two-day intervals progressively closer to their becoming paired. The change in the percentage of birds engaged in the various activities as pairing approached is shown; standing in the nest ($m = -0.8$, $y = 52$, $r = 0.6147$, $P > 0.05$), lying in the nest ($m = 2.0$, $y = 19$, $r = 0.9345$, $P < 0.05$), social interaction ($m = -0.7$, $y = 20$, $r = 0.9244$, $P < 0.05$), nest building ($m = -0.4$, $y = 8$, $r = 0.7106$, $P > 0.05$).

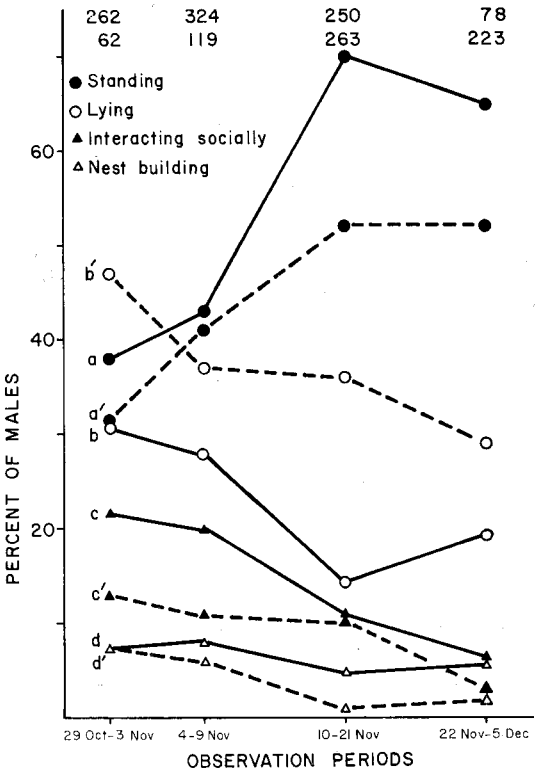

FIGURE 4. Behavior of lone males during the courtship and egg laying period; birds separated according to whether they remained unpaired or eventually paired and bred that season. Points show percentages of birds occupied in various ways. Changes in percentages of behaviors were analyzed by linear correlation: breeders, solid line (a) ($m = 6.8$, $y = 33$, $r = 0.8430$, $P > 0.05$), (b) ($m = -3.1$, $y = 32.3$, $r = 0.7676$, $P > 0.05$), (c) ($m = -3.8$, $y = 26.1$, $r = 0.9817$, $P < 0.05$), (d) ($m = -0.4$, $y = 7.7$, $r = -0.5934$, $P > 0.05$); non-breeders, dashed-line (a') ($m = 4.6$, $y = 30.2$, $r = 0.8375$, $P > 0.05$), (b') ($m = -3.5$, $y = 47.8$, $r = -0.9305$, $P < 0.05$), (c') ($m = -2.1$, $y = 15.6$, $r = -0.9590$, $P < 0.05$), (d') ($m = -1.3$, $y = 7.8$, $r = -0.8386$, $P > 0.05$). Numbers at the top of the figure are sample sizes for each observation period; upper numbers for breeders and lower numbers for non-breeders. During the time periods, 3 and 4, and 5 and 6 were combined to increase and equilibrate sample sizes.

ber. Some of the later six-days periods were combined to increase sample size similarity (Fig. 4). Both groups showed changes similar in pattern but very different in degree. Social activity in eventual breeders dropped 16% from the first period until the combined last periods 22 Nov.–5 Dec. ($P < 0.05$), inactivity decreased 11% ($P < 0.05$), standing in the nest increased 31% ($P < 0.05$), and nest-building dropped 3% ($P > 0.05$). In males that never paired, over the same time periods, social interaction declined 10% ($P < 0.05$), inactivity decreased 18% ($P < 0.05$), standing in the nest increased 21% ($P < 0.05$), and nest-building practically ceased ($P > 0.05$). Combining all observations for eventual breeders ($n = 976$) and non-breeders ($n = 651$), and comparing them, heightens the differences between the two groups. The values in the four occupations for the breeders and non-breeders, respectively, were: lying in the nest or sleeping (25 vs. 36%; $P < 0.05$), standing awake in the nest (51 vs. 52%; $P > 0.05$), nest building (7 vs. 3%; $P < 0.05$), and interacting socially (17 vs. 9%; $P < 0.05$). Eventual breeders were generally more social and more active than non-breeders.

TABLE 3. Length of first visits in days by penguins of different sex and breeding status during 1974–75.

Penguin	Mean	SD	Range	N
Breeding male	28.2	12.4	10–45	328
Non-breeding male	16.3	7.8	2–36	99
Breeding female	10.2	2.5	4–18	171
Non-breeding female	5.3	1.9	2–8	12

The quality of a bird's nest may indicate the amount of time spent in nest-building activities. Judging nests on the four-point scale, the mean score for the maximum quality attained by a non-breeder during his first tenure in the rookery was 0.9 ($SD = 0.9$, $n = 135$); the average quality of a breeder's nest just prior to his pairing was 1.3 ($SD = 0.9$, $n = 337$). The difference was significant ($P <$

TABLE 4. Percent positive responses to the model relative to male's age and breeding status. Data from Ainley (1974b: Table 21.3) are included.

Age	N	Positive responses N (%)	Complete N (%)	Incomplete N (%)	Solicitation N (%)
			Breeders		
6	2	1(50)	1(100)	0(0)	0(0)
7	5	3(60)	3(100)	0(0)	0(0)
8	13	9(69)	8(89)	1(11)	0(0)
9–11	8	4(50)	4(100)	0(0)	0(0)
12–13	5	2(40)	1(50)	0(0)	1(50)
TOTAL	33	19(58)[a]	17(90)[b]	1(5)	1(5)
6–11	28	17(61)	16(94)	1(6)	0(0)
			Non-breeders		
3	11	2(18)	0(0)	1(50)	1(50)
4	31	18(55)	8(44)	9(50)	1(6)
5	30	23(77)	14(61)	6(26)	3(13)
6	33	13(39)	9(69)	3(23)	1(8)
7	20	9(45)	7(78)	2(22)	0(0)
8–11	3	1(33)	1(100)	0(0)	0(0)
TOTAL	128	66(52)[c]	39(59)[d]	21(32)	6(9)
6–11[e]	56	23(41)	17(74)	5(22)	1(4)

[a] Frequencies of positive responses are independent of age; $P > 0.05$, G-test.
[b] Frequencies of complete vs incomplete/solicitations are independent of age; $P > 0.05$, G-test.
[c] Frequencies of positive responses are not independent of age; $P < 0.05$, G-test.
[d] Frequencies are related directly to age; $P < 0.05$, $r = 0.9531$.
[e] Frequencies between breeders and non-breeders are not statistically significant, $P > 0.05$; equality of percentages tested according to Sokal and Rohlf (1969:608).

0.05; Wilcoxon two-sample test). Building a nest is not a social activity among unpaired males, and I do not know whether a female considers the quality of a male's nest as a criterion for selecting him as a mate. The comparison of average scores supports such a relationship, but it may be only that active males build better nests and attract females more easily.

SOCIAL INTERACTION

A female lying in the nest and inviting copulation is important in pair formation and pair-bond maintenance (Ainley 1974b). This situation lends itself easily to experimentation. I presented males with a model female to compare how breeders and non-breeders of various ages behaved during an irresistible social situation. As discussed earlier (Ainley 1974b), responses among young penguins depended on the male's age. Here I compare observations of older birds to those reported earlier of younger ones. Results are further separated by whether or not the males eventually bred.

Positive responses included complete copulation (semen deposited), incomplete copulation (mounting only), and solicitation (vibrating the bill on the female's bill or head). All three responses occur in natural situations; birds copulating naturally and with the model are shown in Figure 1. The proportion of positive responses in eventual breeders ranged from 50% in 6-year-olds to 69% in 8-year-olds and thereafter declined to 40% in 12- to 13-year-olds (Table 4). Almost all (90%) were complete copulations. No statistical relationship to age existed in the incidence of complete copulations. Among non-breeders, the proportion of positive responses increased from 18% in 3-year-olds to 77% in 5-year-olds and then declined to 33% in 8- to 11-year-olds. These proportions were related to age ($P < 0.05$; G-test). The incidence of complete copulations increased with age ($P < 0.05$) from none among 3-year-olds to 100% for 8- to 11-year-olds; correspondingly, incidence of incomplete copulations and solicitations declined with increasing age.

Some differences were revealed by comparing responses among 6- to 11-year-olds in both groups, thereby equilibrating age representation. Non-breeders responded incompletely (22%) much more often than breeders (6%). About 20% more breeders responded positively, and more performed complete copulations. None of these differences was significant statistically ($P = 0.07$), but all consistently "favored" breeders.

Further insight into behavioral differences among males of different ages and breeding status was gained by analyzing responses to the model before copulation (see Ainley 1974b for detailed discussion of displays). The first analysis (Table 5) showed that younger birds displayed often but, older birds prefaced their actions less and less with other behavior; beyond 7 years, most males copulated without previous display. Except for an inclination, which declined with age ($P < 0.05$), to Gakker and Peck at the model, no other statistically significant behavioral trends were apparent. Similar trends occurred among males who refused copulation (Table 6). Responses tended to become more uniform with increasing age, and birds became less likely to avoid the nest until I removed the model. Younger birds that did not copulate avoided the model ($P < 0.05$) or displayed in ambivalent ways. With age, particularly after seven, a male was more likely to act directly: if he did not copulate (Table 4), he tried to expel the model through Alternate Stare ($P < 0.05$) or Gakkering and Pecking ($P < 0.05$). Among birds who refused copulation, the Locomotory Hesitance Vocalization (LHV),

TABLE 5. Relationships of bird's age to its behavior prior to copulating with the model; includes data from Ainley (1974b: Table 21.4).

		Ambivalence		Interaction				Hesitance	
Age	N	Bow[a]	SlWgFp	HdW	Gk[b]	EV	BAx	AlSt	LHV[c]
3	2	2(100)[d]							
4	18	2(11)	1(6)	3(17)	6(33)	1(6)	1(6)	1(6)	5(28)
5	23	2(9)		4(17)	11(48)				9(39)
6	13	2(15)		2(15)	2(15)			1(8)	2(15)
7	9	1(11)		1(11)	1(11)		2(11)	1(11)	1(11)
8	8				1(12)	1(11)			3(38)
9–13	6								1(17)

[a] Displays as in Ainley (1974b); Bow = Bow, HdW = Head Wave, Gk = Gakker and Peck, EV = Ecstatic Vocalization, SRe = Stone Rearrangement.
[b] Correlation to age: $r = -0.8484$, $P < 0.05$.
[c] Correlation to age: $r = -0.2736$, $P > 0.05$.
[d] Figures in parentheses represent percentages.

given upon first approaching the model, was gradually used more with age ($P < 0.05$).

Comparing non-breeders with eventual breeders in these ways revealed additional differences. About half the non-breeders did not display before copulating; the remainder were quite diverse in behavior (Table 7). Eventual breeders, except for three that gave LHV first, merely mounted the model upon return to their nest. Among males that refused copulation (Table 8), non-breeders, again in marked contrast to eventual breeders, displayed often, and almost a third completely avoided the situation. Only one eventual breeder avoided the model, and the remainder of those refusing copulation tried to expel it.

DISCUSSION

The habits of breeders and non-breeders differ in ways that provide insight into understanding the proximate factors relating to an individual's breeding status. I will not discuss here any ecological or evolutionary implications of non-breeding in penguins, having considered them earlier (Ainley 1974a, b).

Results in this paper have centered on males, whose great outnumbering of females (ca. 3:1 as non-breeders older than 4; Table 1) is explained by a difference in mortality rate (Ainley, unpubl. data). This creates a surplus of males who are physiologically capable of breeding, intensifying the competition among them for mates (see also Spurr 1975).

Non-breeding is uncommon in mature female Adélie Penguins. Tardy migration, which could be related to a physiological factor or merely to chance (for example, distance from the rookery), may be the only major reason why a female does not breed. Of the 12 non-breeding females at least 5 years old in 1974–75, 10 were present during their first visit for six days or less, and the others visited for only seven days. These short visits correlated statistically with their late arrival. Judging from the rather poor record of breeding females who stayed less than seven days, the short visit of non-breeders may have had a direct effect on their breeding status. Only 11 (5.8%) of the 171 breeding females (5 years and older) were present for less than seven days. Five laid eggs that did not hatch; three laid clutches of which only one egg hatched; one laid only one egg (which

TABLE 6. Relationship of a bird's age to its behavior in refusing to copulate with the model; includes data from Ainley (1974b: Table 21.5).

		Ambivalence			Interaction				Hesitance		
Age	N	Bow	SRe	SlWgFp	HdW	Gk[a]	EV	BAx	AlSt[b]	LHV[c]	Avoid[d, e]
3	9	1(11)	2(22)			2(22)				1(8)	8(89)
4	13	2(15)	1(8)	1(8)		3(23)	1(8)			1(8)	9(69)
5	7	1(14)	1(14)	2(29)		2(29)			1(14)	1(14)	5(71)
6	12	4(33)		6(50)	1(8)	8(67)			5(42)	1(8)	9(75)
7	16	4(25)	2(12)	6(38)	2(12)	8(50)	2(12)	2(12)	5(31)	3(19)	2(12)
8	4			1(25)		1(25)	2(50)		1(25)	1(25)	1(25)
9–10	4				1(25)	3(75)		1(25)	3(75)	2(50)	
11–12	6			1(17)		4(67)	1(17)	1(17)	3(50)	2(33)	

[a] Correlation to age: $r = 0.7136$, $P > 0.05$.
[b] Correlation to age: $r = 0.8289$, $P < 0.05$.
[c] Correlation to age: $r = 0.8309$, $P < 0.05$.
[d] Correlation to age: $r = 0.9075$, $P < 0.05$.
[e] Displays as in Table 5.

TABLE 7. Comparison of behavior between breeders prior to pairing and non-breeders prior to copulation with the model. All males were 6–11 years old; includes data from Ainley (1974b: Table 21.4).

	No prior display	Ambivalence	Interaction				Hesitance	
N	N (%)	Bow	HdW[a]	Gk	EV	BAx	AlSt	LHV
				Non-breeders				
23	12(52)	3(13)	3(13)	3(13)	1(4)	2(9)	2(9)	4(17)
				Breeders				
17	15(88)	0	0	0	0	0	0	3(18)
P[b]	<0.05	<0.05	<0.05	<0.05	>0.05	>0.05	>0.05	>0.05

[a] Displays as in Table 5.
[b] Equality of percentages tested according to Sokal and Rohlf (1969:608).

hatched); and the remaining two laid and hatched two eggs. That record is very poor compared to females present for seven days or longer. For example, 98% of the 50 breeding females present for 7 or 8 days, who did not lose both eggs during incubation, hatched at least one egg. Also, more breeding females were present for just 7 or 8 days than in any other length-of-first-visit category. Evidently, the 7-to-8 days represents a minimum period that female Adélie Penguins must be present during courtship to insure production of viable eggs. Because date and length of visit are related to fat reserves (Ainley 1974a), these older females who arrive late and stay only briefly, like the younger ones discussed earlier, may not have adequate nutritional reserves for egg-laying.

Most non-breeding males at least five years old arrive in ample time to breed, and many arrive as early and remain as long as breeding males. Their reason for not breeding must be different from that just hypothesized for females, and hence, also different from many of the younger males discussed in Ainley (1974a). A few (ca. 6%) become non-breeders because they pair with females similar to the 12 previously discussed. For the remainder, failure to compete successfully for the limited number of females seems to be the proximate cause for non-breeding, which, in turn, is related to their behavior. Lone males who did not breed, in contrast to those who eventually bred, were less active socially and individually, made poorer nests, and, when confronted with a social situation of major significance (albeit artificial), displayed rather than acting directly and copulating. Active males were thus more successful in competing for females. Additional factors may define the "quality" of males (see the recent discussion of Black-legged Kittiwakes (*Rissa tridactyla*) by Wooler and Coulson 1977).

Factors underlying the different quality of males are not known. In addition to unknown physiological or hormonal factors, a personality factor, not necessarily age-related, also may be involved because many non-breeders tended to be thus for many years, breeding for the first time at a late age (Ainley, unpubl. data). Older non-breeders, unlike many of the younger ones, were more likely to behave appropriately in social situations. Another age-related factor may be experience, but this applies more to younger birds than to those older than about seven years. In the model experiments, including males who accepted or refused copulation, birds at least eight years old acted differently than younger ones. They displayed less, rarely avoided the model and responded directly. The development of such behavior might be aided by previous breeding experience, a characteristic shared by all males older than seven years (LeResche 1971,

TABLE 8. Comparison of behavior between breeders prior to pairing and non-breeders who refused copulation with the model. All males were 6–11 years old; includes data from Ainley (1974b: Table 21.5).

		Ambivalence			Interaction			Hesitance		
N	Avoid	Bow	SRe[a]	SlWgFp	HdW	Gk	EV	AlSt	BAx	LHV
					Non-breeders					
33	10(30)	8(24)	3(9)	12(36)	4(12)	19(57)	2(6)	12(36)	3(9)	5(15)
					Breeders					
11	1(9)			3(27)		2(18)	1(9)	3(27)		2(18)
P[b]	>0.05	<0.05	>0.05	>0.05	<0.05	<0.05	>0.05	>0.05	>0.05	>0.05

[a] Display symbols as in Table 5, and Ainley 1974b.
[b] Equality of percentages tested according to Sokal and Rohlf (1969:608).

Ainley 1974a). Owing to the lapse between my visits to Cape Crozier, I have no direct evidence for any of the birds' total prior breeding experience. My results indicate though that social maturation for some Adélie Penguins may take seven years, a longer period than I had previously suspected.

Among males who copulated with the model, younger ones often vacillated between responses, possibly the result of inexperience. On the other hand, among males who refused copulation, younger birds mostly avoided the situation or expressed ambivalence. Among older birds, fewer avoided the model, more gave an LHV upon return to the nest, and more pecked or displayed direct aggression (AlSt). These birds seemed to better understand the situation or what should occur. Their use of the LHV is interesting for it is a display given when the distance changes between the signaler and a meaningful situation (see Ainley 1974b). The fact that older (more experienced) males more often gave the LHV upon returning to find a penguin (model) in their nest may indicate recognition of the need for direct interaction with another penguin, surely a meaningful situation.

SUMMARY

The behavior of breeding and non-breeding Adélie Penguins five years old and older was compared to gain insight into the factors determining their breeding status. About 24% of males and 10% of females at least five years old were non-breeders at Cape Crozier; all should have been physiologically capable of breeding. Non-breeders on the average arrived later and remained at the rookery for less time than breeders. Some non-breeding males, however, remained as long and possessed as centrally located territories as many breeders. Older non-breeders visited the rookery twice each season for long periods compared to 35–45 shorter visits by breeders. Many non-breeders spent as many total days at the rookery as breeders.

The activity level of a male correlated with pairing. Non-breeding males were less active socially and individually than males that eventually bred. Non-breeders made poorer nests than eventual breeders. Non-breeding males, particularly younger ones, either tended to avoid a female model placed in their nests or they displayed more to it and otherwise acted less directly. Breeding males prior to pairing and older non-breeders acted directly toward the model, either copulating or attempting to expel it from the nest. Responses to the model also correlated in many respects with a male's age, especially among birds less than eight years old.

Non-breeding among mature female Adélie Penguins is most likely related to poor nutritional reserves at the time of arrival in spring. An unequal sex ratio creates strong competition among mature males for a smaller number of females. Success in competing for females is related to a male's general level of activity and the degree to which he acts directly in social interactions. Neither of these factors is necessarily related to behavioral maturity, which is important in the social behavior of younger birds, yet some birds are still maturing socially through their seventh year of life.

ACKNOWLEDGMENTS

I thank W. J. L. Sladen for the opportunity to work in the Antarctic during the 1968–69 and 1969–70 austral summers, and G. A. Llano for the chance to continue and finish the work in 1974–75 and 1975–76. In some subtle fashion, conception of this project on non-breeders grew from discussions with R. E. LeResche. I thank also R. C. Wood, S. H. Morrell, R. E. LeResche, R. J. Boekelheide, and R. P. Schlatter for help in the field. R. W. Schreiber offered clarifying suggestions on the manuscript. Logistic support was provided by the U.S. Antarctic Research Program (USARP) and the U.S. Navy Operation Deepfreeze. The penguins were banded by the USARP Bird-banding Program, largely the effort of W. Sladen and R. Wood. Without these banded birds my studies would never have been possible. This project was supported financially by grants from the Division of Polar Programs, National Science Foundation, to W. Sladen and to the author. This is contribution 130 of the Point Reyes Bird Observatory.

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Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970. Accepted for publication 20 July 1977.