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Influence of Desert Nesting and Foraging Distance on Growth Rates in Gray Gulls (*Larus modestus*)

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By nesting 35–100 km from the coast in the waterless pampas of the interior Atacama Desert of northern Chile, Gray Gull adults limit themselves to a single daily foraging trip (Howell et al. 1974; Guerra et al. in press [a, b]; Fitzpatrick et al. in press [a]). Limitations on feeding frequency and the amount of food that adults can carry (ca. 18 g dry weight; Fitzpatrick et al. in press [a]; unpubl. data), presumably affects growth rates in young Gray Gulls. General conditions of the Atacama and specific descriptions of the Gray Gull nesting sites were reported by Howell et al. (1974), Guerra and Cikutovic (1983) and Guerra et al. (in press [a]). Information on Gray Gulls and their problems associated with nesting far from food and water in the Atacama, where daily surface and air temperatures range from 2–61°C and 2.5–38°C, respectively, are well documented (Howell et al. 1974; Guerra and Fitzpatrick 1987; Guerra et al. 1988, in press [a, b]; Cikutovic et al. in press; Fitzpatrick et al. in press [a, b]).

We studied growth rates in free-ranging and captive Gray Gull young, and compared them to other semiprecocial species within the Laridae. We hypothesized that, because of food and water limitations imposed by nesting far from the coast, Gray Gulls would have a lower mass growth-rate than other Laridae.

During early January 1986 we hand-captured 23 Gray Gull chicks (33–250 g; 1–ca. 45 days old) at a nesting site located at Cerro Negro, 100 km east of Antofagasta (23°41'S), in the Atacama Desert. Cerro Negro nesting sites were described by Cikutovic and Guerra (1983) and Guerra et al. (in press [a]). Each gull was tagged with a numbered metal band (Model 1242-M, size 10, Nat. Band and Tag Co., Kentucky, USA). Chicks were weighed with Pesola scales, and wing, culmen, tarsus and total lengths measured as described in Fitzpatrick et al. (in press [b]). Twelve gulls were released and 11 were taken to the outdoor aviary on the Universidad de Antofagasta campus, located several hundred meters from the beaches where free-ranging gulls forage. We attempted to recapture and remeasure the released gulls on six occasions between 17 January and 10 February 1986. Eight were recaptured four times; three, three times; and one, twice. The free-ranging gulls were also used to study water-turnover and feeding energetics using labeled water (MS in prep.).

Gulls maintained in the aviary were fed once daily an *ad libitum* diet of fresh or previously frozen sardines (*Sardinops sagax*) and anchovies (*Engraulis ringens*), the principal fish component of Gray Gulls' diet (Guerra et al. in press [b]). We weighed and measured captive gulls every 2–10 days, depending on size, until the age of 100 days. Free-ranging gulls beyond 50 days were not recaptured easily and growth data on them are limited.

We estimated age of chicks from an empirically determined wing length-age curve (Ricklefs et al. 1980). The curve was based on wing length-age relationships for free-ranging and captive chicks which

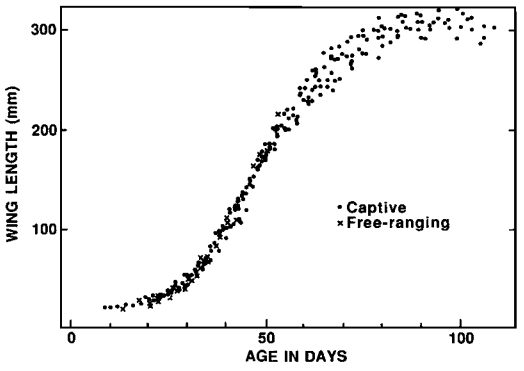

Fig. 1. Comparative age-specific wing growth in captive and free-ranging desert Gray Gull (*Larus modestus*) chicks.

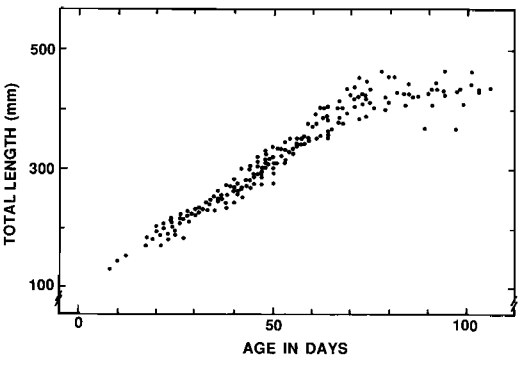

Fig. 3. Age-specific total body length increase in captive Gray Gull (*Larus modestus*) chicks.

we had first banded on the day of hatching. Chicks of unknown age when first measured were compared with those of known age. Growth rate (K) as derived from body mass change was calculated according to Ricklefs' (1967) method which determines the best model (Logistic, Gompertz or Von Bertalanffy) for describing growth.

Increase in wing length was most rapid between 40 and 70 days and became asymptotic at ca. 90 days (Fig. 1). Most fledglings departed from the coast between 50 and 60 days (unpubl. data), which is coincident with the age when banded chicks disappeared from the nesting site. Culmen length increased uniformly until an asymptote at ca. 100 days (Fig. 2). Total length (TL) was not measured in free-ranging chicks to avoid overstressing them. In captive chicks (Fig. 3) TL increased uniformly to the asymptote at ca. 80 days. Tarsus growth was the fastest, becoming asymptotic at ca. 50 days (Figs. 4 and 5). At hatching (<1 h) wing, culmen, body and tarsus lengths represented 5.1, 42.5, 2.3, and 46.7 percent of their respective asymptotic values at complete fledging, demonstrating that culmen and tarsus were in the most advanced condition (Fig. 5). Between 15 and 50 days, mass growth rates differed significantly between free-ranging and captive chicks ($0.025 > P$ ($t = 2.077$) > 0.01) (Fig. 6). Both groups of chicks showed significant relationships between mass and age (15–50 days) (Fig. 7).

Growth data from captive chicks were compared with other Larid species (Ricklefs 1973). The difference between the asymptotic masses of fledglings in the aviary ($\bar{x} \pm SD = 304.0 \pm 31.5$ g; $n = 12$) and those of contemporary fledglings captured on the beaches ($\bar{x} \pm SD = 312.2 \pm 42.1$ g; $n = 16$) was not significant ($t = 0.5615$, $P = 0.2896$). Adult Gray Gulls are considerably heavier than fledglings (females: 342.9 ± 34.7 g, $n = 125$; males: 382.2 ± 39.1 g, $n = 117$; Fitzpatrick et al. in press [b]). The logistic growth model (Ricklefs 1967) most appropriately described Gray Gull growth pattern. From the logistic conversion factor (CF = −0.730 + age in days 0.0222; $r^2 = 0.994$; $n = 12$), the logistic constant, KL, which is directly proportional to growth rate, was 0.0888. Thus, according to the logistic model, mass (M) at any age can be calculated as:

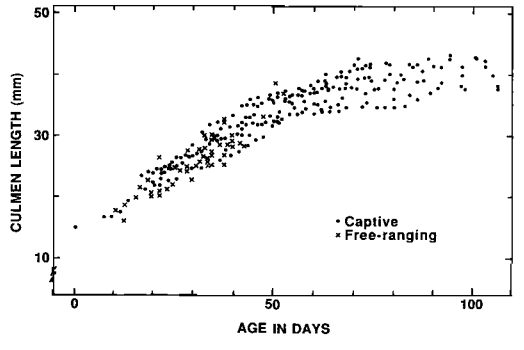

Fig. 2. Comparative age-specific culmen growth in captive and free-ranging Gray Gull (*Larus modestus*) chicks.

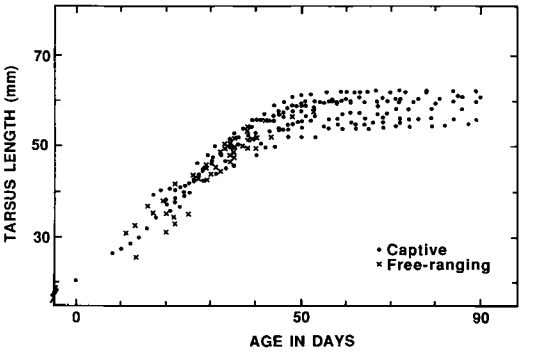

Fig. 4. Comparative age-specific tarsus growth in captive and free-ranging Gray Gull (*Larus modestus*) chicks.

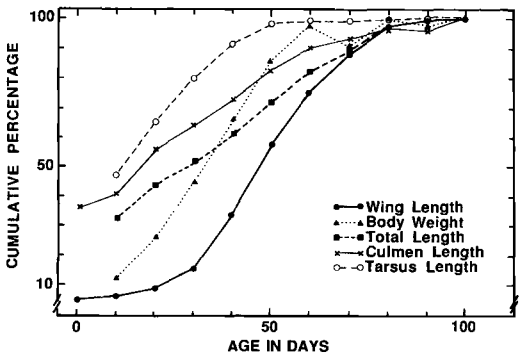

Fig. 5. Increase in morphometric measure of wing, culmen, tarsus, total length, and body mass of captive Gray Gull (*Larus modestus*) chicks as cumulative percentage of their respective asymptotic values.

$$M = \frac{314}{1 + e^{-0.0888(t-32.6)}} \quad (1)$$

where 314 = asymptotic body mass in grams; 32.6 = inflection point on the curve that corresponded to the age when chicks reach 50% asymptotic mass (also = point of maximal growth rate); 0.0888 = K_L, the logistic constant; and t = age in days.

To compare Gray Gull growth with other species, we converted the logistic K_L to the Gompertz K_G (Ricklefs 1973). Thus, following Ricklefs (1973), the Gray Gull K_L = 0.0888 becomes $K_G = 0.68 \cdot K_L = 0.0604$, allowing for direct comparison with other species (Fig. 8; Ricklefs 1973). K_G is significantly correlated to asymptotic mass, but with different slopes that depend on maturity at hatching or mode of development (Ricklefs 1973). Laridae growth rates are correlated to the respective asymptotes for each species (Ricklefs 1973). Using Ricklefs' (1973) data (asymptote, K_G and adult mass) for several of the Laridae (Table 1), we found $K_G = 1.928A^{-0.456}$; $r^2 = 0.977$; $P = 0.0001$.

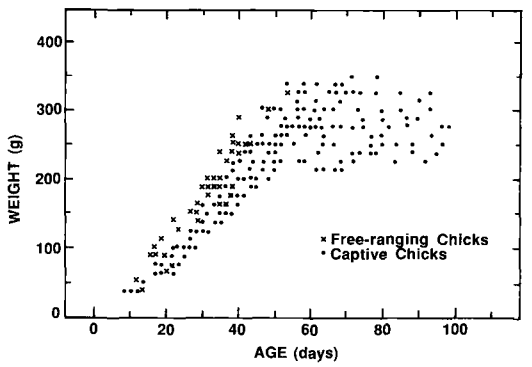

Fig. 6. Comparative age-specific body mass in captive and free-ranging Gray Gull (*Larus modestus*) chicks.

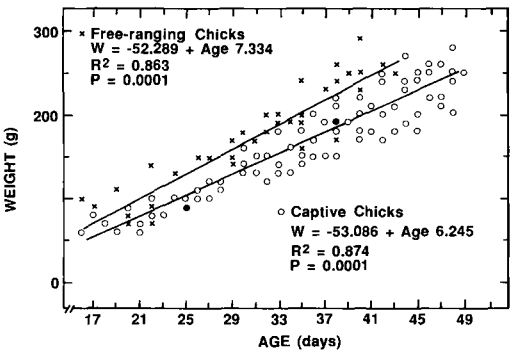

Fig. 7. Comparative age-specific growth rates in captive and free-ranging Gray Gull (*Larus modestus*) chicks.

Because our objective was to test the hypothesis that *L. modestus* had a lower mass growth rate than other members of the Laridae, we omitted it and *L. furcatus*, another long distance forager, from the model (Fig. 8). Both *L. modestus* and *L. furcatus* fell well below the values predicted by the model and outside the lower 95% confidence limit (Fig. 8).

Difference in mass growth (but not in growth of body parts) between captive and free-ranging chicks may be explained by greater activity and stress of captive birds. Normally, chicks in the desert are inactive during the day and expend minimal energy. They become active at night when adults return with food. In the aviary chicks were fed once during the day, but were often disturbed by noise and movement. During the night they were alert especially during the period when adult gulls were heading to the desert and calling among themselves as they flew over the aviary. Although mass growth differed be-

TABLE 1. Growth rate (K_G), asymptotic mass of chicks and adult mass of several species of Laridae (semiprecocial) based on data in Ricklefs (1973).

Species	Asymptote (g)	Growth rate (K_G)	Adult mass (g)
Larus glaucescens	885	0.091	900
L. argentatus	1,080	0.070	1,012
L. fuscus	1,650	0.064	1,600
	850	0.099	854
L. marinus	1,650	0.069	1,659
L. canus	400	0.130	404
L. occidentalis	900	0.080	900
L. tridacytla	380	0.139	407
L. furcatus	660	0.063	690
Sterna paradisaea	105	0.230	105
S. hirundo	130	0.204	125
S. sandvicensis	180	0.175	237
L. modestus[a]	315	0.060	360

[a] Data for *Larus modestus* were determined in this study.

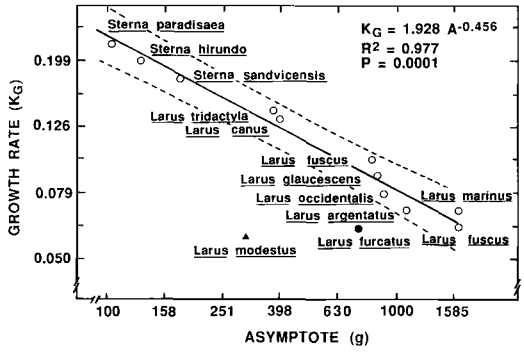

Fig. 8. Regression (log-log) model of Gompertz growth constants (K_G: growth rate) of several Laridae species, excluding *Larus modestus* and *L. furcatus*. Data are from Ricklefs (1973), except for *L. modestus* (this study). Dashed lines represent upper and lower 95% confidence limits of the regression model. Empirical values below this range (*L. modestus* and *L. furcatus*) are significantly lower than predicted values from the model (indicated as closed symbols).

tween free-ranging and captive chicks, the difference in mass between captive fledglings and those contemporaries collected on the beaches was not significant. This suggests that both captive and free-ranging young reached similar masses at the same time.

Laridae are semiprecocial (Nice 1962, Ricklefs 1973, O'Connor 1984), but the growth pattern of some body parts is similar to altricial species (Dunn and Brisbin 1980). The same is true for Gray Gulls when compared to the altricial Brown Pelican (*Pelecanus occidentalis*; Schreiber 1976, Guerra and Cikutovic 1984, unpubl. data). Compared to the larger Herring Gulls, Gray Gulls grow more slowly (Harrison 1983). For example, they require 40–50 days for tarsal growth vs. 20 days in Herring Gulls. Gray Gulls require nearly twice as long to reach their maximal mass as do Herring Gulls. Laughing Gulls (*L. atricilla*; Schreiber and Schreiber 1980) which are closer in size to Gray Gulls than to Herring Gulls, also grow much faster, and reach an asymptotic mass (340 g) in 34–36 days. Tarsus growth in Laughing Gulls is also faster, reaching the asymptote in 36 days.

Chick growth rate is determined by food availability and predation (Lack 1968). Rapid growth reduces chick vulnerability to predation. Thus, in areas without predation such as oceanic islands, chick growth may be expected to be slower than where predation occurs. Gray Gulls at Cerro Negro do not experience predation (Guerra et al. in press [a], unpubl. data). However, Ricklefs (1973) and O'Connor (1984) disagreed with Lack's contention (1968) regarding predation and growth rate. Ricklefs stated that most larids have both high growth rates and high mortality rates, and both are attributed to predation (2%/day). O'Connor (1984) suggested that predators commonly follow adults when they return from their foraging flights to feed the chicks. Therefore, higher growth rates should require an increased frequency of foraging flights which in turn would increase probability of predators finding nests. Ricklefs (1973, 1984) suggested that growth rate was first determined by physiological limitations set by adult size and, second, by precocity of development. The latter has an inverse relation with growth rate (Ricklefs 1973). Altricial chicks which are naked, blind, and have low mobility commonly have a high growth rate. Precocial chicks grow more slowly. Semiprecocials (i.e. larids), which hatch covered with down, eyes open, but with less mobility, should have intermediate growth. Paradoxically (Ricklefs 1973, O'Connor 1984), larids have high growth rates. Ricklefs (1973, 1983) explained higher growth rates among gulls and terns by the fact that chicks are fed by their parents and do not expend large amounts of energy on daily activities.

The growth rate in Gray Gulls may be a compromise related to the long foraging distances that limit chicks to a single daily meal of approximately 67 g wet mass (Fitzpatrick et al. in press [a]). That mass represents a feed size of 17.5 and 19.6% of adult male (382 g) and female (342 g) body mass, respectively (Fitzpatrick et al. in press [b]). According to Ricklefs (1983), pelagic seabirds have a feed size of 14–18 percent of their body mass. The amount of food carried to each chick is close to the daily consumption of anchovies (14–29 g dry mass; $\bar{x} \pm SD = 20.1 \pm 4.3$ g) in captive chicks (Fitzpatrick et al. in press [a]).

Growth in Gray Gulls is comparable to *L. furcatus*, another long distance forager. Also (Howell et al. 1974), the reduced egg mass and clutch size relative to other seagulls, make *L. modestus* and *L. furcatus* more comparable since both species may have difficulties in meeting energy requirements for reproduction. Both *L. furcatus* (Harris 1970) and *L. modestus* are capable of rearing twins. The energy content and quality of food carried daily by adults may be the ultimate factor determining mass growth rate in Gray Gull chicks, as well as clutch size (1 vs. 2 eggs) or whether adults reproduce at all (Guerra et al. in press [b]; Fitzpatrick et al. in press [a]).

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Molt of Primaries and Age Determination in Tengmalm's Owl (*Aegolius funereus*)

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In Tengmalm's Owls (*Aegolius funereus*) which are partly nomadic and band recovery rates are low (e.g. Löfgren et al. 1986, Korpimäki et al. 1987), banding is inadequate for age determination. Some European owls (Strigiformes) molt all primaries annually, while Tengmalm's Owls take more than 1 yr to replace primaries of the juvenile plumage (Glutz von Blotzheim and Bauer 1980, Ginn and Melville 1983, Haarhaus 1983). At 1 yr, Tengmalm's Owls in Germany molt an outermost primary group; at 2 yr, a neighboring middle group; at 3 yr, normally the 7–8 outermost primaries for the second time. They commonly do not molt the 2 innermost primaries until 4 or 5 yr (Glutz von Blotzheim and Bauer 1980: 538; referring to B. Kondratzki and R. Altmüller). While there must be deviations from this pattern from the third year, it should be possible to use the molt pattern to age the owls (Schwerdtfeger 1984).

We investigated the possibility of aging Tengmalm's Owls in northern Sweden from postmolt records. We investigated the pattern of molt in relation to age and sex, and the timing of molt relative to breeding and season. These data are a prerequisite for accurate aging from postmolt records.

We studied birds north of Umeå in northern Sweden (about 64°N, 20°E) in the middle and northern boreal zone (Ahti et al. 1968). The breeding biology of Tengmalm's Owl has been studied here since 1980 (Löfgren et al. 1986, Carlsson et al. 1987). The breeding season is variable and laying dates range from early March until mid-June (Carlsson et al. 1987, Hörnfeldt et al. unpubl.). We followed molt in both captive and wild birds.

We studied 8 captive 1-yr-old owls (collected as nestlings in 1984) and 3 birds when 2 yr old (in 1985–

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