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GROWTH PATTERNS OF TWO RACES OF CALIFORNIA GULL RAISED IN A COMMON ENVIRONMENT[1]

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Abstract. Chicks of two races of California Gull (*Larus californicus*), which differ by 27% in adult body mass, grew to fledging at similar rates when maintained in a common environment and provided with food ad libitum. There were sexual differences in growth rates; males, which were larger, developed more slowly than females. Racial differences in size were maintained, but appeared to be smaller in captive adults and juveniles than in wild birds, indicating that both genetic and environmental components influence body size; racial differences in plumage were maintained and seemed to be under genetic control. Growth patterns and asymptotic size of captives differed from those reported for wild birds, reflecting both captivity effects and procedural bias in determining asymptotes in field studies.

Key words: Morphology; Larus californicus; *environmental influences; body size; growth.*

INTRODUCTION

Factors that determine body size have long interested evolutionary biologists. Interest was rekindled by James (1983), who exchanged eggs between several races of Red-winged Blackbird (*Agelaius phoeniceus*) in North America. She found that the shape of the nestlings was shifted toward that of their foster parents and concluded that there was a significant amount of nongenetic variation in the normal phenotype. Alatalo and Gustaffson (1988) conducted a similar experiment on island vs. mainland populations of Coal Tit (*Parus ater*) in Sweden, but detected no environmental effects. Slagsvold and Lifjeld (1985) reported nongenetic differences in plumage color in Great Tits (*Parus major*) reared in different habitats and determined that these reflected dietary influences.

In this paper we report observations involving two races of the California Gull (*Larus californicus*). *Larus c. albertaensis* is a pale-mantled race that nests mainly east of the Rocky Mountains. It averages 27% larger in body mass than *L. c. californicus,* a darker-mantled form that breeds mostly in the Great Basin (Jehl 1987); it also lays larger eggs, and tends to have a larger mean clutch size (ca. 2.45; Jehl, unpubl.) than *californicus,* especially the population at Mono Lake, California (ca. 2.0, Winkler 1985).

To further investigate the basis for the well-defined morphological differences, which have not yet been shown to be associated with genetic differences (Karl et al. 1987), we studied the growth and development of juveniles of both races raised from the egg in a common environment, and we continued our observations on a small subsample maintained to adulthood.

METHODS

In 1986 Jehl collected a single egg from each of 11 nests of *L. c. albertaensis* at Beaverhill Lake, Alberta, and of 12 nests of *L. c. californicus* at Mono Lake, California. Eggs were placed in a portable incubator and transported to San Diego, California, where they were weighed and measured and transferred to a commercial incubator until the chicks hatched (Day 0), between 31 May and 13 June. Chicks were individually color-marked and housed together in a commercial brooder. At about Day 7 chicks were transferred to an identical brooder to minimize competition with later-hatched, smaller young. At about Day 14 (or at a mass of ca. 200 g) they were moved to an outdoor pen with a large freshwater pool and maintained there under ambient conditions for the duration of the experiment (in some cases up to 36 months), except that during the first 2 months they were provided heat lamps for additional warmth at night.

The birds had unlimited access to food throughout the experiment. For the first week they were fed small krill (*Euphausia* sp.) by hand three times daily, but they also fed themselves readily on krill that was always available in food trays. At Day 8 they were switched to a diet of

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50% krill and 50% diced herring, and after Day 14 to intact herring and other small fish. The birds were measured (exposed culmen, wing length from carpal joint to tip, tarsus) and weighed (before feeding) regularly, usually on alternate days, until 10 August (Day 63–68), which was several weeks later than the fledging period of wild birds (ca. 43 days at Mono Lake). Three chicks in each sample failed to thrive and their data were excluded from the growth analysis. The resulting sample sizes were: *albertaensis,* 4 ♂, 4 ♀; *californicus,* 5 ♂, 4 ♀.

After the chicks had fledged, space limitations made it necessary to reduce the flock to six birds (*albertaensis,* 3 ♂, 1 ♀; *californicus,* 1 ♂, 1 ♀). This was done with no conscious selection for size, the retained birds being representative of their race and sex pool. They were maintained until 10 January 1989, when one male from each population was killed for a museum specimen (specimens in San Diego Natural History Museum). The *albertaensis* female disappeared in March 1989; three birds are still under observation.

After Day 75 the birds were measured sporadically. Measurements of living birds are difficult to make with precision. Accordingly, the dimensions of birds assumed to be fully grown (= adults) were calculated as the mean of several measurements taken when the birds were 27–36 months old, except for wing length, which was determined once, from freshly molted birds at 27 months. Weights of individuals varied seasonally, although in parallel, by up to 35%. We averaged the weights of individuals at 11, 19, and 25 months to provide a rough index to body size.

To analyze growth, we applied weight data to the logistic, von Bertalanffy, and Gompertz curves (Ricklefs 1967); in all cases, the logistic curve provided the best fit. We determined the growth constant (K_L) and the t_{10-90} value (the time a chick required to grow from 10% to 90% of asymptotic size), which may be the most useful parameter for comparing growth rates (Ricklefs 1967, Bradley et al. 1984). The determination of the asymptote is a subjective procedure (cf. Zach 1988), which is affected by the duration over which data are obtained. In our study, increase in body mass was not continuous; it reached a plateau at about Day 40, then sometimes dropped for several days before resuming. Therefore, to allow comparison with previous work, we restricted our analysis of weight data to Days 0–45. No limit was placed on determining asymptotes for bill, wing, and tarsus dimensions.

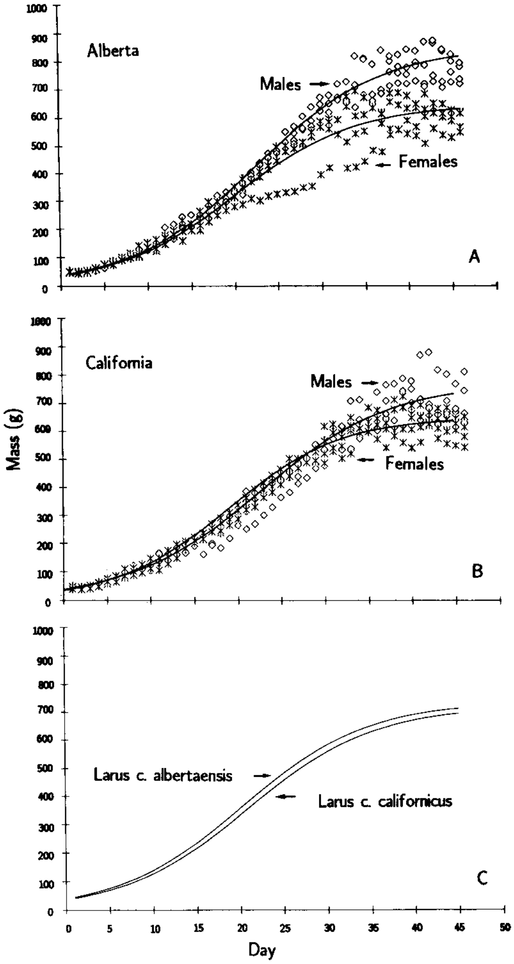

FIGURE 1. Growth curves of (A) *Larus c. albertaensis* and (B) *L. c. californicus* raised under common captive conditions. Diamonds = males, stars = females. In (C) mean weights for each race and day (sexes combined) are fitted to the logistic equation.

Because of significant size dimorphism in California Gulls (Jehl 1987), we analyzed the data by sex, which we determined by external measurements when the gulls were about 2 months old and later confirmed by laparoscopy or postmortem examination.

RESULTS

GROWTH OF CHICKS (DAY 0–68)

At all ages, *albertaensis* chicks averaged larger than *californicus* chicks (Fig. 1); this was a result of the greater average size of the egg (*albertaensis*

TABLE 1. Growth parameters of California Gulls (*Larus californicus*).

Race	Character	Sex	Asymptote	Days	K_L	t_{10-90}
Captive						
L. c. californicus						
Mono Lake[1]	Culmen	♂	45 mm	53		
	Wing	♂	392 mm	73		
	Tarsus	♂	60 mm	33		
	Mass	♂	782 g	38	0.13	33.3
	Culmen	♀	42 mm	55		
	Wing	♀	380 mm	65		
	Tarsus	♀	58 mm	30		
	Mass	♀	656 g	37	0.15	28.7
L. c. albertaensis						
Alberta[1]	Culmen	♂	47 mm	61		
	Wing	♂	404 mm	73		
	Tarsus	♂	61 mm	33		
	Mass	♂	833 g	40	0.14	31.4
	Culmen	♀	44 mm	59		
	Wing	♀	376 mm	65		
	Tarsus	♀	58 mm	30		
	Mass	♀	632 g	38	0.15	30.1
Wild						
L. c. californicus						
Mono Lake[2]	Mass	♂, ♀	~604 g	36	0.20	21.9
Alviso, California[3]	Mass	♂, ♀	620 g	??	0.21	21.1
Bamforth Lake, Wyoming[4]	Mass	♂, ♀	608 g	~36	0.16	27.5

[1] This study.
[2] Winkler 1983.
[3] Jones 1986.
[4] Smith and Diem 1972.

70.5 ± 4.6 cc vs. *californicus* 65.9 ± 4.8 cc) and, consequently, larger hatching weights of the chicks (*albertaensis* 47.5 ± 4.2 g vs. *californicus* 44.9 ± 3.8 g) ($P < 0.05$ in both cases).

There was little difference in the mean growth rates in body mass (sexes combined) of the two populations: *californicus* reached asymptotic mass slightly earlier (ca. Day 37.5 vs. Day 39), but t_{10-90} values were similar (*albertaensis* 30.7 vs. *californicus* 31.0). An intrasexual comparison indicated that males of *albertaensis* grew slightly faster than those of *californicus* (t_{10-90} 31.4 vs. 33.3), whereas females of *albertaensis* grew slower (t_{10-90} 30.1 vs. 28.7). We ascribe the interracial differences to sampling error. Tarsus and wing lengths of both races reached asymptotic size at the same time (tarsus ca. Day 31.5 wing ca. Day 69), but bill length did not (*albertaensis* Day 60, *californicus* Day 54).

Both races showed consistent sexual differences in growth rates, with males taking 1–2 days longer to reach asymptotic size in body mass (Table 1). Similar sexual differences were evident in bill (2 days), wing (8 days), and tarsus (3 days) growth; the only exception was bill length in *californicus*, perhaps owing to errors in measurement.

POSTFLEDGING DEVELOPMENT (DAY 75–36 MONTHS)

As adults, *albertaensis* average 5–12% larger in bill, wing, and tarsus and 27% larger in body mass than *californicus* (Jehl 1987). In the captive flock, the greater size of *albertaensis* was evident in males in all characters by Day 70–75; in females this was true only in bill and body mass (Table 2).

The captives continued to grow slowly, and at 27–36 months *albertaensis* was larger in all characters except body mass of males. In all dimensions, however, the degree of size difference between captive adults and juveniles of each race was less than between wild adults (Table 2).

We did not detect any consistent differences in coloration or markings in either of the two groups in the downy, juvenal, or first basic (winter) plumages. At age 14 months, both forms began to molt into the second basic plumage and

TABLE 2. Dimensions of California Gulls (*Larus californicus*).

	Exposed culmen			Wing (flat)			Tarsus			Mass		
	No.	Mean	Range	No.	Mean	Range	No.	Mean	Range	No.	Mean	Range
					L. c. albertaensis							
Males												
Wild adults[1]	49	53.0	47.3–57.4	48	412.2	385–431	48	63.1	58.6–72.0	32	841	635–1,045
Captive juveniles[2]	4	48.6	45.3–52.3	4	405	391–423	4	60.6	59.5–62.4	4	843	786–866
Captive adults[3]	3	51.9	50.1–54.2	3	416.3	413–422	3	61.1	59.9–63.0	3	793	767–832
Females												
Wild adults	38	47.8	41.2–52.0	38	391.3	369–408	36	57.7	52.8–65.1	19	710	568–903
Captive juveniles	3	43.5	41.0–45.3	3	376	363–386	3	57.6	56.7–59.0	3	740	667–833
Captive adults	1	46.5		1	391		1	58.1		1	689	
					L. c. californicus							
Males												
Wild adults	145	47.3	40.5–59.2	146	395.7	365–415	132	59.0	47.7–65.0	64	657	490–885
Captive juveniles	4	44.2	43.0–45.7	4	392	383–407	4	60.2	58.0–61.5	4	758	715–831
Captive adults	1	48.6		1	415		1	60.7		1	793	
Females												
Wild adults	165	42.6	38.0–48.4	202	372	341–390	153	54.8	43.8–60.5	84	556	432–695
Captive juveniles	4	40.9	40.0–42.3	4	380	370–390	4	58.2	57.3–59.0	4	677	622–767
Captive adults	1	45.0		1	382		1	57.0		1	648	

[1] From Jehl 1987.
[2] Age 70–75 days.
[3] Age 27–36 months.

to acquire gray feathers of similar hue on the mantle. At 25 months, the start of their third year, five of six birds (three of each race) had molted into definitive basic (adult winter) plumage; the remaining bird retained black spots or smudges on a few rectrices. By that time the difference in mantle color that characterizes wild birds of the two populations was obvious.

The California Gull usually does not attain definitive basic plumage until the start of its fourth year (Behle and Selander 1953, Johnston 1956). Its acquisition at the start of the third year has also been observed in captive Kelp Gulls (*L. dominicanus*; F. S. Todd, pers. comm.), another species considered to have a 4-year plumage cycle (Kinsky 1963). Whether the accelerated development observed in these two species is a result of captivity is not known.

In June 1989 (age 36 months), the legs of the *californicus* female had turned bright yellow, as in breeding birds; she was also head tossing and soliciting the attention of the *albertaensis* males, whose legs were still pale gray-green, as is typical of nonbreeders. She made a scrape but no eggs were found. In April 1990 (age 46 months), she produced a clutch of three eggs.

DISCUSSION

GROWTH TO FLEDGING

Larus c. albertaensis is much larger in body size, with larger eggs and a larger average clutch than *californicus*, especially at Mono Lake, where the very small mean clutch size has been linked to low food availability in the prelaying period (Winkler 1985). Because both Alberta and Mono Lake captives achieved similar t_{10-90} values in a common environment, it appears that there are no intrinsic differences in growth rates between the populations. However, growth curves for body mass of captives from Mono Lake differ from those described for wild *californicus* (Table 1); the latter appeared to grow more rapidly until about Day 20, then slowed (Fig. 2); their overall growth rates were higher (Table 1); and wild birds were judged to have reached asymptote 1–2 days earlier, but at 20% less mass (600 vs. 719 g).

Like Smith and Diem (1972), we consider the faster early growth of wild birds to result from the greater ability of adult gulls, than humans, to provision very small chicks. On the other hand, the observation that weight increase in wild birds begins to slow down when they attain a mass of ca. 525 g (Day 20), whereas captives of 525 g (Day 28) are still growing rapidly (Fig. 2) suggests environmental influences, e.g., that wild adults are unable to provide larger chicks with either the quality or quantity of food available to captives, which results in lower asymptotic weight; an alternative view is that adults slow their provisioning rate in order to stimulate the young to fledge faster, and thereby to minimize the risk of loss to terrestrial predators.

Comparisons of growth patterns, however, rely upon accurate estimates of the asymptote, which in our view are likely to be greatly underestimated in field studies. The usual method of studying growth is to fence off part of a colony and weigh chicks until they fledge. But large chicks at any age are more mobile than small chicks, and as fledging nears are more likely to escape. This leads to a diminishing pool of subjects, especially after about Day 30 (e.g., table 35 in Vermeer 1970, p. 44), which then becomes progressively biased in favor of undersized birds. Accordingly, what is commonly reported as "asymptotic mass" (or days to reach asymptote) is more likely to represent the average minimum weight (or age) a chick can attain before it can flutter away (cf. Smith and Diem 1972). Accordingly, published data on growth rates in gulls and other precocial or semiprecocial birds should be carefully evaluated before being used comparatively (see Zach 1988 for a critical review).

POSTFLEDGING DEVELOPMENT

Birds raised in captivity maintained their expected relative sizes, but captive adults differed less in size than wild adults, mainly because *californicus* seemed to attain greater size than in the wild. We emphasize that the sample sizes for adults are, in themselves, too small to sustain this finding, but also note that it is consistent with data from the larger sample of juveniles (Table 2), in which size differences between the races were diminished by Day 70–75. Although additional studies are needed, the results indicate that both genetic and nongenetic factors were affecting body size. In adults there was no evidence of environmental effects on coloration; racial differences were maintained and appeared to be entirely genetic.

Indications of genetic differences between two populations suggest an evolved response to different selective regimes. Earlier, Jehl (1987) proposed that the smaller *californicus* likely evolved in arid, shrub-steppe habitats of the Great Basin, where food is dispersed and patchy, whereas *albertaensis* was associated with freshwater lakes of the prairies and Great Plains, where nearby food supplies may be more predictable and substantial (Vermeer 1970, Kennedy 1973, Baird 1976). Small size is thermally advantageous in hot areas, because small birds can cool off faster, and probably also in areas of low food availability, because small birds can survive on absolutely less food and can replenish their reserves faster after adverse conditions end (Downhower 1976, Monaghan and Metcalfe 1986). Small body mass and associated low wing loading can also enhance foraging at greater distances from the colony, as well as aerial agility (Jehl and Murray 1986). Indeed, *californicus* conspicuously uses aerial foraging to exploit emergences of flying insects (Jehl, pers. observ.), but so does *albertaensis* (K. Vermeer, pers. comm.).

Zink (1989) and Rising (1989) encouraged further studies to assess genetic vs. environmental influences on morphology. We concur, but caution that such studies are labor-intensive, expensive, and more difficult than they may seem. The challenges of maintaining birds under optimal conditions in captivity are minor compared to those involved in cross-fostering studies in the wild, where a season's effort can be forfeited overnight to a predator (e.g., Jehl and Chase 1987). In either instance it is difficult to obtain consistent measurements from living birds, even if they are taken by the same observer (which cannot be done in cross-fostering experiments). Also, because of logistical problems in the field, and of space problems in captivity, sample sizes may be too small to instill much confidence, especially if (as in this study) the data are partitioned by sex. But if that is not done, or accounted for (cf. James 1983), the pooling of data from unequal sex classes in dimorphic species could inflate or reduce the estimates of external influences on phenotypic development.

The growth constants (K_L) for our captives, when converted to Gompertz (K_G) values (*albertaensis* 0.010, *californicus* 0.095), were within the confidence limits plotted for larids by Guerra et al. (1988, fig. 8). Nevertheless, given the potential complications introduced by differences in sampling duration, estimating asymptotes, capture bias, and the pooling of data from birds of unknown sex, we suspect that most of the available data on growth in wild birds, though superficially precise, are too crude to allow detailed quantitative comparisons between different colonies or different species, or between wild and captive populations of the same species. Indeed, we agree with Zach (1988) that data are often overanalyzed and that "simple observed growth statistics rather than growth curve analysis" are sufficient for most studies.

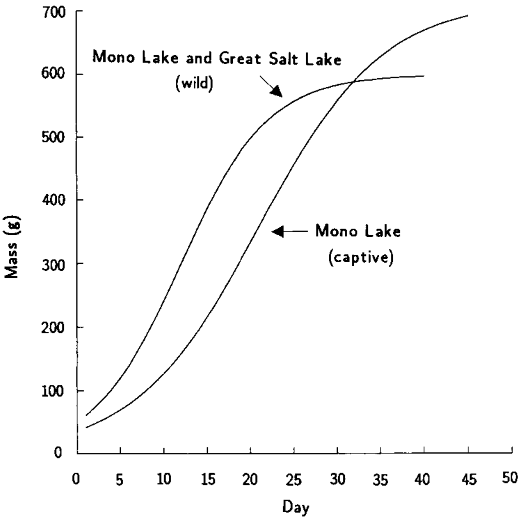

FIGURE 2. Growth curves of captive *Larus c. californicus* from Mono Lake, California, compared with that of wild birds from Mono Lake and Great Salt Lake, Utah (data from Winkler 1983, fide Jones 1986).

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