POPULATION DYNAMICS OF THE GALÁPAGOS FLIGHTLESS CORMORANT *PHALACROCORAX HARRISI* IN RELATION TO SEA TEMPERATURE

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SUMMARY

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The Flightless Cormorant *Phalacrocorax harrisi* is restricted to c. 400 km of the western coastline of the Galápagos archipelago, coinciding with the local occurrence of seasonal upwelling oceanic currents. Here we report data from a 10-year historical study of a colony of c. 118 adult birds stretching c. 2 km along the coastline and representing about 12% of the total population of the species. The number of clutches laid and juveniles fledged were positively associated with the persistence of cold nutrient-rich surface water in offshore foraging grounds, suggesting that availability of food brought about by changes in marine productivity is both the proximate and ultimate factor controlling the timing and outcome of breeding. Individuals frequently made more than one breeding attempt per year, usually changing mates. Males invested more in nest-building and feeding of the offspring than their mates, and we relate this to male and female reproductive strategies. Most Flightless Cormorants were extremely sedentary, having attachments to local stretches of coastline several hundred metres long. However, a few birds travelled many kilometres, sometimes between colonies. Adult survival and condition was not associated with breeding effort or success. Adult survival, recruitment through births and minimal net immigration validate a published demographic model of the species (Valle 1995).

Key words: Flightless Cormorant, Galápagos, breeding strategy, dispersal, sea temperature, parental investment.

INTRODUCTION

The Flightless Cormorant *Phalacrocorax harrisi* is one of the world's rarest seabirds (~1000 pairs; Jiménez-Uzcátegui 2006), restricted to <400 km of the coasts of Fernandina and Isabela Islands in the Galápagos archipelago (from 1°40′N to 1°36′S, and from 89°16′W to 92°01′W). The species is distributed in 9–10 "populations" (Duffie *et al*. 2009) or "colonies" (Valle, 1995) separated by c. 7–45 km, where the birds nest in groups of about 2–15 nests close to the water's edge, with easy access to the sea (Fig. 1). Sporadic nests are found between colonies. This range coincides with cold nutrient-rich water forced to the surface by upwelling of the eastward-flowing Equatorial Undercurrent (or Cromwell current) meeting the western edge of the islands (Houvenag 1974). The resulting high prey density and predictability of a wide range of benthic prey can be exploited by Flightless Cormorants in shallow-water foraging areas within a few hundred metres of the colony (Wilson *et al*. 2008). Around Fernandina and Isabela islands, fishes are unusually diverse and abundant (Edgar *et al*. 2004). Earlier studies suggested that breeding effort and outcome are likely linked to the occurrence of cold water in foraging areas, although this has not been formally demonstrated (Snow 1966, Harris 1974, Wilson *et al*. 2008).

During El Niño–Southern Oscillation (ENSO) events, which in this area persist for 11–18 months (Vargas *et al*. 2006), the Equatorial Undercurrent weakens, leading to warmer, nutrient-poor surface waters, poor primary production and reduction in fish numbers (Chavez *et al*. 1999). These events have a profound effect on the Flightless Cormorant. In 1971–1972 the population was estimated at 800 pairs but numbers reached a low of about 400 birds in 1983 following an extreme ENSO event (Harris 1979, Valle & Coulter 1987). A further strong ENSO event occurred in 1997/98. In 2006, 1 396 birds were recorded (Jiménez-Uzcátegui *et al*. 2006).

Flightless Cormorants are resident at breeding colonies throughout the year and are rarely seen more than a few hundred metres offshore (Harris 1979). While some previous studies have suggested that individuals remain within c. 2 km of their natal colony to breed (Snow 1966, Harris 1979, Jiménez-Uzcátegui *et al*. 2006), the extent of sedentary behaviour has not been quantified. Dispersal of birds, creating gene flow within the species range, has been reported (Valle 1995).

Compared with other seabirds, the breeding strategy of the Flightless Cormorant has several unusual features. The birds frequently make more than one breeding attempt per year, usually change mates and nest sites, and females may desert juveniles to the further care of their mates who complete the rearing alone (Harris 1979, Tindle 1984). Harris (1979) recorded that while 76.1% of clutches contained three eggs, the mean clutch size was 1.7 young per clutch at hatching, and in 74.2% of cases only one juvenile fledged per clutch. Young that died were usually emaciated, presumably due to starvation.

Here we report on a decade-long study of the population dynamics of the species and relate the unusual features of breeding to a prolonged breeding season coinciding with temporal cold nutrient-rich waters in foraging areas, and to the sedentary behaviour of the birds, predisposing them to in-breeding. We equate our findings with conclusions reached from a demographic model of the Flightless Cormorant that used estimates of annual adult survival, age-specific fecundity and juvenile recruitment (Valle 1995).

STUDY AREA AND METHODS

Colony, population and breeding

The study colony of c. 118 birds consisted of seven groups of 3–15 nests ("locations") spread along c. 2 km of bare basaltic, gently sloping, coastline at Punta Espinosa, Fernandina Island (0°22′0 S, 91°31′20 W). The seven locations were separated by c. 100–600 m of coastline, punctuated by natural physical barriers (mangrove inlets, rough lava, beaches). This was 10%–14% of the world population at the time (Harris 1979). During the decade 1970–1980, the colony was visited every c. 2 weeks during 1970–1975 (by MPH and co-workers) and 1977–1979 (by RWT and LET); however, in 1976 it was visited only in July, and in 1980 it was visited only four

Fig. 1. Principal breeding colonies of the Flightless Cormorant in Galápagos (large dots). Other nesting places occur sporadically between some colonies (for details see Valle 1995); their approximate distribution is shown here for the eastern coast of Fernandina Island (small dots).

times (by RWT and S. Harcourt). Observations were confined to March–October. This was the main breeding season, and clutches laid at other times were usually unsuccessful. In some years there were two peaks of laying, and for convenience of analysis we split the season into two equal periods, March–June and July–October.

At each visit, nests were checked; the ring numbers, location and breeding status of all birds present were noted; and unringed individuals were ringed. Between 1971 and 1980, virtually all resident birds were marked with hard-metal rings with numbers large enough to be read without catching the bird. Birds were sexed by size (there being little overlap between the sexes) and by position during copulation. At most visits, the coastline up to 2 km on either side of the colony was also checked for Flightless Cormorants, and the ring-numbers of ringed birds were recorded. During 1970–1973 all known nesting areas within 5 km of the Punta Espinosa colony were visited irregularly to ring adults and young, and to check for emigrants from the colony.

Population data were analysed as below (see Data analysis). No survival data were available for 1979–1980 due to incomplete coverage in 1980, and only sub-adult survival data were available for the period 1970–1975. Breeding was considered to be successful if the chick survived two months when it took to the sea. No breeding success data were available for 1974–1976.

Sea surface temperature and breeding

Sea surface temperatures (SST) in the tidal foraging area immediately offshore from the colony were recorded at most visits, using a thermometer hand held at a depth of c. 15 cm. In about half the visits, single monthly measurements were made. In the remainder, >1 measurement was made per month, and measurements were averaged for purposes of analysis.

Movement and dispersal

Distribution within the colony

The extent to which individual adult birds moved among the seven nesting locations (see above) within the c. 2 km stretch of coastline constituting the colony was determined by recording the locations of re-sightings of ringed birds throughout the study. For purpose of analysis, "re-sightings" were defined as at least two months apart. Only birds that incubated two or more clutches were included, and the collated data were analysed as described below (see Data analysis).

Movement between colonies

Flightless Cormorants were also ringed elsewhere in the species range. During 1970–1971, 282 birds (c. 18% of the then-total population) were ringed with site-specific colour rings visible at several hundred metres at Cabo Hammond, Cabo Douglas, Punta Mangle, Punta Tortuga, Punta Albemarle, Cabo Berkeley and Bahia Urvina (Fig. 1; details in Harris 1979). A majority were also ringed with numbered rings. During 1977–1979, a further 106 were ringed with numbered rings at Punta Albemarle (7), Punta Espinosa (57), Cabo Marshall (3), Cabo Hammond (12), Caleta Negra (9) and Puerto Bravo (18). Searches for these birds were made throughout most of the species range at intervals during 1970–1973, in August 1977, and in August 1980, either from an offshore dinghy with binoculars (coloured rings) or by 0.5–4 h visits to the colonies and
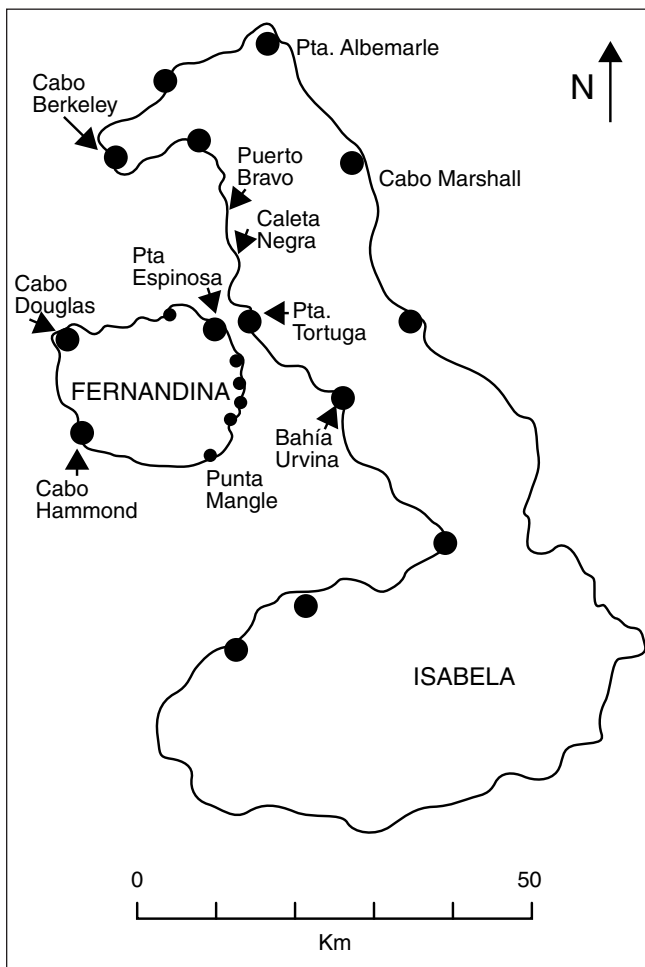
isolated nest(s) outside the colonies (coloured rings and numbered rings). Visits were made every two weeks to the colony at Punta Tortuga, Isabela, the nearest colony to the study colony, c. 5 km across open sea, during April 1970–September 1971. Further checking of ringed birds was carried out by opportunistic visits to individual colonies at other times during the decade.

Parental investment

During May–June and July–September 1977–1980, groups of up to eight nests at each of two locations were observed constantly for 4–6 week periods by teams of three to six observers. Observations were conducted during 153 days for all daylight hours (06h00–18h00) and for seven nights (18h00–06h00). Data were collected on 2100 nest-days of observation for 40 pairs from early nest construction to when the young were aged 120 days. For each adult we recorded the per day frequency of bringing nesting material to the nest site, the amount of time spent at the nest site and incubating or brooding, and the frequency of giving feeds to the young. When breeding, Flightless Cormorants do not come ashore elsewhere other than at the vicinity of the nest site, and do not remain in the water unless foraging or collecting nest material (Wilson *et al.* 2008, and RWT pers. obs.). Hence, we could determine the cumulative time investment in breeding and foraging activities by individual male and female parents.

During 1978 and 1979, adult female and male breeding Flightless Cormorants were weighed when incubating clutches, and/or when brooding young to age 40 d, and/or at brood age c. 70 d; hence, birds were each weighed (to the nearest 50 g) up to five times. Juveniles were weighed in 1977 and 1978.

Data analysis

Population metrics

Mark-live recapture data obtained from banded Flightless Cormorants at the study colony were analysed for annual colony attendance and survival, and for recruitment into the population, using the Jolly-Seber method of the MARK program (http://www.phidot.org/software/mark) implemented with POPAN formulation (Arnason & Schwartz 1999). Recapture data were fitted to a model of time-varying survival (ϕ), recapture (p) and recruitment (b). Goodness of fit of the model was compared with other testable models (n = 10) where time-dependence of ϕ or p or b, or combinations thereof, was replaced with constant. Goodness of fit was estimated from Akaike's Information Criteria (AIC) score for each model (lowest score indicating preferred model), and by comparison of models using the Likelihood Ratio Test (LRT). Reference to the numbers and survival of Flightless Cormorants in this article refers to derivations from this analysis unless otherwise stated.

Nesting location

To examine whether birds nested preferentially at locations at which they had previously nested, three statistical models were fitted.

The first model assumes that birds have a preference for locations but that these locations are not necessarily adjacent. Some locations were assumed to be more preferred, on average, than others. This was done by fitting "Bird" and "Location" as random effects. This model assumes that there is independence between locations.

The second model also assumes a location effect but with adjacent locations being positively correlated. Thus, if a location is occupied, there is a preferential choice for locations adjacent to the occupied location. This can be analysed by using a Conditional Auto Regression (CAR) correlation structure (Barnett & Dobson 2010) for location random effect. Thus, the location effect is assumed to be from a multivariate normal distribution with adjacent location co-variance(s) being positive, i.e., a Toeplitz correlation structure for adjacent nests. No "Bird" effect was fitted. Thus, the choices of individual birds are not affected by previous location choices: each bird will try to randomly occupy a location, with all birds preferring on average some locations compared to other. This assumes that some locations are "prime property" for all birds.

The third model is a combination of the above two models: (i) there is a location effect (i.e., some locations are "prime property"); (ii) there is a spatial effect with adjacent nests being preferred; and (iii) individual birds have a preference for particular locations, irrespective of their quality.

The above three models were implemented in R using the package R2WinBUGS, using a Bayesian framework. The package "Season" was used for defining the correlation matrix for the CAR. Weak priors were used. The models were fitted separately for male and female birds. Model selection was based on the Deviance Information Criterion (DIC) (Spiegelhalter *et al.* 2002), with a lower DIC indicating a better model.

The correlations of water temperature and breeding, of laying dates, of number of daily feeds received per young versus brood age, and of population size versus year were tested by linear regression analysis. Percent population decline was derived from the line of best fit. Where relevant, deviation from the line of best fit was determined by the Wald–Wolfowitz *(*Runs) test.

Weights of groups of birds were compared using the Mann–Whitney test (2-tailed). For other groups of data, comparisons of significance of difference were made using the χ^2-test. Arithmetic means are presented ± standard deviations.

RESULTS

The population

A total of 220 adults and sub-adult Flightless Cormorants (105 males, 104 females and 11 unsexed) were recorded at the colony during 1970–1979 (Fig. 2A). The mean number recorded annually was (mean ± SD) 89.4 ± 5.2 (43.0 ± 8.8 males, 46.4 ± 9.2 females). The numbers of males and females present each year did not differ significantly (χ^2 = 4.203, df 9, P = 0.90). We observed a mean decline in the population of 3.0 birds per annum.

Mark-live recapture data for 105 banded males (456 annual recaptures) and 104 banded females (381 annual recaptures) best fitted the model "time-varying survival, time-varying recapture, time varying recruitment into the population" (LRT versus all other testable models P < 0.0001). The mean derived number of adults attending the colony per annum was 118.1 ± 7.6 (60.4 ± 10.5 males and 58.2 ± 4.6 females; Fig. 2B). The total derived population over the decade was 221 ± 2.5 adults (108 ± 1.7 males, 102.5 ± 1.7 females, 11 unsexed). The population declined, but not significantly, by 2.9% (4.1 birds) per annum (r^2 = 0.219, P = 0.18). There was

no significant difference between the annual survivals of males (89.4 ± 2.9%) and females (92.9 ± 2.1%; $\chi^2 = 2.35$, df 9, $P = 0.98$; Fig. 2C).

Annual recruitment of 11.1 ± 4.0 individuals by birth and/or net immigration was required to sustain the population (Fig. 2B). We recorded a 15.1 ± 3.5 juveniles fledged per annum, of which 8.0 ± 3.19 (50.0%) survived to the second year of life in the years for which we have data (no data for 1979; Fig. 2A). The year 1978 was a particularly good one, as 19 (79%) of 24 juveniles survived, whereas 1977/78 was poor, and not one of the 12 juveniles was seen again. Sub-adult survival (i.e., second year of life) was 85.7% during 1970–1975 (the years for which we have data).

Breeding

A mean of 52.9% ± 20.2% of males and 51.5% ± 16.3% of females bred each season (Table 1), with extremes in 1978 (88.2% males, 76.1% females) and in 1972 (27.1% males, 30.3% females). The mean number of clutches incubated per annum by all males (0.60 clutches) did not differ significantly from the mean number of clutches incubated per annum by all females (0.62 clutches) (Table 1). All but three of the adults recorded at the colony bred. The mean number of clutches laid in the eight years for which we have records was 31.5 ± 10.3 (range 19 in 1972 to 52 in 1978; Table 2). Breeding success averaged 0.43 ± 0.19 juveniles taking to the sea per clutch laid; 1972 was particularly unsuccessful with only three juveniles reared, compared with 29 in 1970. Eleven males and 12 females whose full breeding histories were known over 11 years reared a mean of 3.5 juveniles and 3.8 juveniles at rates of 0.49 and 0.45 juveniles per clutch, respectively. Adult males and females (i.e., breeding and non-breeding) reared 0.31 ± 0.24 and 0.30 ± 0.21 juveniles per annum, respectively ($\chi^2 < 0.01$, df 1, $P = 0.99$).

In most years there were two clear periods of laying (Table 2). Birds laying "late" were those that had not bred that year or whose first clutch or brood had failed, and females that had already successfully raised juveniles. Forty-two females laid two clutches in the same season, significantly more than the 25 males that incubated clutches (Table 3). Eleven females that had raised juveniles from their first clutches deserted these offspring and bred again with new mates. No male deserted its young and re-nested. The number of females and males incubating a second clutch following the failure of the first clutch or brood was not significantly different (Table 3). All the birds incubating second clutches within a season changed partners between nesting attempts, and no pair laid a replacement clutch.

Female desertion

Female desertion was followed in detail in 1978. Of 12 females that raised juveniles, at least 11 deserted them, 10 were later found nest-building or courting, and at least six laid second clutches. At least one and probably two females successfully raised a juvenile from their second clutches, but it is not known how long they remained with it. The outcomes of the other second breeding attempts were unknown.

In all cases where the female deserted the young (usually at approximately 70 d), the male carried on feeding the young for a further 50–80 d, i.e., until the young were four to five months old. One male was seen to feed a nine-month-old juvenile. Eight of 10 juveniles abandoned by females, whose fates were known,
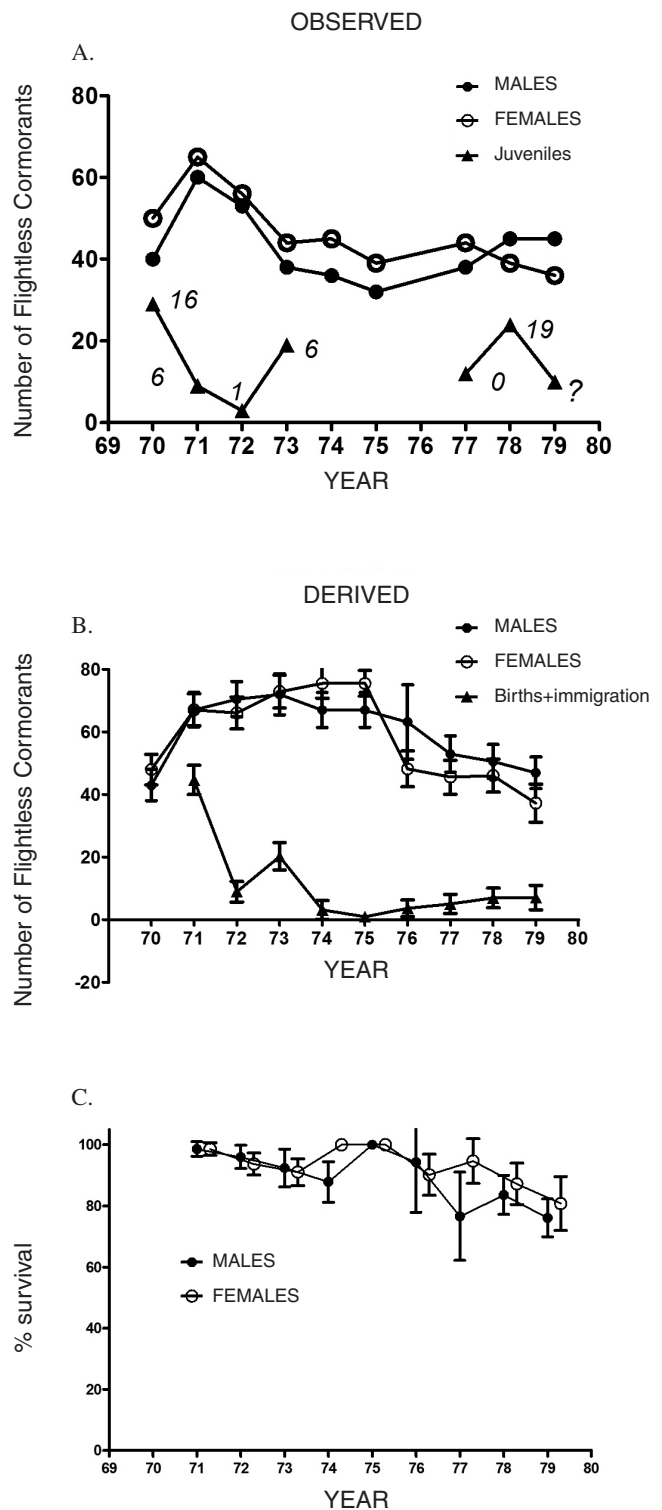
Fig. 2. Numbers, survival and recruitment of Flightless Cormorants at Punta Espinosa 1970–1980. (A) Observed numbers of adult males, females and juveniles (numbers in italics indicate juveniles surviving to second year of life). (B) Derived numbers of males and females, and recruitment (births and immigration) into the population. (C) Derived annual survival of adult males and females. Derivations were obtained from mark-recapture analysis. Mean annual derived recapture was 72.5% ± 7.9% (males), 72.2% ± 5.2% (females). No data were available for juvenile recruitment during 1974–1976.

were alive the following year. Clearly, the male can successfully complete the rearing of the young.

MATE FIDELITY

Fidelity to mate was very low; in only 22 out of 210 (10.4%) cases in which both members of a pair were alive did the pair remain intact. Mate fidelity was not influenced by previous nesting success, as pairs that remained together for consecutive attempts did not raise significantly more juveniles in their second attempt together than pairs that changed partners between attempts ($\chi^2 = 0.213$, df 7, $P = 0.62$). In only 45 of 252 (17.8%) cases did two birds nest together more than once.

The 11 males for which breeding histories were fully documented during the decade incubated a mean of 7.1 ± 2.6 clutches with 5.8 ± 2.3 different mates. The 12 fully documented females incubated a mean of 8.6 ± 2.7 clutches with 6.7 ± 2.2 different mates.

SEA SURFACE TEMPERATURE AND BREEDING EFFORT AND SUCCESS

Most laying occurred between March and October, coinciding with the usual prevalence of cold (18–23°C) nutrient-rich water in the offshore feeding grounds. Outside this period, the surface water was frequently warmer, at 23–28°C (Fig. 3). The number of clutches laid per annum was inversely and significantly related to water temperature (Table 2; Fig. 3B). In 1970, 1973 and 1978, when higher numbers of clutches were laid (Table 2), water temperatures recorded from April to October were consistently in the range 18–23°C (Fig. 3A). In 1979, water temperatures did not fall to below 24°C until June (Fig. 3A), and there was less laying until the July–October period. Water above 24°C persisted late into the year in 1972 (due to the ENSO phenomenon) (Wyrtki *et al.* 1976, Chavez *et al.* 1999). Fewer clutches (19) were laid that year (Fig. 3B), and most (18) were laid "late" in August–September (Table 2), when waters were coldest for the year.

TABLE 1
Percentage of adults that incubated clutches, and number of clutches per annum,
by male and female flightless cormorants 1971–1973, 1977–1980

Year	% adults that incubated clutches		Mean number of clutches per adult			
	Male	Female	Breeding males	All males	Breeding females	All females
1970	65.2	56.3	1.31	0.90	1.40	0.79
1971	37.3	55.2	1.16	0.43	1.00	0.43
1972	27.1	30.3	1.00	0.27	1.00	0.29
1973	41.7	31.4	1.00	0.42	1.10	0.42
1977	57.3	60.3	1.17	0.67	1.35	0.77
1978	88.2	76.1	1.13	1.04	1.41	1.13
1979	53.4	50.8	1.04	0.53	1.04	0.54
1980	?	?	1.00	?	1.04	?
Mean ± SD	**52.9 ± 20.2[a]**	**51.5 ± 16.3[a]**	**1.10 ± 0.11**	**0.60 ± 0.27[b]**	**1.16 ± 0.18**	**0.62 ± 0.29[b]**

[a] $\chi^2 < 0.01$, $P = 0.895$
[b] $\chi^2 < 0.01$, $P = 0.986$

TABLE 2
Annual totals of clutches laid and juveniles produced at Punta Espinosa 1970–1973, 1977–1980

Year	Number of clutches laid (juveniles produced)			Juveniles per clutch	Juveniles per adult (all adults)	Peaks of laying	
	Mar–Jun	Jul–Oct	Total			Early	Late
1970	22 (20)	16 (9)	38 (29)	0.76	0.31	Apr–Jun.	Sep.
1971	19 (5)	10 (4)	29 (9)	0.31	0.07	Apr.	Jul.
1972	1 (0)	18 (3)	19 (3)	0.16	0.02	–	Aug–Sep.
1973	25 (14)	5 (5)	30 (19)	0.63	0.13	Apr–May	Oct.
1977	21 (10)	14 (2)	35 (12)	0.33	0.12	Apr.	Aug–Sep.
1978	27 (13)	25 (11)	52 (24)	0.46	0.25	Apr.	Aug–Sep.
1979	8 (?)	17 (?)	25 (10)	0.40	0.12	Jun.	Jul.
1980	2 (1)	22 (9)	24(10)	0.42	–	–	Jul–Aug.
Mean ± SD	**16.7 (8.9)[a]**	**15.7 (6.1)[a]**	**31.5 (14.4)**	**0.43 ± 0.19**	**0.15 ±0.10**		

[a] 1979 data omitted.

The number of juveniles raised per adult was related inversely to water temperature, though the trend was only just significant ($P = 0.048$, Fig. 3C). Significantly more juveniles were raised in 1970, 1973 and 1978 (24.0 ± 5.0, n = 3; Table 2), the only years when water temperatures of 18–23°C were consistently recorded from April to October (Fig. 3A), compared with other years (8.5 ± 3.8, n = 5; $\chi^2 = 7.39$, df 1, $P = 0.01$). Fewest juveniles were fledged per adult in 1972 when warm water persisted late into the year (Fig. 3A). In 1977, when the seasonal cold waters terminated early and temperatures above 23°C were recorded from August onwards (Fig. 3A), only two of 14 clutches laid during July to October resulted in juveniles (Table 2). Young were light in 1977; the mass of two male and two female juveniles soon after they went into the sea (2427 ± 556 g) was significantly less than that of four male and four female juveniles in 1978 (3226 ± 498 g; Mann–Whitney U = 4.00, $P = 0.048$). Further, none of eight ringed juveniles of 12 reared in 1977 was seen again. These data indicate that juvenile production was enhanced when cooler water persisted in offshore foraging areas.

The number of clutches incubated and juveniles produced in 1973, the year immediately following the "bad" year of 1972 characterised by high SST, did not differ significantly from that of 1979, the year immediately following the "good" year of 1978 (clutches incubated, $\chi^2 = 0.455$, df 1, $P = 0.50$; juveniles produced, $\chi^2 = 0.05$, df 1, $P = 0.82$; Fig. 3B, C; Table 2). Thus, reproduction was not compromised in the season following a season in which SSTs had been suboptimal for breeding.

Movement and dispersal

*Flightless Cormorants exhibited restricted distribution within the colony*

Individual females were sighted at a mean of 3.36 of the seven locations in the colony and incubated clutches at a mean of 2.06 of the locations (n = 287 clutches; Table 4). Individual males were sighted at a mean of 3.43 of the seven locations and incubated clutches at 2.37 of the locations (n = 205 clutches).

TABLE 3
Number of Flightless Cormorants incubating a second clutch in a season in relation to the outcome of their first clutch

	Number incubating a second clutch	
Fate of first laying	**Male**	**Female**
Eggs failed to hatch	14	16
Young lost within 40 days of hatching	6	7
Young lost within 40–70 days of hatching	1	3
No young raised, reason for failure unknown	4	5
Subtotal	**25**[a]	**31**[a]
Juvenile raised to more than 70 days	0	11
Total	**25**[b]	**42**[b]

[a] $\chi^2 = 0.643$, $P = 0.423$
[b] $\chi^2 = 4.31$, $P = 0.038$
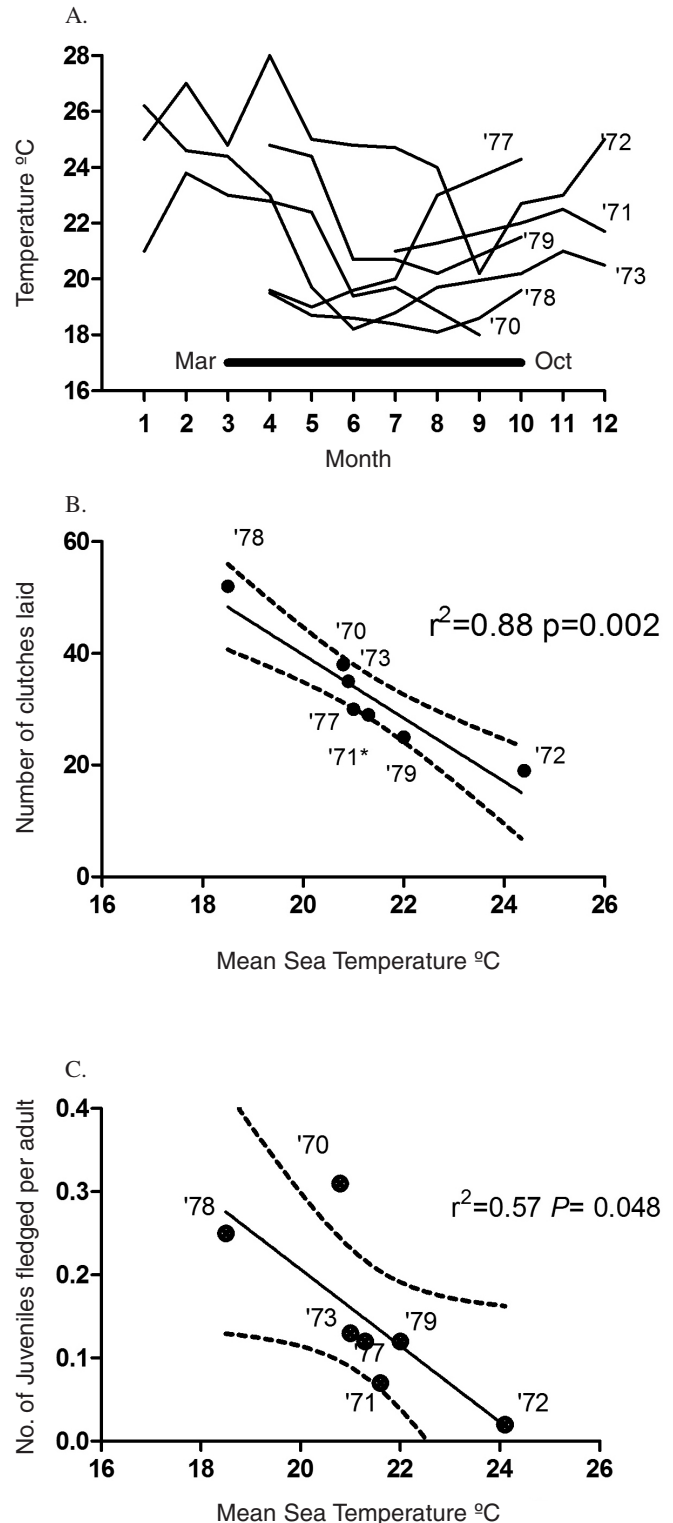
Fig. 3. Reproductive effort and success in Flightless Cormorants are correlated with surface sea water temperature in the offshore feeding area adjacent to the colony. (A) Surface water temperatures by year (lines) and month (x-axis). (B) Number of clutches laid in March–October per year against sea temperature. (C) Number of juveniles fledged per adult per year, relative to mean sea temperature during this period. (B and C: linear regression and 95% confidence limits [dashed lines] are shown.)

Of clutches recorded, 82.2% incubated by females and 73.9% incubated by males were at the same or adjacent location to the location where those individuals had incubated their immediately preceding clutches (Table 5). Most clutches were incubated at three of the seven locations (female 24.7%, 19.1% and 35.8%; male 24.3%, 22.4% and 32.6%, respectively), designated as prime locations. The rest were distributed over the remaining four locations. There was no significant difference between males and females in the distribution of clutches among the locations (Mann–Whitney U = 23.00, *P* = 0.90).

Of the three models of spatial distribution (see Methods), model three was statistically the most appropriate for both males and females (Table 6). Thus, (i) individual birds have particular preferences for location, and (ii) there is a spatial relationship between preferences, i.e., adjacent locations were preferred. In addition, (iii) for the population as a whole, particular locations were prime locations, preferred over others.

Together, the above data demonstrate that individual Flightless Cormorants show a highly restricted range of movement within the colony. Both males and females tended to frequent one or several adjacent locations, among which they breed.

Pairs incubating clutches together for a second time in consecutive breeding attempts (n = 10) showed no significant preference for the same location over another location within the colony (χ^2 = 0.20, df 1, *P* = 0.65). Similarly, pairs nesting together for a second time after breeding with other partners in the interim (n = 6) had no preference

for the same location over another location within the colony in their second nesting together (χ^2 = 0.34, df 1, *P* = 0.56).

Limited immigration/emigration at the study colony

Only six adult birds (2.7% of the 220 recorded at the colony; see below) and nine juveniles (9.3% of the 96 recorded) immigrated into the Punta Espinosa area during 1970–1980. Of 220 adults and sub-adults ringed at the Punta Espinosa colony, 10 (4.6%) were caught once outside the area, but all were within 2 km of the study area and later returned. Twenty-two of 25 juveniles ringed in 1970–1972 remained within the study area after reaching independence.

Movement of Flightless Cormorants between colonies

Of 282 birds ringed in 1970/71 and searched for during the subsequent 8–9 years along approximately 240 km of coastline (c. 62% of the entire range of the species), two adults ringed c. 4 km away moved into the Punta Espinosa colony and bred (Table 7). Three other adults immigrated into the Punta Espinosa colony from nearby sites on Isabela Island (Fig. 1), which involved journeys of 5–7 km across open sea. In two cases, the birds (both females) subsequently bred at Punta Espinosa. Two further cases of long-distance dispersal were recorded: one re-sighting indicated an inter-colony journey of c. 28 km involving c. 5 km across open sea from Isabela Island to Fernandina Island and a further c. 23 km travelling (presumably) along the coastline; the second re-sighting indicated a c. 9 km journey along the west coast of Fernandina Island. Of a further 106 birds ringed in 1977–1979 and checked until 1980, two

TABLE 4
Number of locations among the total locations (n = 7) at the study colony where individual Flightless Cormorants were recorded and bred during the decade 1970–1980

Sex (n)	Mean ± SD (% of total locations)	
	No. of locations where re-sighted	No. of locations where clutches incubated
Males (53)	3.43 ± 1.20[a] (49.0)	2.37 ± 1.00 (33.8)
Females (74)	3.36 ± 1.09[b] (48.0)	2.06 ± 0.83 (29.4)

[a] Mean no. of re-sightings per individual male 9.09 ± 4.79 per 7.09 ± 3.07 years.
[b] Mean no. of re-sightings per individual female 9.01 ± 4.43 per 6.81 ± 2.61 years.

TABLE 5
Location of clutches incubated by male and female Flightless Cormorants in relation to location of their immediately prior clutch

Sex	% of clutches		
	Same location	Adjacent location	Non-adjacent location
Female[a]	51.2	30.7	18.5
Male[b]	38.8	35.6	25.8

[a] n = 205 clutches
[b] n = 143 clutches

TABLE 6
Conditional Auto Regression (CAR) analysis of breeding locations of individual Flightless Cormorants at Punta Espinosa

CAR model	Males			Females		
	DIC score	DIC[a] difference	Effective parameter numbers	DIC score	DIC[a] difference	Effective parameter numbers
Model 1	1071	447	55.56	916	133	22.46
Model 2	698	74	82.10	852	66	111.60
Model 3	624	0	61.55	786	0	105.71

[a] Deviance Information Criterion (DIC) statistic for the three models for males and females. The DIC difference for the three models uses the best model (model 3) as the benchmark. A difference of 10 units in DIC indicates that the "Model with the smaller DIC is... definitely better" (http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/dicpage.shtml)

were recorded as having dispersed; one made a 7 km journey from Isabela Island to Punta Espinosa, the other a 20 km journey between colonies on the east coast of Isabela Island.

Parental investment

For 11–20 d before the first egg was laid, and during incubation and raising of the offspring, both sexes brought nesting material (predominantly algae) to the nest-site. Before laying, males brought significantly more items than females ($\chi^2 = 8.13$, df 113, $P < 0.001$; Fig. 4). There was considerable day-to-day variation. In one case, in the 11 d before the clutch was laid, a male brought (per day) 5, 32, 15, 13, 35, 17, 20, 16, 13, 10 and 11 items to the nest. After the clutch was laid, collection of nesting material by males was drastically reduced, and males and females contributed approximately equally to fetching nesting material, progressively diminishing until the brood was c. 70 days old (Fig. 4A).

Both sexes were at the nest site for c. 5–5.5 h per day prior to laying, and then contributed equally to incubation and brooding until the young were 20 d old (Fig. 4B), in shifts of 2.59 ± 1.06 h (n = 104 shifts, male) and 2.77 ± 1.33 h (n = 94 shifts, female). By the time that the chicks were 40 d old, female attendance at the nest site fell by c. 31% relative to male attendance ($\chi^2 = 15.7$, df 70, $P < 0.001$; Fig. 4B).

After incubating and brooding, birds entered the water and fed within c. 200 m of the shore before returning to the nest. Birds only very rarely came ashore elsewhere. Thus, during incubation and caring for the brood to c. 20 d old, both male and female parents spent a total c. 6.5 h per day foraging. When the brood reached 40 d, however, females spent c. 1.6 h per day more foraging than did their mates. Once they reached an age of c. 70 days, young were left unattended at the nest except when the male (but not the female, see below) returned to feed the brood.

Female parents fed their offspring aged 0–20 d 2.9 ± 0.3 times daily, declining to 1.2 ± 0.1 times daily at age 60–70 d. Males fed their offspring aged 1–20 d 2.0 ± 0.2 times daily, the rate declining to 0.9 ± 0.2 times daily at age 60–70 days. The mean cumulative number of feeds given by female parents (125 ± 3.3 feeds per brood) was 40.4% greater than that of their mates (89 ± 2.5 feeds per brood) at the time of the females' desertion at c. 70 days ($\chi^2 = 25$, df 2, $P < 0.001$; Fig. 5A). Males continued to feed offspring 0.9 ± 0.05 times daily to 110 days of age (when systematic observations ceased). Beyond brood age 110 d, males (but not females) occasionally fed juveniles to age 5–9 months. The number of daily feeds received by the brood declined near-linearly, and was not significantly affected by female desertion (Fig. 5B). The fall observed at day 80 (i.e., following female desertion) was within the 95% confidence limits and did not differ significantly from the line of best fit (Runs test, $P = 0.9$).

Adult survival and condition are not associated with breeding effort or success

In 1971, 1972, 1979 (when mean SSTs were higher; see Fig. 3B), the mean percentage of all males and females incubating clutches (39.2% male, 45.4% female; Table 1) was significantly lower than in 1978 (when mean SST was low), when c. 88% of males and females incubated clutches (male, $\chi^2 = 9.81$, df 1, $P = 0.002$; female, $\chi^2 = 7.14$, df 1, $P = 0.007$). Similarly, a significantly smaller mean percentage of males (12.9%) and females (18.4%) raised juveniles in these years than in 1978 (male 53.3%, $\chi^2 = 24.7$, df 1, $P = 0.0001$; female 61.5%, $\chi^2 = 23.2$, df 1, $P < 0.0001$; Fig. 2A,B). However the mean annual survival of adults (Fig. 2) during these three years (male 90.4%, female 91.0%) did not differ significantly from that in 1978 (male 83.3%, $\chi^2 = 0.25$, df 1, $P = 0.617$; female 87.2%, $\chi^2 = 0.08$, df 1, $P = 0.776$). Thus, adult survival was not compromised in years when breeding effort and success within the population was suboptimal.

TABLE 7
Re-sightings of banded adult Flightless Cormorants >4 km from colony/site of banding

Banded		Re-sighted			
Colony or site/island	Date banded	Colony or site/island	Date re-sighted	Distance, km	Comment
West coast/Fernandina	Apr.–Jun. 1970	Pta. Espinosa/Fernandina	1973	<5	Female. Incubated clutch at Pta. Espinosa 1973
West coast/Fernandina	Apr.–Jun. 1970	Pta. Espinosa/Fernandina	1973	<5	Incubated clutch at Pta. Espinosa 1973
Pta. Tortuga/Isabela	Oct.1972	Pta. Espinosa/Fernandina	Jul. 1979, Apr. 1980	5[a]	Female. Raised chick at Pta. Espinosa
Pta. Tortuga/Isabela	Apr. 1971	Pta. Espinosa	Aug 1980	5[a]	
Pta. Tortuga/Isabela	Jul.1973	Pta. Espinosa	1975, 1976, 1977, 1978, 1979, 1980	5[a]	Female. Incubated clutches with 5 males at Pta. Espinosa; raised at least three juveniles
Pta. Tortuga/Isabela	Oct. 1972	Cabo Douglas/Fernandina	Aug.1980	28[a]	
Cabo Hammond/Fernandina	Apr.–Jun. 1970	West coast/ Fernandina	Sept. 1974	9	
Puerto Bravo/Isabela	May 1977	Pta. Espinosa/Fernandina	Aug. 1980	7[a]	
Caleta Negra/Isabela	May 1977	Pta. Albemarle/Isabela	Aug. 1980	20	

[a] Includes 5 km across open sea.

The mass of females incubating in 1979, which had raised juveniles 8–10 months earlier in their most recent previous nesting in 1978, did not differ significantly from that of females weighed in 1978 at the time of deserting their juveniles (Table 8). Similarly, the mass of females who deserted their juveniles and who laid a second clutch in the same season did not differ from that of females who deserted and did not lay a second clutch in the same season. Thus, females did not lose condition when raising offspring, or, alternatively, were able to recover, and could thus embark on a new cycle of breeding in the same or following season.

The mass of males when raising juveniles alone after their mates' desertion did not differ significantly from that of males weighed after abandoning their clutches or broods (Table 8). Similarly, the mass of females after raising and deserting juveniles did not differ significantly from that of females after abandoning their clutches or broods. These data suggest that body mass of both sexes is independent of breeding outcome.
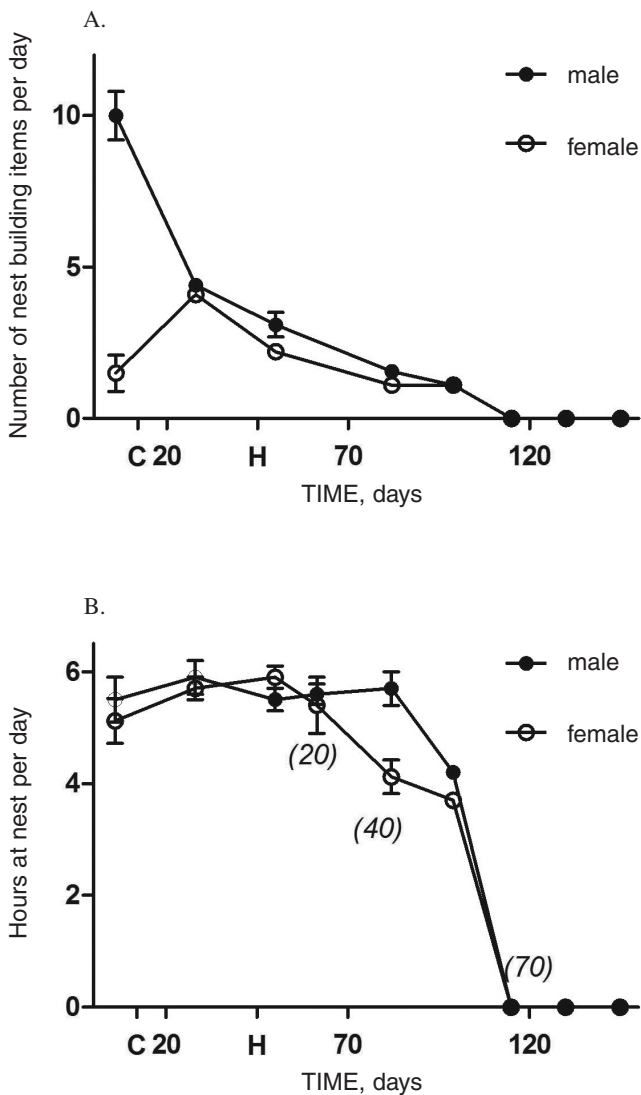

Fig. 4. Number of items of nesting material brought to the nest site (A), and number of daylight hours spent at the nest site (B), by male and female Flightless Cormorants. Numbers on the x-axis refer to time elapsed since the commencement of nest-building. C, clutch laid; H, hatching. Numbers in italics denote the age of the brood.

DISCUSSION

Sea surface temperature and breeding

Most females laid between March and October when surface waters water was cold (18–23°C) due to the upwelling of the Equatorial Undercurrent and Humboldt current (Houvenag 1974, Wyrtki *et al.* 1976). Between November and March, water temperatures usually exceeded 23°C due to warm water moving south to seas off Ecuador and Peru. This warm water is associated with a low biological productivity, which directly affects the numbers and/or availability of many of the fish eaten by cormorants (Harris 1979, Valle 1994, Edgar *et al.* 2004). During the ENSO event of 1972, warm waters persisted late into the year, few clutches were laid, and breeding success of the few birds that bred was very low. No bird ringed as a young, juvenile or immature bred for its first time in 1972. In other years, the number of clutches laid correlated significantly with sea temperature during the breeding season; fewer clutches were laid when water temperatures exceeded 23°C (Fig. 3B). There was a strong trend for fewer juveniles to be raised per adult when mean water temperatures for the season were higher, although the trend was only just significant ($P = 0.048$). Data for only one of the
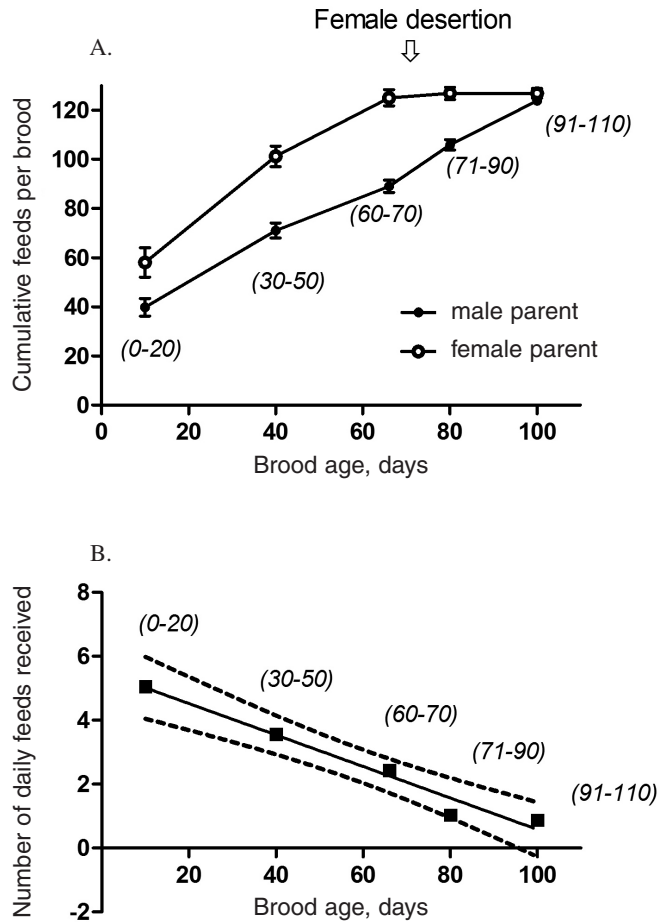
Fig. 5. Parental feeding of the Flightless Cormorant brood. (A) Mean cumulative number of feeds (error bars show SD) received from male and female parents (n = 257 feeds). (B) Number of daily feeds received per brood to age 110 days (95% confidence limits are shown [dashed lines]). Arrow indicates mean age of offspring at the time of female desertion. Numbers in italics indicate age range of brood.

seven years (1970) lay outside the 95% confidence limits (Fig. 3C). Furthermore, significantly more juveniles were raised when cold water persisted throughout the season, compared with other years. Complete failures of clutches were most common between January and March, when the sea was warmest and least birds nested (Harris 1979). During a severe ENSO event in 1983, when water >23°C persisted in the islands until September (Valle 1994), no more than five clutches were laid, and no juveniles were reared at Punta Espinosa although only about half the area was surveyed (D. Day, pers. comm.).

Availability of food brought about by changes in marine productivity is probably both the proximate and ultimate factor controlling the timing of breeding. The Flightless Cormorant is presumably adapted to an unpredictable food supply and breeds opportunistically whenever cold waters occur. Cold waters usually persisted for about seven months, sufficient time for a pair to raise one brood to independence (4–5 months), but not two. However 11 of 61 females managed to rear two broods by deserting the first brood and nesting again that season with another male. Among females that had raised a juvenile to three months, but did not relay immediately, the interval between successive nesting attempts was significantly less than for males that had raised a juvenile to three months (Harris 1979). This suggests that females deserting young even in less optimal seasons could recover and regain breeding condition more quickly than their mates that fed the young for several months longer. Thus, by deserting, a female accelerates her reproduction in any conditions. However, during the decade of the study, females did not breed significantly more often or raise more juveniles than did males. While the strategy of female desertion enhances outcome in years when optimal sea temperatures persist for much of the year, it apparently accrues no long-term advantage to females over males.

TABLE 8
Mass of Flightless Cormorants relative to breeding status

Breeding status	Mass, g, mean ± SD
Females	
Incubating 1979. Raised juvenile 8–10 months earlier (n = 11)	2769 ± 174[a]
Recently deserted juvenile in 1979 (n = 9)	2769 ± 226[a]
Incubating. Raised juvenile earlier that season (n = 4)	2805 ± 301[b]
Incubating. Did not raise juvenile earlier that season (n = 7)	2801 ± 168[b]
Recently deserted juvenile (n = 15)	2784 ± 224[c]
Abandoned clutch or brood (n = 7)	2867 ± 164[c]
Males	
Raised juvenile after mate desertion (n = 8)	4018 ± 109[d]
Abandoned clutch or brood (n = 8)	3961 ± 224[d]

Mann-Whitney test
[a]   U = 45.00, $P = 0.761$
[b]   U = 12.00, $P = 0.77$
[c]   U = 39.50, $P = 0.563$
[d]   U = 26.00, $P = 0.561$

Over the decade, the mean annual recruitment of breeding offspring at three years of age per pair was 0.13, calculated from juvenile production per adult (Table 2), and first- and second-year survival rates of 50.0% (Fig. 2) and 85.7% (Harris 1979), respectively. In 1978, a year with "good" oceanographic conditions in which most adults laid clutches and juvenile production per adult was high, the calculated recruitment rate was 0.22. In 1972, a year with poor oceanographic conditions, when only c. 20% of adults laid clutches and juvenile production per adult was very low (Table 2), the recruitment rate was 0.02.

Our mean recruitment rate of 0.13, though lower, was not significantly different from the figure of 0.19 computed by Valle (1995) ($\chi^2 < 0.01$, df 1, $P = 0.916$). We cannot exclude the possibility that we may have underestimated juvenile survival because of some unrecorded juvenile emigration from the colony (see above). With a recruitment rate of 0.13, an adult would replace itself in c. 8 years. Allowing for adult survival, this equates to a lifetime recruitment of c. 2 per adult bird, in accord with the Valle model (1995) and the observed long-term relatively stable status of the population (Valle & Coulter 1987).

Movement and dispersal

Individual Flightless Cormorants tended to reside and breed at a cluster of two to three locations along a few hundred metres of coastline for at least c. 7 years (the mean time for which we have data) (Table 4). This restriction occurred even though all seven nesting locations spread along c. 2 km of coastline at the Punta Espinosa colony were within easy reach and accessible to all birds at the colony. Furthermore, 11 males and 12 females ringed during 1970/71 were regularly re-sighted and recorded breeding throughout the decade. Assuming a mean adult life span of c. 13 years (Valle 1995), this suggests that cormorants tend to remain within the same small strip of coastline for most, and possibly all, of their lives. However some longer movement occurred. We recorded nine movements of >5 km, five of which involved a sea crossing to another island (Table 7). In four instances, birds were recorded breeding at their new site (Table 7). Re-sightings were likely to under-record actual movement between sites, as colonies other than the study colony were less intensively checked. Two further inter-island migration events have been recorded subsequently (Larrea 2007).

Other observers have proposed that Flightless Cormorants may be sedentary, and generally do not disperse >2 km from the colony (Snow 1966, Harris 1979). Based on dispersal of 38 non-breeding and breeding Flightless Cormorants marked with Global Positioning System recorders, Wilson *et al.* (2008) found that birds tended to stay in the same colony, did not usually venture more than 200 m from the coast, and never ranged more than 7 km from the colony over a 3-year period. Valle (1995) recorded 2%–8% of adults dispersed >4 km between consecutive breeding attempts and c. 24% of juveniles spread >4 km from their birthplace before attempting to breed for the first time.

The overall sedentary habit of Flightless Cormorants is supported by genetic analysis of individual birds throughout the species range, which demonstrated significant genetic differentiation among colonies on the same island, and particularly between the two islands where the species occurs (Duffie *et al.* 2009). Together, the findings are consistent with low dispersal and behavioural philopatry, which serve to promote genetic differentiation as a

function of distance (Duffie *et al.* 2009). Separation of the colonies is presumably determined by coastline topography, which in turn determines suitable nesting locations. Philopatry in Flightless Cormorants argues against previously inferred extensive gene flow and panmixia (Valle 1995).

Genetic variability within the colony is facilitated by overlap of clusters of breeding locations preferred by individual birds, by individuals occasionally straying from "their" cluster to other proximal breeding locations within the colony, by occasional immigration/emigration, and by mate changing. While these factors facilitate some gene flow, the direct genetic analysis data (Duffie *et al.* 2009) indicate that their impact does not override prevailing genetic differentiation between colonies.

Mate fidelity

The percentage of pairs remaining together in consecutive breedings (10.4%) was greater than expected by chance (3.2% among the mean of c. 32 breedings per annum). This likely reflects the trend for individuals to remain in clusters of locations within the colony, rather than disperse throughout the colony, thereby limiting mate choice. The 10.4% of cases in which two birds did nest together more than once consecutively were not associated with previous nesting success by the pair, suggesting that there is no premium on breeding with the same mate for Flightless Cormorants.

Parental investment

Tindle (1984) suggested that the putative sedentary behaviour of Flightless Cormorants predisposed them to in-breeding and that this may be a factor driving their reproductive strategy. In this paper we demonstrate that, some dispersal notwithstanding, Flightless Cormorants are indeed extremely sedentary, individual birds being re-sighted only at c. 50%, and incubating clutches at c. 33%, of locations within the colony over the decade.

Although the sex ratio in the colony did not differ significantly from parity (Fig. 2), in all years (except perhaps 1978 when most birds bred successfully), there was a supply of unattached males with which deserting females could make their second breeding attempt that season. The surfeit was made up of those males whose first breeding attempts had failed and those that had not bred that season. The latter group likely included young males, whose first breeding attempt occurs at an earlier age (c. 15–18 months) than that of young females (Harris 1979, Valle 1995).

Males spent significantly more time than their mates bringing nest material before the clutch was laid (Fig. 4A). Both sexes contributed equally to incubation. After hatching, both sexes attended the nest equally, but when the brood reached about 40 days of age, females spent significantly less time at the nest (Fig. 4B) and fed the brood significantly more frequently than their partners. The mean number of cumulative feeds given to the brood by the female exceeded that of the male by 46.7% (135 vs. 92 feeds) at the time of her desertion. Males continued to feed the brood at least a further 40 times, but probably not more than 70 times after their partners had deserted. The female Flightless Cormorant's strategy is to invest heavily in the chick-rearing before deserting the nest and re-mating, leaving her mate to finish rearing the brood. Female desertion did not significantly impact the gradual decline in the number of daily feeds received by the brood (Fig. 5B).

Males do not usually pre-empt their mates' desertion, since females may be stressed in making their contribution to chick feeding before desertion at times when vacillating food supplies are limiting (Tindle 1984, Valle 1994). Thus, by the time the brood reaches c. 40 days of age, females spend 39% more time away from the nest foraging than males (Fig. 4). Therefore, there is doubt that females could feed themselves and complete the rearing of the brood alone were the male to desert first. Males certainly can, as eight out of 10 juveniles in 1978 abandoned by the females and subsequently fed only by the males were alive the following year.

While the pattern of investment differs, the cumulative time invested by males and females before female desertion does not differ significantly; both sexes invest between 640 and 690 hours (Tindle 1984). In terms of energy, the female has probably invested more than her mate at the time of her desertion at brood age c. 70 days, as foraging is likely to be more energetically expensive than gathering nesting material.

Although it is normally the female that deserts the brood, we observed a male courting a new female while still feeding a juvenile deserted by his previous mate. Subsequently, Valle (1994) recorded a male deserting a female that was "late" in deserting the brood herself, and a male raising a brood with a new partner while still feeding the juvenile from the previous mating; only the juvenile from the second brood survived.

The Flightless Cormorant is the most sexually dimorphic member of the Phalacrocoracidae. Males are about 30% heavier than females and can dive deeper and for longer than females, allowing them to forage further offshore (Tindle 1984, Valle 1994, Wilson *et al.* 2008), and can take larger bottom-dwelling prey species (Schreer *et al.* 2001). Both sexes forage primarily within c. 200 m of the shore adjacent to the Punta Espinosa colony (Wilson *et al.* 2008, Tindle unpublished obs.). Rapid drop-off in the depth of water limits foraging at greater distances. Intimate knowledge of local submarine topography arising from extreme sedentary behaviour likely confers foraging advantages. Differential foraging behaviour associated with water-depth may serve to maximise habitat exploitation by a pair, thereby enhancing the chances of successfully raising a juvenile in times of food shortages (Wilson *et al.* 2008).

Population dynamics

The demographic parameters of the Flightless Cormorant population have been modelled by Valle (1995). Our data over a 10-year period substantively support the model. An annual adult survival of 91.2% acting on a mean of c. 118 birds would produce a gross loss of c. 11 adult birds per annum. The derived mean annual recruitment of 0.13 breeding offspring per pair (above) indicates a gross annual recruitment of 7.7 breeding birds into the population per annum, indicating an annual decline in the population of 3.3 birds per annum. This is similar to the losses we observed and those derived by MARK analysis (3 birds and 4.1 birds per annum, respectively; see above). These data suggest that immigration into the colony was minimal, and this accords with our observations of movement of birds into the colony from peripheral areas and by long-distance immigration. The adult annual survival rates we report (89.4% male, 92.9% female) support those computed by Valle (89.4% male, 94.3% female) and are congruent with a proposed mean adult lifespan of c. 13 years (Valle, 1995). The long lifespan is also

suggested by the fact that nine of 18 (50%) of birds ringed as adults (of unknown age) and juveniles in 1960–1962 (Lévéque 1964) we recorded as surviving at the colony for a further 12–14 years. Jiménez-Uzcátegui *et al.* (2012) reported five Flightless Cormorants of banded ages 11.1–15.9 years.

Adult survival was not compromised in years of reduced breeding effort and reduced success associated with suboptimal oceanic conditions and putative food shortage. In other years, female mass did not change significantly when measured in consecutive breeding attempts (in which the first attempt was successful), indicating that females did not lose condition when raising offspring, or alternatively were able to recover in time to embark on a new cycle of breeding in the same or the following season. We found no significant decline in body weight in either sex associated with successfully raising a juvenile, suggesting that they do not sacrifice body condition during chick-rearing. Together, the above observations support a model predicting that food availability selects for high adult survival and maintenance of condition rather than increased reproductive effort (Harris 1979, Horn & Rubenstein 1984, Valle 1995).

Threats to the species from oceanographic change

Seasonal cold water may have shaped the breeding strategy of the Flightless Cormorant for 500 000 to 1 million years (Wilson *et al.* 2008). A rise of several degrees of SST in foraging areas during the breeding season (Fig. 3) or persisting throughout the breeding season (i.e., during ENSO events) results in low breeding success. The Flightless Cormorant population reached a low of about 400 birds in 1983 following the extreme ENSO event of 1983 when food was very scarce (Valle & Coulter 1987). A further strong ENSO event occurred in 1997/98. Flightless Cormorant numbers have recovered from each of these events (Jiménez-Uzcátegui *et al.* 2006), indicating the demographic potential for increase when optimal food conditions return. ENSO events have occurred in Galápagos for at least the last 6 000 years (Riedinger *et al.* 2002). However, their frequency and severity appear to have increased (Rodbell *et al.* 1999, Riedinger *et al.* 2002, Vargas *et al.* 2006), possibly associated with global climate change (Sachs & Ladd 2010).

Habitat restriction determined by oceanographic conditions, foraging range restricted by flightlessness and the high degree of specialisation embodied in flightlessness itself, constrain the population to numbers barely considered adequate for long-term persistence of the species (Mace & Lande 1991, Henle *et al.* 2004). Long-term and/or frequent short-term rises in SST in foraging areas pose a threat to this vulnerable (IUCN Red List) species, which is dependent on cold upwelling water for breeding and survival.

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