AGE, RESOURCE AVAILABILITY, AND BREEDING EFFORT IN BRANDT'S CORMORANT

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ABSTRACT.—We gathered life-history data on banded Brandt's Cormorants (*Phalacrocorax penicillatus*) at Southeast Farallon Island, California, from 1972 to 1984, and documented breeding performance as affected by age and annual variation in food availability.

Females bred at a younger age than males, but did not live as long. Birds of both sexes that bred at least once bred the same number of years. Mate fidelity was low (9%) because of poor synchrony in the arrival of mates and low site fidelity by females. Prior breeding experience had little influence on reproductive success. The most successful individuals fledged 10-20 chicks over their lifetime, and averaged 2.5 chicks/breeding year over four to eight years.

Cormorants experienced significant interannual differences in food availability. "Poor" food years occurred frequently and, consequently, all adults skipped breeding at least one season during their reproductive lifetimes. Food availability also affected age at first breeding, as well as age-related breeding phenology, reproductive effort and success, and return rates of banded juveniles and adults. The reproductive traits of Brandt's Cormorant allow it to exploit an unpredictable environment; previously proposed life-history models relegate cormorants to stable environments. *Received 5 May 1986, accepted 24 January 1989.*

MANY vertebrates can adjust reproductive effort to the amount of energy available each year (Giesel 1976). Schaffer (1974) hypothesized that life-history characteristics in variable environments depend on when significant mortality occurs during the life cycle. If variable conditions lead to variable success, then breeding effort should be adjusted to insure survival until the next favorable year. If conditions instead lead to variable adult survival, then breeding effort should be increased in order to reproduce immediately, before death occurs.

In seabirds, which are long-lived and thus should have ample opportunity to adjust breeding effort, many life-history traits are strongly influenced by age and this relationship has been the subject of much research. Age-influenced traits include the proportion of individuals that breed, nest-site characteristics, mate selection, phenology, clutch size, and various components of reproductive success (see review by Ryder 1980, and more recent studies: e.g. Pugesek 1983, Pugesek and Diem 1983, Ainley et al. 1983, Shaw 1986). Yet, interannual variations in breeding behavior and success, as influenced by age, have received scant attention.

The California Current is one of the world's five major eastern boundary-current systems. These ocean systems are the most biologically productive in the world, and depend upon wind-driven transport of surface waters for nutrient input (through upwelling and advection). Considerable interannual fluctuation in oceanographic climate, biological productivity, and development of the food web is characteristic of these systems (Glantz and Thompson 1981, Chelton et al. 1982, McLain and Thomas 1983, McLain et al. 1985). The most dramatic of the periodic anomalies in production are known as El Niño-Southern Oscillations (ENSO). During ENSO, biological productivity decreases radically and the food web collapses (Glantz and Thompson 1981, McLain et al. 1985, Ainley and Boekelheide 1990).

The seabirds of eastern boundary currents are abundant and unique, with a high incidence of endemism in respective avifaunas (Brown 1976, 1980). Brandt's Cormorant (*Phalacrocorax penicillatus*) is unique to the California Current, but is less abundant than its ecological counterparts, the Guanay Cormorant (*P. bougainvillii*) of the Peru Current and the Cape Cormorant (*P. capensis*) of the Benguela Current (Ainley and Boekelheide 1990). The latter two species are important commercially because of the guano they produce and they have been the subject of appreciable study. Little work has been directed toward Brandt's Cormorant. We collected information on the reproductive success of known-age Brandt's Cormorants from 1972 to 1984, and analyzed patterns in relation to food availability to determine the validity of Schaffer's hypothesis with regard to this species.

STUDY AREA AND METHODS

We studied Brandt's Cormorants on Southeast Farallon Island (SEFI), 48 km west-southwest of San Francisco, California, at 37°42'N, 123°00'W, the largest of the South Farallon Islands. Between 1971 and 1983, cormorant numbers averaged 16,000 and ranged between 4,300 and 23,800 individuals (Ainley and Boekelheide 1990).

We observed known-age individuals from a blind overlooking a colony of about 500 pairs on the northwest shore of SEFI (for details, see Ainley and Boekelheide 1990). Between 1970 and 1983, workers from Point Reyes Bird Observatory (PRBO) banded 5,866 cormorant chicks in the study colony. From 1971 on, each chick was given two bands: a USFWS individually numbered metal band on one leg and a colored, wrap-around plastic band on the opposite leg. Leg position, band number, and band color designated year class. We banded chicks at night to minimize gull predation on nestlings and eggs. In 1970–1978 (except 1971) we used aluminum bands; those used in 1971 were monel and all were soon lost. After 1978 we used stainless-steel (incoloy) bands, and through 1985 none had fallen off. We corrected for loss of aluminum bands from estimates made on the double-banding system.

We monitored banded birds daily from April to August in 1972–1985. We read band numbers with a 20–60× spotting scope, mapped the location and movement of each bird, recorded the condition or absence of metal and color bands, described plumage, and noted sexually distinct behaviors. We noted the date when each bird began to occupy a site continuously, date of pairing, egg-laying and chick-hatching dates, and nest condition. From 1979 to 1983, we also recorded date of first arrival in spring.

We calculated age at first breeding, effects of breeding experience, and lifetime breeding records only for individuals with complete annual records. Variation about means are given as ±1 standard deviation. Breeding chronology, clutch size, and reproductive success were analyzed for similarity of variance (ANOVA) and between-age differences were tested using the Student-Newman-Keuls multiple comparison (SNK) (Sokal and Rohlf 1969).

We sexed cormorants according to criteria discussed by Williams (1942). We excluded from analyses birds that we were unable to sex, visited only a few times, or nested out of sight within the colony.

We determined return rates of banded birds after correcting for band loss. Because of an unknown rate of emigration, return rates were considered minimal. The majority of banded birds observed elsewhere on SEFI nested within 300 m of the natal colony, but a few nested as much as 1 km away. On the basis of site fidelity information, we assumed that once a bird nested within a colony it was unlikely to emigrate. In support of this assumption, Potts (1969) found that only 8% of Shags (*P. aristotelis*) breeding for the first time nested outside their natal colony, and that <1% moved after having bred once. Consequently, return rates of established breeders more accurately reflect true survival rates.

We used four principal criteria to rate years on the basis of food availability: (1) tendency of cormorants to feed within 5 km of SEFI (vs. as much as 80 km away), (2) proportion of juvenile rockfish (*Sebastes* spp.) in the diet of Farallon piscivorous birds (including Brandt's Cormorants), (3) breeding population size of Brandt's Cormorants relative to the 13-yr mean, 1970–1983, and (4) the occurrence of significant nest abandonment during the breeding period (see Ainley and Boekelheide 1990 for more details). Subsequent direct assessment of prey abundance and distribution in 1985–1988 indicates that these criteria were accurate (unpubl. data, PRBO and National Marine Fisheries Service, Tiburon Laboratory). Years of "good" food availability were 1977, 1979, and 1981; 1980 and 1982 were "moderate" years; and 1976, 1978, and 1983 (all years of oceanographic anomaly; McLain et al. 1985) were "poor" years.

RESULTS

Age of first sighting and first breeding.—On average, female and male Brandt's Cormorants first returned to the breeding colony at the same age (female 2.7 ± 1.3 yr, $n = 96$; male 2.9 ± 1.2 yr, $n = 212$; $t = 0.91$, df = 306, $P > 0.2$; Fig. 1). The modal age of first sighting for both sexes was 2 yr, but <5% of birds of either sex returned as 1-yr-olds. Among all birds eventually sighted, about 90% returned by their fourth year.

Despite similar ages of return, males and females differed in the average age of first breeding (Fig. 1). Females first bred at 3.5 ± 1.5 yr ($n = 40$), and males at 4.2 ± 1.3 yr ($n = 70$; $t = 2.61$, df = 108, $P < 0.02$). The modal age of first breeding for females was 2 yr, but only 2 out of 131 two-yr-old males bred. The modal peak for males occurred at 4 yr.

The average age of birds sighted or breeding for the first time varied annually; many young birds appeared and attempted to breed in years of good food availability but few or none did so in poor years. For example, in the 1983 ENSO year, no 2-yr-olds (out of 600 chicks banded in 1981) were observed. This contrasts with 1979, an exceptionally good year, when we observed

60 of the 592 birds banded as chicks in 1977. In 1979, 64% ($n = 11$) of 1977-cohort females that eventually bred did so as 2-yr-olds.

Breeding phenology.—Spring arrival dates varied strongly with age among males (Table 1). The oldest appeared first, and usually by mid- to late March. Peak arrival for previous breeders fell between mid-April and early May. Few males visiting or breeding for the first time arrived before May, and many, particularly 2-yr-olds, arrived during June and July. Therefore, youngest males arrived 2–8 weeks later than older birds. The pattern was altered in years of poor food availability. No males occupied sites until late April, and all arrived during a brief period extending through mid-May.

Arrival dates of females were not clearly stratified by age except that youngest females arrived last (Table 1). Most females old enough to have bred previously (>3 yr) arrived slightly later than similarly aged males. The oldest females did not arrive any earlier than others that had bred before. Youngest females (i.e. 2- and 3-yr-olds nearly all of whom were visiting for the first time) did not arrive until late May and June, a pattern similar to that of young males.

Laying dates followed the pattern of arrival, and younger birds laid later (Table 2). Males comprised two groups, older individuals who had bred at least once and younger birds who were breeding for their first or occasionally the second time. Youngest females began to lay significantly later than older ones; the oldest females laid earlier than all other age groups. Clutch initiation dates among youngest birds of both sexes exhibited a large coefficient of variation, which indicated little laying synchrony.

The elapsed time between arrival and laying measured how quickly a bird could pair, complete nest building, and begin a clutch. Among females during the period 1979–1982, age groups did not differ (Table 1), and the arrival-laying interval averaged 13.6 ± 5.8 days ($n = 48$, range 5–30 days). According to Grau (1984), Brandt's Cormorants require 16 days for yolk development, plus additional time for albumen synthesis and shell deposition. Apparently, most females began to form yolks before they first arrived at the colony.

Among males, the time between arrival and the date their mate laid the first egg was longer among the oldest individuals. This disparity is likely due to the early arrival of oldest males, which occupied sites in March, weeks before females appeared. Early males did not occupy their sites continuously, and spent less time during initial visits than did later-arriving males.

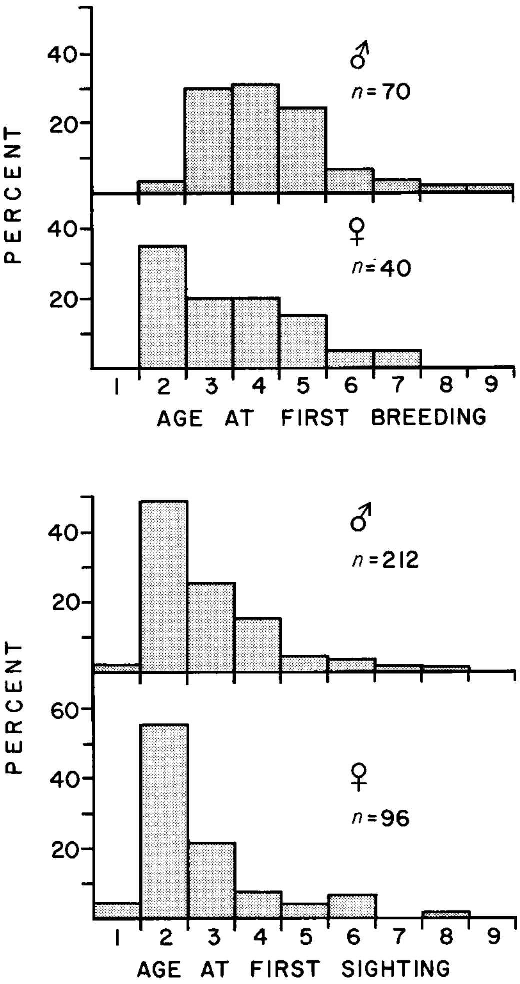

Fig. 1. Age of first sighting and first breeding of Brandt's Cormorants banded 1972–1977.

Nest and mate choice.—The percentage of pairs with older males (56%) outnumbered pairs with older females (21%) and those with mates of the same age (24%; $n = 34$ known-age pairs). In 65% of pairs, mates were within one year of age.

Among the 34 known-age pairs, only 3 remained intact in following years, and none persisted longer than two years. The 3 pairs that remated used the same nest site during both years. In 24% of the dissolved pairs ($n = 8$), both mates returned, but in 56%, one failed to return.

TABLE 1. Mean arrival dates (SD in days) and number of days elapsed between arrival and clutch initiation for known-age Brandt's Cormorants, 1979-1982.

Age (yr)	Arrival date	n	SNK[a]	Days elapsed	n	SNK[a]
			Males			
2	19 Jun ± 23.2	22	A		0	
3-4	31 May ± 22.6	66	B	24.7 ± 9.4	9	A
5-6	11 May ± 14.3	55	C	23.7 ± 11.1	28	A
7-8	3 May ± 18.8	72	D	27.5 ± 10.1	34	A
9-12	21 Apr ± 28.0	39	E	37.8 ± 17.3	24	B
			Females			
2-3	7 Jun ± 15.6	18	F	11.2 ± 6.9	5	C
4-5	18 May ± 18.2	18	G	12.6 ± 4.3	10	C
6-7	9 May ± 13.4	21	G	14.5 ± 5.7	19	C
8-10	9 May ± 16.6	17	G	14.2 ± 6.8	14	C

[a] Student-Newman-Keuls multiple comparison; values with the same letter do not differ significantly, $P > 0.05$.

Males, more than females, used the same nest site year after year (Table 3). From 1980 to 1982, 70% of returning males ($n = 110$) and 32% of returning females ($n = 28$) reoccupied their previous site. The percentage of males that reoccupied the same site increased with age. Among 9- to 12-yr-old birds, reoccupation was two times more likely than for 3- and 4-yr-olds. We found no pattern among females, but this may have been a consequence of a small sample. If we include in the sample females that returned to a nest that was different but within the same subcolony (usually within 10 m of the previous year's nest), then they indeed exhibited no pattern.

The majority of Brandt's Cormorants did not remate in successive seasons. Even if both birds survived the winter, only a synchronous arrival in spring would favor remating, since pair bonding took place quickly among birds returning to the colony. When a male returned, his previous site had to be vacant or he had to successfully evict the new occupant. Fights between males were common, even when many suitable sites existed nearby. It appeared that such fights ensued when a previous site holder encountered a stranger at his spot. Fights ranged from minor threats to battles that continued for several hours or sporadically over several days. Females occasionally fought for sites if they were displaced from where they had bred the year before, but their fights were rarely as intense as those between males.

Breeding effort and success.—Nesting space was not limited during this study (though it likely was historically; Ainley and Boekelheide 1990), so any bird that so desired could have occupied

TABLE 2. Mean clutch initiation dates for known-age Brandt's Cormorants, 1972-1984.

Age (yr)	Dates ($\bar{x}$ ± SD)	n	SNK[a]
	Males		
3-4	2 Jun ± 23.3	60	A
5-6	29 May ± 15.1	72	A
7-8	22 May ± 11.9	60	B
9-12	18 May ± 12.0	43	B
	Females		
3-4	5 Jun ± 17.7	27	C
5-6	27 May ± 15.5	27	D
7-8	23 May ± 14.1	35	D
9-12	12 May ± 12.3	16	E

[a] Student-Newman-Keuls multiple comparison; values with the same letter do not differ significantly, $P > 0.05$.

TABLE 3. Fidelity (percentage of returnees) of known-age Brandt's Cormorants to nest sites, 1980-1982.

			Different site	
Age (yr)	n	Same site[a]	Same subcolony	Different subcolony
		Males[b]		
3-4	9	44	33	22
5-6	29	59	31	10
7-8	41	71	22	7
9-12	31	87	10	3
		Females[c]		
3-6	9	56	33	11
7-10	19	21	68	11

[a] Return rates of males significantly greater than females ($\chi^2 = 13.62$, df = 1, $P < 0.001$).

[b] Return rates significantly different by age ($\chi^2 = 8.91$, df = 3, $P < 0.05$).

[c] Return rates no different by age group ($\chi^2 = 3.33$, df = 1, $P > 0.05$).

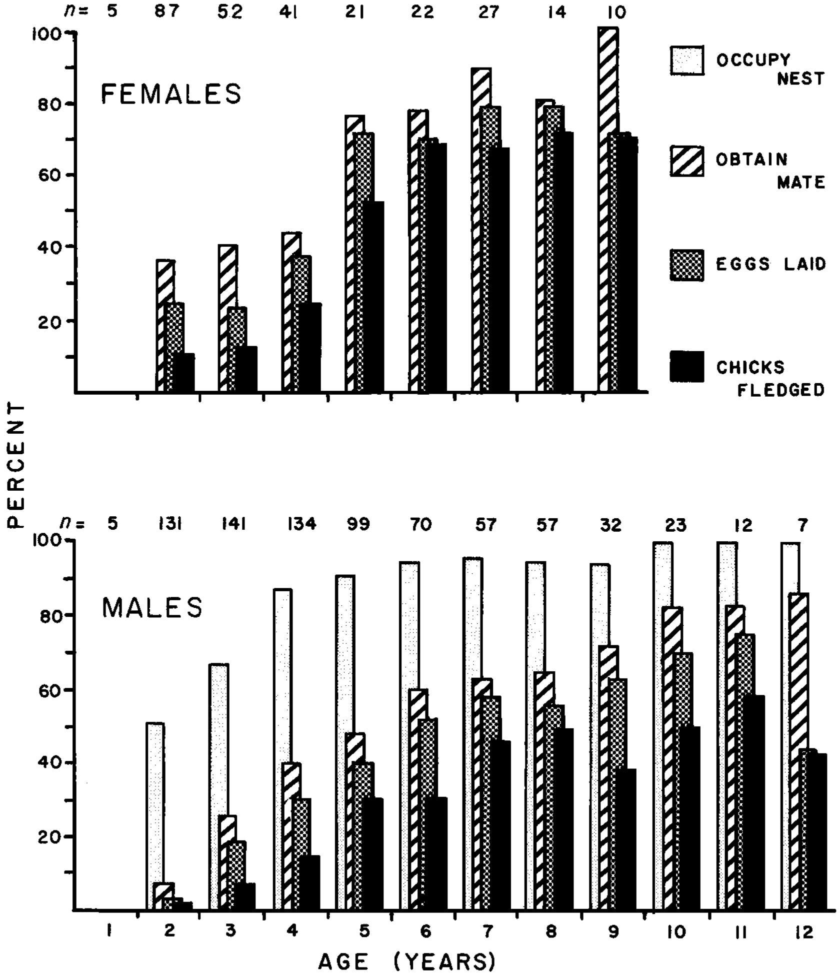

Fig. 2. Percentages of known-age male and female Brandt's Cormorants who occupied nest sites, paired (constructed a substantial nest), produced eggs, and fledged at least one chick; n = sample size within each age class.

a site, regardless of age. Nest-site occupation increased with age, and reached a plateau of 90–100% among males at least 5 yr old (Fig. 2). Only 51% of 2-yr-old males occupied sites; the remainder merely wandered through the colony or roosted nearby. A sharp increase in site occupation was evident between ages 2 and 4 yr, and nearly all surviving males that had bred before occupied sites in subsequent years.

The percentage of males who obtained a mate, or who remained until nest construction had progressed appreciably, increased steadily through all ages up to 10 yr (Fig. 2). The youngest males were unlikely to pair, even if they occupied a site. In fact, the failure of 2-yr-olds to breed was largely due to their inability to obtain a mate. Among older males that had bred at least once, 14–36% (depending on age class) did not obtain mates. In food-poor years few males obtained mates, regardless of age. In better years, some males did not pair, including individuals that occupied sites for 2–3 months and advertised daily for passing females.

The percentage of males whose mates laid eggs, and who eventually fledged chicks, also increased with age, especially among the youngest age classes (Fig. 2). Youngest males were unlikely to fledge chicks. Among older

TABLE 4. Comparison of clutch size and breeding success at nests of known-age Brandt's Cormorants.

	Males by age				Females by age			
	3-4	5-6	7-8	9-12	2-3	4-5	6-7	8-10
Nests with eggs	56	62	60	39	28	22	32	17
Clutch size[a] ($\bar{x} \pm$ SD)	2.9 ± 0.6	2.9 ± 0.7	3.0 ± 0.7	3.3 ± 0.5	2.5 ± 0.6	2.9 ± 0.7	3.4 ± 0.6	3.3 ± 0.7
n	49	55	52	36	24	20	28	15
Significance[b]	A	A	A	B	C	D	D	D
% eggs								
Lost prematurely	46	21	21	25	40	34	21	17
Lost at hatch	10	9	4	6	9	4	9	8
Addled	5	10	10	7	10	10	8	10
Hatched	39	60	65	62	41	52	62	65
% chicks								
Dead <11 days	17	11	10	12	21	14	7	3
Dead 11-20 days	9	11	8	11	3	14	11	8
Dead >20 days	5	5	2	4	0	3	3	8
Fledged[c]	69	73	80	73	76	69	79	81
% total success[d]	27	43	52	45	31	36	50	53
Fledglings/nest[e] ($\bar{x} \pm$ SD)	0.7 ± 0.9	1.2 ± 1.0	1.6 ± 1.2	1.5 ± 1.3	0.8 ± 1.0	1.0 ± 1.0	1.8 ± 0.9	1.9 ± 1.0
n	56	62	60	39	28	22	32	17
Significance[b]	A	B	B	B	C	C	D	D

[a] Does not include incomplete clutches or replacement clutches.

[b] Student-Newman-Keuls multiple comparison, within each sex only, for mean clutch size and mean number of fledglings per nest; values with the same letter do not differ significantly, $P > 0.05$.

[c] On the basis of eggs hatched.

[d] On the basis of eggs laid.

[e] Includes nests with replacement clutches.

males, less than 50% fledged chicks. Curiously, the percentage of males that succeeded dropped for both 9- and 12-yr-olds, in part because of the large proportion that reached these ages during the strong 1982–1983 ENSO.

Among females, the youngest birds (ages 2–4) differed distinctly from older birds in the proportion that paired, laid eggs, and fledged chicks (Fig. 2). Youngest birds were usually either visiting the island or breeding for the first time. Less than 40% paired and approximately 25% laid eggs. By 5 yr of age, breeding effort became consistent across age classes, but even among the oldest females >20% did not lay eggs and ca. 30% did not fledge chicks because of the general reproductive failure of all birds in food-poor years.

All females (ages grouped) were more successful than males in pairing, obtaining eggs, and fledging chicks (Fig. 2). This was particularly evident between ages 5–9 yr, when females were much more likely to fledge chicks. This pattern may relate to the tendency of males to pair with females younger than themselves, as noted previously. Perhaps more importantly, our sample of males includes a greater proportion of individuals present during food-poor years when few females returned. As a result most of the males present then remained unpaired.

Clutch size.—Clutches laid by 2- and 3-yr-old females were smaller than those laid by females older than 5 yr (Table 4). No 2- or 3-yr-old females laid four-egg clutches, whereas 10% of those laid by 4- and 5-yr-olds, 36% of those laid by 6- and 7-yr-olds, and 43% of those laid by 8- to 10-yr-olds were four-egg clutches. We observed only one five-egg clutch and it was laid by a 6-yr-old.

Among known-age males, clutch sizes of the oldest birds (9–12 yrs) were significantly larger than clutches of younger birds (Table 4). Mates of the oldest males produced clutches equal in size to those laid by older females, confirming that older males are likely to pair with older females.

Breeding success (all years combined).—Hatching success differed by age for both males and females (male $\chi^2 = 25.86$, df = 3, $P < 0.01$; female $\chi^2 = 10.53$, df = 3, $P < 0.02$; Table 4). Younger birds had poor hatching success because they lost eggs, either through nest abandonment or incidental loss during incubation. The number of eggs that disappeared at expected hatch dates, or that never hatched despite full-term incubation, did not differ among age or sex classes.

TABLE 5. Incidence of relaying and success of replacement clutches by known-age Brandt's Cormorants, 1972–1984. Sample sizes in parentheses.

Age	% lost 1st clutch[a]	% relaid after loss	Mean no. chicks fledged/nest
		Male	
3–4	52	14	0.0 ± 0.0 (2)
5–6	26	38	1.2 ± 1.6 (5)
7–12	19	42	1.0 ± 0.9 (8)
		Female	
2–3	36	30	0.5 ± 0.7 (2)
4–5	27	33	1.0 ± 1.4 (2)
6–9	20	80	2.3 ± 0.9 (8)

[a] On the basis of data from Table 4 (no. nests with eggs).

In contrast to hatching success, the proportion of chicks successfully fledged did not differ relative to parental age (male $\chi^2 = 2.56$, df = 3, $P > 0.25$; female $\chi^2 = 2.00$, df = 3, $P > 0.25$; Table 4). Youngest breeders lost a higher percentage of chicks 0–10 days old, suggesting difficulty with the transition from incubation to chick care. Chicks 0–10 days old of older parents fared no worse than chicks 11–20 days old. Chicks older than 20 days experienced little mortality regardless of their parents' age.

Overall breeding success also differed among age classes (male $\chi^2 = 21.21$, df = 3, $P < 0.01$; female $\chi^2 = 10.00$, df = 3, $P < 0.05$). The number of chicks fledged per nest was significantly lower for youngest breeders, but thereafter performance did not improve with age (Table 4).

Older birds were much more likely to relay if their first clutch was lost, and were similarly more successful at fledging chicks from replacement clutches (Table 5). Older breeders laid first clutches early in the laying period and had more time to relay if their first clutch was lost. Only one known-age female, a 9-yr-old, laid two replacement clutches in one season. This occurred in the good-food year of 1979.

Breeding success (interannual variability).—Comparisons among years of differing food availability reveal that age classes did not fare equally (Table 6). Youngest birds bred only in the most favorable years. The proportion of young females that laid eggs declined from >33% of those present in good years to <10% in moderate to poor years. The proportion

TABLE 6. Breeding effort and success of Brandt's Cormorants in years of different food availability.

	Males			Females		
Age:	3–4	5–6	7–12	2–3	4–5	6–10
			Good years (1977, 1979, 1981)			
No. birds observed	95	66	67	34	30	37
% attempting breeding[a]	31	47	66	35	57	81
Mean clutch size	3.0 ± 0.7	2.8 ± 0.7	2.9 ± 0.6	2.6 ± 0.5	2.9 ± 0.3	3.3 ± 0.7
n	22	26	36	9	11	24
% fledging chicks[b]	17	35	49	15	47	73
Mean fledglings/pair[c]	1.1 ± 1.1	1.3 ± 1.0	1.6 ± 1.2	1.0 ± 1.3	1.4 ± 1.0	1.9 ± 0.9
n	29	31	44	12	17	30
			Moderate years (1980, 1982)			
No. birds observed	40	43	66	15	6	26
% attempting breeding[a]	13	65	67	7	83	81
Mean clutch size	2.0 ± 0.0	3.1 ± 0.5	3.2 ± 0.6	2.5 ± 0.7	3.3 ± 0.5	3.4 ± 0.5
n	2	22	37	2	4	16
% fledging chicks[b]	0	47	55	7	50	77
Mean fledglings/pair[c]	0.0	1.2 ± 1.0	1.4 ± 1.0	1.0	1.0 ± 1.2	1.7 ± 0.9
n	5	28	44	1	5	21
			Poor years (1976, 1978, 1983)			
No. birds observed	95	32	26	35	17	12
% attempting breeding[a]	16	28	12	9	12	25
Mean clutch size	2.7 ± 0.7	2.6 ± 1.0	3.0 ± 0.0	2.3 ± 0.5	1.0	3.0 ± 1.4
n	11	7	2	4	1	2
% fledging chicks[b]	4	16	0	3	0	17
Mean fledglings/pair[c]	0.3 ± 0.6	0.6 ± 0.5	0.0	0.7 ± 1.2	0.0	0.7 ± 0.6
n	15	9	3	3	2	3

[a] No. with eggs/no. occupying sites × 100.

[b] No. fledging chicks/no. occupying sites × 100.

[c] Includes only those that had eggs.

among young males with eggs dropped by 50%. In contrast, the percentage of older birds that laid eggs did not decline between good and moderate years. The percentage of middle-aged birds that laid eggs even rose in moderate years. The trends in clutch sizes were consistent with those discussed above (see *Clutch size*), but sample sizes were too small to test statistically in any but the good-food years. Then, only the youngest females laid clutches smaller than those of the oldest females (SNK test, $P < 0.05$). The data for moderate and poor years indicate the possibility that between-age-class differences may increase as resources diminish, but more data are required to test this hypothesis. Older birds fledged equivalent numbers of young in both good and moderate years, whereas youngest birds fledged young in good years only. In poor years, few birds of any age attempted to breed and they failed.

Effect of breeding experience on success.—We considered those birds that had attempted breeding (i.e. produced eggs) in a previous year to be "experienced." Though our samples were small, we found no definitive increase in clutch size or breeding success with increased experience (Table 7).

Individual performance.—The average bird bred 2–3 seasons and fledged 2–4 chicks during its lifetime (Table 8). This was due not only to mortality, but also to the frequency with which birds skipped breeding. Unfavorable years occurred often enough that 75% ($n = 20$) of cormorants that bred four or more years skipped breeding at least once following their first breeding year. Nearly all birds failed to breed during 1978 and 1983, and all known-age birds that laid eggs during those years later abandoned their efforts.

Some birds greatly outperformed the average values. The stellar male reared 20 chicks to independence, an average of 2.5 chicks/yr for the 8 yr in which he bred. Several other males bred 4–7 yr and reared 9–12 chicks. The two females with the best record bred in 4 and 5 yr, fledged 10 and 12 chicks, and averaged 2.5 and 2.4

TABLE 7. Clutch sizes and breeding success of known-age Brandt's Cormorants with different levels of experience.

Sex	Age	Year as breeder	Clutch size Mean	Clutch size *n*	Percentage eggs hatched	Percentage chicks fledged	Fledglings/nest Mean	Fledglings/nest *n*
Male	2	First	2.0 ± 0.0	2	25	100	0.5 ± 0.7	2
	3	First	2.7 ± 0.6	20	42	67	0.7 ± 0.9	24
	4	First	3.0 ± 0.6	23	37	77	0.8 ± 1.1	25
		Second	2.9 ± 0.6	8	61	50	0.9 ± 0.8	8
	5	First	2.8 ± 0.7	21	61	78	1.3 ± 1.0	21
		Second	3.1 ± 0.6	10	46	74	1.2 ± 1.1	12
		Third	3.0 ± 0.0	2	83	60	1.5 ± 0.7	2
Female	2	First	2.7 ± 0.5	15	45	174	0.8 ± 0.7	17
	3	First	2.0 ± 0.6	6	30	83	0.6 ± 1.1	8
		Second	3.0 ± 0.0	2	67	75	1.5 ± 0.7	2
	4	First	2.6 ± 0.5	7	67	63	1.1 ± 0.9	9
		Second/third	2.5 ± 1.3	4	40	100	1.0 ± 1.2	4
	5	First	3.0 ± 0.7	5	55	80	1.6 ± 1.1	5
		Second/third	3.0 ± 0.0	4	55	67	1.0 ± 0.8	4

chicks/yr, respectively. One female laid 26 eggs during 7 yr, including two replacement clutches, but she fledged only 8 chicks. Birds of both sexes averaged the same number of breeding years despite the earlier recruitment of females (Table 8). This phenomenon appeared to be related to a longer reproductive life span, more years skipped by males, or both (see Discussion).

Return rates of banded birds.—We subsequently observed 17% of the 2,876 chicks banded from 1972 to 1977 as adults (i.e. birds ≥2 yr of age). The 1976 cohort returned at a much lower rate than the five other cohorts (Fig. 3). A weak ENSO occurred in 1976, and an aberrant warm-water year occurred in 1978 (McLain et al. 1985). Food availability was poor during both years (Ainley and Boekelheide 1990), and this must have affected postfledging and prebreeder survival. A stronger ENSO occurred in 1972–1973, but it ended by the fall of 1973 and was followed by 2 yr of good food availability.

All age and sex groups exhibited lowest return rates during 1982–1984, with the sole exception of 1975 males (Fig. 3). These low rates coincided with the 1982–1983 ENSO, a period when nearly all Farallon species failed at breeding and dispersed widely from the Gulf of the Farallones (Ainley and Boekelheide 1990). Mortality during this period was exceptionally severe for older females, as all 1972- to 1975-year-class females failed to return after 1983. A few males from those cohorts, however, were still alive in 1988.

In contrast, only slight decreases in return rates occurred following the 1976 ENSO for birds of the 1972 and 1973 cohorts (Fig. 3). Return rates of adults in 1979, following the 1978 warm-water event, were among the highest observed, even though nearly all Brandt's Cormorants abandoned their breeding efforts mid-season in 1978 (Ainley and Boekelheide 1990). As noted in the latter report, the Farallon population rebounded immediately in both 1977 and 1979 when prey populations returned in abundance. These data reveal that catastrophic adult mortality did not occur during these years, in contrast to 1982–1983.

TABLE 8. Number of years in which known-age Brandt's Cormorants bred.

Years bred	Males (*n* = 73) No.	Males (*n* = 73) %	Females (*n* = 38) No.	Females (*n* = 38) %
1	32	44	17	45
2	12	16	9	24
3	16	22	5	13
4	4	5	3	8
5	4	5	3	8
6	3	4		
7	1	1	1	3
8	1	1		
Median	2		2	
Mean	2.4 ± 1.7		2.2 ± 1.4	

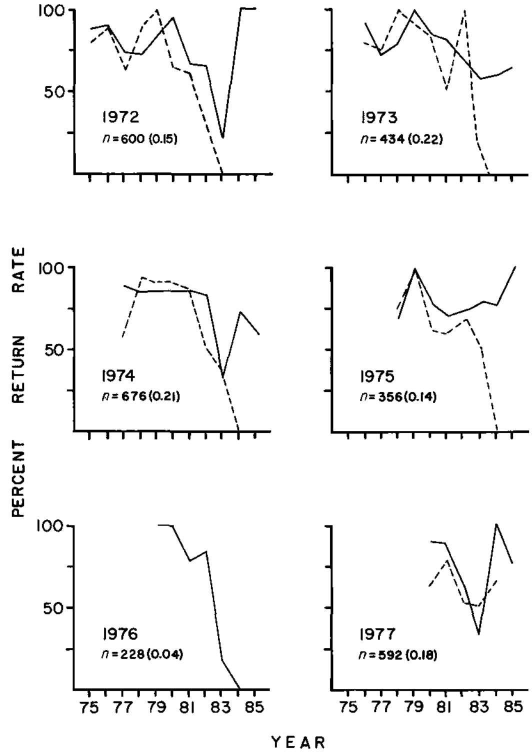

Fig. 3. Annual return rates of Brandt's Cormorants ≥ 2 yr old for 1972-1977 cohorts in 1975-1985; solid lines = males, dashed lines = females (no banded 1976 females seen).

All years combined, females returned at a slightly lower rate than males between the second and third years (2% and 5% decreases in rates, respectively). Among 3-yr-old females, low return rates occurred in the 1974 and 1977 cohorts where only 56% and 64% of 2-yr-olds entered their third year (Fig. 3). The 1974 birds were possibly handicapped by poor conditions in 1976, similar to those that affected 1976 fledglings. Females of the 1977 cohort, however, experienced exceptionally good feeding conditions in 1979; that cohort exhibited the highest proportion of females first breeding as 2-yr-olds (64%, $n = 11$). Lower return rates in 1980 suggest that these females incurred a substantial cost by breeding as 2-yr-olds, but data for all 2-yr-old females suggest otherwise. Return rates of females that bred as 2-yr-olds were no different than those that visited but did not breed ($\chi^2 = 0.379$, df = 1, $P > 0.5$). A possibility still remains that more females who first visited as 3- or 4-yr-olds survived than did those first visiting as 2-yr-olds, but we cannot sample birds that do not visit the island to prove this.

Among 2- to 7-yr-olds, males averaged slightly higher return rates than females, but the difference was not significant (male 0.82 ± 0.06, female 0.79 ± 0.06; Mann-Whitney *U* test, $P > 0.05$). After 7 yr of age, females exhibited a substantial drop in return rates; only a few banded females in the cohorts under investigation lived beyond 10 yr. Males also exhibited a decrease in return rates at 9 yr of age. In large part, the precipitous decline in return rates among older birds is due to the effects of the 1982-1983 ENSO, as reported above. Whether significant numbers of Brandt's Cormorants survive beyond these ages must remain for future study.

DISCUSSION

Brandt's Cormorants are endemic to the California Current. Consequently, they display several life-history traits appropriate for maximizing lifetime reproductive success in the annually variable environment. For a seabird, they have a relatively young age at first breeding, which enables young birds to respond to favorable conditions. Second, there is a large interannual variation in the age of first breeding, which results from young birds breeding in favorable years but delaying breeding in poor years. They demonstrate low mate fidelity, which permits immediate remating if former mates are not available. Females show low site fidelity, which similarly permits an immediate switch to a new male if the former mate does not return on time or at all. The inconsequential role of breeding experience relative to environmental experience means that adequate social and breeding skills are attained at an early age. Finally, they abandon or skip breeding in poor years, which insures survival to a later year. Their plasticity in reproductive effort is further illustrated by the smaller clutches laid in years when breeding was delayed—the mean clutch sizes varied by more than one egg between years—and by the marked asynchrony in egg laying in better years. That is, the population egg-laying period could extend over more than 3 months (Ainley and Boekelheide 1990). In more southerly populations, this species may lay eggs from mid-winter to early summer (Michael 1935, Williams 1942). In general, the above traits are typical of most seabirds, and in total they combine elements from both of Schaffer's (1974) reproductive models, but unlike most seabirds, Brandt's Cormorants are capable of balancing investment in reproduction and survival depending on annual conditions.

No information is available on the breeding effort of known-age Guanay or Cape cormorants, the Brandt's Cormorant analogs in the Peru and Benguela systems, respectively. Like the California Current, both systems display strong interannual variation in oceanographic climate and prey abundance (Shannon et al. 1984, McLain et al. 1985). Breeding populations of both the Guanay and Cape cormorants change dramatically from year to year depending on food supply (Murphy 1925; Rand 1960, 1963; Jordán 1967; Glantz and Thompson 1981; Duffy 1983; Duffy et al. 1984). For example, Guanays in Peru dropped from 28 million in 1955 to 6 million during the 1957–1958 ENSO. By 1959 numbers had returned to 11 million and by 1963, 18 million (Jordán 1967). At the Galápagos Islands, which are strongly affected by the Peru Current, the Flightless Cormorant (*Nannopterum harrisi*), a close relative of the Brandt's (Siegel-Causey 1988), displays even greater extremes in breeding effort (Harris 1979, Tindle 1984). This species breeds year-round if conditions permit, and the age of first breeding averages 2.5 yr. Females may breed when as young as 17 months, but during the 1972 ENSO, no young birds bred. Also like Brandt's Cormorant, individuals are not faithful to either mates or nest sites, and breeding effort and success fluctuate greatly between years. During 1972, few adults attempted to breed but there was no subsequent decrease in adult survival (Harris 1979).

Cormorants breeding in more stable environments exhibit less variability in effort than Brandt's or Flightless cormorants. Kortlandt (1942) found that 2-yr-old Great Cormorants (*P. carbo*), in Holland, may pair and build nests but rarely lay eggs. Most individuals bred at 3 yr, but others at 4 or 5 yr of age. (He did not separate sexes.) Coulson et al. (1969) found that most female Shags start to breed at 3 yr, a few breed at 2 yr, and some delay until 4 or 5 yr. No Shags in Snow's (1960) small sample bred as 2-yr-olds. Snow (1963) also found that 93% of marked males and 41% of marked females reused the same nest in successive years. Both Snow (1960) and Potts (1969) recorded little annual variation in either the number of chicks fledged or in breeding population size during 11 sample years. On the basis of mathematical simulation, Aebischer (1986) proposed that a marked 3-yr decline in Shag numbers at another site was due to extensive nonbreeding by adults and low recruitment of young breeders when feeding conditions were poor. Our results show that this is indeed feasible for cormorants. Finally, in the Blue-eyed Shag (*P. atriceps*) of the Antarctic, where the vagaries of pack-ice concentration determine access to food, mate retention has been found to be very low (Shaw 1985, see also Cuthbert 1985), and little effect on breeding performance by a change in mate is evident (Shaw 1986). As in the Brandt's Cormorant, Shaw (1986) also found that breeding experience had little influence on success. Blue-eyed Shags first breed when 3 yr old.

Lack (1968) and Nelson (1983) theorized that the breeding strategy of members of the Phalacrocoracidae is related primarily to their inshore feeding habits. Compared with tropical pelagic pelecaniforms and other pelagic seabirds, the cormorants' restriction to coastal habitats, large brood size, and rapid chick growth require that they nest near abundant, reliable food. This may be true for many cormorant species, but although eastern boundary currents are high in productivity, food availability is not reliable. Yet cormorants are principal avian components of such systems. All inshore habitats, thus, are not alike. Those of eastern boundary systems are clearly not similar to those where most seabird studies have been conducted (i.e. shallow-water, high-latitude systems; see Ainley and Boekelheide 1990). Lack and Nelson based their model of the cormorant breeding strategy on the average minimum of food availability. It is apparent though that cormorants can cope with extreme variability in the abundance of food, and that they do so by being exceedingly plastic in their breeding traits. In this way they are far better able than other seabirds to exploit periods of food abundance, and like other seabirds can forgo breeding when conditions are poor (see also Boersma 1978, Ainley and Boekelheide 1990).

Cormorants are major components of the highly variable eastern boundary currents, and one could perhaps consider them to be boundary current specialists. An ENSO occurs on average every 5.4 yr, with a strong event every 12.3 yr (Quinn et al. 1978, Chelton et al. 1982, McLain et al. 1985). Years when food is superabundant, in the California Current at least, come at a frequency similar to that of ENSOs (Ainley and Boekelheide 1990). Each adult cormorant, therefore, will likely experience the extremes of food availability, including at least one, and likely more, food-poor and food-rich years during its lifetime. It is strongly possible that such extreme events have much more important effects on population size, age structure, and ecological adaptation in cormorants of eastern boundary systems than do the "average" years (Murphy 1981, Duffy 1983, Ainley and Boekelheide 1990).

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