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Patterns of Egg Laying and Breeding Success in Humboldt Penguins (*Spheniscus humboldti*) at Punta San Juan, Peru

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Abstract.—We analyzed patterns of egg laying and breeding frequency of Humboldt Penguins (*Spheniscus humboldti*) between 1993 and 1997 at Punta San Juan, Peru. Egg-laying extended from mid-March to the first week of December, showing two well-defined peaks in April and August–September. The extended breeding period of these birds was the result of individuals having a second clutch. About half of the females (n =189) had two clutches per year, most of which were double broods (73%). The date of completion and outcome of reproduction, or whether a change of mates occurred from the previous year, did not affect timing of egg laying. The majority of first clutches (62%) were laid in April each year. Two-clutch breeders that started laying eggs early in April had a higher breeding success than those starting in late April, and double brooders had greater success than single brooders. Two-clutch breeders started to lay eggs earlier than single-clutch breeders. Taking into account that a penguin breeding cycle (from egg laying to fledging) lasts ~4 months, laying eggs early in April increases the chance of rearing two successful broods per year. During three consecutive years, females tended to have two clutches instead of only one clutch and an average breeding success of 4.54 fledglings over 3 years. Having as many clutches as possible when conditions are favorable appears to be a strategy used by Humboldt Penguins to maximize their lifetime reproductive success within a productive but unpredictable environment.

Resumen.—Entre 1993 y 1997 analizamos los patrones de puesta de huevos y frecuencia reproductiva de *Spheniscus humboldti* (Pingüino de Humboldt) en Punta San Juan, Perú. La puesta de huevos se extendió desde mediados de marzo hasta la primera semana de diciembre, mostrando dos picos bien definidos en abril y agosto-septiembre. El largo período de nidificación de estas aves se dió como resultado de la puesta de una segunda nidada por parte de algunos individuos. Aproximadamente la mitad de las hembras (n = 189) pusieron dos nidadas por año, la mayoría de las cuales presentaron dos crías (73%). La fecha de finalización y el resultado reproductivo, o si ocurrió un cambio de pareja desde el año anterior, no afectó la coordinación en la puesta de huevos. La mayoría de las primeras nidadas (62%) fueron puestas en abril de cada año. Las parejas con dos nidadas que comenzaron a poner sus huevos al comienzo de abril tuvieron un éxito reproductivo mayor que las que comenzaron a fines de abril. Las parejas que criaron dos pichones fueron más exitosas que las que criaron un solo pichón. Las parejas con dos pichones comenzaron a poner sus huevos más temprano que las parejas con una sola cría. Considerando que el ciclo de cría de un pingüino (desde la puesta del huevo hasta dejar el nido) dura ~4 meses, poner los huevos a principios de abril incrementa las chances de criar exitosamente dos nidadas por año. Durante tres años consecutivos, las hembras tendieron a presentar dos nidadas en lugar de una sola y un éxito reproductivo promedio de 4.54 volantones en tres años. La estrategia de *S. humboldti* parece basarse en tener la mayor cantidad posible de nidadas cuando las condiciones son favorables para así maximizar el éxito reproductivo total en un ambiente productivo pero impredecible.

Most species of birds restrict energy-demanding events, such as breeding and molt, to a time of year when environmental conditions including food availability are favorable (Lack 1968, Perrins 1970, Immelmann 1973). The endangered Humboldt Penguin (*Spheniscus humboldti*) breeds along the coasts of Peru and Northern Chile, regions associated with the cold and highly productive Humboldt Current. Besides the richness of those waters, food availability is seasonal within years, and highly variable and unpredictable between years in Peru (Guillen et al. 1971, Barber and Chavez 1986, Bakun 1987). The periodic occurrence of El Niño events dramatically affects marine mammals (Majluf 1987, Ono et al. 1987, Trillmich and Ono 1991) and sea birds (Tovar et al. 1985, Hays 1986, Paredes and Zavalaga 1998). Under such conditions, timing of the breeding cycle of penguins should be flexible, which was suggested by Stonehouse (1967) for penguins that breed in tropical

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and subtropical latitudes. In Peru, Humboldt Penguins have been reported to breed from March to December (Murphy 1936, Hays 1984, Zavalaga and Paredes 1997a). In Chile, two peaks of egg laying have been described, one in May and one in October (Population Habitat Viability Analysis 1998). However, detailed information about laying patterns and factors affecting timing of egg laying of this species are not available. Factors found to influence timing of breeding in other penguin species include food supply (Bost and Jouventin 1990, Olsson 1996, Olsson and Brodin 1997), outcome of the previous reproduction (Bost and Jouventin 1990, Van Heezik et al. 1994), sea surface temperature (Warham 1975, Reilly and Cullen 1981), and breeding experience (Ainley et al. 1983).

The extended breeding season of penguins may coincide with the occurrence of replacement clutches. Gentoo Penguins (*Pygoscelis papua*) at Crozet Islands, can re-lay eggs if their first clutch or brood is lost (Bost and Jouventin 1990). Little Blue Penguins (*Eudyptula minor*; Reilly and Balmford 1975, Woodell et al. 1984), African Penguins (*Spheniscus demersus*; La Cock and Cooper 1988, Randall and Randall 1981), Galapagos Penguins (*Spheniscus mendiculus*; Boersma 1975), and Humboldt Penguins (Zavalaga and Paredes 1997a) can re-lay eggs after successfully raising chicks (double brooding).

The aim of this study was to provide the first detailed analysis of egg-laying pattern and breeding frequency of Humboldt Penguins. We examine how outcome of breeding affects the timing of the next laying, and how Humboldt Penguins optimize breeding decisions within a year.

Study area and methods.—Data were gathered from 1993 to 1997 at Punta San Juan (15°22′S, 75°12′W), which holds the largest breeding colony of Humboldt Penguins in Peru. Detailed information about Punta San Juan is provided elsewhere (Zavalaga and Paredes 1997a, Battistini and Paredes 1999). The overall penguin population increased from 1,260 to 1,843 pairs during the study period. Penguins molt between January and February, followed by the breeding period in March to December. After three weeks of fasting on land, they spend two to three weeks at sea recovering weight lost during the molt (30%; C. B. Zavalaga unpubl. data). Females lay one to two eggs per clutch during a four day interval. Incubation lasts for 42 days, chicks hatch over a two day period and chick rearing lasts 75 days on average (Zavalaga and Paredes 1997a).

In spite of the positive anomalies in sea surface temperatures (SST) in 1997, penguins laid eggs and raised chicks, which suggests that adequate food supply was available throughout most of the year. A massive abandonment of chicks started in late December when SST anomalies began to climb to extreme levels (Paredes and Zavalaga 1998)

Two groups of nests were monitored in regular intervals from the last week of March to the first week of January each year. Nests were checked between 1000 and 1300, when number of penguins at their nests was at its lowest. Each year one group consisted of 120–165 nests (surfaces and burrows) on the cliff top and 50–100 nests on the slopes. This group was checked every two to four days from a blind 100 m away using spotting scopes to avoid disrupting penguins on surface nests. It was possible to determine content of nests (egg, chicks, and adults) from that distance because of the inclination of the terrain where nests were located. Nests were mapped and numbered using PVC stakes or rocks as reference points. The second group (33–97 nests) consisted of those in crevices, burrows, and sea-caves. Protection afforded eggs and chicks by these covered nests allowed us to mark 247 individuals with stainless steel bands and check nests with a minimum of disturbance. Each nest was checked weekly between 1993 and 1995. In 1996 and 1997, nests were checked weekly during peaks of egg laying, hatching, and fledging and biweekly after that. During nest checks, we recorded nest content, adult band number, and egg biometry or chick measurements. Other breeding areas were checked April–May and opportunistically in other months of the year to detect possible movements of banded individuals, but none was found in other colonies.

The laying date of the first egg of a clutch was considered the beginning of laying. ''Fledging'' was defined as the first departure to sea of the last chick in the nest, and breeding success was estimated by number of chicks successfully fledged per pair per year. Breeders were categorized according to number of clutches laid per year. Single-clutch breeders, or single brooders, laid only one clutch. Two-clutch breeders laid two clutches. Within this category, double brooders laid a second clutch after successfully rearing chicks (double brooding), and replacement brooders had a second clutch after failing to fledge their first clutch (replacements). Successful double brooders were those that had at least one fledgling during the second reproduction. Clutches of single and replacement brooders did not necessarily produce chicks. Reference to first clutch, unless otherwise stated, includes the first clutch of all three brooding categories.

Both groups of nests were used to determine the phenology of laying, which was estimated from direct observations of eggs laid between nest checks and by subtracting 42 days (Zavalaga and Paredes 1997a) from hatching dates. Within a brood, only first chick hatching dates were used for the analysis. Egg laying, hatching, and fledging dates were measured with an accuracy of ±3.5 days. Only those pairs using covered nests and that were banded the previous year were used for analysis of breeding frequency. Whereas comparable quality data are not available for surface nesting birds, casual observations suggest double brooding is common in this situation too. Adults were sexed using morphometric characters (Zavalaga and Paredes 1997a). Pairs with both individuals banded and pairs with only females banded were pooled because there was no difference in the frequency of the different clutches between those groups ($\chi^2 = 1.88$, df = 8, $P > 0.05$). Pooled data from 1993–1997 were used for the overall analysis. The pairs that laid three clutches were not included in posterior analysis due to the small sample size. To examine whether a change in partner influenced timing of egg laying, we considered that a female changed partner when it bred with a different male the next reproduction. We did not distinguish between changes of partners due to divorce or male mortality. For analysis of timing of first clutches and breeding success, we categorized pairs as ''early'' or ''late'' breeders on the basis of whether they laid the first clutch before or after the total median date of egg laying in each year (Table 1).

We tested normality in the samples using the Kolgomorov-Smirnof test. Parametric tests (Students *t* ANOVA) or nonparametric tests (Mann-Whitney or Kruskal-Wallis) were used to make comparisons between two or more sample means. Chi square tests were used to compare proportions and Pearson Product Moment test was used for correlation analysis. α was set at $P < 0.05$. SIGMA STAT 2.0 was used for statistical analysis. Means are expressed ±SE.

Results.—Humboldt Penguins had an extended period of egg laying, starting in mid-March and ending the first week of December. Laying patterns were cyclical and similar among years, showing a bimodal distribution of clutches each year (Fig. 1). The first peak of laying was very consistent between years and occurred during April, whereas the second peak was much more variable, occurring between the first week of August and last week of September. Additional small peaks in June 1993 and 1995 and in August 1997 may be explained by replacement clutches resulting from nest abandonment. Several nests were flooded by sea waves during ocean swells in May 1993 (25%, $n = 237$), May 1995 (41%, $n = 213$), and June 1997 (11%, $n = 26$), and by exceptional rainfall in September 1997. In 1993, 7% of the adult-banded population died by accidental entanglement in gill nets. The duration of the egg-laying period varied between 229 and 282 days for the 5 years of the study.

The bimodal distribution of egg laying (Fig. 1) appears to be the result of individual birds having sequential multiple clutches within a year (Fig. 2). Of a total of 189 pairs (59 pairs were represented more than once), on average 53, 43, and 4% had one clutch, two clutch and three clutches each year, respectively. Of pairs that had two clutches per year ($n = 82$), 73% were double brooders and 27% replacement brooders. Of pairs that had three clutches per year ($n = 7$), most were replacement brooders during their second (86%) and third breeding attempt (71%).

First clutches of banded pairs were laid over an extended period from 13 March to 8 December (Table 1); however, the majority (62%, $n = 181$) were laid in April. Interannual differences in laying dates of first clutches were mainly due to single-clutch breeders (Table 1). Laying dates of first clutches of two-clutch breeders did not differ among years, except for double brooders, for which the median laying date in 1996 was later than in the other years (Kruskal-Wallis $H = 15.07$, $P = 0.004$; Table 1). Second clutches of replacement brooders were laid from 10 May to 17 November, with 55% of them laid during June and July. Second clutches of double brooders were laid from 12 August to 23 October, but 80% of them were laid between August and September. There were significant differences in median laying dates of second clutches of replacement brooders among years (ANOVA, $F = 4.085$, $P = 0.012$). In contrast, laying dates of second clutches of double brooders did not differ among years (ANOVA, $F = 1.256$, $P = 0.299$; Table 1).

We examined the effect of the ending date and success of the previous reproductive episode and the change of partners on timing of subsequent laying. Within a given year, there was a strong relationship between the end of first and beginning of second reproduction (Pearson, $r = 0.216$, $n = 87$, $P < 0.05$). In contrast, between two consecutive years, there was no relationship between end of reproduction and beginning of laying the next year (Pearson, $r = 0.161$, $n = 45$, $P = 0.29$). Even though the range in dates of when chick rearing ended was large, covering 227 days from 20 July to 4 March, most pairs (82%, $n = 45$) started laying in April the second year. The outcome of the second breeding attempt did not affect timing of laying the next year. The median date of egg laying of successful pairs (16 April, $n = 32$) was similar to that of those that failed their second breeding attempt the previous year (14 April, $n = 15$, Mann-Whitney $U = 310$, $P = 0.259$).

Changing partners between years did not affect timing of egg laying in the next year. Females that retained mates (60%, $n = 33$) had similar mean laying dates (15 April ± 7 days, $n = 20$) to those that bred with a different male (17 April ± 8 days, $n = 13$, Mann-Whitney $U = 233.5$, $P = 0.658$) the previous year. In contrast, timing of egg laying of the second clutch within a year was affected by a change in male for females that successfully reared chicks during the first clutch. Mean egg-laying dates of females that changed partners (20 October ± 8.4 days, $n = 4$) was significantly later than those of females that bred with the same males (10 September ± 2.7 days, $n = 37$, $t = 2.457$, $P = 0.019$).

First clutches of two-clutch breeders (double and replacement brooders) were started on similar dates (Kruskal-Wallis $H = 0.211$, $P = 0.64$) and were earlier

Table 1. Humboldt Penguin egg-laying dates of first and second clutches for three breeding categories[a] from 1993 to 1997 at Punta San Juan.

	First clutches				Second clutches		
	SB	DB	RB	Total	DB	RB	Total
1993							
Median	12 Apr	8 Apr	11 May	12 Apr	13 Sep	20 Sep	13 Sep
Range	5 Apr–8 Dec	20 Mar–12 Apr	28 Apr–7 Jul	20 Mar–8 Dec	18 Aug–13 Oct	2 Jul–17 Nov	2 Jul–17 Nov
n	3	4	4	11	4	4	8
1994							
Median	5 May	12 Apr	8 Apr	20 Apr	8 Sep	27 Jun	26 Aug
Range	6 Apr–15 Aug	13 Mar–24 May	1 Apr–18 May	13 Mar–15 Aug	14 Aug–23 Oct	13 Jun–28 Jul	13 Jun–23 Oct
n	22	14	6	43	14	6	20
1995							
Median	9 Apr	4 Apr	4 Apr	8 Apr	4 Sep	3 Jul	26 Aug
Range	31 Mar–13 Sep	31 Mar–20 May	28 Mar–12 Apr	28 Mar-13 Sep	24 Aug–21 Oct	10 May–19 Aug	10 May–21 Oct
n	19	12	8	41	12	8	20
1996							
Median	26 May	24 Apr	20 Apr	30 Apr	11 Sep	11 Jul	9 Sep
Range	15 Apr–10 Nov	9 Apr–14 May	6 Apr–10 Jul	6 Apr–10 Nov	12 Aug–28 Sep	3 Jul–22 Sep	3 Jul–28 Sep
n	30	13	6	49	13	6	19
1997							
Median	16 Apr	9 Apr	16 Apr	14 Apr	25 Sep	7 Jun	22 Sep
Range	2 Apr–28 Sep	7 Apr–29 Apr	16 Apr–16 Apr	2 Apr–28 Sep	3 Sep–3 Oct	29 May–17 Jun	29 May–3 Oct
n	21	14	2	37	14	2	16

[a] SB = single brooders, DB = double brooders, RB = replacement brooders.

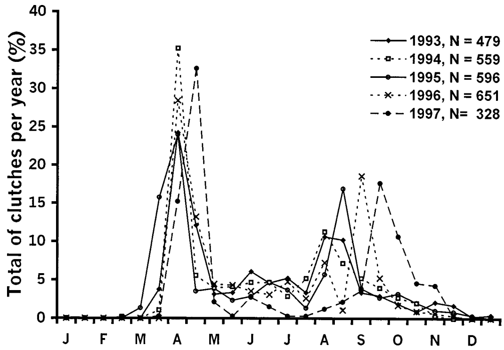

FIG. 1. Phenology of Humboldt Penguin egg-laying during 1993–1997 at Punta San Juan, Peru.

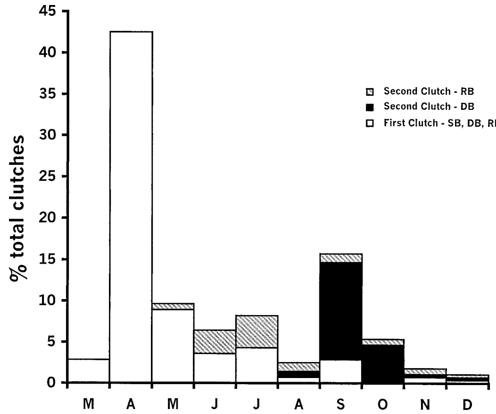

FIG. 2. Distribution of Humboldt Penguin breeding by month for different breeding categories: single brooding (SB), double brooding (DB), and replacement brooding (RB) for the period 1993–1997. $n = 282$.

than those of single brooders (Kruskal-Wallis $H = 25.91$, $P < 0.001$; Table 1). Breeding success of double brooders (2.61 fledglings per pair per year, $n = 59$) was significantly higher than single brooders (0.98 fledglings per pair per year, $n = 94$) and replacement brooders (1.07 fledglings per pair per year, $n = 28$) (Kruskal-Wallis $H = 67.58$, $P < 0.001$). There was no difference between breeding success of replacement and single brooders (Mann-Whitney $U = 1754.5$, $P = 0.777$). On average 58% (range 21–92%, $n = 60$) of double brooders successfully reared at least one chick during their second reproduction.

Early two-clutch breeders had a higher breeding success (2.34 fledglings per pair per year, $n = 58$) than those that laid eggs after the median date (1.65 fledglings per pair per year, $n = 29$, Mann-Whitney $U = 1020.5$, $P = 0.022$). The majority of successful double brooders (80%, $n = 30$) laid first clutches before the median date, whereas single brooder pairs that laid eggs early had a similar success to those that laid later (0.97 vs. 1.00 fledglings per pair per year, $n = 39$ and 55; Mann-Whitney $U = 1834.5$, $P = 0.89$). Thirty-seven percent ($n = 95$) of single brooders overlapped laying dates of first clutches of successful double brooders.

The breeding frequency and success of 11 females were analyzed during three consecutive years. Sixty-four percent of females had two clutches per year during two years and 27% during three years. Most females (73%) had five to six clutches during the three years. The mean combined breeding success of the 11 females over the three years was 4.54 fledglings per pair.

Discussion.—The frequency of a bird's reproduction and time of year at which it occurs are important aspects of its reproductive strategy (Perrins and Birkhead 1983, Löfgren 1984). As expected for a subtropical species, Humboldt Penguins had an extended egg-laying period from March to December, but showed two marked peaks of egg laying in April and August–September. Similar patterns of egg laying have been observed at Pachacamac Island along the northern coast of Peru (Paz-Soldan and Jancke 1998). In Chile, Humboldt Penguins also have two peaks of egg laying, although both peaks are offset by one month (May and October) from timing of breeding in Peru (Population Habitat Viability Analysis 1998).

Birds adjust breeding and molting schedules when conditions are favorable and food is abundant to optimize successful chick rearing (Lack 1954). During this five-year study, most females (62%) began egg-laying after the molt in April, suggesting that it may be the optimal time for reproduction. On the southern Peruvian coast, the catch per effort of anchovy (*Engraulis ringens*), the Humboldt Penguin's main prey (Zavalaga and Paredes 1997a), is highest during summer (December–March) and lowest during winter (July–September) when anchovy schools are more dispersed and in deep waters (Guillen et al. 1971, Bakun 1987). The boom in reproduction during summer in other seabirds that feed on anchovy also suggests that food supply is very abundant. However, Humboldt Penguins molt during this time rather than breed. This suggests that recovery of condition (30% of initial weight lost) might be important for adult survival and a constraint on timing of breeding. In addition, extreme temperatures of summer (up to 35°C) may not be suitable for penguin breeding because of high costs of thermoregulation. Thus, Humboldt Penguins appear to favor breeding immediately after molt when food is still abundant but solar radiation is reduced. Individuals that breed during winter may use other resources, perhaps in conjunction with the higher cost of foraging on anchovies at deeper depths, to sustain breeding activities.

The onset of egg laying following reproduction the previous year in Humboldt Penguins was not affected by date of completion of reproduction, fledging success, or whether a change of mates occurred. These results may be explained in part by the fact that the majority of penguins finished reproduction in December, avoiding overlap with molting and having enough time to recover energy stores before beginning breeding again. In contrast, the timing of the end of the first reproductive episode and the changing of mates affected the timing of the second breeding attempt within a year. This is likely the result of the short time to get ready to breed again when producing two clutches.

The second breeding peak, occurring in August–September, was mainly the result of the capacity of Humboldt Penguins to have a second clutch. The greater among-year variability in the timing of this second peak compared to the first peak appears to be a product of nest abandonment because double brooders had very consistent peaks of egg laying between years, whereas replacement breeders were highly variable.

Timing of egg laying may be particularly important for strictly seasonal penguins because they have relatively short periods when food is abundant or environmental conditions are suitable for breeding (Van Heezik et al. 1994, Williams 1995). In contrast, the subtropical Humboldt Penguin has an extended breeding season and can produce several clutches per year. Although there may be optimum times for laying eggs, timing should not be as constrained because they can breed during most of the year in a productive environment. Nonetheless, we did find that laying eggs early in April might increase the likelihood of having two clutches and a higher annual breeding success. Two-clutch breeders that started to lay eggs before the median date in April had a higher annual breeding success than those females that laid eggs later. In fact, the majority (73%) of successful double brooders started to breed early. Taking into account that a breeding cycle (from egg laying to fledging) lasts ~4 months, laying eggs early in April increases probability of rearing up to four chicks per year.

Timing of egg laying does not seem to be the only factor restricting single brooders to have two clutches per year. Even though single brooders started egg laying later than two-clutch breeders, some individuals laid clutches (37%) on dates similar to birds that had successful double broods. Inexperienced birds (Hario 1997) may be more likely to breed only once. Also, environmental conditions in some years may make it difficult for birds in marginal condition to recover energy stores in the interim to begin a second clutch.

The relatively large percentage of individuals laying one or more clutches following successful fledging of a clutch suggests that high rates of reproduction during years of food abundance may be adaptative for Humboldt Penguins in a productive but unpredictable environment. In fact, a high proportion of penguins (58%) successfully reared two broods per year. During El Niño years, penguins failed or skipped reproduction (Hays 1986, Paredes and Zavalaga 1998). Therefore, having as many clutches as possible when conditions are favorable can maximize the lifetime reproductive success of Humboldt Penguins.

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