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Effects of parental age and food availability on the reproductive success of Heermann's Gulls in the Gulf of California

Leticia Vieyra,[1] Enriqueta Velarde,[2,4] and Exequiel Ezcurra[3,5]

[1]*Oriente 257 Number 165, Col. Agrícola Oriental, México, D.F. C.P. 08500 Mexico*
[2]*Unidad de Investigacón de Ecología y Pesquerías, Universidad Veracruzana, Hidalgo 617,*
Col. Río Jamapa, Boca del Río, Veracruz, C.P. 94290 Mexico
[3]*Biodiversity Research Center of the Californias, San Diego Natural History Museum,*
P.O. Box 121390, San Diego, California 92112-1390 USA

Abstract. Parental age, body condition, and food availability have been found to influence breeding parameters in seabirds, such as clutch size, number of chicks hatched and fledged, hatching, fledging, and reproductive success. In this paper we analyze the influence of parental age and body condition estimated by body mass, and food availability estimated from catch per unit effort (CPUE) statistics for Pacific sardine (*Sardinops caeruleus*) + northern anchovy (*Engraulis mordax*) by the local fishing fleet, on the breeding parameters of the Heermann's Gull (*Larus heermanni*; a vulnerable species according to Mexican federal law) nesting in Isla Rasa, Gulf of California, Mexico. Results are based on data from 1123 recaptures of known-age individuals, ranging from 4 to 13 years of age, during seven observation years between 1989 and 1997. Ages of mated male and female gulls were positively correlated. Breeding parameters showed their lowest values in 1992, an El Niño year in which the birds also showed significantly lower individual masses for both males and females, and in which the local CPUE of sardine + anchovies was lowest. All breeding parameters increased significantly with parental age and were highest at 10–12 years. No significant statistical interactions were found between food availability and parental age on the breeding parameters. Through a path analysis we found that there is a strong chained relationship between variables: food availability, which is strongly driven by oceanographic conditions, affects both the survival of eggs into hatchlings and the survival of hatchlings into fledglings. This external factor and parental age, a biological factor intrinsic to each nesting couple, explain 41% of the observed between-nest variation in fledgling success.

Key words: age; El Niño; food availability, Gulf of California; Heermann's Gull; Larus heermanni; reproductive success.

Introduction

In seabirds, as in many other species, breeding is seasonal and occurs several times in an individual's life (Lack 1968, Perrins 1970, Murton and Westwood 1977). Avian breeding is influenced by various factors such as age, probability of acquiring a nesting territory and a mate, egg-laying date, clutch and egg sizes, reproductive success, and adult survival (Sæther 1990, Robertson et al. 1994). Reproductive success in seabirds has several components, such as clutch size, hatching success, and fledging success, and they are all important components of the individual's fitness. Each one of them may be affected by diverse factors, both intrinsic to the parents (age, feeding and breeding experience, physical condition, and breeding effort) (Pugesek 1981, 1984), and to the environment (food availability, availability of nesting sites, and climatic conditions).

Age

Breeding parameters have been reported to vary with the age of the parents in several species of birds. Clutch size, a main estimator of reproductive effort, has been observed to increase with age in the Yellow-eyed Penguin (*Megadyptes antipodes*; Richdale 1957), the Black-legged Kittiwake (*Rissa tridactyla*; Coulson 1966), the Arctic Tern (*Sterna paradisea*; Coulson and Horobin 1976), the Common Tern (*Sterna hirundo*; Hays 1978), the California Gull (*Larus californicus*; Pugesek 1983), the Lesser Snow Goose (*Chen caerulescens caerulescens*; Rockwell et al. 1993), the Brandt Cormorant (*Phalacrocorax penicillatus*; Boekelheide and Ainley 1989), and other species of seabirds (Coulson and White 1958, Haymes and Blokpoel 1980, Pugesek and Diem 1983, Pyle et al. 1991, Sydeman et al. 1991). However, Haymes and Blokpoel (1980) for the Ring-billed Gull (*L. delawarensis*), report a middle-age peak in clutch size and a subsequent decline in this parameter for older individuals.

Hatching success and fledging success have also been reported to increase with age in various seabird species, coinciding with an increase in parental breeding effort or experience, as older, more experienced parents improve their ability to feed and defend their broods. Both parameters have been observed to stabilize, or even decrease, in older individuals (Pugesek and Diem 1990, Pyle et al. 1991).

Food availability

Food availability has been found to affect the breeding parameters of various species. Clutch size, fledging success, and reproductive success are directly related to food availability in the California Brown Pelican (Anderson et al. 1980, 1982, Sunada et al. 1981), the Brandt Cormorant (Boekelheide and Ainley 1989), and the Western Gull (Penniman et al. 1990, Sydeman et al. 1991). Food availability also interacts with age of the breeding individuals because in years of low food availability fewer young breeders will nest, or they will have lower reproductive success (Boekelheide and Ainley 1989, Sydeman et al. 1991).

Nesting site

Most studies on nesting seabirds have shown that the older birds are the first to return to the colony, occupy the best nesting territories, and breed (Coulson and White 1958, Mills 1973, Coulson and Horobin 1976, Ainley et al. 1983, Pugesek 1983, Boekelheide and Ainley 1989, Pyle et al. 1991). Pugesek and Diem (1983) found that older individuals of *L. californicus* tend to nest further away from the colony edges and are better protected from the wind. Other authors have found that younger birds are unable to defend an optimal nesting site due to their being less competitive or socially less dominant, less knowledgeable of the best sites to raise their chicks, less aware of external dangers, less able to defend their chicks from predators, or less experienced in providing shelter and food for them (Forslund and Larsson 1992, Gilchrist et al. 1994, Pärt and Gustafson 1994, Wiebe and Martin 1994).

Body mass of the breeding adults

In several seabird species individual body mass has been observed to affect breeding performance. In the Common Tern (*Sterna hirundo*), Wendeln and Becker (1999) observed that heavier individuals had a higher reproductive success and their chicks showed a higher growth rate. Chastel et al. (1995) found that reproductive success in male Blue Petrels (*Halobaena caerulea*) was directly related to individual body mass, and that breeding individuals were heavier than nonbreeding ones, during the same breeding season.

Objectives and scope of our work

All the previous issues raise a series of interesting questions on the factors that have an influence on the reproductive success of some seabird species. On the one

hand, we know that some extrinsic factors having a bearing on seabird reproductive success, such as sea surface temperatures and the intensity of marine upwellings, may change dramatically from one year to the next in synchrony with the warm phase and the cold phase of ocean–atmosphere oscillations such as the El Niño phenomenon (Velarde and Ezcurra 2002, Velarde at al. 2004). These oscillations add a random component to the reproductive success of the birds that may be of critical importance to their overall reproductive fitness. On the other hand, reproductive success is also highly dependent on the birds' intrinsic ability to secure a good nesting site, take care of their nests, and feed their chicks, a series of factors that are known to vary with age. Thus, the age and experience of the nesting couple adds a systematic component to reproductive success that may also have a significant bearing on reproductive fitness. In short, the reproductive success of a nesting couple may depend on (1) their age, an intrinsic and biologically driven factor, and (2) local environmental conditions, a set of extrinsic environmental factors largely driven by unpredictable oceanographic conditions.

The main question that we wanted to explore with this study was how does the birds' reproductive ability change as they age, or when oceanographic conditions vary inducing marked changes in food availability, and how do these two sets of factors (one systematic and intrinsic to the species, the other one random, driven by the large-scale dynamics of the global environment and extrinsic to the species) interact in the overall reproductive fitness of seabirds. We explored these questions by analyzing the breeding performance of known age Heermann's Gulls (*Larus heermanni*) nesting in Isla Rasa in the Midriff region of the Gulf of California. With our research we tested three hypotheses: (1) As birds age they will tend to increase their reproductive success until the onset of senescence. (2) Oceanographic warm-phase anomalies and the ensuing decline in available pelagic fish will induce a decline in reproductive success. (3) Older birds should show a higher ability to cope with low food availability during anomalous years, i.e., there should be a marked interaction in the joint effect of parental age and food availability on reproductive success.

Our data set contains one of the longest data records for nesting seabirds, where Heermann's Gulls have been banded and individually followed for up to 13 years, allowing us to make unique inferences on the effect of aging patterns on the reproductive biology of this little known species, which is listed as "vulnerable" under Mexican federal law. Most (95%) of the nesting population of this unique species concentrates in Isla Rasa, which is part of the protected area of the Islands of the Gulf of California (Anderson et al. 1976, Velarde and Anderson 1994, Velarde 1999, Velarde and Ezcurra 2002). The information provided here is part of an ongoing, 29-year effort at monitoring the reproductive

TABLE 1. Nesting valleys studied in Isla Rasa, Gulf of California, Mexico (see also Fig. 1) and years in which they were sampled.

Valley	1989	1990	1991	1992	1995	1996	1997
1) La Casita			×	×	×	×	×
2) El Estero	×		×	×	×	×	×
3) Gran Estación Central				×	×	×	
4) Tapete Verde	×	×	×	×	×		
5) Casitas Viejas de Arriba	×	×	×	×	×	×	×
6) Casitas Viejas de Abajo	×	×	×	×	×	×	×

aggregation of seabirds on this island, which has been a central part in the recovery, management, and conservation of this species in particular, and of the biodiversity of the area in general.

THE STUDY AREA

The study was carried out in Isla Rasa, Gulf of California, Mexico (28°49′24″ N, 112°59′03″ W). The island is low in elevation (only 33 m above sea level, from which its Spanish name Rasa, meaning "flat" is derived), volcanic in origin, and with an approximate area of 0.6 km^2. It has two main topographic zones: low-lying rocky hills intersected by valleys filled with deep guano deposits. The climate is very dry and vegetation is scant, dominated by spiny chollas (*Cylindropuntia fulgida* and *Cylindropuntia alcahes*), *Atriplex barclayana*, and other halophytes (Velarde 1999). The island is situated in the Midriff Region, the most productive part of the Gulf of California and one of the most productive marine regions in the world (Álvarez-Borrego 1983, Álvarez-Borrego and Lara-Lara 1991). Marine productivity is significantly reduced during El Niño years, affecting the reproductive success of at least some of the seabirds (Anderson et al. 1980, 1982, Velarde and Ezcurra 2002, Velarde et al. 2005). The island is the nesting site of 95% of the world population of Heermann's Gulls (*Larus heermanni*; ~260 000 individuals) and Elegant Terns (*Sterna elegans*; ~180 000 individuals). Also, ~10 000–15 000 Royal Terns (*S. maxima*) nest there every year (Velarde 1999). These seabirds, protected under Mexican federal law, nest on the island between early April and early July of each year. Heermann's Gulls and Elegant Terns feed mainly on Pacific sardine (*Sardinops caeruleus*) and northern anchovy (*Engraulis mordax*; Velarde et al. 1994, 2004). The island was declared a protected area in 1964 by the Mexican federal government, and on-site protection and monitoring has been carried out continuously since 1979 (Velarde and Anderson 1994).

METHODS

Heermann's Gulls are very synchronous in their breeding, and the laying period of the entire nesting population generally extends for no more than three weeks. The average nesting density in the valley areas, where our monitoring was carried out, is 71 nests/100 m^2 (Velarde 1999). Clutch size varies from one to three eggs,

and mean and mode vary in different years (Velarde-González 1989, Velarde 1999, Vieyra 2004).

Our study was carried out with information from years 1989–1992 and 1995–1997. Only adult, banded, known-age Heermann's Gulls were monitored. These individuals were banded as fledglings in the valley areas of the island, as part of a banding program carried out between 1984 and 1993, when ~4000 fledglings were banded annually (excluding 1988 and 1992), using aluminum bands provided by the U.S. Fish and Wildlife Service. Heermann's Gulls reach sexual maturity at four years of age, so no reproductive individual was younger than that age.

During the first two weeks of April, we searched for banded individuals in the study areas (six of the 11 valleys were monitored during the seven years, but not all valleys were monitored every year, see Table 1). We entered the nesting areas walking very slowly and searched for bands while the nesting individuals rose momentarily from their nests and bands could be seen. Each nest where a banded individual was found was marked with a numbered wooden stake. Stakes were placed 5 cm to the left of each nest as seen from a previously established observation point. During the laying period each observation area was monitored at least every other day, and new eggs were marked and weighed, differentiating between first, second, and third egg. An egg was considered lost if it disappeared from the nest or was found broken. Clutch size was determined as the total number of eggs laid in a nest, including the lost eggs. During the last 10 days of incubation of the first incubating birds, adult gulls from the marked nests were captured using a funnel-entrance chicken-wire trap (3-cm mesh size). The trap is cylindrical with walls and ceiling ~30 cm high and 60 cm in diameter, respectively. Up to six traps were placed simultaneously in the study area. Entering the nesting areas very slowly, and using slow movements, the traps were placed over the nests, ideally directing the entrance away from other territories and toward the edge of the valley, in the direction from where the person would be entering the area. Captures were carried out during the first hours of the morning and late afternoon, so eggs would not be exposed to strong sun. Also, a small cloth was placed over the trap, to shade the eggs while the adult on duty was trying to enter the trap. The adult gull would walk around the trap and eventually find the entrance, sitting on the eggs to proceed with incubation.

The captured gull was carefully taken out of the trap, a cotton hood was placed over its head, with which it readily relaxed, and was taken to a processing station a few meters away from the nesting area. A cotton wrapper was placed temporarily around its body to weigh the animal using a 1000-g Pesola scale (Baar, Zug, Switzerland). Bill depth was measured using a caliper to determine the sex of the individual (E. Velarde, *personal observation*), and the band number was registered (from 1988 onward, aluminum bands on recaptured adults were replaced with stainless steel or Incoloy U.S. Fish and Wildlife Service bands, which last several decades). The band number indicated the year and the valley in which the individual was born. Finally, the individual was released and the trap removed from the nest. Once hatching started, the captures were suspended in order to avoid disturbance (chicks will flee their nests if approached by a person and may be pecked by neighboring adults). The study areas were monitored daily with binoculars from designated observation points from that moment until mid-June, when crèches start to form and chicks can not be followed individually.

Chick survival was estimated as the proportion of chicks surviving to a certain age. Food availability was inferred indirectly through the annual values of catch per unit effort (CPUE) for Pacific sardine and northern anchovy landings (data in metric tons per standard boat-day) and for the fishing fleet of the State of Sonora. The data are generated by the Regional Center for Fisheries Research (Centro Regional de Investigación Pesquera, CRIP) in Guaymas and regularly used by researchers for fisheries research (e.g., Cisneros et al. 1995, Lluch-Cota et al. 2007). Historically, the fleet fished mostly from October to May in the Guaymas Basin, although now, with modern refrigerators, it fishes almost year-round with a short rest period in September. The Mexican Fisheries Commission may increase this no-fish period in any given year according to their stock estimates (DOF 1993). In a previous study (Velarde at al. 2004) we have shown that food availability for the Heermann's Gulls in the Gulf's Midriff is strongly correlated with the catch of the fishing fleet. Lower food availability and lower catches are related to the descent of the thermocline during the warm phase, which reduces ocean productivity in the surface layer and induces fish to dwell deeper, making them unavailable to both the seabirds and the purse-seine nets.

All regression analyses were done using generalized linear models (McCullagh and Nelder 1989) with the GLIM Package (NAG 1998). A Pearson linear correlation test was run to determine if there was a relation between the ages of mated male and female. Mean and standard deviation were obtained for clutch size, hatching success, number of chicks hatched and fledged per nest, fledging success and reproductive success by year, age of the breeding adult, and site (valley where individuals were nesting, see Fig. 1). Log-linear regres-

sion models were run to determine if there was a significant difference in the number of eggs laid per nest, the number of hatchlings, and the number of fledglings (a Poisson-type frequency data), among breeding adults of different ages and masses, during different years, and in different sites, while offspring survivorship (a binomial variate) was analyzed using a logistic model. For all these models, year and valley were treated as discrete factors with seven and six levels, respectively, and age, body mass, and food availability (estimated from the CPUE proxy values) were treated as continuous predictors. To analyze the possibility of curvilinear responses, we also tried squared and cubic terms on age and CPUE, but did not find any significant higher-order terms in any of the analyses. Finally, in order to see if the effect of catastrophic years had a larger effect on birds of certain ages or on certain valleys, we analyzed the interaction terms between year and age, and between CPUE and age. Because different nesting valleys were sampled in different years, their effect on the statistical model is unbalanced and, for this reason, we did not analyze the interactions between nesting site and the other variables included in the analysis, and only the main effect of the nesting site was included in each model.

Cumulative chick mortality curves were obtained in relation to chick age, measured in days after hatching. The body mass of adult breeding individuals was analyzed separately for males and females and regressed through linear models against year and age. Simple *t* tests for two samples with unequal variances were used to estimate differences in the mass of males and females among years.

Finally, we performed a path analysis on our data set. The technique, originally developed by Wright (1921), is a combination of a graphic representation of the main functional pathways between variables and relatively simple algebraic manipulations that allow testing for alternative relational hypotheses on the system under study (for a detailed explanation on the theory of path analysis see Sokal and Rohlf 1995). Because male and female birds differ in their body mass, we reduced all mass values to sex-specific standardized deviations from the seven-year mean, and then pooled the data of males and females together, averaging the two values in those nests in which both members of the couple had been banded. We then calculated the correlation matrix between all the seven variables used in the study: (1) oceanographic anomalies estimated from the values of the Southern Oscillation Index (SOI; Velarde et al. 2004), (2) food availability (using the sardine + anchovy CPUE proxy estimator), (3) parental mass anomaly (standardized deviation from the mean), (4) parental age, (5) clutch size, (6) number of hatchlings, and (7) number of fledglings. We then selected only those pathways that accounted for >1% of the observed variation between variables (partial $r^2 > 0.01$), and calculated the path coefficients for each relationship
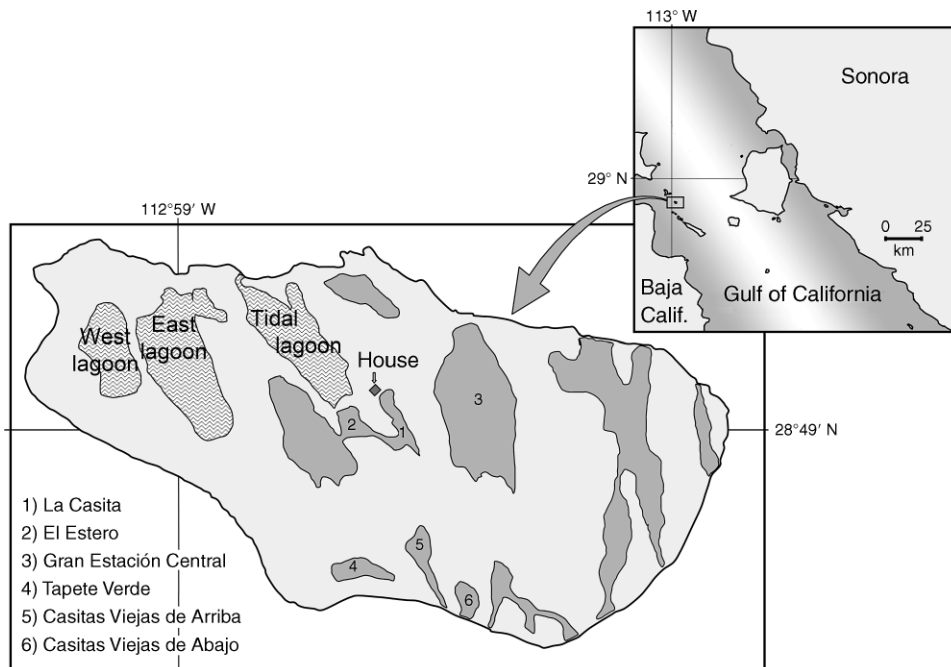
Fig. 1. Map of Rasa Island with the valleys where Heermann's Gulls nest shown in gray. The valleys where sampling was conducted are indicated by numbers. In the top-right insert, the dark area in the Gulf of California shows the sardine fleet's traditional fishing grounds (modified from Lluch-Belda et al. [1986] and DOF [2004]).

(path coefficients are standardized regression coefficients showing only the direct effect, and removing indirect effects, of an independent variable on a dependent variable in the path model). Finally, in order to test the adequacy of our path model we calculated the variance in fledgling success accounted for by our model, and compared it with the variance accounted for by a standard multiple regression model with one dependent variable (number of fledglings per nest) and six independent predictors.

RESULTS

A total of 1552 Heermann's Gulls (967 males and 585 females) were captured in 1081 marked nests; 1123 of these were banded, known-age individuals (852 males and 316 females). In 40 of the nests both parents were banded. The age range of the captured gulls was from four to 13 years. The youngest breeders found were four years old, indicating that this species takes at least four years to reach sexual maturity. The correlation coefficient of the age of the individuals in pairs where both male and female were banded was positive ($r^2 = 0.59$, $P < 0.0005$, $n = 40$). Because these two variables were strongly aliased, male and female data were pooled for all the following statistical tests.

Parental age and reproductive success

The age of parents had a significant effect on all breeding parameters (Table 2). Clutch size, number of hatchlings, and number of fledglings tended to increase with age, although they did so at different rates (Fig. 2). Heermann's Gulls in this study showed the highest average clutch size and highest average number of chicks hatched at age 13 and the lowest at age four. The highest average number of fledged chicks was observed for individuals 10 years of age, after which they tend to stabilize, and the lowest for age four parents. No

TABLE 2. Effect of food availability (sardine + anchovy catch per unit effort [CPUE] proxy), age of parents, body mass, and nesting valley within the island on clutch size, number of hatchlings, and number of fledglings.

Factor	χ^2	df	P
Clutch size			
Parental age	8.87	1	0.003
Body mass	6.28	1	0.009
Number of hatchlings			
Food availability	80.96	1	<0.001
Parental age	23.29	1	<0.001
Body mass	20.05	1	<0.001
Number of fledglings			
Food availability	44.42	1	<0.001
Body mass	21.82	1	<0.001
Parental age	9.56	1	0.002
Valley	19.15	5	0.002

Notes: The analysis was done with a log-linear model for absolute frequencies using both continuous variables (food availability, age, and body mass) and discrete factors (nesting valley) as model predictors. In all analyses the number of data points was 1081, corresponding to the cumulative number of nests analyzed during the seven-year study period. Only the significant terms of the model are shown.
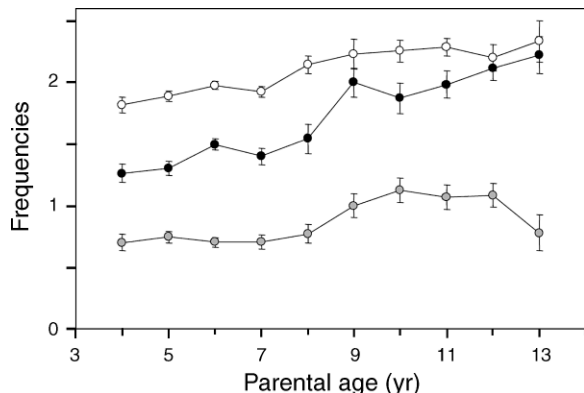
FIG. 2. Breeding parameters by age of parents: clutch size (open circles), number of chicks hatched (black circles), and number of fledglings (gray circles). The cumulative number of nests analyzed during the seven-year study period for parents of ages 4–13 corresponded, respectively, to 103, 208, 349, 162, 70, 39, 47, 59, 36, and 8 nests.

significant correlation (or higher-order curvilinear relationship) was found between the age of the birds and their body mass either for males ($r^2 = 0.002$, $n = 967$, $P = 0.21$) or females ($r^2 = 2.2 \times 10^{-10}$, $n = 584$, $P = 0.99$).

The effect of food availability on reproductive success

There was a significant effect of the calendar year in breeding parameters according to the generalized linear model, but a similar, and statistically more parsimonious, fit could be achieved simply by replacing the calendar year by food availability (sardine + anchovy CPUE) as the predictor (Table 2). Clutch size was not significantly related to food availability, but the number of hatchlings and fledglings was strongly dependent on the food estimate and also on the body mass of the parents, a parameter also significantly correlated with food availability ($r^2 = 0.08$, df = 1079, $P < 0.001$). This pattern, however, was largely due to one single season, the spring of 1992, which corresponded to an El Niño year (Fig. 3) when food availability was low and birds had an extremely low body mass. A test on the parameters of the log-linear regression model showed a significant difference ($P < 0.00001$) in hatchling and fledging numbers between 1992 (an El Niño year, when hatchlings and fledglings were in very low numbers) and the rest of the years, but not among the latter.

The survival of chicks was also highly related to food availability. During non-El Niño years, highest chick mortality occurred during the first 10 to 15 days of life of the chicks, and then tended to level off. With the exception of the El Niño event of 1992, final chick survival ranged between 67% and 55%, but did not differ significantly between years (Fig. 4). During the 1992 El Niño, mortality maintained a fast rate after the first two weeks, leading final survival to drop to 22%, significantly lower than during normal years ($\chi^2 = 32.5$, df = 5, $P < 0.0001$).

The body mass of both male and female gulls varied considerably between years. In all cases the mass of the males was always ~17% higher than that of the female within each pair, and both data sets varied synchronically (Fig. 5a). In the El Niño year of 1992, when the lowest CPUE values of our observation years occurred (Fig. 5b), the lowest masses were observed for both males and females. Significant differences ($P < 0.01$ for paired t tests) were found for the average mass of both male and female Heermann's Gulls between the El Niño year of 1992 and all the other years, which in turn did not differ among themselves. As would be expected, a significant ($P < 0.05$) correlation was found between mean annual male and female body mass and sardine + anchovy CPUE ($r^2 = 0.59$ and $r^2 = 0.41$, respectively; and $r^2 = 0.51$ for the relative deviations of both sexes pooled together; df = 5 in all cases), but this relationship was entirely attributable to only one data record: the low CPUE values for the 1992 El Niño year.
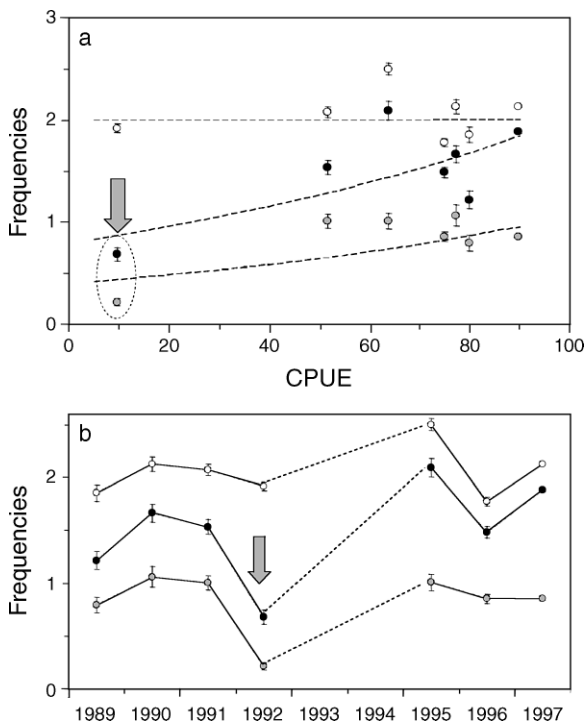

FIG. 3. (a) Breeding parameters plotted against food availability (sardine + anchovy annual catch per unit effort [CPUE]). The dotted lines mark the predictions of the log-linear model. (b) Breeding parameters plotted against year. In both graphs, the arrows show the decrease in the number of hatchlings and fledglings observed during the 1992 El Niño year. Key to symbols: clutch size (open circles), number of chicks hatched (black circles), and number of fledglings (gray circles). In both graphs, each point corresponds to an annual cycle. The number of nests analyzed each year was 69, 63, 133, and 158 for 1989–1992; and 96, 237, and 325 for 1995–1997.
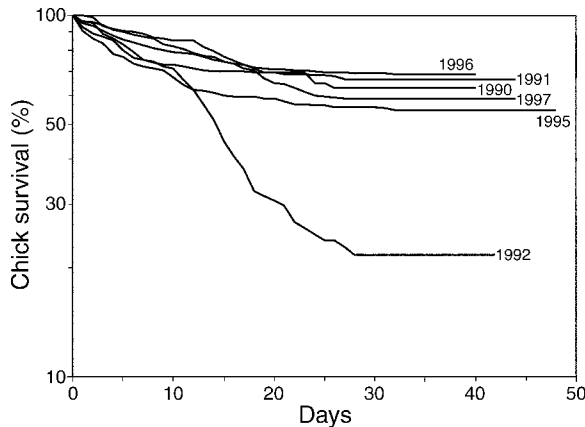
FIG. 4. Survivorship curves for chicks during years 1990 (108 chicks were followed, 68 survived to fledglings), 1991 ($n = 204/136$), 1992 ($n = 101/22$), 1995 ($n = 188/103$), 1996 ($n = 413/284$), and 1997 ($n = 532/314$).

Nesting site and reproductive success

The nesting site showed no significant influence on clutch size or number of chicks hatched, but had a significant effect on the number of fledglings (Table 2). However, a test of the model parameters showed that this significant effect ($P < 0.0001$) is only due to one site, the Grand Central Station Valley, where fledgling survival is higher than in all the other stations, which, in turn, did not differ among themselves.

Interactions among variables

No significant interactions were found between the effect of age and food availability on any of the reproductive parameters (Table 2), nor between age and calendar year. Because most of the variation observed from one year to the next is attributable to the low food availability observed during year 1992, it is clear that the depression in reproductive success observed during that year affected birds of all ages in a similar manner.

Path analysis

Based on the intensity of the correlations between variables, we constructed a path model with 12 functional relationships and calculated the path coefficients for each relationship (Fig. 6). The mean number of fledglings produced per nest (a measure of reproductive success) was defined as the criterion or dependent variable. Oceanographic anomalies (the mean December-to-May values of the Southern Oscillation Index) and parental age were introduced as exogenous variables, i.e., defined by factors external to our model. Food availability (the sardine + anchovy CPUE proxy) was strongly related to oceanographic conditions, and was, in turn, a main factor driving adult body mass, and the number of hatchlings and fledglings. Down the sequence, adult body mass was related to clutch size and, less intensely, to the number of hatchlings. Finally, on an

independent branch of the functional pathway, parental age was also related to clutch size and number of hatchlings and fledglings. The proportion of variance explained by this model ($R^2 = 0.41$) was higher than that of a standard multiple regression model with no chained variables ($R^2 = 0.32$), a fact that strongly suggests that our chained-effects model is a more accurate representation of our study system. Our model also allowed us to confirm the absence of significant interactions between variables, as no correlated relational links between predictors of the same hierarchy in the chain were found.

DISCUSSION

Our results clearly highlight a network of chained effects driving reproductive success: oceanographic anomalies have an impact on food availability, which in turn affects the birds' body mass and their ability to tend to their nests and feed their chicks. Bird age, clearly related to past nesting experience, is an indicator of the couple's ability to lay eggs and take care of the nest. In the following sections we will analyze how these variables relate to each other, and we will discuss their usefulness as predictors of reproductive success.
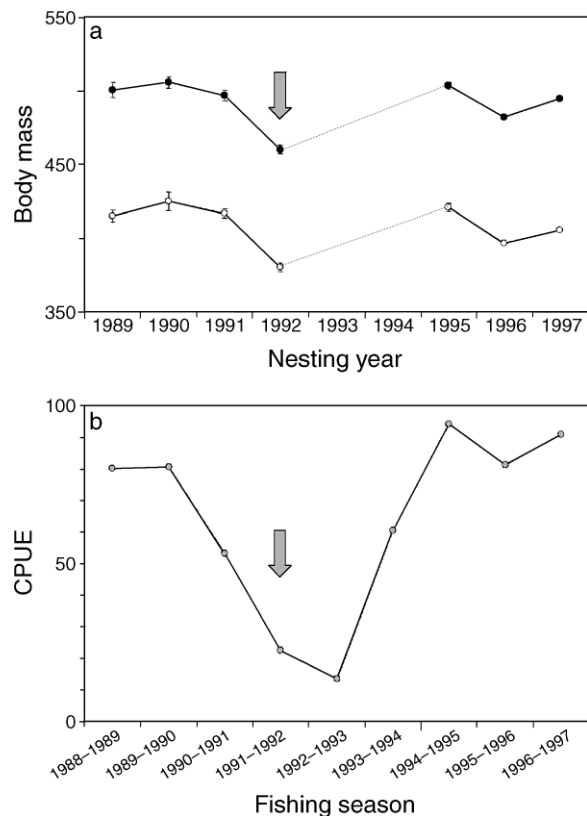

FIG. 5. (a) Average mass of male (solid circles) and female (open circles) Heermann's Gulls ($n = 967$ and 585, respectively), and (b) CPUE for sardine and anchovy for the Sonoran fishing fleet in the study years. The gray arrows show the effect of the 1992 El Niño year on both gull mass and sardine + anchovy CPUE.

The effect of age

In our study we found a high correlation between the ages of nesting males and females. In the Heermann's Gull, both members of a pair unite in the breeding territory several weeks before eggs are laid. This gives individuals some time to reclaim their old breeding territories and reunite with their previous mate. When first time breeders (four-year-old individuals) arrive at the nesting areas, all will be bachelors and most of their potential mates will belong to their same cohort. A marked correlation between the ages of male and female in a nesting couple has been reported for several species of seabirds and waterbirds (Coulson 1966, Coulson and Horobin 1976, Jouventin et al. 1999). This is due to high mate fidelity in most of these species, but also to the fact that older birds arrive at the breeding grounds earlier than younger ones (Coulson and White 1958, Coulson 1966, Coulson and Horobin 1976). If an individual's mate of the previous year is not back at the breeding territory, for whatever reason, the bachelor individual at the colony, at that particular time, will be surrounded by individuals of similar age because the younger birds tend to arrive to the breeding grounds later in the season. For this reason, when the younger breeding adults arrive at the colony, most of the older adults will have already found a mate among similar-aged adults (Coulson 1966).

Reproductive success in Heermann's Gulls tends to increase monotonically with age, but some noteworthy differences occur between the different nesting stages. Average clutch size increased in our data set continuously until the birds were 13 years old. The pattern was even more marked with the number of hatchlings: in young birds only ~70% of the eggs hatch successfully, while in 12–13-year-old birds 97% of the eggs hatch. After hatching, chick survival was similar in all nests: around 40–50% of the chicks that hatched became fledglings in all age classes, and no age-related differential survival was found. However, because they hatch more eggs, older birds are generally able to produce more fledglings. Last, in the 13-year-old age class we observed a decrease in the number of fledglings. Although this last decrease was nonsignificant, the data suggest that the reproductive success of older couples may level off after age 10 to around one chick per nest, possibly starting to decline after 13 years of age.

A pattern of increase of clutch size with age has also been observed in other species of gulls such as the Ring-billed Gull (Haymes and Blokpoel 1980), the Black-legged Kittiwake (Coulson and White 1958), the California Gull (*L. californicus*; Pugesek and Diem 1983), and the Western Gull (*L. occidentalis*; Pyle et al. 1991, Sydeman et al. 1991). Clutch size in the Heermann's Gull, as in other species, may be linked to their food reserves and their ability to obtain food which, in turn, is likely related to age (Wunderle 1991).
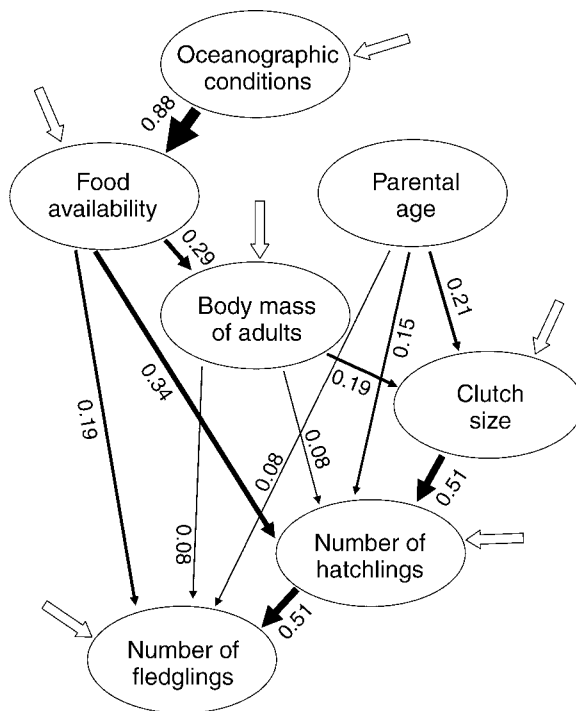

FIG. 6. Path diagram of the main factors affecting the breeding success of Heermann's Gulls in Isla Rasa. Black arrows and the associated numbers indicate pathway coefficients between related variables; open arrows indicate the incidence of independent factors, which were uncontrolled (and undefined) in our study but add variation to our data set.

An increase in the number of chicks hatched per nest with age suggests an increased capacity in the more experienced adults for incubation and nest defense, as found by other studies (Coulson and White 1958, Coulson 1966, Sydeman et al. 1991). Although other authors have reported a constant increase, or increase with eventual stabilization in hatching success with age (Pugesek and Diem 1983, Sydeman et al. 1991), in our case hatching success continued to increase at least up to 13 years of age of the parents, which is the maximum age of the Heermann's Gulls in our sample.

The number of fledglings in Heermann's Gulls increased with parental age up to age 10 years and then tended to stabilize. Studies on Adelie Penguins have shown that the number of fledglings per nest increases constantly with parental age (Ainley and Schlatter 1972), a pattern attributed to the greater experience of older individuals to obtain food.

The mean number of fledglings per nest in Heermann's Gull reached a maximum at 10 years of age and then seemed to level off. In most gull species it has been observed that reproductive success, or some of its components, increases constantly with age (Mills 1973, Ryder 1975, Pugesek 1983, Pugesek and Diem 1983, Sydeman et al. 1991), or reaches a plateau (Pyle et al. 1991). However, using a longer time series than for their earlier studies, Pugesek and Diem (1990) found that

older California Gulls exhibited a declining fledging success. Although not statistically significant, the declining trend in reproductive success in 13-year-old Heermann's Gull observed in our study may be a first evidence of senescent reproduction. Future analyses of the Isla Rasa nesting colony, with more data for older birds, may confirm this hypothesis.

The effect of food availability

Although clutch size was not significantly related to food availability, the number of hatchlings and fledglings, as well as their survival probability and the body mass of their parents, were all strongly influenced by the availability of sardines and anchovies. The pattern, however, was defined to the El Niño conditions of 1992, as no significant differences were found between the other years.

During the 1992 El Niño year, when food availability was low, clutch size did not decrease, at variance with reports for other species, such as the Western Gull (Sydeman et al. 1991, Penniman et al. 1990). In 1992 we noticed that, after the hatching period, parents took a longer time to return to their nests and relieve their mates, often forcing the guarding adult to leave the nest in search of water or food, leaving the nest unprotected. Under such conditions, the probability of chick mortality increased, triggered by fatal attacks from neighboring adults, hunger, or predation from the Yellow-footed Gull (*L. livens*; Velarde 1992). The positive correlation between reproductive success and food availability is similar to that reported for other seabird species, such as the California Brown Pelican (*Pelecanus occidentalis californicus*) (Anderson et al. 1982, Anderson and Gress 1984), and Western Gull (Penniman et al. 1990, Sydeman et al. 1991).

The effect of nesting site

The number of fledglings per nest was significantly higher in the Grand Central Station Valley. This is the largest nesting area within the valleys we sampled, and also the one with the highest nest density. Although we did not explicitly investigate the possible causes for this difference, it is likely a result of the better protection against predation provided by a large and dense colony, especially against successful incursions of the Yellow-footed Gull, which tend to be lower in high nesting-density areas (Velarde 1992).

Interactions between age and food availability

The fact that we found no significant interactions between food availability and parental age in their joint effect on reproduction suggests that in our study the effect of the 1992 El Niño year affected birds of all ages in a similar manner. This result contrasts with other studies that did find marked interactive patterns. For example, Ainley and Schlatter (1972) and Wunderle (1991) report that in other seabird species age is positively correlated with feeding experience. Boekel-heide and Ainley (1989) report that older Brandt Cormorants (*Phalacrocorax penicillatus*) produce the same number of fledglings in good and moderate years, while younger ones only attempt to breed in years with good food conditions.

Path analysis

Our path model shows a strongly chained relationship between variables. Jointly, food availability and parental age explain 41% of the observed between-nest variation in fledgling success. Food availability, which is in turn strongly driven by oceanographic conditions ($r^2 = 0.77$), affects both the survival of eggs into hatchlings and the survival of hatchlings into fledglings, very likely because when food is abundant parents both spend more time tending their nests and have more fish to feed their chicks. Parental age was positively correlated with clutch size and number of hatchlings and fledglings, because, as shown in the previous analyses, older parents are better at laying eggs and taking care of their nest.

Conclusions

Our study shows that breeding performance of the Heermann's Gulls is heavily affected by the age of the breeding adults and by food availability. Food availability also affects the body mass of the breeding adults, as well as their hatching and reproductive success. The age of the male and female parents is closely correlated, highlighting the trend in this species for mate fidelity. Successful breeding in the Heermann's Gull increases with parent age, reaching a peak between 10 and 13 years, and then tending to stabilize (or even perhaps decline). The species could be showing a senescent period after 13 years of age, a factor that deserves further attention as the individuals may live as much as 23 years or more. The two main factors having a bearing on reproductive success, age and food availability, operate in the seabird colony at Isla Rasa in a largely independent manner and do not have a significant interaction in their overall impact on the reproductive fitness of seabirds.

We finish this study by accepting two of our original hypotheses and rejecting the third one: (1) In Isla Rasa, as the Heermann's Gulls age they significantly increase their reproductive success. (2) As reported in previous studies (Velarde and Ezcurra 2002, Velarde et al. 2004), we confirmed that oceanographic warm-phase anomalies produce a marked decline in the reproductive success of Heermann's Gulls, triggered by a reduction in the availability of sardines and anchovies, their main food source. (3) Contrary to our original hypothesis, during the period of low food availability that took place during the 1992 El Niño event, the older birds showed a relative decline in reproductive success similar to that of younger birds. We conclude that the two main factors driving successful reproduction, parental age and random variations in the ocean's productivity, seem to operate simultaneously and with relatively similar

importance on the overall reproductive fitness of each nesting couple. Older couples are in general better at successful breeding, but collapses in the availability of sardines and anchovies hit young and older nesting couples with similar intensity.

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