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NESTING ECOLOGY AND REPRODUCTIVE CORRELATES  
IN THE DESERT-NESTING GRAY GULL  
*Larus modestus*

DISSERTATION

Presented to the Graduate Council of the  
University of North Texas in Partial  
Fulfillment of the Requirements

For the Degree of

DOCTOR OF PHILOSOPHY

By

Roberto E. Aguilar Pulido

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During the 1991-92 breeding season, the largest known active nesting colony of gray gulls *Larus modestus* in the Atacama Desert of Chile consisted of 2930 nesting pairs. Nest dispersion was clumped, facilitating group defense against avian predators. Clutch size, which averaged 1.56 eggs with relative frequencies of 0.44, 0.55 and 0.01 for one-, two- and three-egg clutches, was similar to other colonies throughout the Atacama. Egg volumes were similar to those in other colonies. First-laid eggs were larger (48.9 cc) than second-laid (45.5 cc) and single eggs (47.5 cc). Mean incubation time differed significantly between first-(28 days) and second-laid (29 days) eggs. Single eggs required 28 days to hatch. Hatching success was higher in two-egg (0.90) than single-egg (0.67) nests. Overall, 1.6 hatchlings were produced per nest, 4042 for the colony. Chicks from single-egg nests grew faster than those with nest mates, demonstrating food restriction effects imposed by the single daily foraging flight by their parents to the coast 15 km away.

Egg temperature during incubation ranged from 30°C, during the night (24:00-02:00 h) when eggs were exposed while nesting adults interacted with their mates which had returned from foraging, to 39°C, when adults stood during the day (14:00-16:00) for convective thermoregulation. Chicks developed thermoregulatory ability 5 days post hatching, coincident with the time when both adults began to forage at the coast. Chick thermal neutral zone was between 25° and 40°C, somewhat higher than for other larids. Thermal tolerance of embryos (17° - 41°C) was similar to other seagulls.

## ACKNOWLEDGMENTS

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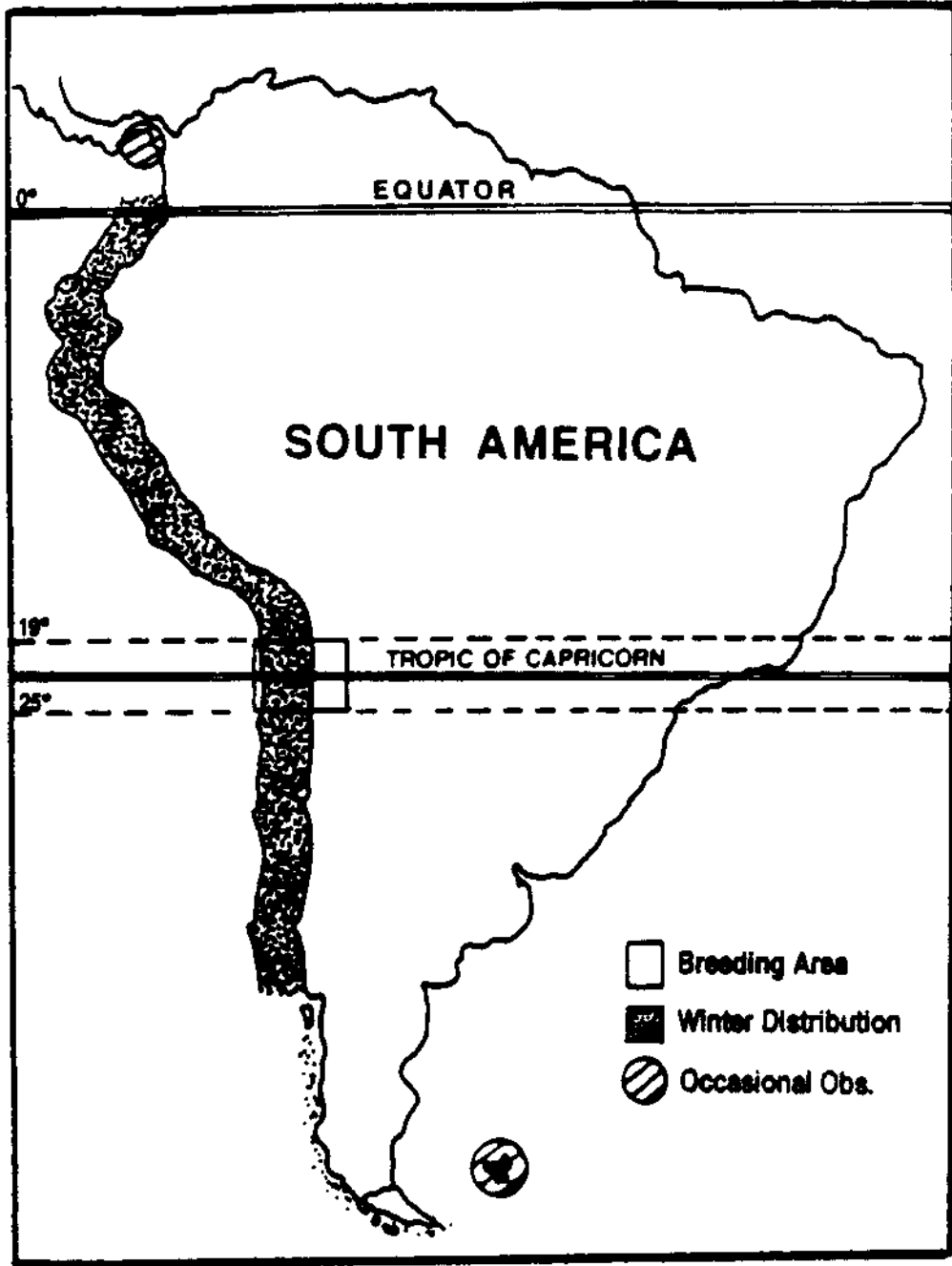
## CHAPTER I

### INTRODUCTION

Gray gulls (*Larus modestus*) are abundant on the Pacific coast of South America between 0° and 40° S lat. (Goodall et al. 1951; Howell et al. 1974; Meyer de Schauensee 1982). During the reproductive season (August to March), their geographic distribution is restricted to northern Chile where they nest 25 - 100 km from the coast in the Atacama, the driest and most barren desert on earth (Howell et al. 1974) (Figure 1). The nesting ecology of gray gulls, which requires daily foraging flights to the coast and exposes them to extreme daily meteorological conditions (e.g., ground temperature = 2-61°C, air temperature = 2.5-38°C, wind velocity = 0-55 km/h, radiation = 0.15-1.4 Kw/m<sup>2</sup>, relative humidity = 5-99%) (Howell et al. 1974; Guerra et al. 1988a), has resulted in several unique adaptations and evolutionary compromises among life history, physiological and behavioral traits, and their demographic consequences (e.g., Murphy 1936; Yañez 1949a, 1949b; Goodall et al. 1951; Johnson 1967; Tovar 1968; Moffett 1969; Chapman 1973; Howell et al. 1974; Devillers and Terchuren 1976; Cikutovic and Guerra 1980; Guerra and Cikutovic 1983a, 1983b; Guerra 1987; Fitzpatrick et al. 1992)

Figure 1. Geographic distribution of gray gulls *Larus modestus* during breeding (September-March) and non-breeding seasons (April-August), including occasional observations in the Gulf of Panamá and the Falkland Islands.



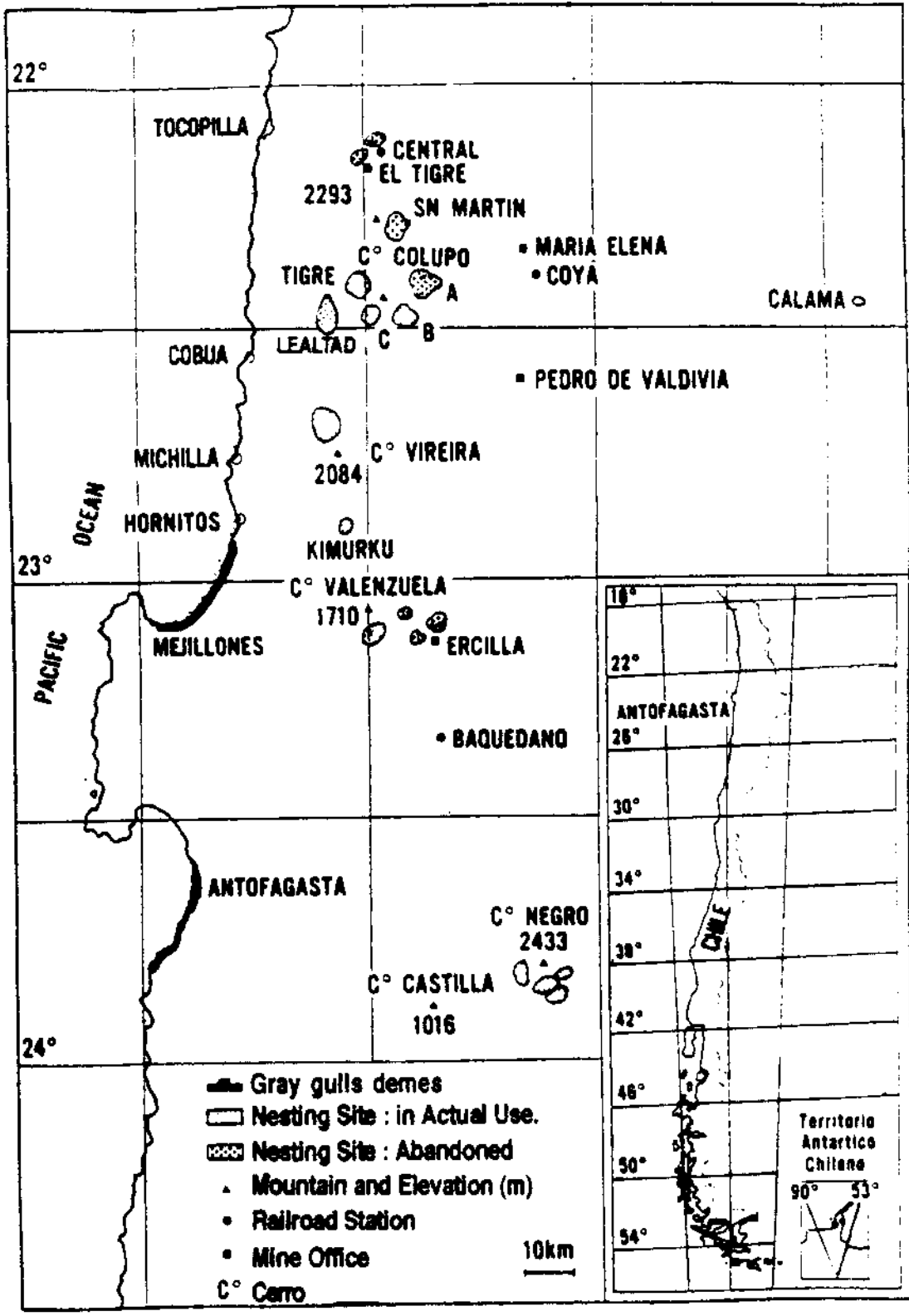


Several explanations have been offered for the unique reproductive behavior of gray gulls. Howell et al. (1974) suggested that they breed in the same place where their ancestors did during the Pleistocene, when there was a large saline lake from which the "salares" or nitrate deposits developed. This explanation would account for the behavior of *L. modestus* that nest in the Colupo area (Figure 2), but not for those nesting further inland, beyond where the prehistoric lake existed. A second explanation considers reduced aggressiveness in gray gulls compared to the other sympatric and coastal-nesting kelp (*Larus dominicanus*) and band-tailed gulls (*Larus belcheri*): to avoid interspecific competition for nest sites, gray gulls nest in the desert. However, coastal censuses have shown *L. modestus* to be numerically the dominant species, especially during the reproductive season, when other gulls reduce their presence (Guerra 1987, 1990). Thus, interspecific competition for nest sites would appear to be minimal. A third explanation relates to nest predation, principally by turkey vultures (*Cathartes aura*) and humans. According to Guerra and Cikutovic (1983a), Guerra (1987) and Fitzpatrick et al. (1992), gray gulls may be relocating their nests deeper into the desert to escape predation and human exploitation of their eggs. Gray gull eggs from the Colupo colony (Figure 2) were sold commercially in Tocopilla before the nesting site was abandoned. Local residents observed that both turkey

vultures (*C. aura*) and condors (*Vultur gryphus*) started visiting the Colupo colony prior to departure of gray gulls. Additionally, mining activities and use of explosives in the nitrate pampas have been implicated as other factors promoting the movement of colonies of gray gulls (Guerra 1987; Fitzpatrick et al. 1992).

The first gray gull nesting sites were discovered in 1919 by A. Johnson in the area of Centro Lagunas (nitrate mines) (Goodall et al. 1951) and in 1943 by J.D. Goodall, A. Johnson and R.A. Philippi (Goodall et al. 1951) to the east of the Colupo mountains ( $22^{\circ}66' S$ ;  $69^{\circ}59' W$ ), 35 km. from the coastal city of Tocopilla (Figure 2). However, the large Colupo colony, which covered  $5.5 \text{ km}^2$  and contained ca. 10,000 nesting pairs (Howell et al. 1974), was abandoned in the early 1970's (Devillers and Terschuren 1976; Guerra and Cikutovic 1983a). Locations of active nesting colonies were unknown until 1980, when C.G. Guerra discovered a small colony several kilometers NE of the railroad station known as Palestina at the base of Cerro Negro ( $23^{\circ}52' S$ ;  $69^{\circ}43' W$ ; Figure 2), ca. 90 km from Antofagasta (Guerra and Cikutovic 1983a). Later in 1983, additional colonies were discovered at Cerro Negro and Kimurku (Guerra et al. 1988c). The former, located 100 km SE from Antofagasta, is the most inland site known. The latter is near the Kimurku mountains 35 km east of the coastal city of Mejillones (Figure 2).

Figure 2. Active and inactive gray gull *Larus modestus* nesting sites in the Atacama Desert.  
(Modified from Guerra et al. 1988c. After Guerra 1987).



Simultaneous breeding of two distinct gray gull demes at Kimurku and Cerro Negro provided an opportunity for Guerra, Fitzpatrick and collaborators (Guerra and Cikutovic 1983a; Guerra 1987; Guerra and Fitzpatrick 1987; Cikutovic et al. 1988; Fitzpatrick and Guerra 1988; Fitzpatrick et al. 1988a; Fitzpatrick et al. 1988b; Guerra et al. 1988a; Guerra et al. 1988b; Guerra et al. 1988c; Guerra et al. 1988d; Fitzpatrick et al. 1989 Guerra et al. 1989; Guerra 1990; Fitzpatrick et al. 1992) to compare and quantify the effects of different daily foraging trips (ca. 200 vs. 70 km) on their life history biology and energy allocation. Their research has demonstrated that *L. modestus* is uniquely adapted to and constrained by its nesting of up to 100 km from the coast in the desolate pampas of the Atacama Desert of northern Chile. Nesting in the Atacama exposes gray gulls to intense solar radiation and the inseparable combination of high temperatures and water scarcity: diurnal surface temperatures far exceed the upper limit for most animals, especially homeotherms (e.g., 61°C), and absence of water requires them to commute long distances for food and water. Thus, nesting under severe physiologically-challenging desert conditions, at distances from the coast sufficient to limit foraging to once per day, places major constraints on time, energy and water budgeting in gray gulls, and affects their overall life history tactics for resource allocation between somatic maintenance and reproduction (Fitzpatrick et al. 1992).

Consequently, gray gulls exhibit adaptations and evolutionary divergence from other larids, including those inhabiting desert environments.

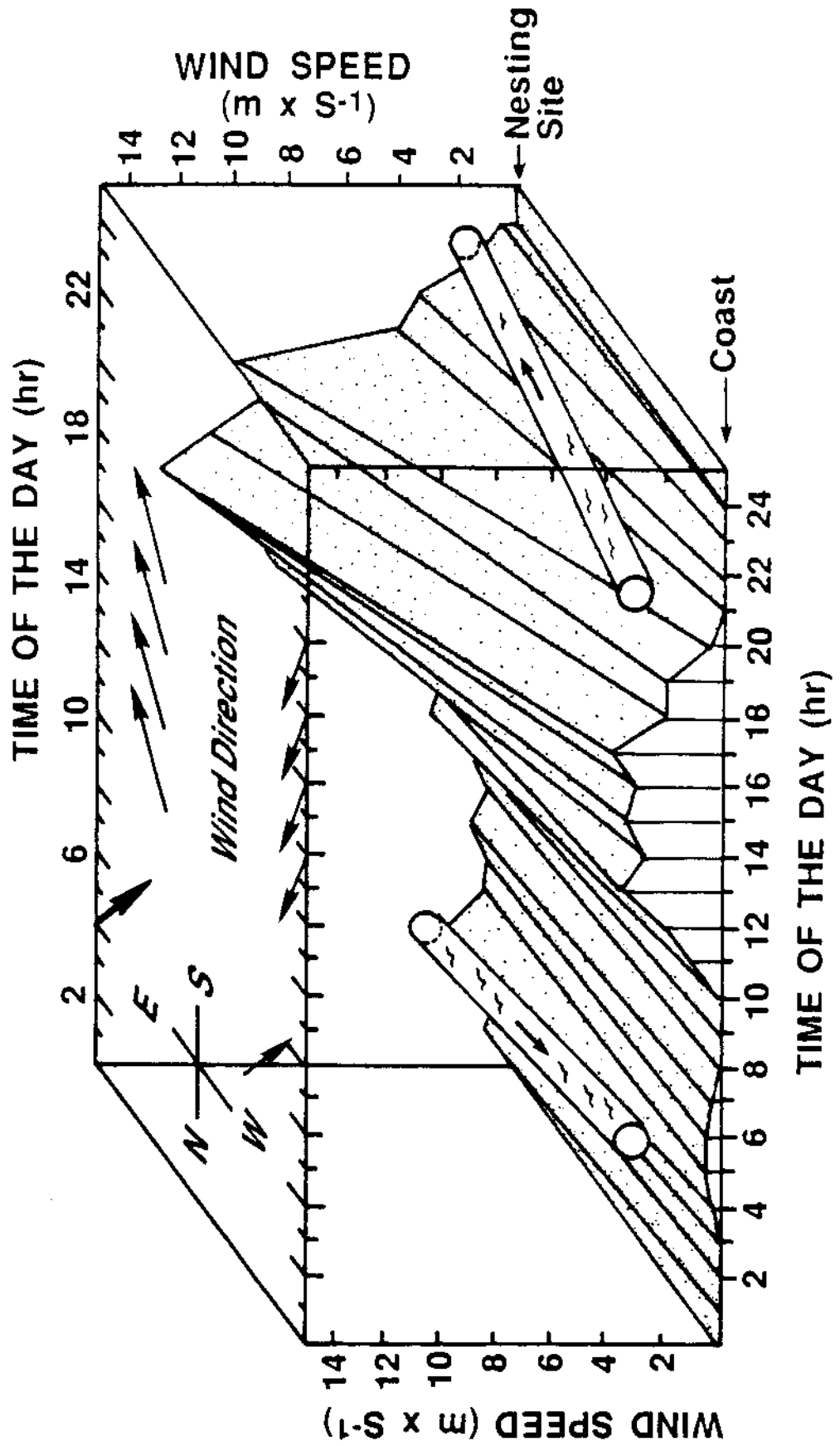
During the breeding season, beaches from Tocopilla to Antofagasta ( Figure 2) are densely populated with gray gulls (ca. 10,000 at Mejillones). As sunset approaches, they congregate offshore in flocks that ascend in spirals to heights over 1,000 m. After sunset, they fly inland to nesting sites in the Atacama. These flights coincide with decreasing wind velocity at the coast and in the desert (19:00-21:00 h)(Fitzpatrick et al. 1988a). Gulls depart the desert at ca. 04:00 h, catching a tail wind from the Andes, and arrive at the coast just before sunrise (Fitzpatrick et al. 1988a). According to Guerra (1987) and Fitzpatrick et al. (1988a), daily flights correspond to three major environmental factors: (1) wind patterns and thermals; (2) food availability; and (3) predator avoidance. Taking advantage of wind and thermal patterns should reduce energy requirements for gaining altitude to cross the coastal mountains and decrease the average flight time to the coast. Since food availability is high in the early morning and gray gulls are visual predators, early morning light hours should be optimal for their foraging. Return to the desert after dark reduces chances of being tracked by predaceous birds, such as turkey vultures which are the most important predators on their eggs and hatchlings. When gray gulls fly

to the desert (Figure 3), turkey vultures have already returned to their nocturnal roosts.

Nesting sites, characterized by Fitzpatrick and Guerra (1988) and Guerra et al. (1988c). Consist of sandy substrate covered with small rocks and frequently cut by dry channels in alluvial fans. Nests are of two types: (1) simple shallow scrapes in the sand away from rocks; and (2) shallow depressions surrounded by guano deposits juxtaposed to the SW side of small rocks. The former are used by adults during incubation and tending chicks for the first week post-hatching. During incubation and brooding, nesting pairs alternate daily foraging flights to the coast. Afterwards, both forage, leaving chicks unattended for 20 h from 04:00 to 24:00 h for ca. 2 mo when they are old enough to leave for the coast (Guerra et al. 1988d). Sites on the SW side of small rocks are used by chicks as refuges. During the hottest period of the day (11:00-14:00 h) the lowest ground temperatures coincide with the chick refuges, where the highest wind velocities occur during the same period, facilitating convectional thermoregulation by chicks. In contrast, when the cool desiccating night wind blows from the Andes, the lowest wind velocities occur at the rock refuges, enabling chicks to avoid their chilling effects (Fitzpatrick and Guerra 1988).



Figure 3. Relation of foraging flights in gray gulls *Larus modestus* to wind velocity and direction at nesting site and on the coast. (taken from Fitzpatrick et al. 1988. After Guerra 1987).



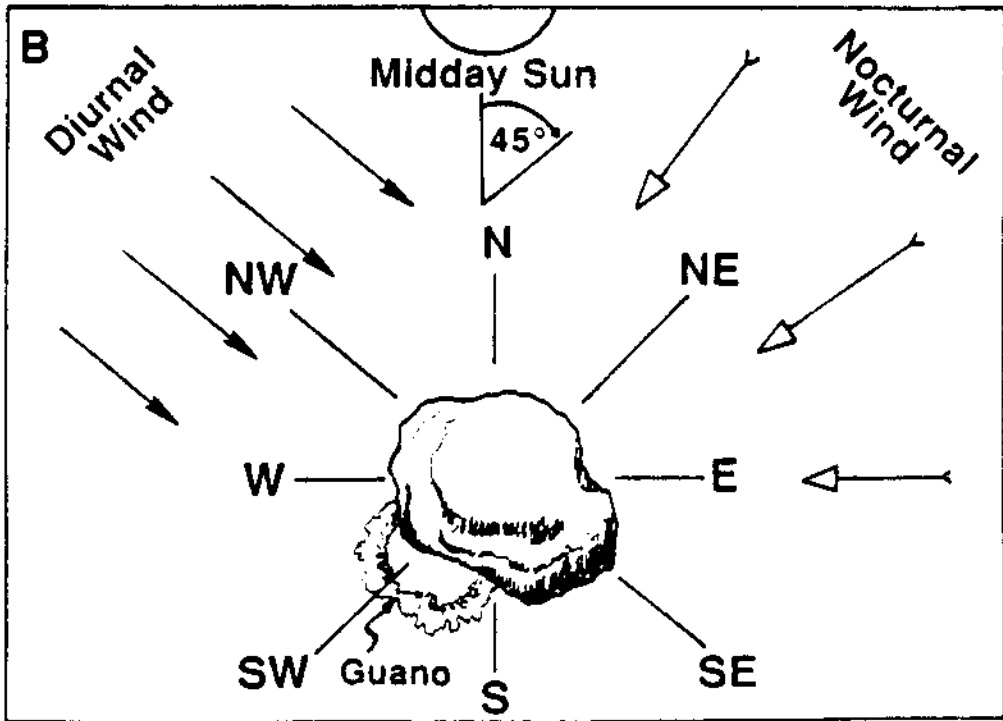
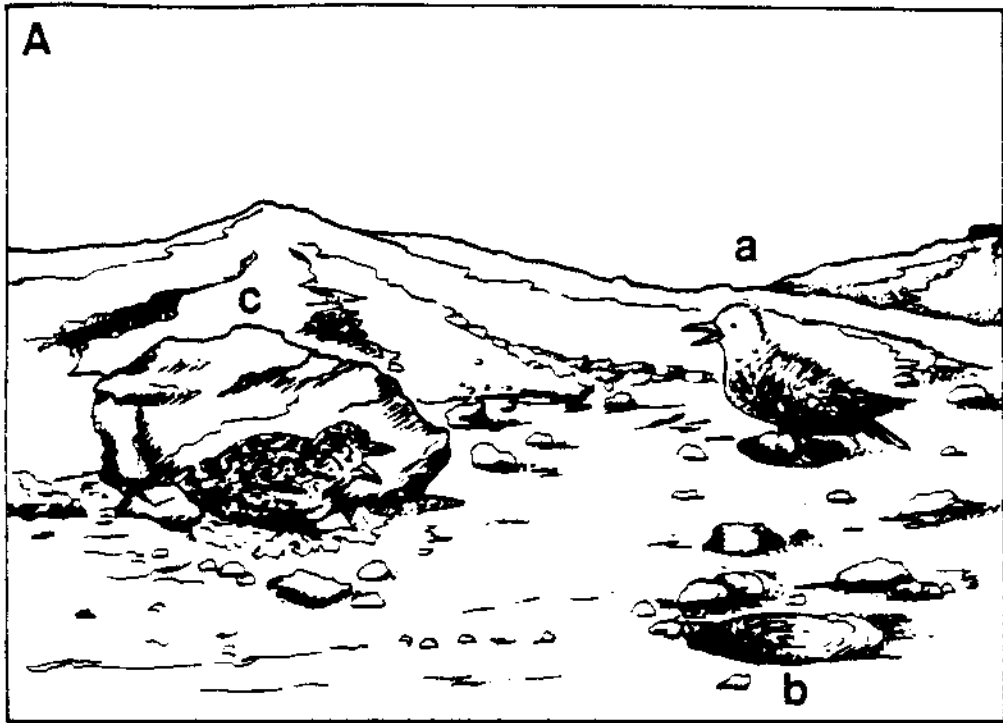
Since rocks usually are too small to afford similar protection for adults, they incubate and tend newly-hatched chicks in the open, where they take advantage of the wind for convective cooling, by erecting their dark plumage and standing with spread wings during the hottest hours (Figure 4). According to Walsberg et al. (1978), erected feathers, especially dark ones, reduce heat load transmitted to the skin. When adults stand, their eggs are exposed to a highly desiccating environment (Guerra et al. 1988a). Additionally, incubating adults leave their nests, to distract turkey vultures and falcons (*Falco sp.*), exposing eggs to both dry air and direct sunlight (Guerra 1990; Fitzpatrick et al. 1992). However, it appears that gray gull eggs have been selected for reduced functional pore area to reduce water loss (Guerra et al. 1988a). This, combined with thermoregulatory behavior are among the most important adaptations in gray gulls for successful reproduction in the Atacama Desert (Guerra et al. 1988a). Wide daily fluctuations in ambient temperature and adult nest-tending behavior, also have resulted in additional adaptations relative to other larids: (1) wide thermal neutral zone (TNZ); (2) capacity to tolerate hypothermia and hyperthermia; (3) low standard metabolic rate (SMR); and (4) efficient thermoregulatory behavior (Fitzpatrick et al. 1992).

According to Guerra et al. (1989) and Fitzpatrick et al. (1992), metabolic rate in gray gull is temperature-

Figure 4. A. Sketch of a typical gray gull *Larus modestus* nesting site, showing an incubating adult thermoregulating and shading eggs (a); an empty incubation scrape (b); a chick within a refuge next to a rock(c).

B. Relation of a chicks refuge, defined by a ring of guano, to daily winds and sun at midday.

(Taken from Fitzpatrick and Guerra 1988; Fitzpatrick et al. 1991. After Guerra 1987).



independent within 26-32<sup>0</sup> C, their TNZ. Although their standard metabolic rate (SMR = 0.0209 KJg<sup>-1</sup>h<sup>-1</sup>) is significantly lower than those reported or predicted (0.0227 KJg<sup>-1</sup>h<sup>-1</sup>) for sea birds of the same body mass as gray gulls (Ellis 1984), the lower limit of their TNZ is higher than for other gulls (Champell et al. 1984). The higher or lower limits may result from different nocturnal behavior of young gray gulls. Between 24:00 and 04:00 h young gulls (chicks and fledgling) are active, increasing metabolic heat production, as they are fed by and interact with adults which have returned from foraging (Guerra et al. 1989). After adults depart, the young gulls are inactive during the coldest hours (04:00-07:00 h), taking shelter from the cold Andean winds next to rocks or within shallow dry channels (Fitzpatrick and Guerra 1988; Guerra et al. 1988c). During those hours, young gulls may increase heat generation metabolically through post-feeding heat increment associated with digestion (specific dynamic action) and shivering thermogenesis. Low nightly temperatures and cold wind may be more challenging to small chicks than diurnal ambient conditions. Clearly, they must have ability to generate and maintain heat when left unattended before adults arrive and after they depart. Metabolic rate in young gray gulls is 1.31-1.91 times higher during the 3 h after feeding, and

nearly four times their SMR at ambient temperature of 6–10°C (Guerra et al. 1989; Fitzpatrick et al. 1992).

According to Guerra et al. (1989) and Fitzpatrick et al. (1992), gray gulls post fledging effectively thermoregulate between 14 and 29°C, but become slightly hypothermic below and hyperthermic above that range. Hyperthermia, which decreases both water and energy loss through lowering the body-ambient temperature gradient, should reduce dependence on evaporative cooling and allow adult gray gulls to stand above their nests during the hottest hours of the day for convective thermoregulation. Thermoregulatory behavior in gray gulls is less costly than for the sympatric congener, *L. belcheri*, an adaptation for desert nesting that reduces both water and energy loss (Fitzpatrick et al. 1989).

Although gray gulls are well-adapted in terms of color, behavior, physiology and thermal tolerance to nesting in the Atacama Desert, there are several trade-offs affecting their reproductive biology relative to other sea gulls. These include: (1) longer incubation time; (2) slower growth rate; (3) reduced clutch size; and (4) sensitivity to marine productivity (Fitzpatrick et al. 1992). Guerra et al. (1988a) stated that prolonged embryonic development (28–30 days) is a consequence of reduced functional pore area of egg shells, which results in both low water vapor conductance and exchanges of metabolic gases, CO<sub>2</sub> and O<sub>2</sub>. Although Laridae

are classified as semi-precocial (O'Connor 1984; Ricklefs 1973), growth in gray gulls is the lowest of those reported for the family. Slow growth may be one of the effects of the long distance adults travel to obtain and food. The limited amount of food carried daily by gray gull adults may be the ultimate factor determining chick growth rate (Guerra et al. 1988b) and an important regulator of clutch size (Guerra et al. 1988d).

According to Guerra et al. (1988d), gray gulls did not reproduce during the 1982-83 El Niño-Southern Oscillation (ENSO), or the following breeding season of 1983-84. The population appeared to recover from ENSO during 1984-85, but laying was delayed until late December-early January. Normal laying resumed in 1985-86, coincident with the return of high densities of anchovies, the principal food of gray gulls. Coastal census during February 1986 showed a large fledgling recruitment (54.4% of total individuals censused). Gray gull females appear to "bet hedge" (Stearns 1976), altering their clutch size from zero to one or two according to food availability (Guerra et al. 1988d; Fitzpatrick et al. 1992).

Information obtained from previous work by Guerra, Fitzpatrick and collaborators seems sufficient for quantitative comparisons of different activities and testing certain hypotheses concerning effects of desert nesting on the evolution of several life history parameters in gray gulls. Time-budgets and energetics of foraging, and their



relations to reproduction demonstrate that gray gulls are well adapted to nesting in the Atacama Desert (Fitzpatrick et al. 1988a). However, information is still incomplete about: (1) demographic patterns; (2) thermal profiles and metabolism in embryos; (3) ontogeny of thermoregulation; (4) growth rates of chicks in nesting sites close to the coast; and (5) comparative growth rates of chicks from one vs. two-egg clutches. The main reason for this incompleteness is that, until 1989, the only known gray gull nesting colonies were composed of relatively small widely dispersed groups or subcolonies, as much as 10 km apart, with individual nests separated by up to several hundred meters. Hyperdispersed nesting within and among subcolonies has made it extremely difficult to study nesting gulls (Fitzpatrick et al. 1992).

Three years ago Guerra and collaborators discovered the largest known currently active nesting colony of gray gulls, NE of Lealtad mountain ca. 15 km from the coast and 45 km SE of Tocopilla (Guerra 1990; pers. obs) (Figure 2). Guerra estimated that the Lealtad colony consists of ca. 5472 breeding adults, with a nest density (3420 /km<sup>2</sup>) significantly greater than other known active nesting sites. The large number of breeding gulls and high nest density provided an excellent opportunity to conduct studies necessary to continue the comprehensive study begun in the early 1980's by Guerra, Fitzpatrick and collaborators, and to provide insight for the protection of this unique species,

now officially considered susceptible to becoming endangered by human activities (e.g., intensive anchovy fishing, pollution, mining activities and egg exploitation; Fitzpatrick et al. 1991).

General objectives of my study were to describe the reproductive ecology of gray gulls in the large Lealtad colony, with emphasis on demographic parameters and physiological adaptations of eggs and chicks, which would complete some original objectives established in the early 1980's by Guerra and Fitzpatrick. Specifically, my study focused on describing, then comparing with other desert and non-desert nesting larids, interactive effects of ambient physical conditions and nest-site predation on eggs and chicks. I addressed the following specific hypotheses:

**Hypothesis 1** - As suggested by Guerra (1990), the presence of avian predators should select for tactics of spatial and temporal nest dispersion, and clutch size that maximize egg and chicks survival. Preliminary observations suggest that nest density at Lealtad increases from the edge toward the center. Thus, I hypothesized that nest dispersion is clumped, which should facilitate efficient group defense against turkey vultures and minimize egg exposure to dry environment when adults fly to distract or defend nests from predators.

**Hypothesis 2** - As suggested by Lack (1968), reduced clutch size in birds that feed far from their breeding site is an

adaptative response to the cost of obtaining food for their chicks. According to Guerra et al. (1988d) and Fitzpatrick et al. (1991), clutch size in *L. modestus* reflects the pattern observed in long distance-foraging seabirds (i.e., pelagic). Comparing clutch sizes during 1985-87 of two populations breeding at different distances from the coast (100 vs. 35 km), they speculated that the lower average clutch size and frequency of two-egg clutches at 100 km may be a function of the greater cost of commuting 200 km daily to provision offspring. Thus, I hypothesized that clutch size of the population breeding in Lealtad (15 km from the coast) should be greater than for the more inland sites.

**Hypothesis 3** - As an extension of Hypothesis 2, clutch size of one vs. two eggs should show differences in mass/energy content and/or incubation time. Therefore, I hypothesized that the average incubation time of two-egg clutches should be longer than single-egg clutches.

**Hypothesis 4** - Since Schreiber et al. (1979) and Sydeman et al. (1991) have indicated lower egg-hatching success in smaller than larger clutches and Guerra (1987) suggested that during years of normal marine productivity single eggs are laid predominantly by young females in their first reproductive season, I hypothesized that egg-hatching success in should be higher in two-egg is than single-egg clutches.

**Hypothesis 5** - Because of gray gull nest defense and thermoregulatory behavior during the day, and exchange of

incubation duties between parents during the night (Fitzpatrick and Guerra 1988; Fitzpatrick et al. 1989), their eggs and nestling are often exposed to desiccating wind, intense solar radiation and high temperatures, and low temperatures and cold wind, respectively, which increase the probability of egg mortality. Therefore, I hypothesized that embryos, which are ectothermic, should have a wider range of thermal tolerance (i.e., lower critical thermal minimum and higher maximum) than embryos of congenics.

**Hypothesis 6** - Guerra et al. (1988a) established that, as an adaptative response to frequent exposure to high temperatures and solar radiation, shells of gray gull eggs have reduced functional pore area that minimizes water loss. However, this may prolong embryonic development because of concomitant attenuation of  $O_2/CO_2$  exchange. Thus, I hypothesized that the overall metabolism of developing gray gull embryos should be lower than in embryos of other gulls.

**Hypothesis 7** - Since food is limited by the amount (18 g dry mass; 317 KJ) an adult carries during its single daily foraging flight (Fitzpatrick et al. 1988a), simultaneous foraging by both adults would be adaptive. Therefore, I hypothesized that chicks should develop the capacity for thermoregulation earlier than other semi-precocial larids.

**Hypothesis 8** - As an extension of Hypothesis 7, I hypothesized that the onset of thermoregulation should

coincide with the time chicks are first left alone in the desert, when both parents begin forage simultaneously.

**Hypothesis 9** - Dawson and Bennett (1973) pointed out that desert homeotherms show relatively low standard metabolic rates (SMR), which would reduce caloric demands in environments of low food availability. Since gray gull adults have lower SMR than other gull species of similar mass (Guerra et al. 1989), I hypothesized that chicks also should have lower SMR than similar sized chicks of other species.

**Hypothesis 10** - Because chicks are left alone in the desert, they are exposed to a wide range of ambient temperatures (e.g., surface temperature = 4-61°C, air temperature = 2.5-38°C) during each day, I hypothesized that gray gull chicks should exhibit a wider thermal neutral zone (TNZ) than chicks of species inhabiting environments having less extreme thermal variation.

**Hypothesis 11** - Since, as stated by Guerra et al. (1988b), chick growth rate is limited by the amount of food that adults carry during their single daily foraging trip, single chicks should receive more energy for growth than those with nest mates. Thus, I hypothesized that single chicks should grow faster than those in two-chick nests, and that differences between growth rates should be greatest during low productivity years (see Guerra et al. 1988d)

**Hypothesis 12** - According to Lack (1968), chick growth rate is determined by food availability and predation; rapid

growth reduces the time when chicks are vulnerable to predation. In areas without predation chick growth should be slower than where predation occurs, such as on oceanic islands or deep in the Atacama. Therefore, I hypothesized that chicks at Lealtad (predators present), should grow faster than those in Cerro Negro (predators absent).

## CHAPTER II

### MATERIALS AND METHODS

I conducted the study reported herein during the 1991-92 breeding season on the gray gull population that occupies the sandy beaches between Tocopilla and Mejillones and nests 15 km from the coast near Lealtad Mountain (Figure 2). Experimental studies were conducted at the Lealtad site and in Dr. Carlos G. Guerra's laboratories at the Instituto de Investigaciones Oceanológicas of the Universidad de Antofagasta (IIO/UDA).

I focused, according to my specific objectives, on describing and/or determining: (1) ambient physical conditions (temperature, solar radiation, wind velocity); (2) spatial dispersion of nests; (3) clutch size; (4) length of and temperature incubation; (5) egg-hatching success; (6) thermal profile and metabolism of embryos; (7) ontogeny of thermoregulation and metabolism in chicks; and (8) chick growth rates.

#### Meteorological Measurements

I determined variations in ambient meteorological conditions to establish information necessary to test

hypotheses related to thermal response by embryos and ontogeny of thermoregulation in chicks. I measured and recorded diel fluctuations in wind velocity ( $W_V$ ), air ( $T_A$ ) and soil temperature ( $T_G$ ), and solar radiation ( $R_S$ ) using a micrologger system (model 21X; Campbell Scientific, Inc. Utah), following the methods used by Fitzpatrick and Guerra (1988), Guerra et al. (1988c) and Guerra (1990). Because of equipment difficulties, wind direction was not recorded and data from Guerra (1990) were used. Temperature sensors were placed on and 1 m above the ground, an anemometer at the same height above and a pyranometer on the ground in the open desert. Ambient conditions were recorded every 10 min for 27 h on 17-18 January, 1992.

#### Nest Dispersion

**Hypothesis 1** - To test the hypothesis that the spatial dispersion of nests was clumped, I determined the dispersion of 179 nests within an area of 51334 m<sup>2</sup> using the nearest neighbor method (Clark and Evans 1954). Measurements consisted of selecting a nest (nest A) at random and tape-measuring the distance to its nearest neighbor (nest B). From nest B, the measurement continued to its nearest neighbor (nest C) and from nest C to its nearest neighbor (nest D) and so on. The series of measurements was continued



until there were no neighbors closer than the last nest measured. Then another series of measurements was begun.

Nearest neighbor methods are based on the ratio (R) between the mean of the observed distances ( $\bar{r}_A$ ) and the mean expected distances if the population were distributed randomly ( $\bar{r}_E$ ). This ratio of the observed mean distance ( $\bar{r}_A$ ) to the expected mean distance ( $\bar{r}_E$ ) serves as the measure of the deviation from randomness. In a random distribution, R is equal to 1, and under conditions of maximal aggregation, R is equal to 0, since all the individuals occupy the same locus; therefore, the distances among them is 0.

Nest dispersion was calculated as follows:

$$R = \bar{r}_A / \bar{r}_E$$

$$\bar{r}_E = 1/2\sqrt{d}$$

where:

$\bar{r}_A$  = mean distance observed

$\bar{r}_E$  = mean distance expected

d = nest density

Significant departure of R from expectation of random nest dispersion was tested using the normal variate C, where

$$C = \frac{\bar{r}_E - \bar{r}_A}{s\bar{r}_E}$$

$$s\bar{r}_E = \frac{0.26136}{\sqrt{Nd}}$$

and:

$sr_E$  = standard error of  $r_E$

N = number of nests measured

#### Clutch Size

**Hypotheses 2** - To test the hypotheses that clutch size should be greater in nesting sites closer to the coast than those more inland, I counted eggs in 277 nests located within an area of 95 x 836 m selected randomly in the Lealtad colony on 21 December 1991 and 17 January 1992. Resultant data (X clutch size and relative frequency of one-, two- and three-egg clutches) were compared with data published by Howell et al. (1974), Guerra (1987) and Guerra et al. (1988d)

#### Time and Temperature of Incubation and Egg-Hatchling Success

**Hypothesis 3 and 4** To determine if average incubation time is longer in two-egg than single-egg clutches and that egg-hatching success is higher in two-egg than one-egg clutches, I examined 163 nests located near the center of the Lealtad colony. Nests were located on 21 December 1991 and 17 January 1992, and identified by painting a nearby rock, and marking a number on each egg shell with waterproof ink. I visited the nests on 17 and 25 January, and 5 and 11 February 1992 to check on hatchling and/or egg mortality.

Maximal egg diameter and length were measured to the nearest mm using a dial caliper. Weight was measured to the nearest g by placing the egg in a small tared polyethylene bag suspended from a Pesola Scale. Age of the egg (i e., the time since laying) was estimated by means of a floatation technique (Bennett and Dawson 1979), which consisted of placing the egg into a container with water and determining its inclination angle relative to the container bottom. To determine the correspondence between the floatation technique and age of egg, I collected a group of seven freshly-laid eggs and incubated them in a styrofoam box at 36-37°C at Dr. Guerra's laboratory. Before placing the eggs into an incubator, I checked one of them again with the floatation technique, immediately dissected it, and noted the stage of development. I checked egg floatability weekly, at which time I dissected one of the eggs to determine state of development.

I assessed the egg temperature during incubation by means of a "thermo-egg". This consisted of an egg under incubation into which I inserted and fixed a fine thermocouple connected to the micrologger. The egg was then replaced into the nest. Egg and nest (with incubating adult) temperatures were recorded every 10 min for 27 h on 17-18 January 1992. Nest temperatures were measured using a thermocouple connected to the micrologger. Simultaneous measurements of  $T_G$ ,  $T_A$ ,  $R_S$  and  $W_V$  were recorded.

### Thermal Tolerance and Metabolism in Embryos

**Hypotheses 5** - To test the hypothesis that gray gull embryos should have wider thermal tolerance than those of congeners, I collected 14 eggs on 28 and 30 January 1992, determined their ages (2-3 weeks old) using the floatation technique and transported them within a styrofoam container at ambient temperature and adequate humidity to the laboratory at IIO/UDA. There, I measured the physiological response of the embryos to temperature in terms of heart rate (HR = beats per 15 sec), following the method used by Bennett and Dawson (1979). I determined minimal temperature tolerance and the possibility of recovery with increase of temperature in eggs maintained at different temperatures: one egg at 0°C for 1 h, two eggs at 10°C for 45 min, one egg at 15°C for 30 min, and two eggs at 18°C for 15 min. I determined changes in HR with changing temperature and maximum temperature tolerance in eight eggs maintained at 18-20°C for 15 min. HR recovery after maximum temperature tolerated was not tested. After exposure, I dissected the embryos from their shells and placed them in petri dishes containing Ringer's solution (Gaviño et al. (1977): 6.0 gr NaCl; 0.0075 gr KCl; 0.1 gr CaCl; 0.1 gr NaCO<sub>3</sub>; dissolved in 1 l of distilled water) and measured their HR. To increase embryo temperature, the petri dish with its contents, were placed on a heating plate and changes in temperature of the

embryos. HR was determined by observing the embryo through a dissecting microscope and counting beats during 15 sec, timed with a stopwatch.

**Hypothesis 6** - To determine if the overall metabolism of developing gray gull embryos is lower than those of congeneric gulls, I measured metabolic rates at incubation temperatures (30°-40°C) in four embryos (4 weeks old, two of them in piping stage), collected on 12 February 1992, using an Applied Electrochemistry S-3A Oxygen Analyzer (OA) connected to a flow-through acrylic metabolic chamber (6.0 x 9.0 x 6.0 cm) (MC) (Figure 5). During respirometry, the MC was maintained inside a steel chamber (SC) heated with a 45 W red reflex light bulb, and its temperature controlled with a contact thermometer (CT). The MC's temperature, monitored with a micrologger, was considered to be the same as embryo's temperature. Water vapor produced by the embryos was removed from the air leaving the MC, by passing it through a plastic tube containing drierite before entering the OA, where the O<sub>2</sub> concentration was measured, then displayed digitally on the AO panel and recorded continuously with a YSI two-channel graph recorder (Figure 5). Flow rate, controlled by a flow meter (FM), was adjusted according to pre-testing at 35°C of one of the eggs collected. Initial O<sub>2</sub> concentration was calibrated at 20.9% by passing ambient air directly to OA through the two-way valve. Oxygen consumption involved placing an egg of known mass (nearest 0.1 g) in the MC at

36°C, 15-20 min prior to measurement. All determinations were made between 13:00 and 18:00 h. After respirometry, eggs were placed in a styrofoam incubator at 37-38°C until the next measurement. Mass-specific O<sub>2</sub> consumption (VO<sub>2</sub>) was calculated following Tucker (1972) from flow rate and change in O<sub>2</sub> concentration as air passed through the metabolic chamber as:

$$VO_2 = \frac{fr * (0.2090 - OA/100) * t}{Mb}$$

where:

VO<sub>2</sub> = ml of oxygen g<sup>-1</sup> h<sup>-1</sup>

fr = air flow rate in ml min<sup>-1</sup>

OA = percent O<sub>2</sub>

t = 60 min

Mb = mass of embryo in g

VO<sub>2</sub> values were corrected to STPD. Since the embryos measured were very close to hatching (4 weeks), I used the average hatchling mass (35.2 g; SD = 3.83 g; N = 22) to calculate VO<sub>2</sub>.

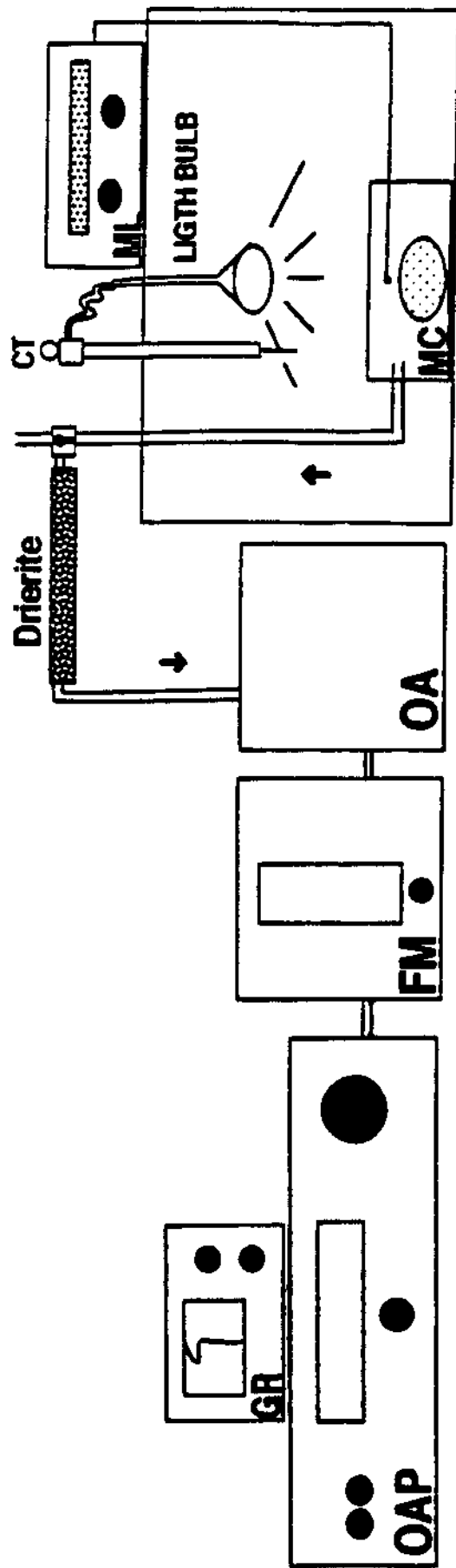
### Ontogeny of Thermoregulation and Metabolism in Chicks

**Hypotheses 7 and 8** - To determine if gray gull chicks are able to thermoregulate earlier than congeneric chicks and/or that the onset of thermoregulation coincides with the time

when chicks are left unattended in the desert, I assessed thermoregulation capacity in 16 0-3 day-old and 11 6-26 day-old hatchlings at the Lealtad site during 24 h periods on 25 January and 5 February, 1992. Chicks, captured by hand, were placed in non-shaded and shaded wire mesh confinements (1.20 x 0.50 m) for 10-15 and 45-50 min, respectively. Chick body temperatures ( $T_B$ ) were measured immediately before placing them into the wire mesh confinements by using a fine thermocouple inserted ca 2 cm into their cloaca. During confinement,  $T_B$  measurements were made hourly, as quickly as possible to reduce stressing the chicks, from 07:00 to 19:00 during the day and every 2 h during the night from 20:00 until 02:00. Simultaneously, meteorological data were recorded in a micrologger.

Figure 5. Respiration system for measuring oxygen uptake ( $VO_2$ ) in *Larus modestus*: (MC) Metabolic chamber, (ML) Micrologger, (AO) Oxygen analyzer, (FM) Flow meter (AOP) Oxygen analyzer panel, (GR) Graph recorder.





**Hypotheses 9 and 10** - I tested the hypotheses that gray gull chicks should have lower SMR and a wider TNZ than other bird species inhabiting extreme environments, in the same manner as previously described for eggs.  $VO_2$  was measured in two chicks, from eggs collected on 12 February 1992, at different temperatures, using an Applied Electrochemistry S-3A Oxygen Analyzer (Figure 5). The MC used was plastic (12 x 12 x 12 cm) and cooled in a refrigerator whose temperature was controlled with a contact thermometer. Chicks were held in the MC for 5-10 min before measurements.  $VO_2$  was measured from low to high temperatures at least twice at given temperatures for each chick and two-three times during their first week (33-45 g).  $VO_2$  was calculated following Tucker (1972), according to the equation previously described for egg metabolism.

#### Growth Rate

**Hypotheses 11 and 12** - I tested the hypotheses that growth rates should be higher in chicks from single egg nests than from two-egg nests, and that Lealtad chicks should grow faster than those nesting at Cerro Negro (reported by Guerra et al. 1988b), following the methods in Guerra et al. (1988b). During February 1992, 70 chicks, weighing 30 to 206 g, were banded with numbered metal rings (Model 1242-M, size 10, National Band & Tag Co. Kentucky) and their nests (one or

two-egg clutch size) identified. All banded chicks were initially and subsequently weighed using 100-500 g Pesola scales, according to their body mass, to the nearest g. Recapture of chicks decreased rapidly after 2 weeks when tarsus development enabled them to move freely around the nesting site.

## CHAPTER III

### RESULTS

During the 1991-92 breeding season, reproductive activities (e. g., spiral flights, courtship and mating) were delayed until December, later than the usual period which occurs during September-October (Guerra et al. 1988d). During October and November 1991, the beaches at Antofagasta and Mejillones were populated densely by gray gulls, but I did not observe any reproductive behavior. To confirm that reproduction was delayed, I made a field trip to the Lealtad site on 16 November 1991 and did not find any nesting gray gulls. I first observed courtship and mating on 29 November. Subsequently, there was rapid increase in the frequency of mating as well as the spiral flights. I took a second field trip to Lealtad on 7 December 1991 and found only a few groups of nesting gray gulls. I could verify a high density of gray gulls nesting only after the third week in December.

Topographic characteristics of the Lealtad site, do not differ from those described by Guerra et al. (1988c) for other Atacama nesting sites. Nests are in areas having sandy substrate and numerous small rocks. As at Cerro Negro nesting sites, dry channels in the alluvial are used by chicks as refuges. Micrometeorological conditions within

those refuges are more moderate than those outside in the open desert (Fitzpatrick and Guerra 1988).

#### Meteorological Conditions

Fluctuations in air ( $T_A$ ) and ground ( $T_G$ ) temperatures are shown in Figure 6, solar radiation ( $R_S$ ) in Figure 7, and wind velocity ( $W_V$ ) and direction in Figure 8. On 17-18 January 1992,  $T_A$ ,  $T_G$  and  $R_S$  increased gradually after sunrise to maximal values between 14:00 and 15:00 h, and decreased after 17:00 h to minimal values between 05:00 and 07:00 h. The highest  $T_A$  recorded was 31°C and  $T_G$  was 51°C, both at 15:00 h. The lowest  $T_A$  was 15°C at 05:40 h and  $T_G$  of 12°C at 05:00 h. The maximal radiation recorded was 1.47 kw/m<sup>2</sup> at 14:00 h.

Daily winds at Lealtad typically are from the NW, reaching maximal measured velocity of 7.8 m sec<sup>-1</sup> at 16:00 h. During the night, (21:00 - 03:00 h) the air is calm, but between 04:00 and 07:00 h the cool-dry Andean wind blows from NE at ca 1-2 m sec<sup>-1</sup>, exposing gray gulls to the lowest diel temperatures.

Figure 6. Daily variations in air ( $T_A$ ) and ground ( $T_G$ ) temperature at the Lealtad nesting site of gray gulls *Larus modestus* recorded during 17-18 January 1992.

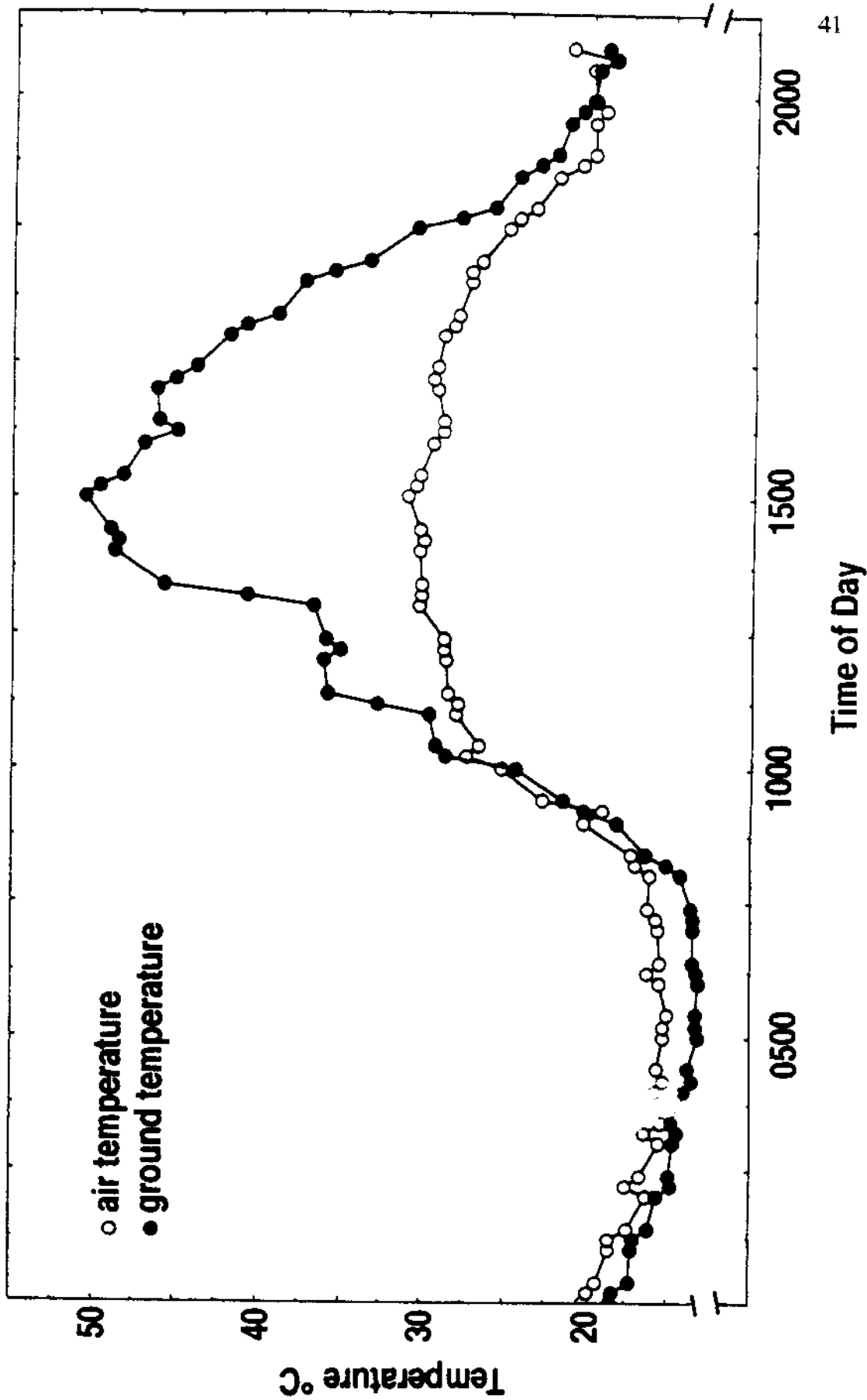


Figure 7. Diel variations in radiation ( $Kw/m^2$ ) at the Lealtad nesting site of gray gulls *Larus modestus* recorded during 17-18 January 1992.



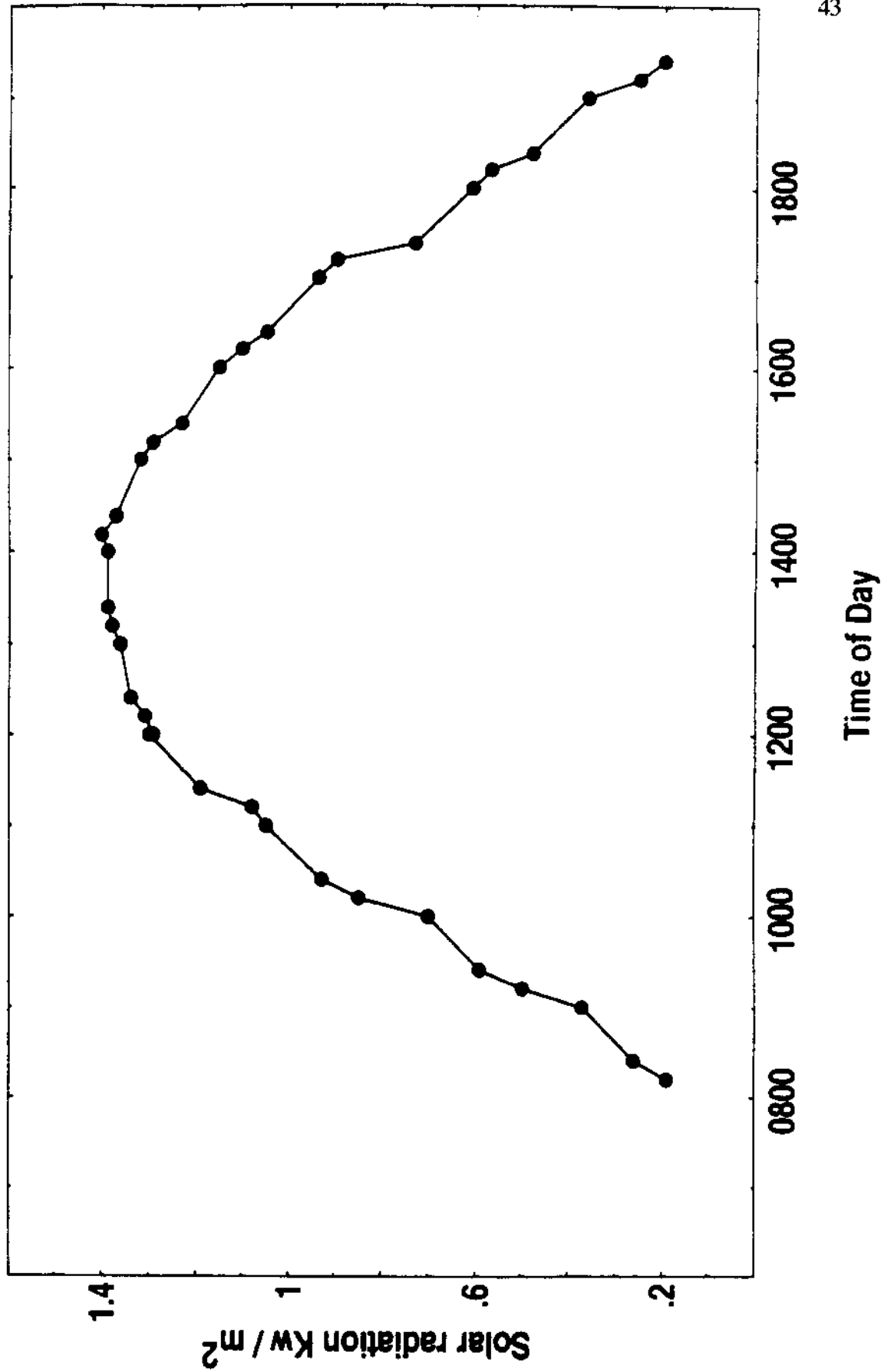
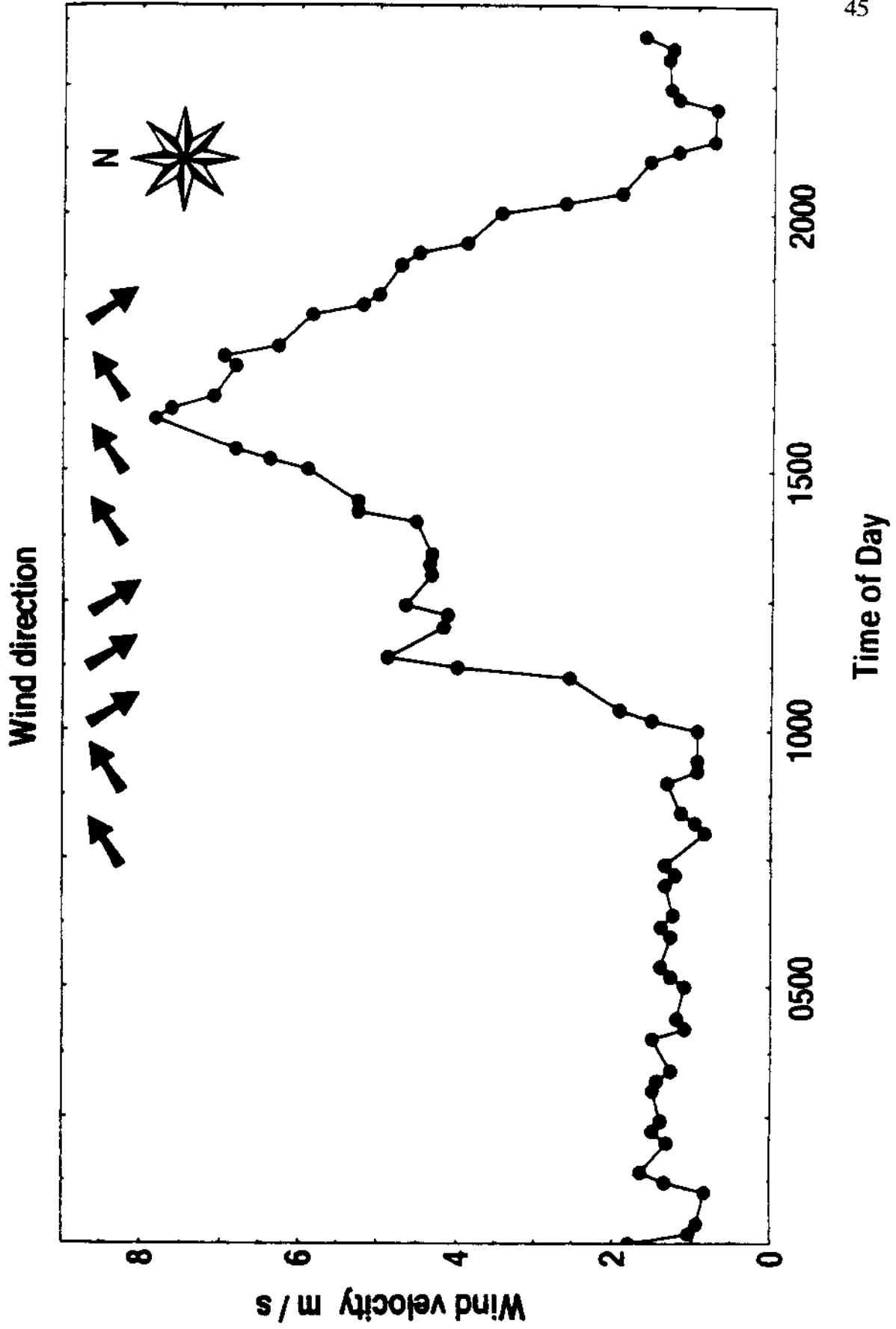


Figure 8. Wind direction and velocity ( $W_V$ ) at the Lealtad nesting site of gray gulls *Larus modestus* measured during 17-18 January 1992.



### Nest Dispersion and Density

**Hypothesis 1** - Estimated nest and adult densities at Lealtad were 3487 and 6974 per km<sup>2</sup> respectively. The actual colony, which covered 0.8 Km<sup>2</sup>, had a total number of 2929 nests and 5858 breeding adults. Nest dispersion is presented in Figure 9, which shows relative and absolute frequencies of distances (m) among nests located near the center of the colony. Of the 179 nests examined 67% had a nearest neighbor between 3 and 7 m. Nearest-neighbor frequencies over 10 m were low; I found only 10 nests at those distances. Nest-dispersion calculations, summarized in Table 1, demonstrate that gray gulls formed an aggregated colony ( $R = 0.5729$ ;  $p \ll 0.0001$ ), supporting the hypothesis that nests in Lealtad colony are clumped.

TABLE 1

Statistics\* for gray gull *Larus modestus* nest  
dispersion in the Lealtad colony

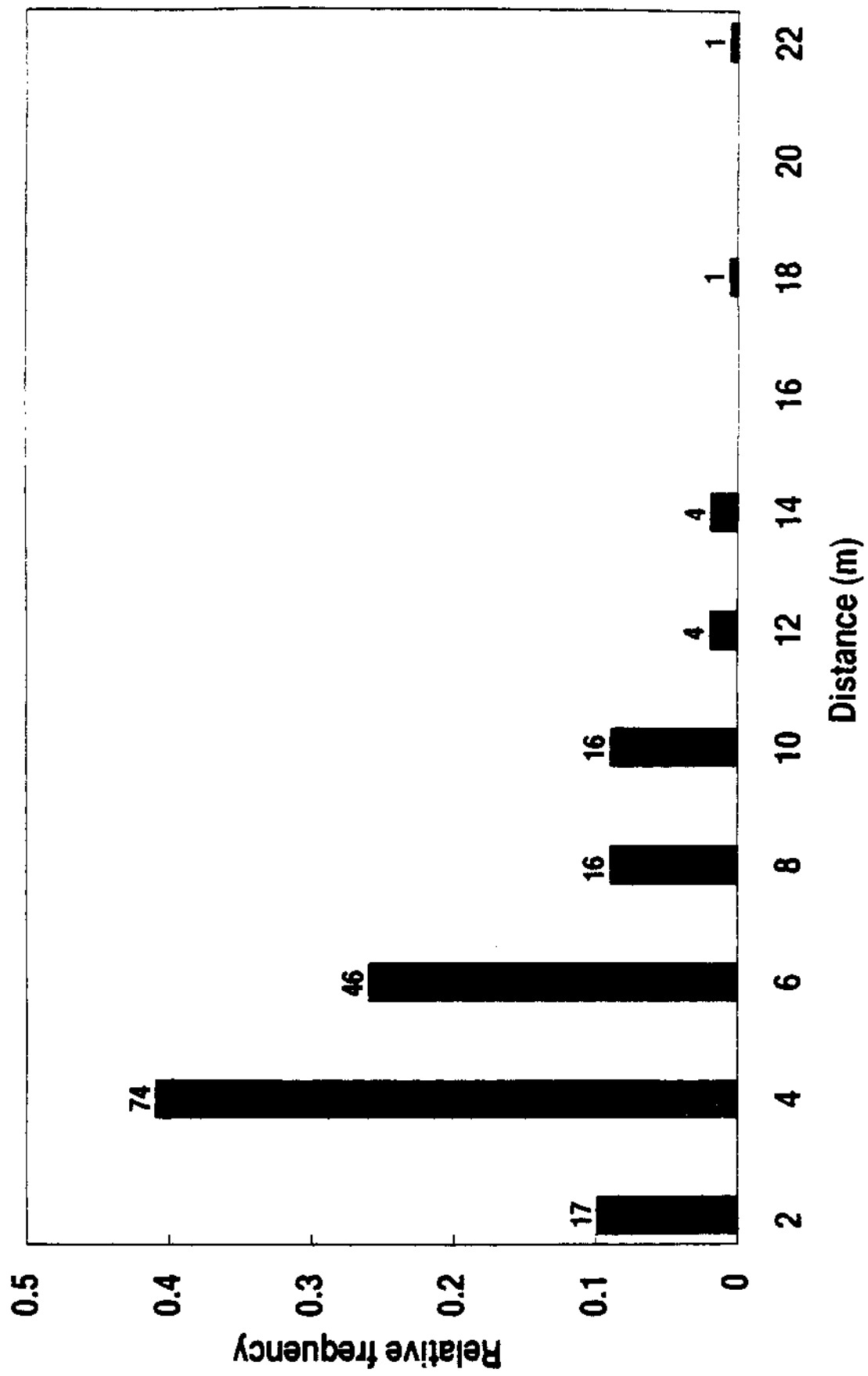
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Mean distance observed ( $r_A$ )	= 4.851 m
Density (d)	= 0.003487 nest/m <sup>2</sup>
Mean distance expected ( $r_E$ )	= 8.467
R ( $0 > 1$ )	= 0.573
N	= 179
Standard error ( $s_{r_E}$ )	= 0.331
Significance of R (c)	= 10.924
Difference between $r_A$ and $r_E$ significant at probability p	<< 0.0001

---

\* Following Clark and Evans 1954.

Figure 9. Frequency histograms showing distribution of nearest neighbor distances among gray gull *Larus modestus* nests within the Lealtad colony. The number above the column represents absolute frequency.



### Clutch Size

**Hypotheses 2** - To test the hypothesis that clutch size is related to distance from the coast that adults must commute, clutch size was determined in nests in an area of 0.08 km<sup>2</sup>, representing approximately 10% of the entire Lealtad colony. Results are summarized in Figure 10. Total nests and eggs counted were 277 and 432, respectively with a mean of 1.56 eggs/nest, and relative frequencies of two-egg clutches higher than single-egg nests (55.2 vs. 44.4%). Table 2 contains summarized data published on clutch size (relative frequencies and average) among different gray gull nesting sites. Comparison suggests, that because of among year variation, there are no clear differences in clutch size among nesting sites. The highest (1.81) and lowest (1.43) mean clutch sizes reported for gray gulls were from Colupo-Kimurku-Valenzuela area in 1984-85 and 1985-87, respectively. All clutch sizes reported for colonies closer or further from the coast fall within that range. Relative frequency of two-egg clutches ranged from 0.43 to 0.81 at Colupo-Kimurku Valenzuela between the same years. Therefore, the hypothesis that clutch size is determined by distance between nest sites and the coast could not be supported.



TABLE 2

Comparison of gray gull *Larus modestus* clutch sizes among desert nesting locations reported for different years.

BREEDING YEAR	CLUTCH SIZE	NESTING SITES			
		LEALTAD 15 km inland	C-K-V* 35 km inland	COLUPO 25 km inland	C°NEGRO 100 km inland
1969-70 (a)	1			0.47	
	2			0.52	
	3			0.01	
	X			1.55 (N=182)	
**					
1984-85 (b)	1		0.57		0.53
	2		0.43		0.47
	X		1.43 (N=21)		1.47 (N=15)
***					
1985- 86-87 (c)	1		0.19		0.34
	2		0.81		0.47
	X		1.81 (N=31)		1.66 (N=68)
1989-90 (d)	1	0.53			0.50
	2	0.47			0.50
	X	1.47 (N=126)			1.55 (N=60)
1991-92 (e)	1	0.44			
	2	0.55			
	3	0.01			
	X	1.56 (N=277)			

Source: (a) Howell et al. (1974)

(b) Guerra (1987)

(c) Guerra et al. (1988d)

(d) Guerra (1990)

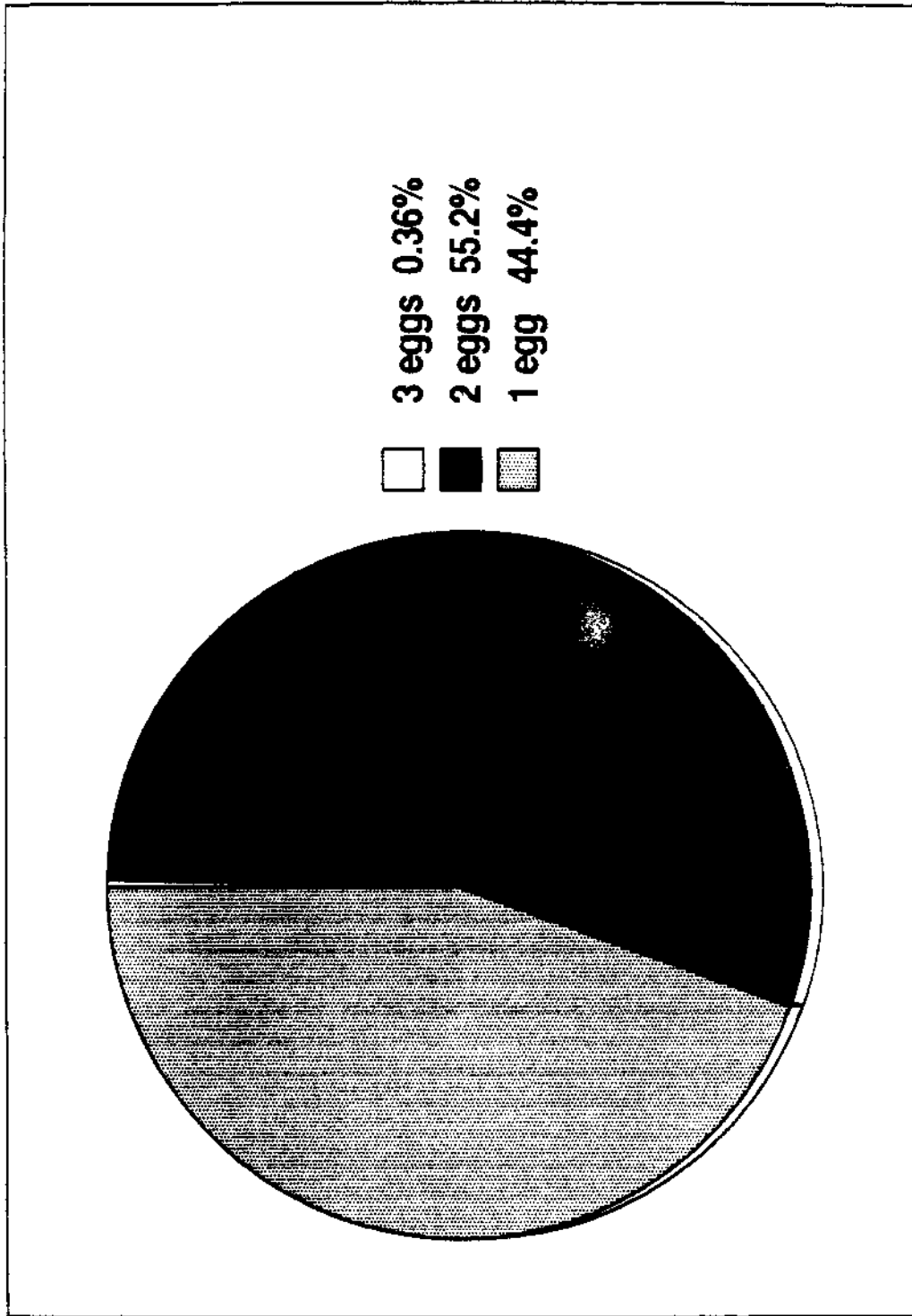
(e) This study

\* Colupo-Kimurku-Valenzuela area (see Figure 2)

\*\* Resumed breeding after ENSO

\*\*\* Both 1985-86 and 1986-87 breeding seasons pooled

Figure 10. Gray gull *Larus modestus* clutch size in the Lealtad colony during the 1991-92 breeding season.



### Time and Temperature of Incubation

**Hypothesis 3** - The hypothesis that clutch size of one vs. two eggs should show differences in mass/energy content and/or incubation time, was examined by measuring egg mass (M), length (L) and diameter (D). Volume comparisons are preferable to using mass because development stage and /or water loss may affect mass do not alter volume. I predicted egg volume using the equation  $V = 0.476 L D^2$  (Harris 1964), which has been evaluated by Guerra (1987) empirically through comparing water displacement and predicted volumes. Table 3 contains egg volumes at Lealtad during 1991-92 breeding season and those reported for Cerro Negro and Colupo-Kimurku-Valenzuela areas (Figure 2). During the 1991-92 breeding season at Lealtad, first laid eggs in two-egg clutches, were significantly larger than the second eggs (one tail, t test,  $p = 0.0001$ ). Also, first-laid egg volumes were significantly larger than for single eggs (one tail, t test,  $p = 0.009$ ), but second-laid eggs were not significantly larger than eggs from single egg nest (one tail, t test,  $p = 0.1088$ ). Volumes of eggs at Lealtad were similar to those reported for other nesting colonies in the Atacama. Based on volume, the hypothesis that clutch size of 1 vs. 2 eggs should show differences in mass/energy content was supported.

To test the hypothesis that the incubation time for single-eggs is shorter than for two-egg clutches, nests were

checked on 21 December 1991 (marking), 17 and 25 January, 5 and 11 February 1992. Because of field logistics, I was able to obtain data from only eight one-egg nests and 11 two-egg nests. Obtaining post-hatching information was difficult because the nests were so close that the highly mobile hatchlings were difficult to associate with particular nests. Tables 4 and 5 contain summaries of incubation times for one and two-egg clutches, respectively. On 21 December (marking day) the marked eggs were determined by floatation as freshly-laid. Tables 6 and 7 show correspondence between floatation degree and embryo development. On subsequent days, many of the marked eggs had hatched. I then weighed those hatchlings to estimate their age from the age:mass regressions developed generated in the growth rate study (see Figures 26 and 27) and to estimate the time when they hatched. According to my observations, embryos in the pipping stage usually hatched the next day. Thus, hatching dates for all eggs that I found in that stage were assigned to the following day. Mean incubation times were not significantly different (one tail, t test,  $p = 0.3454$ ) between one-egg (27.9 days) and two-egg clutches (28.1 days), but significant differences were found in incubation time between first and second laid eggs in two-egg clutches (28 vs. 29 days; one tail, t test,  $p = 0.0001$ ). Since there were no significant differences in overall in incubation times between two and one-egg nests, the hypothesis that incubation

time in two-egg nests are longer than one-egg nests, was not be supported.

TABLE 3

Volume (cc) of eggs within one and two-egg clutches from gray gull *Larus modestus* nests in the Lealtad, Colupo-Kimurku-Valenzuela area and Cerro Negro nesting sites.

SITES	EGG	N	X	SD	MIN	MAX	CV
	**						
LEALTAD (a)	I	109	48.9	3.92	41.1	65.5	8.02
	II	109	45.5	4.19	37.1	64.0	9.21
	*						
C-K-V (b)	I	39	46.6	4.39	37.2	56.1	9.43
	II	26	44.6	3.61	38.5	53.9	8.09
CERRO NEGRO (b)	I	15	49.4	3.50	40.6	52.9	7.09
	II	15	46.2	3.53	40.5	52.2	7.64
LEALTAD (a)	SINGLE	54	47.5	4.27	36.4	58.1	8.98

Source: (a) This study  
(b) Guerra (1987)

\* Colupo-Kimurku-Valenzuela area (see Figure 2)

\*\* I = first laid; II = second laid.

TABLE 4

Clutch size and length of incubation in eggs of gray gulls *Larus modestus* nesting at Lealtad.

ONE-EGG CLUTCH	
NEST ID #	INCUBATION TIME (days)
6	28
7	27*
8	27
18	26*
85	29
129	26*
140	30
160	30
X	27.9 days
SD	1.6 days
N	8 eggs

\* Incubation time estimated from regressions developed in the growth rate study (Figure 26):  
 $\text{Mass} = 11.96 \text{ Age} + 21.87$ ;  $r^2 = 0.98$ ;  $p = 0.0001$ .

TABLE 5

Clutch size and length of incubation in eggs of gray gulls *Larus modestus* nesting at Lealtad.



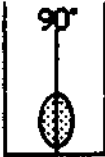
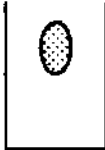
TWO-EGG CLUTCH		
NEST ID #	INCUBATION TIME (days)	
	FIRST LAID	SECOND LAID
25	28	29
31	28	29
39	28*	29
40	27*	28
42	26*	28*
109	28*	29
108	30	30
110	28	30
114	28	29
133	27	28
146	30*	30*
X	28	29
SD	1.2	0.8
N	11	11
X (First and Second pooled)	28.5	
SD	1.1	
N	22	

\* Incubation time estimated by regression models generated in growth rate study (Figure 27):  
 $Mass = 9.41 \text{ Age} + 24.98$ ;  $r^2 = 0.94$ ;  $p = 0.0001$ .



TABLE 6

Correspondence between the degree of egg floatation and embryo development stage in gray gull *Larus modestus* at Lealtad.

FLOATING (degree from the bottom)		EMBRYO DEVELOPMENTAL STAGE*	ESTIMATED INCUBATION TIME
0° egg horizontal at the bottom		A	Freshly-laid
45°		B	2 weeks
90°		C	3 weeks
25-50% of the floating egg above water surface		D	4 weeks chick is ready to hatch

\* For explanation see Table 7.

TABLE 7

Incubation time and embryo developmental stage in gray gulls *Larus modestus*.

INCUBATION TIME WEEK		DEVELOPMENTAL STAGE
1	(A)	Only embryonic button; in some cases, during the first week embryos length had reaches about 2-3 mm.
2	(B)	Embryo clearly identifiable presenting large eyes eyes and heart; part of the digestive system is notice- ceable. Embryo's length is about 7-15 mm.
3	(C)	Embryos nearly fully grown but legs and wings not clearly developed. Heart and blood vessels visible Incipient down appearing on. the embryo's back by end of week.
4	(D)	Early in the week embryo completely covered with down, except the head. Head will be covered by end of week, when embryo is ready to hatch.

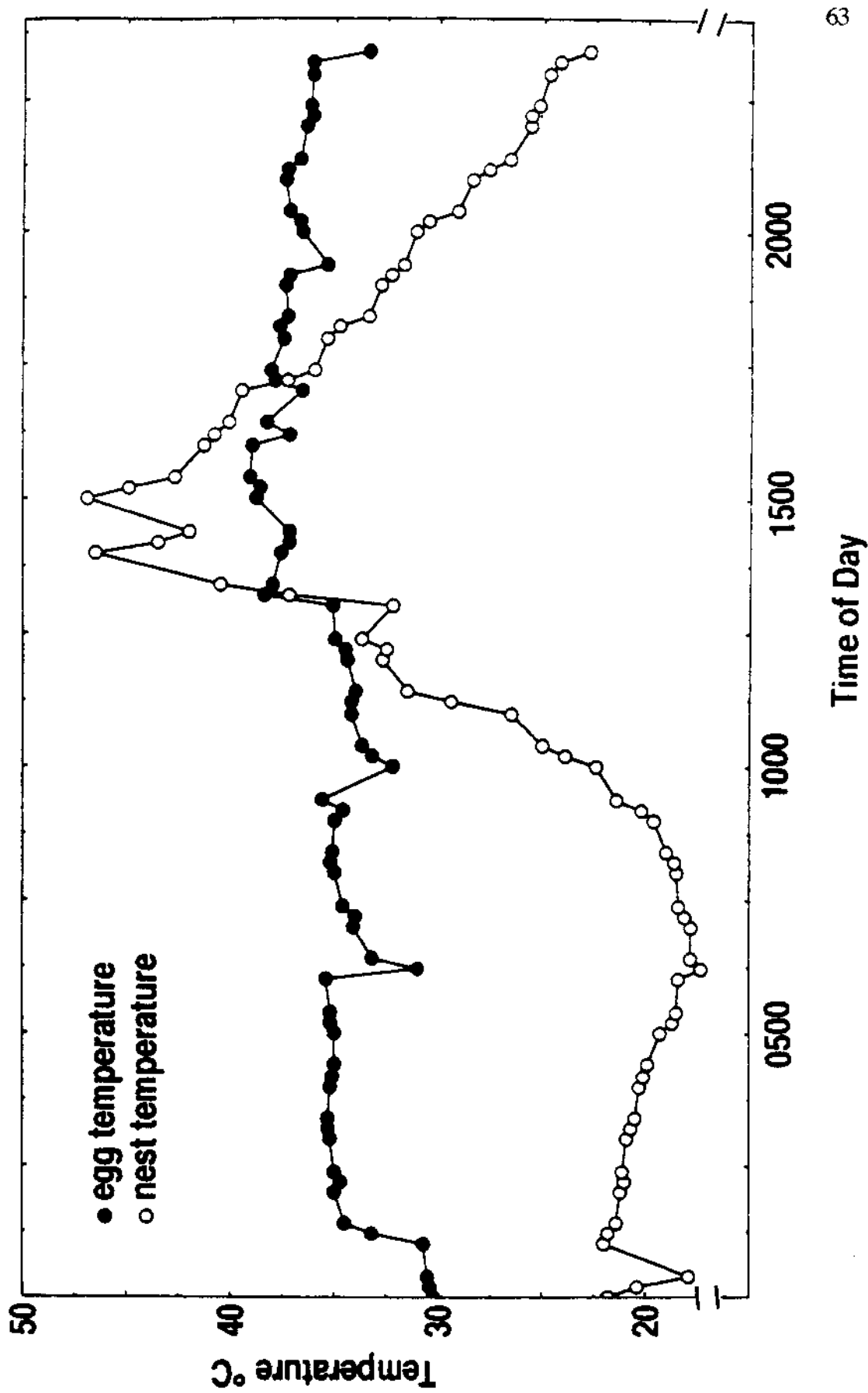
Incubation temperature varied from 30 to 39°C ( $X = 35.44^{\circ}\text{C}$ ;  $SD = 2.05$ ;  $N = 73$ ). Minimal temperatures occurred during the night (24:00-02:00 h) (Table 8) when there was high activity in the colony associated with the arrival of foraging adult gulls from the coast. The mean egg temperature during those hours was 32°C. Highest temperatures were reached in mid-afternoon, coinciding with maximal  $S_R$  and  $T_G$  (Figure 11). The mean egg temperature during that period was 38.6°C

TABLE 8

Gray gull *Larus modestus* incubation temperatures ( $T^{\circ}\text{C}$ ) (one egg measured) at Lelatad nesting colony during 17-18 January 1992.

TIME	$T^{\circ}\text{C}$	TIME	$T^{\circ}\text{C}$
0700	34.1	1900	37.4
0800	35.0	2000	36.6
0900	35.0	2100	37.4
1000	32.8	2200	36.4
1100	34.2	2300	36.1
1200	34.4	2400	30.2
1300	35.1	0100	30.7
1400	37.6	0200	35.0
1500	38.8	0300	35.2
1600	39.0	0400	35.2
1700	36.6	0500	35.0
1800	37.5	0600	35.4

Figure 11. Diel variation in incubation, ground and nest temperatures in the Lealtad nesting site of gray gulls *Larus modestus* during 17-18 January 1992.



## Egg-Hatching success

**Hypothesis 4** - The hypothesis that egg-hatching success is higher in two than one-egg nests was assessed during the same incubation time period. I considered that hatching was successful when egg shell fragments occurred in nests with a new hatchling. I assessed egg condition by gently shaking by hand. Those with loose contents were considered dead. Hatching success is summarized in Table 9 and Figures 12 through 14. A total of 164 nests, 116 with two eggs (71%) and 48 with one egg (29%) were studied. Both eggs hatched in 81 nests (69.8%), and one egg hatched in 20 (17.2%) of the two-egg nests. Because the nests were so close together and hatchlings were highly mobile, I was unable to determine hatching success in 15 nests (12.9%). The total number of eggs hatching from the 101 two-egg nests was 182 ( $182/202 = 90.1\%$ ) with a total mortality of 20 ( $20/202 = 9.9\%$ ).

Assuming that 100% of the nests with undetermined hatching success (15 nests) had zero hatching (worst possible case), the total hatching success in two-egg nests was 78.4% (182) and the total mortality was 21.6% (50). Disregarding the 15 nests that could not be followed to hatching, 100% of the two-egg nests observed from laying to hatching (101) produced at least one egg. Thus, 80% (81/101) of the two-egg nests produced two-hatchlings and 20% (21/101) lost one, producing a single hatchling. In one-egg nests, 32 nests

produced hatchlings (66.7%) and five failed (10.4%). For the same reason given above, I was unable to determine hatching success in 11 nests (22.9%). The total number of hatchlings from the 37 one-egg nests was 32 (86.5%) with a mortality of five eggs (13.5%). Assuming that 100% of the 11 nests having undetermined success produced zero hatchlings (worst possible case), the total hatching success in one-egg nests was 66.7% (32 eggs) and the total mortality 33.3% (16 eggs). Using only those single-egg nests that were observed from laying to hatching, 86% (32/37) were successful; 14% (5/37) failed. Based on the worst possible case, 87.1% of the two-egg nests (101/116) were successful in producing at least one hatchling vs. 66.7% of single-egg nests (32/48). Based on those nests actually followed, 100% of two-egg nests produced at least one hatchling vs. 86% for single-egg nests. Thus, results supported the hypothesis that two-egg nests should have higher egg-hatching success than single-egg nests.

Overall, the 138 nests (37 single-egg + 101 two-egg) that were followed from laying to hatching produced a total of 239 eggs for an average of 1.73 eggs per nest, which was higher than the colony average (1.56) determined for 277 nests (see p 51; Table 2). These 138 nests (i.e. nesting pairs) produced 214 hatchlings for a hatching success of 89.5% (214/239 eggs laid; 37 from single-egg + 202 two-egg nests). Based on these 138 nests, there was 0.78 hatchling per female. Extrapolating to the entire colony (ca.2929

nests and 5858 adult gulls), but using the mean clutch size (1.56) and frequency (single-egg = 0.44; two-egg nests = 0.55; N = 277) data in Table 2, 1.38 hatchlings should have been produced [80% of the 153 two-egg nests (122) produced two hatchlings (= 244); 20% (31) produced one hatchling (= 31); 86% of the 123 single-egg nests (106) produced hatchlings (= 106)] per nesting pair for a total of 4042 hatchlings during the 1991-92 breeding season.



TABLE 9

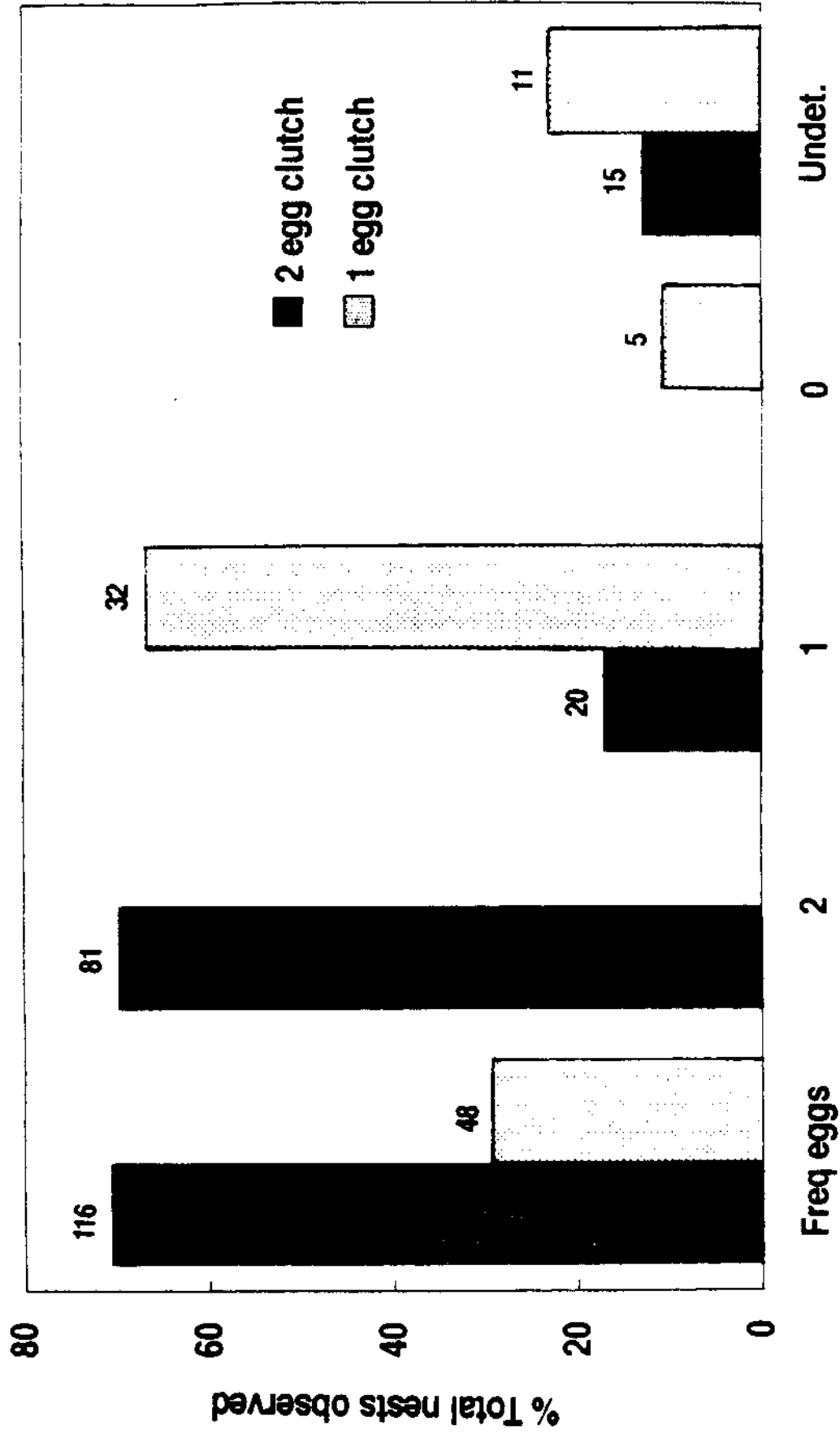
Egg and hatching success in gray gulls *Larus modestus* at Lealtad during the breeding season 1991-92.

TWO-EGG CLUTCHES							
Number/percentage of eggs hatching							
	Total	two eggs hatch		one egg hatch		Und*.	
		N	%	N	%	N	%
Nests	116	81	69.8	20	17.2	15	12.9
Eggs	202	162	80.2	20	9.9		
		** Total Eggs Hatched		182	90.1%		
		** Total Egg Mortality		20	9.9%		
ONE-EGG CLUTCHES							
Number/percentage of eggs hatching							
	Total	one egg		no egg		Und*	
		N	%	N	%	N	%
Nests	48	32	66.7	5	10.4	11	22.9
Eggs	37	32	86.5	5	13.5		
		** Total Eggs Hatched		32	66.7%		
		** Total Egg Mortality		16	33.3%		
** OVERALL TOTAL							
		one and two egg		Hatched	214	76.4%	
		clutches pooled		Mortality	66	23.6%	

\*Und.= undetermined

\*\* Assuming that all undetermined nests produced no hatchlings (worst possible case).

Figure 12. Relative and absolute frequencies of nests with two-egg vs. one-egg clutches and hatching success by clutch size in nests in the Lealtad colony of gray gulls *Larus modestus* during the 1991-92 breeding season.



Hatching success by clutch size

Figure 13. Total hatching and mortality of eggs according to clutch size at the Lealtad nesting colony of gray gulls *Larus modestus* during the 1991-92 breeding season.

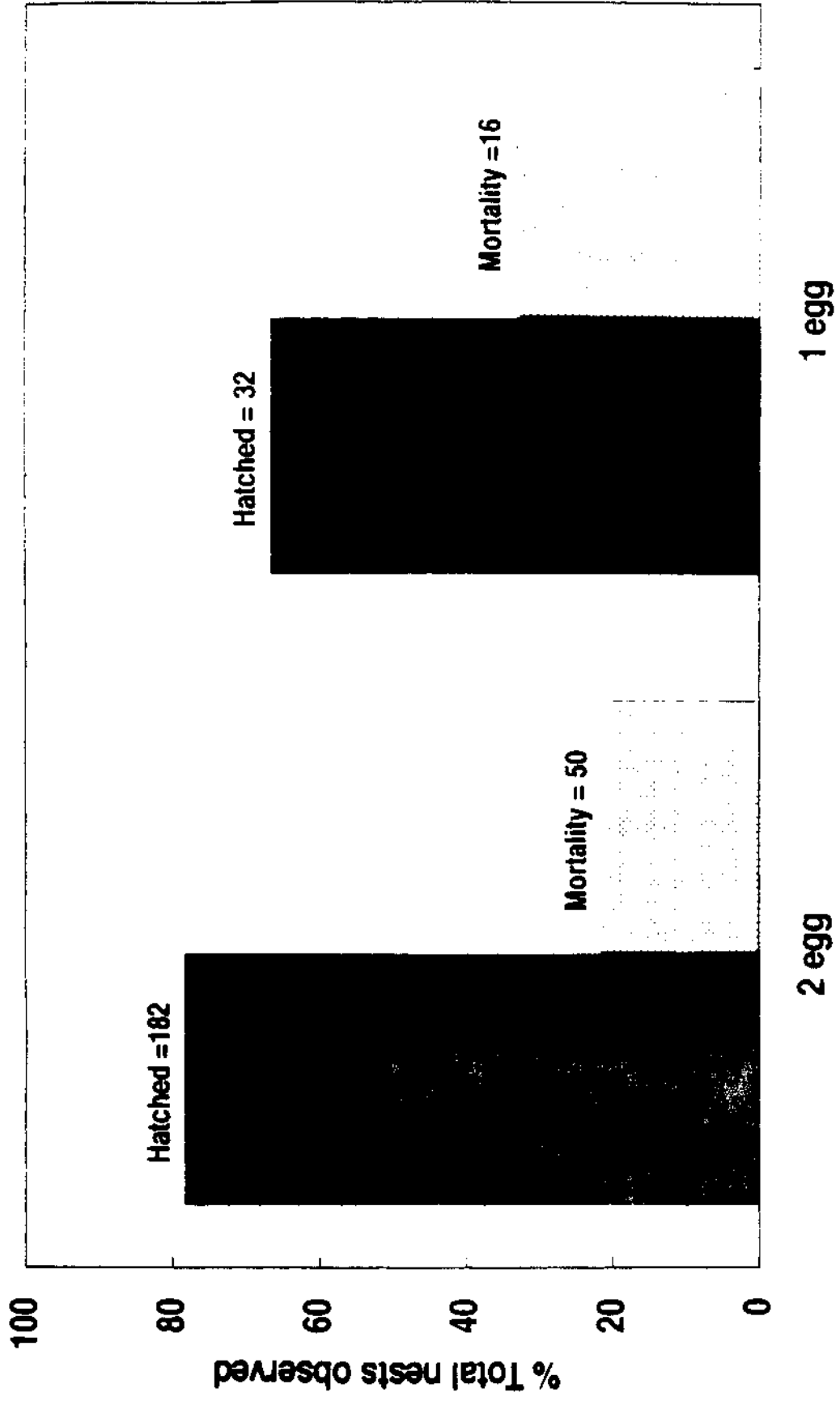
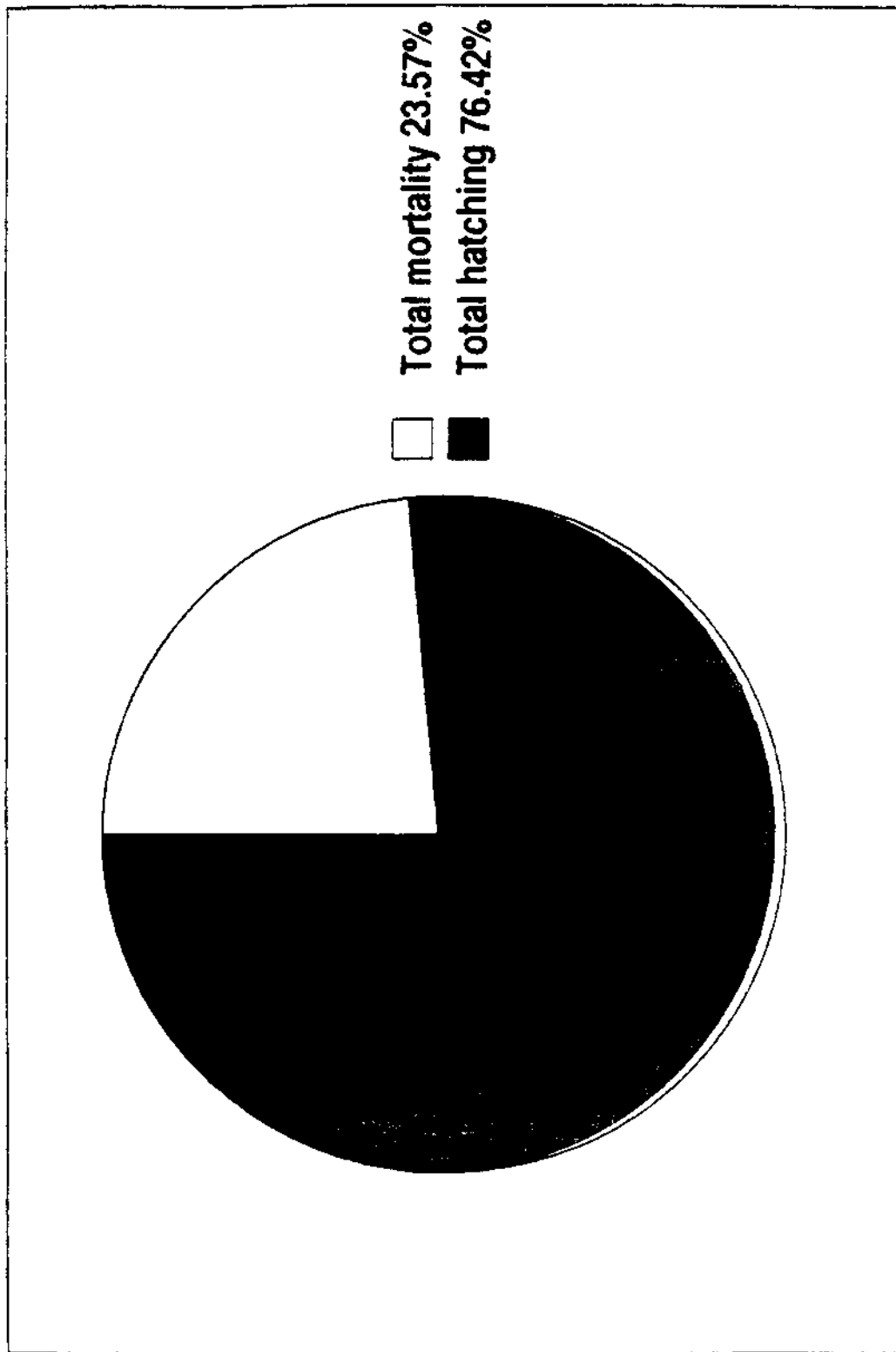


Figure 14. Total hatching and mortality in gray gulls *Larus modestus* eggs at the Lealtad nesting site during 1991-92 breeding season.



### Thermal Profile and Metabolism of Embryos

**Hypothesis 5** - The hypothesis that embryos should have a wider range of thermal tolerance than congeners was assessed by means of heart rate (HR) response to temperature. Assessment of minimal temperature tolerance showed that HR in gray gull embryos was reduced to zero below 18°C (i.e., critical thermal minimum;  $CT_{min}$ ); embryos did not recover as temperature was increased. Assessment of maximal temperature tolerance showed that embryo HR stopped above 42°C. Maximum temperature tolerated was the one at which HR arrhythmia was detected. The mean maximal temperature tolerated was 41.7°C (SD = 1.2°C; N = 7). Recovery with decreasing temperatures was not tested.

Heart rate responses to different temperatures are shown in Tables 10 and 11. Since variations in HR, in both groups of embryos showed the same response pattern to  $T_A$  (t test for slope,  $0.9 > p > 0.5$ ), data were pooled to form Figure 15. Embryo HR was linearly related to the temperature ( $HR = 1.45 T_A - 19.79$ ,  $r^2 = 0.99$ ,  $p = 0.0001$ ). Mean HR, within the incubation temperature range (30-39°C), fluctuated from  $100.8 \pm 16.4$  beat/min (N = 8) to  $146.0 \pm 10.96$  beat/min (N = 6).



TABLE 10

Heart rate (beats/15 sec) in gray gull *Larus modestus* embryos as function of age and ambient temperature ( $T_A$ ).

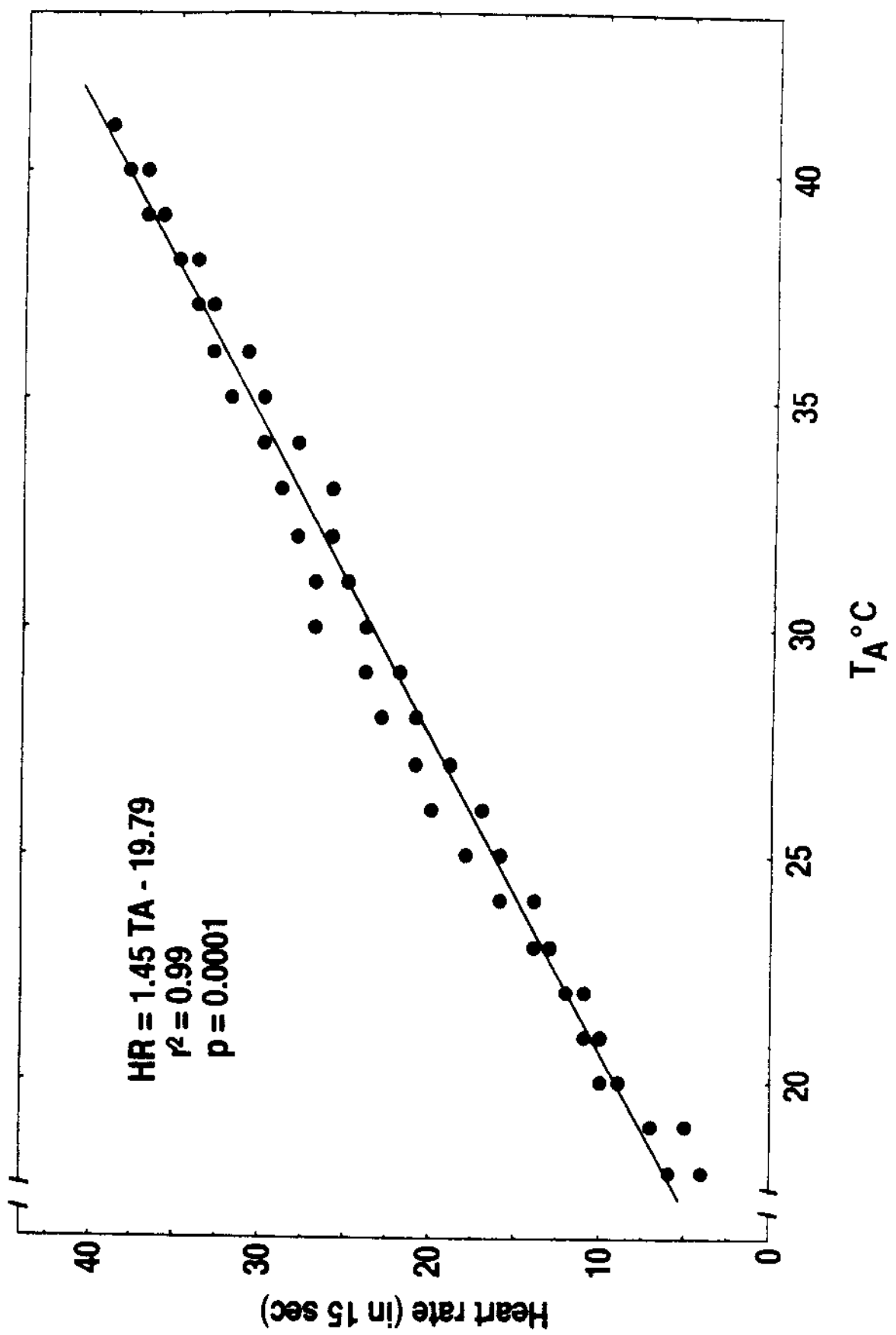
$T_A$ °C	# =	2 weeks old				3 weeks old			
		1	2	3	4	5	6	7	8
18	4								6
19	5								7
20	5	10	9	13		14	7	11	7
21	6	10	9	13		15	7	12	8
22	10	11	10	14		16	8	15	11
23	11	12	12	17		17	8	16	16
24	12	13	12	20		17	10	17	18
25	14	15	13	21		19	16	19	20
26	16	15	14	24		19	18	20	22
27	18	17	16	25		19	21	20	23
28	21	18	17	29		20	24	24	24
29	22	18	19	29		20	30	23	25
30	24	21	20	30		23	32	26	26
31	25	21	22	31		23	32	25	27
32	25	23	23	33		25	33	26	29
33	29	24	25	*		27	34	26	30
34	29	27	27			29	34	27	31
35	34	28	27			33	33	28	32
36	36	29	29			36	34	29	32
37	37	30	31			36	35	31	33
38	37	32	32			37	38	32	34
39	38	35	34			37	41	34	A
40	39	37	35			38	41	35	
41	41	39	37			40	42	36	
42	A	A	39		Arithmia=A	A	A		
43			A		[* death by broken blood vessel]				

TABLE 11

Summary statistics ( $\bar{X} \pm SD, N$ ) for heart rate (beats/15 sec) in gray gull *Larus modestus* embryos as function of age and ambient temperature ( $T_A$ ).

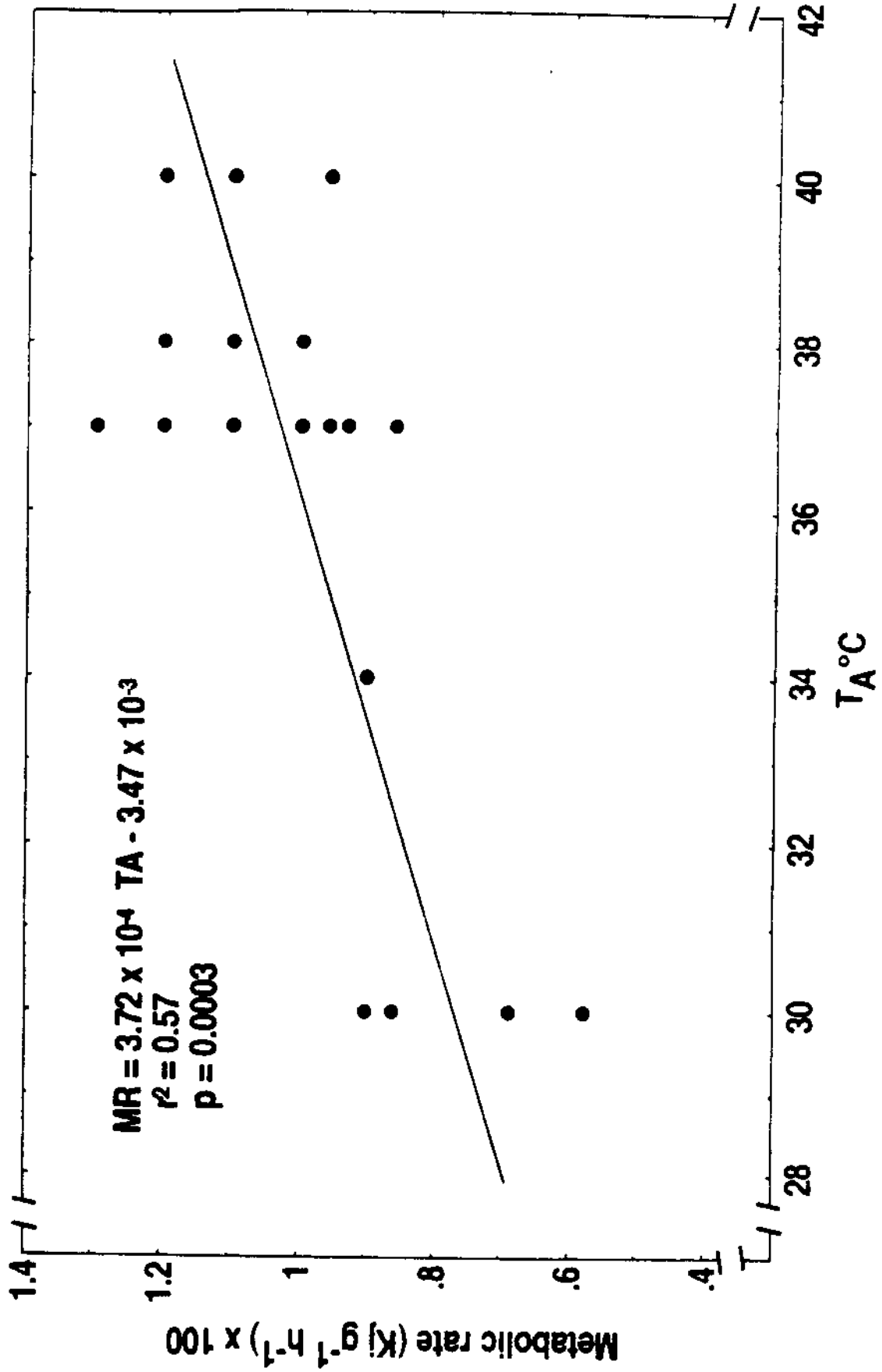
$T_A$ °C	2 weeks old	3 weeks old
20	9.25 ± 3.3, (4)	9.75 ± 3.4, (4)
21	9.50 ± 2.9, (4)	10.50 ± 3.7, (4)
22	11.25 ± 1.9, (4)	12.50 ± 3.7, (4)
23	13.00 ± 2.7, (4)	14.25 ± 4.2, (4)
24	14.25 ± 3.9, (4)	15.50 ± 3.7, (4)
25	15.75 ± 3.6, (4)	18.50 ± 1.7, (4)
26	17.25 ± 4.6, (4)	19.75 ± 1.7, (4)
27	19.00 ± 4.1, (4)	20.75 ± 1.7, (4)
28	21.25 ± 5.4, (4)	23.00 ± 2.0, (4)
29	22.00 ± 5.0, (4)	24.50 ± 4.2, (4)
30	23.75 ± 4.5, (4)	26.75 ± 3.8, (4)
31	24.75 ± 4.5, (4)	26.75 ± 3.9, (4)
32	26.00 ± 4.8, (4)	28.25 ± 3.6, (4)
33	26.00 ± 2.6, (3)	29.25 ± 3.6, (4)
34	27.67 ± 1.2, (3)	30.25 ± 3.0, (4)
35	29.67 ± 3.8, (3)	31.50 ± 2.4, (4)
36	31.33 ± 4.0, (3)	32.75 ± 3.0, (4)
37	32.67 ± 3.8, (3)	33.75 ± 2.2, (4)
38	33.67 ± 2.9, (3)	35.25 ± 2.8, (4)
39	35.67 ± 2.1, (3)	37.33 ± 3.5, (3)
40	39.00 ± 2.0, (3)	38.00 ± 3.0, (3)
41	39.00 ± 2.0, (3)	39.30 ± 3.1, (3)

Figure 15. Relation between heart rate beats (15 sec) and ambient temperature ( $T_A^{\circ}\text{C}$ ) in gray gull *Larus modestus* embryos (aged 2-3 weeks) from the Lealtad nesting colony.



**Hypothesis 6** - The hypothesis that overall metabolism of developing gray gull embryos should be lower than in embryos of other gulls was assessed by means of oxygen consumption ( $VO_2$ ). Metabolic expenditure of embryos at their incubation temperatures is shown in Figure 16. Variation in  $VO_2$  was proportional to temperature change ( $p = 0.0003$ ). Within the incubation temperature range ( $30^\circ$  to  $40^\circ\text{C}$ ), metabolic rate ranged from  $0.0058$  to  $0.012 \text{ Kj g}^{-1} \text{ h}^{-1}$ . At  $37^\circ\text{C}$  (modal temperature), the mean metabolic rate was  $0.0104$  ( $SD \pm 1.52 \cdot 10^{-3}$ )  $\text{Kj g}^{-1} \text{ h}^{-1}$ .

Figure 16. Metabolic rates ( $\text{Kj g}^{-1} \text{h}^{-1}$ ) in gray gull  
*Larus modestus* embryos from the Lealtad nesting colony.



Ontogeny of Thermoregulation and Metabolic Rates  
in Hatchlings

**Hypothesis 7 and 8** - Hypotheses that gray gull chicks should develop the capacity for thermoregulation earlier than chicks of other semi-precocial larids and that the onset of thermoregulation must be coincident with the time chicks are left alone, were tested by comparing chicks  $T_B$  to ambient conditions ( $T_G$ ,  $T_A$  and  $R_S$ ). Average  $T_B$  of hatchlings at different ages and ambient conditions are shown in Tables 12 and 13. In both groups  $T_B$  increased during the morning and decreased during the night, following the pattern of the three principal ambient variables. During the hottest period (12:00 to 16:00),  $T_B$  of 0-3 and 6-13 day-old hatchlings reached similar maximal values in both groups. During the coldest period (18:00 to 07:00)  $T_B$  decreased with decreasing ambient conditions, reaching lower values in 0-3 than 6-13 day-old chicks (34° vs. 37.4°C, respectively). Figures 17 and 18 contain the regression models for both groups of chicks (0-3 and 6-13 day old) and their relation to  $T_G$  and  $T_A$ , respectively. Divergence in the regression line ; (i.e., wider at lower,  $\leq 25^\circ\text{C}$ , than higher temperatures,  $\geq 50^\circ\text{C}$ ), indicates a sigmoidal relation, with asymptotic values over 45°C. Since daily variations in  $T_B$  in both groups of chicks showed the same response pattern to changes in  $T_G$  and  $T_A$  (t test for slope,  $0.4 > p > 0.2$ , for both variables), data were



pooled to form Figures 19 and 20, respectively. The range of  $T_B$  varied in both groups from 37° to 42°C, showing the highest correlation to  $T_A$ . There were no significant differences between  $T_B$  for 0-3 and 6-13-day old chicks (t test,  $p = 0.1385$ ). Table 14, and Figures 21 and 22 present  $T_B$  data for hatchlings under shade, and their relation to  $T_G$  and  $T_A$ , respectively. Both groups of chicks maintained stable and similar  $T_B$ . The higher correlation for  $T_B$ , in both groups, was to  $T_A$  changes. Variation in  $T_B$  for 0-3 day-old chicks with changes in  $T_A$  was not significantly different from the  $T_B$  variation in older chicks (t test for slope,  $0.9 > p > 0.5$ ). Both data sets are pooled in Figure 23. Chicks  $T_B$  under shade ranged from 37.4 to 39.3°C; both groups were pooled (see Table 14) because there was no significant difference between them (t test,  $p = 0.1406$ ).

Mean  $T_B$  of all chicks (0-13 days) exposed to direct solar radiation (1.25 - 1.42 Kw/km<sup>2</sup>) was significantly higher than for those maintained under shade (t test, one tail,  $p = 0.0003$ ). Figure 24 presents  $T_B$  of both groups by age and the regression models during the coldest hours, 18:00 - 07:00 h (see Tables 11 and 12). Although their slopes are not significantly different ( $t = 2.1428$   $0.1 > p > 0.05$ ), there were significant differences between both groups of chicks. Mean  $T_B$  in 0-3 day-old chicks was lower than in older chicks; (t test, one tail,  $p = 0.0059$ ).

TABLE 12

Relation of body temperature ( $T_B$ °C) in gray gull *Larus modestus* chicks (0-3 days old) to ground temperature ( $T_G$ °C), air temperature ( $T_A$ °C) and solar radiation ( $R_S$  Kw/km<sup>2</sup>) at the Lealtad nesting colony on 25 January and 5 February 1992.  
(Ambient variables represent means for both days.)

Time	$T_G$	$T_A$	$R_S$	$T_B \pm SD, (N)$
0900	22.8	19.6	0.39	37.1 $\pm$ 1.80, (15)
1000	34.5	22.6	0.56	40.2 $\pm$ 1.11, (15)
1100	46.4	25.0	0.75	41.7 $\pm$ 0.76, (16)
1200	49.2	28.9	1.29	42.2 $\pm$ 0.90, (16)
1300	53.2	29.0	1.37	42.1 $\pm$ 1.58, (16)
1400	50.1	26.2	1.42	41.3 $\pm$ 0.77, (16)
1500	51.0	25.6	1.31	41.1 $\pm$ 0.54, (16)
1600	49.5	25.7	1.25	40.3 $\pm$ 0.81, (12)
1700	46.1	24.7	1.04	39.2 $\pm$ 1.60, (16)
1800	39.7	23.6	0.73	38.0 $\pm$ 0.92, (16)
2000	23.5	17.9		38.4 $\pm$ 1.49, (4)
2200	12.2	13.9		35.5 $\pm$ 2.31, (4)
2400	7.0	12.0		36.7 $\pm$ 1.11, (3)
0200	6.2	12.8		35.5 $\pm$ 1.17, (3)
0700	4.2	7.5		34.0 $\pm$ 0.46, (3)

TABLE 13

Relation of body temperature ( $T_B$ °C) in gray gull *Larus modestus* chicks (6-13 days old) to ground temperature ( $T_G$ °C), air temperature ( $T_A$ °C), and solar radiation ( $R_S$  Kw/m<sup>2</sup>) at the Lealtad nesting colony on 25 January and 5 February, 1992.  
(Ambient variables represent means for both days.)

TIME	$T_G$	$T_A$	$R_S$	$T_B \pm SD, (N)$
0900	22.8	19.6	0.39	38.9 $\pm$ 0.40, (5)
1000	34.5	22.6	0.56	39.6 $\pm$ 0.48, (5)
1100	46.4	25.0	0.75	42.1 $\pm$ 1.00, (6)
1200	49.2	28.9	1.29	42.1 $\pm$ 0.90, (10)
1300	53.2	29.0	1.37	41.9 $\pm$ 1.86, (10)
1400	50.1	26.2	1.42	41.5 $\pm$ 1.02, (9)
1500	51.0	25.6	1.31	41.8 $\pm$ 0.57, (10)
1600	49.5	25.7	1.25	40.8 $\pm$ 1.10, (5)
1700	46.1	24.7	1.04	39.9 $\pm$ 0.70, (9)
1800	39.7	23.6	0.73	39.0 $\pm$ 0.52, (10)
2000	23.5	17.9		38.5 $\pm$ 0.92, (5)
2200	12.2	13.9		38.7 $\pm$ 0.76, (5)
2400	7.0	12.0		38.7 $\pm$ 1.60, (5)
0200	6.2	12.8		38.6 $\pm$ 0.72, (5)
0700	4.2	7.5		37.4 $\pm$ 0.80, (5)

TABLE 14

Relation of body temperature ( $T_B$ °C) of gray gull *Larus modestus* chicks (0-3 and 6-13 days old) maintained under shade to ground ( $T_G$ °C) and air ( $T_A$ °C) temperature, at the Lealtad nesting colony, on 25 January and 5 February 1992. (Ambient variables represent means for both days.)

TIME	$T_G$	$T_A$	$T_B \pm SD, (N)$	
			0-3 days-old	6-13 days-old
1145	45.9	24.6	38.6 $\pm$ 1.20, (16)	38.8 $\pm$ 1.27, (10)
1245	48.3	25.1	39.2 $\pm$ 0.82, (16)	39.3 $\pm$ 1.59, (10)
1345	52.5	25.5	38.6 $\pm$ 0.87, (16)	39.0 $\pm$ 0.61, (10)
1445	49.2	24.8	39.3 $\pm$ 0.48, (16)	39.1 $\pm$ 0.55, (10)
1545	50.4	24.8	38.7 $\pm$ 0.66, (16)	39.3 $\pm$ 0.44, (10)
1645	48.8	24.6	38.0 $\pm$ 0.56, (12)	38.3 $\pm$ 0.78, (4)
1745	45.5	22.9	37.5 $\pm$ 0.46, (12)	37.4 $\pm$ 0.27, (5)
			$X \pm SD = 38.6 \pm 0.63, (7)$	38.7 $\pm$ 0.68, (7)

Figure 17. Linear regression models relating body temperature ( $T_B$ °C) of gray gull *Larus modestus* chicks (0-3 and 6-13 days old) to ground temperature ( $T_G$ °C) at the Lealtad nesting colony.

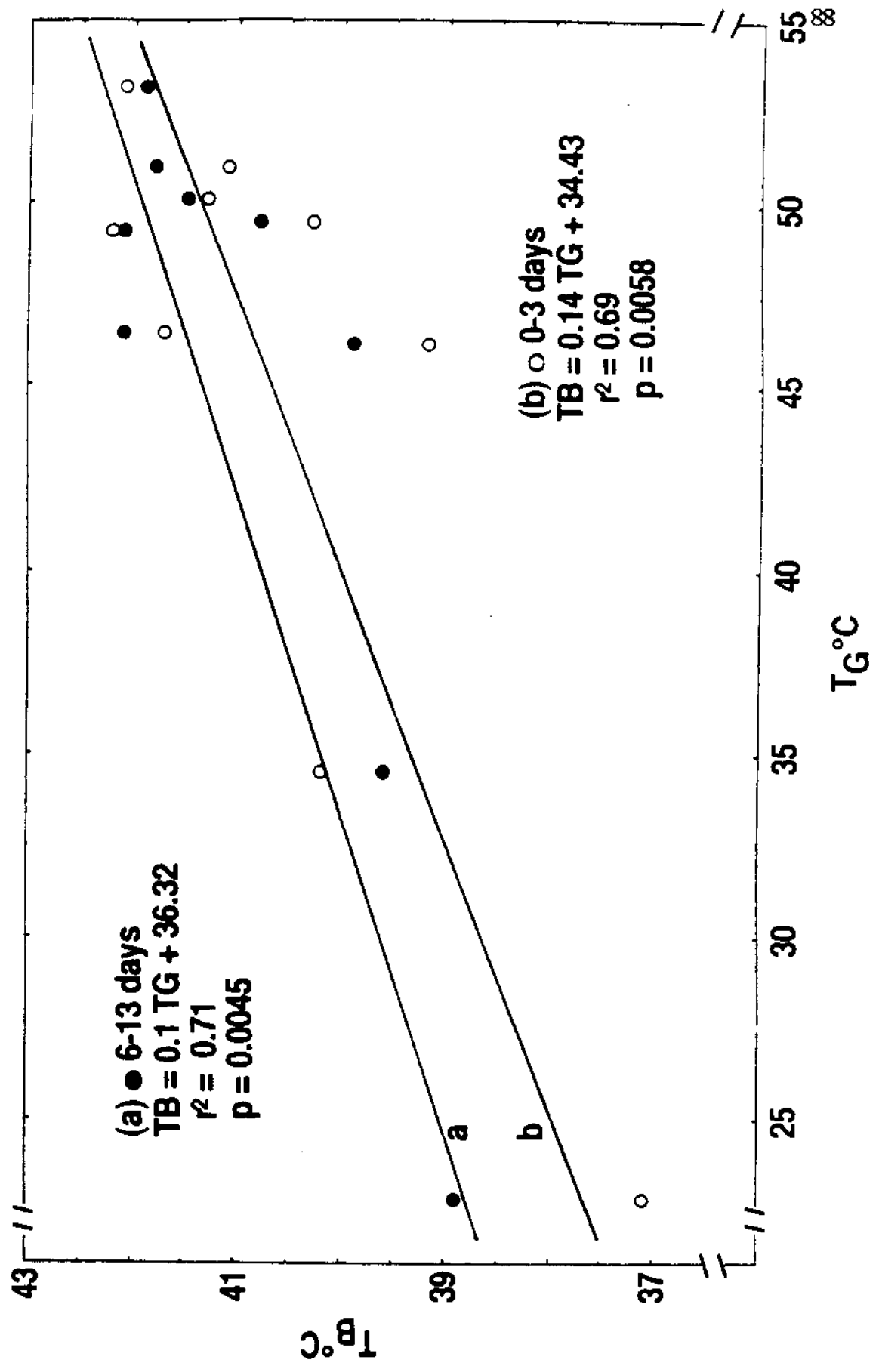


Figure 18. Linear regression models relating body temperature ( $T_B$ °C) of gray gull *Larus modestus* chicks (0-3 and 6-13 days old) to air temperature ( $T_A$ °C) at the Lealtad nesting colony.

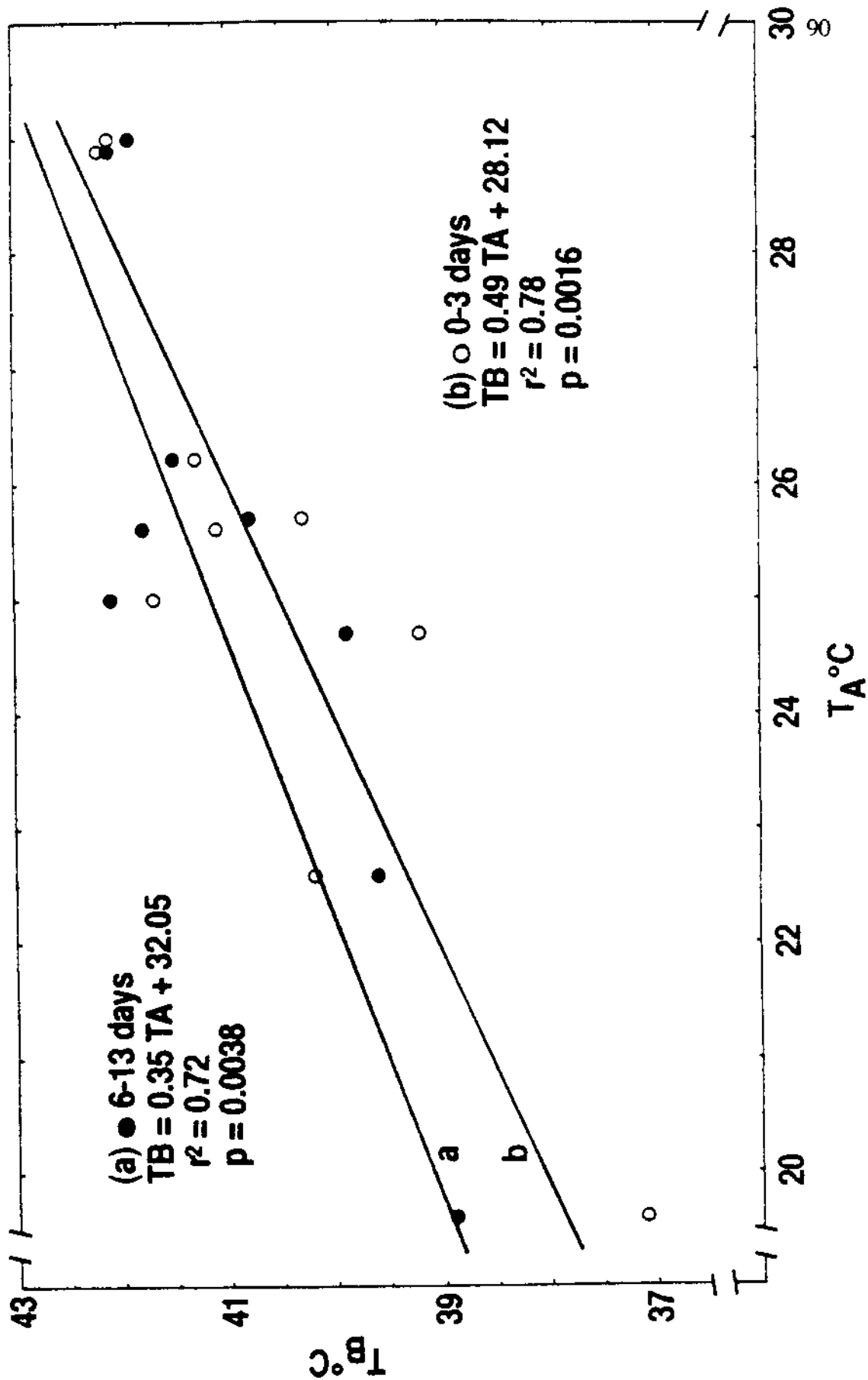




Figure 19. Linear regression model relating body body temperature ( $T_B$ °C) of gray gull *Larus modestus* chicks (0-13 days old; pooled from Figure 17) to ground temperature ( $T_G$ °C) at the Lealtad nesting colony.

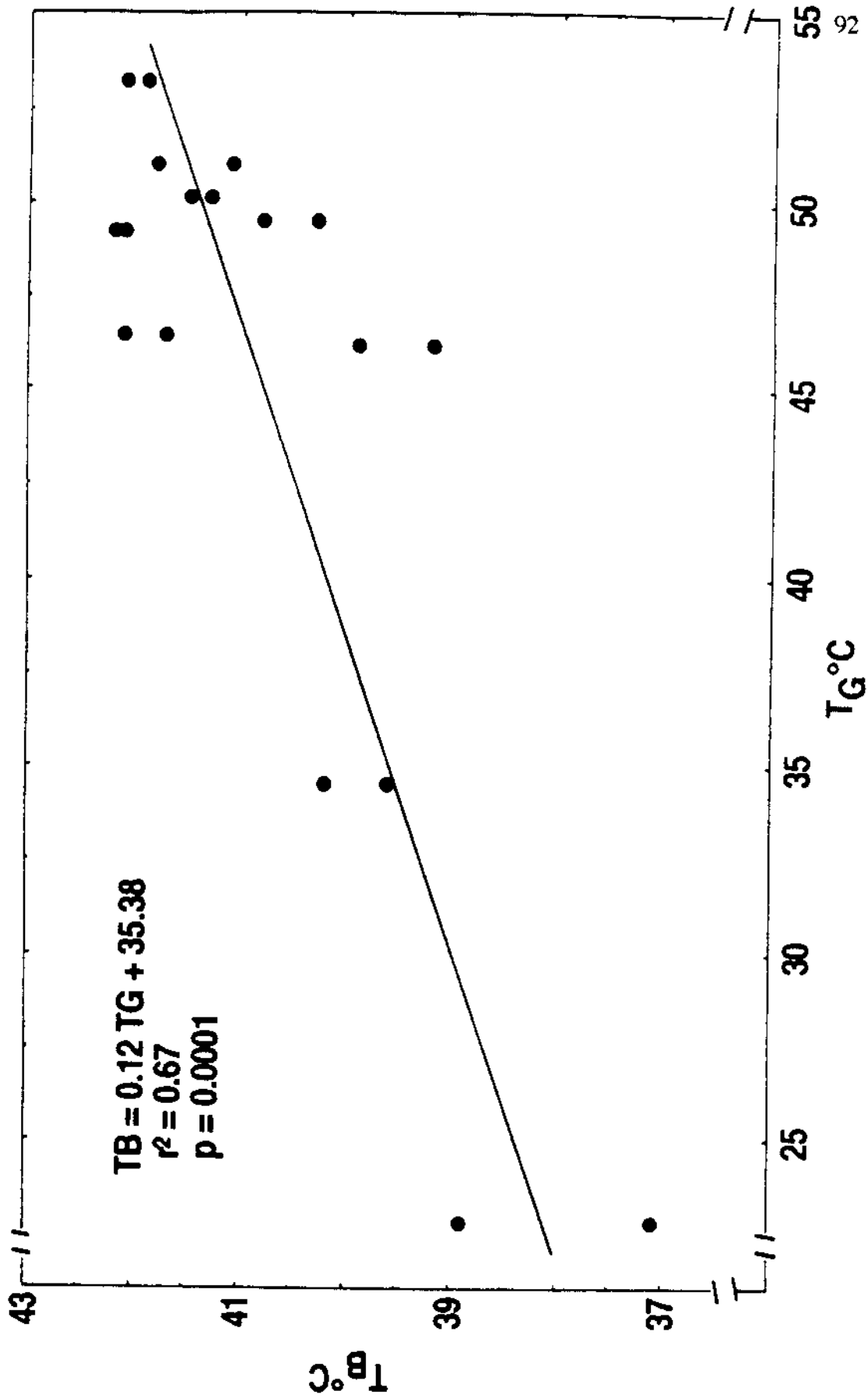


Figure 20. Linear regression model relating body temperature ( $T_B$ °C) of gray gull *Larus modestus* chicks (0-13 days old; pooled from Figure 18) to air temperature ( $T_A$ °C) at the Lealtad nesting colony.

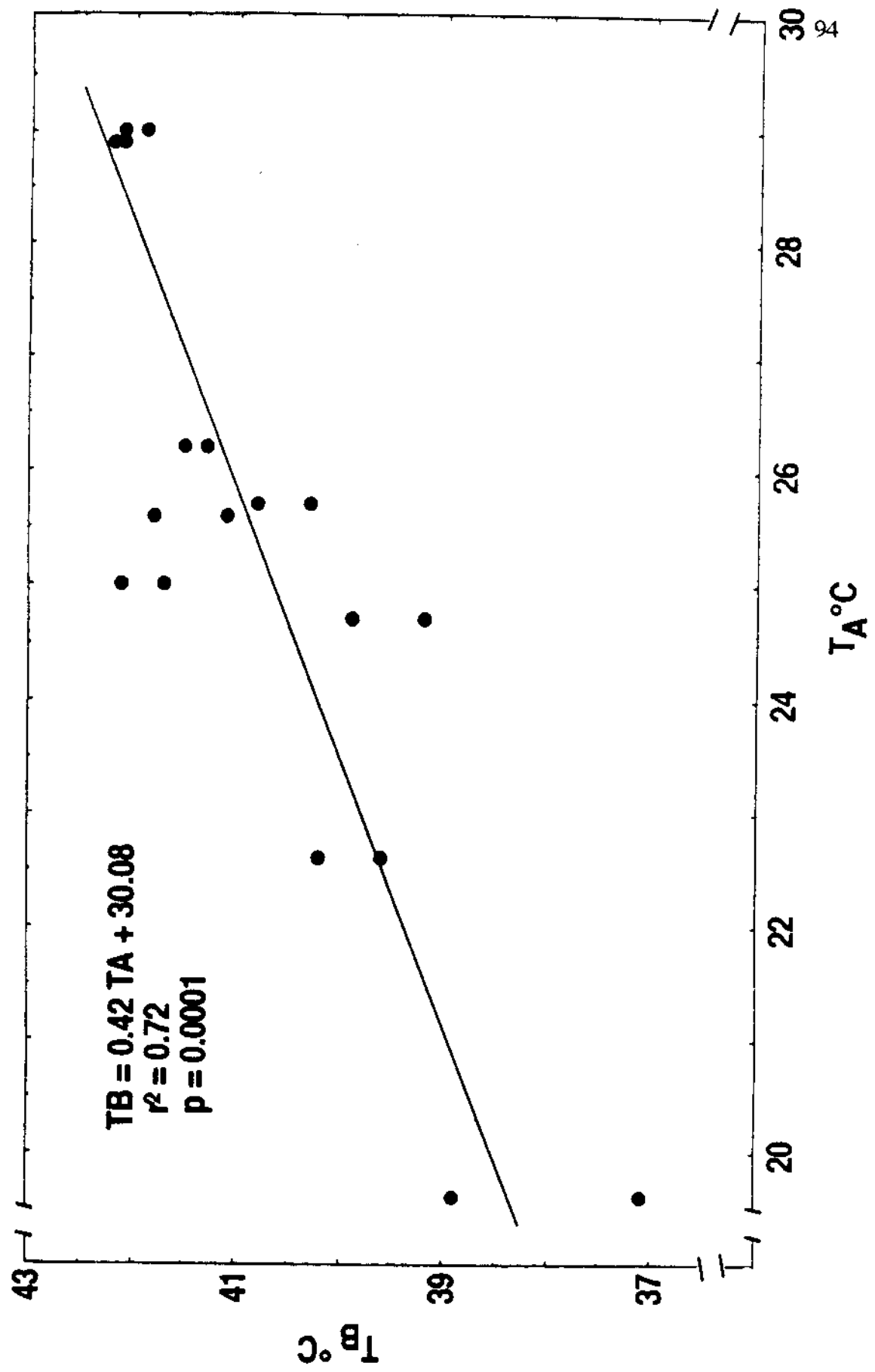


Figure 21. Linear regression models relating body temperature ( $T_B$ °C) of gray gull *Larus modestus* chicks (0-3 and 6-13 days old) maintained under shade to ground temperature ( $T_G$ °C) during the day at the Lealtad nesting colony.

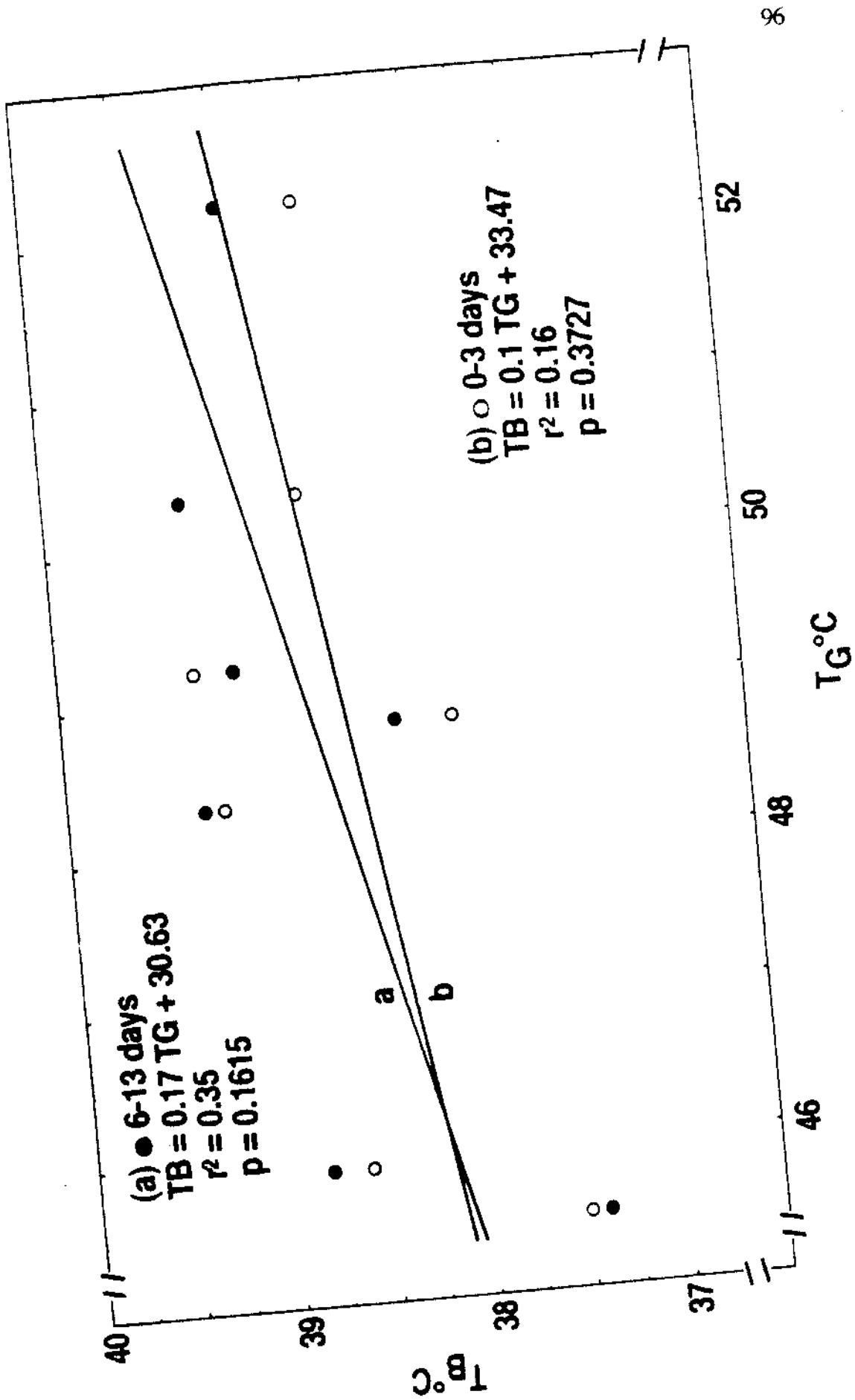


Figure 22. Linear regression models relating body temperature ( $T_B$ °C) of gray gull *Larus modestus* chicks (0-3 and 6-13 days old) maintained under shade to air temperature ( $T_A$ °C) during the day at the Lealtad nesting colony.

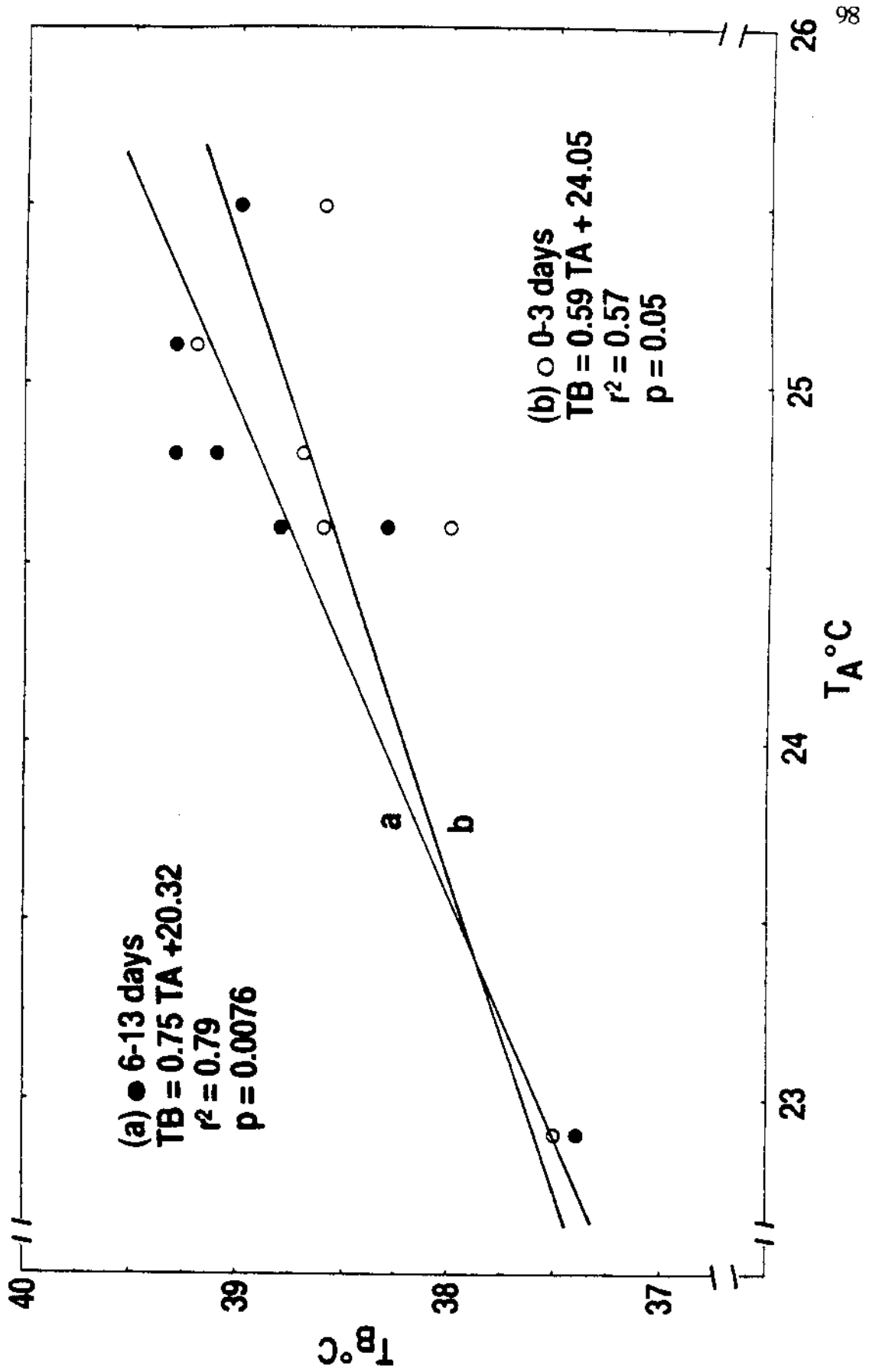




Figure 23. Linear regression model relating body temperature ( $T_B$ °C) of gray gull *Larus modestus* chicks (0-13 days old) maintained under shade to air temperature ( $T_A$ °C) during the day at the Lealtad nesting colony.

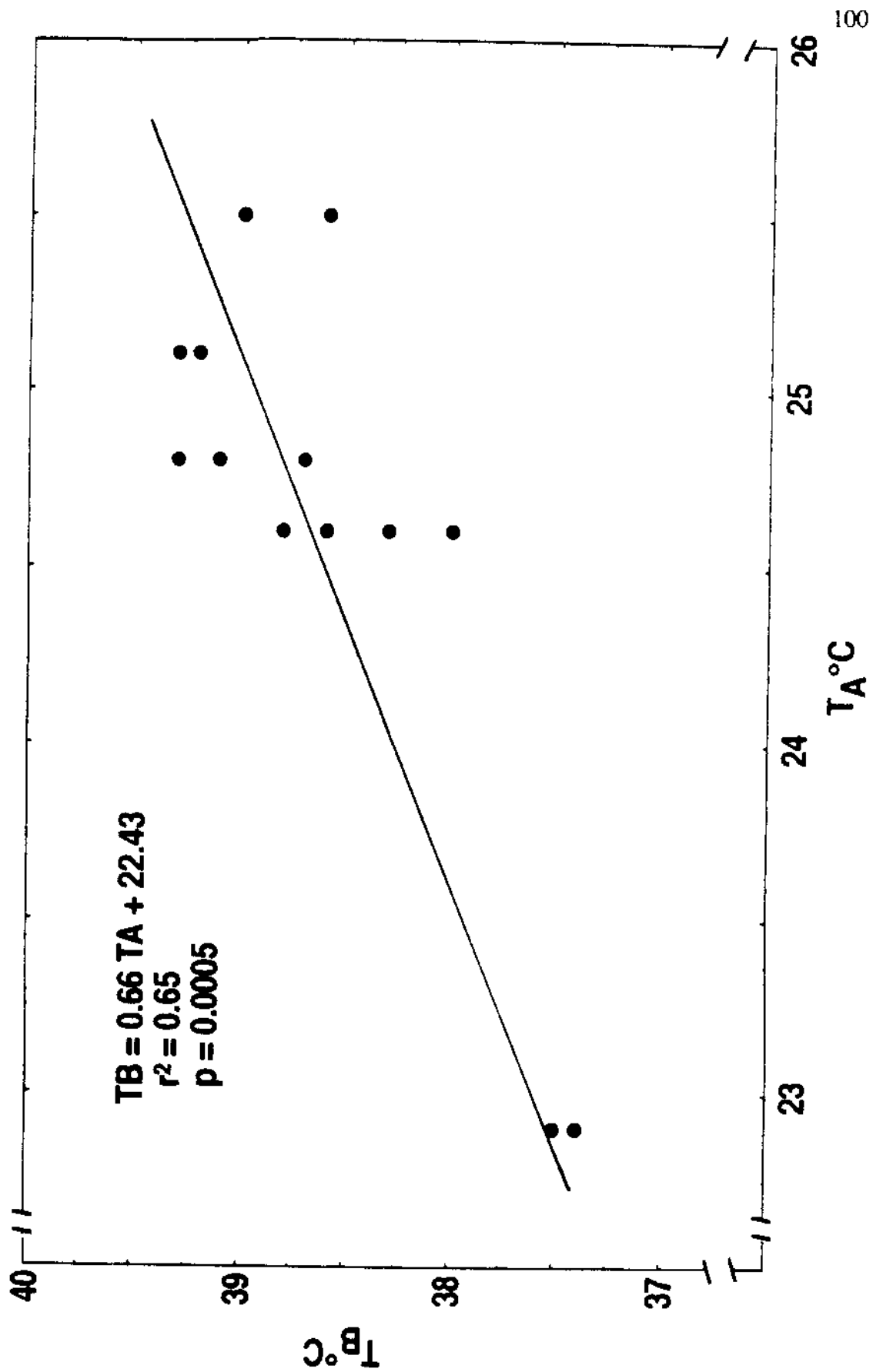
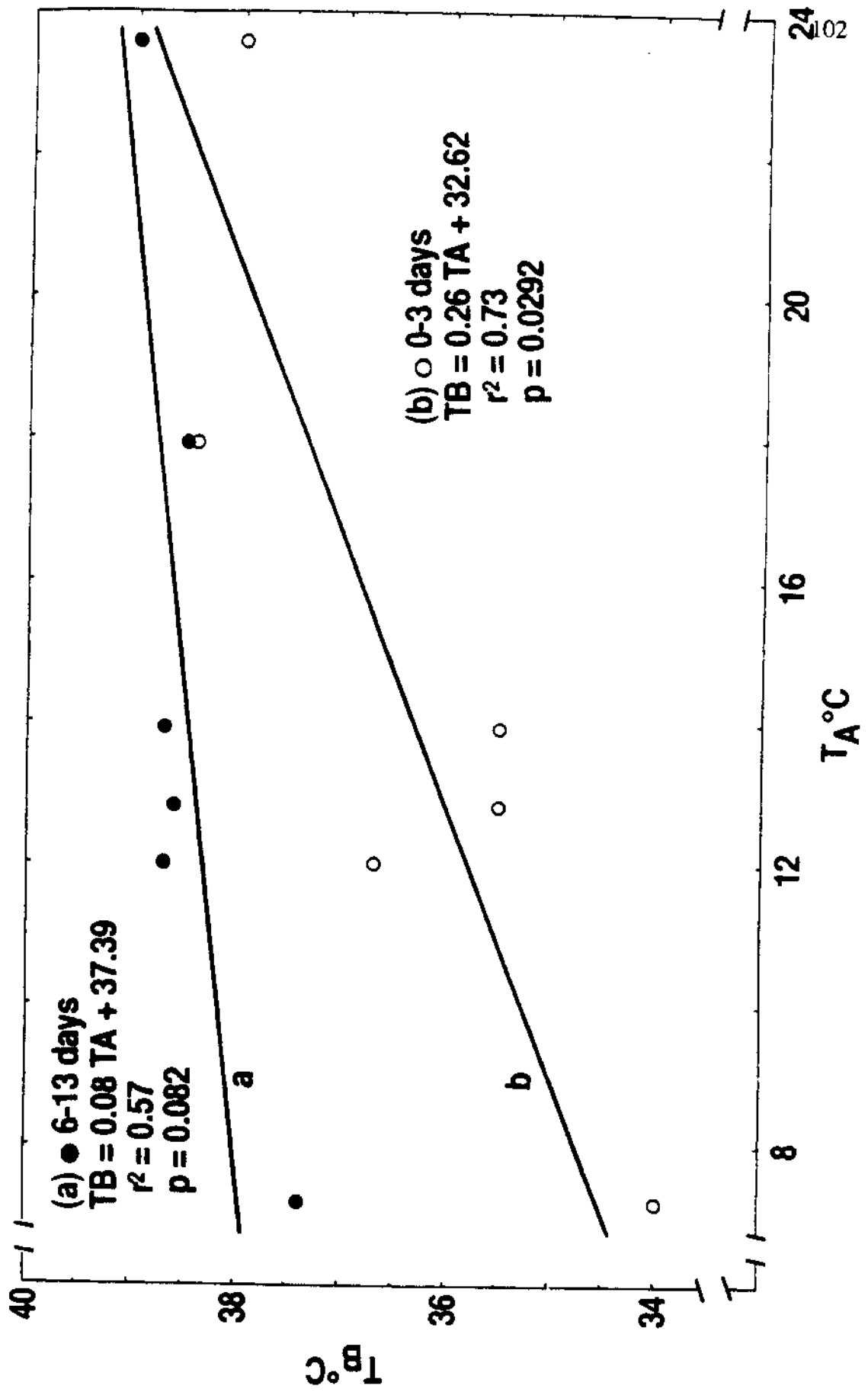


Figure 24. Linear regression models relating body temperature ( $T_B$ °C) of gray gull *Larus modestus* chicks (0-3 and 6-13 days old) to air temperature ( $T_A$ °C) during the coldest hours (18:00-07:00) at the Lealtad nesting colony.



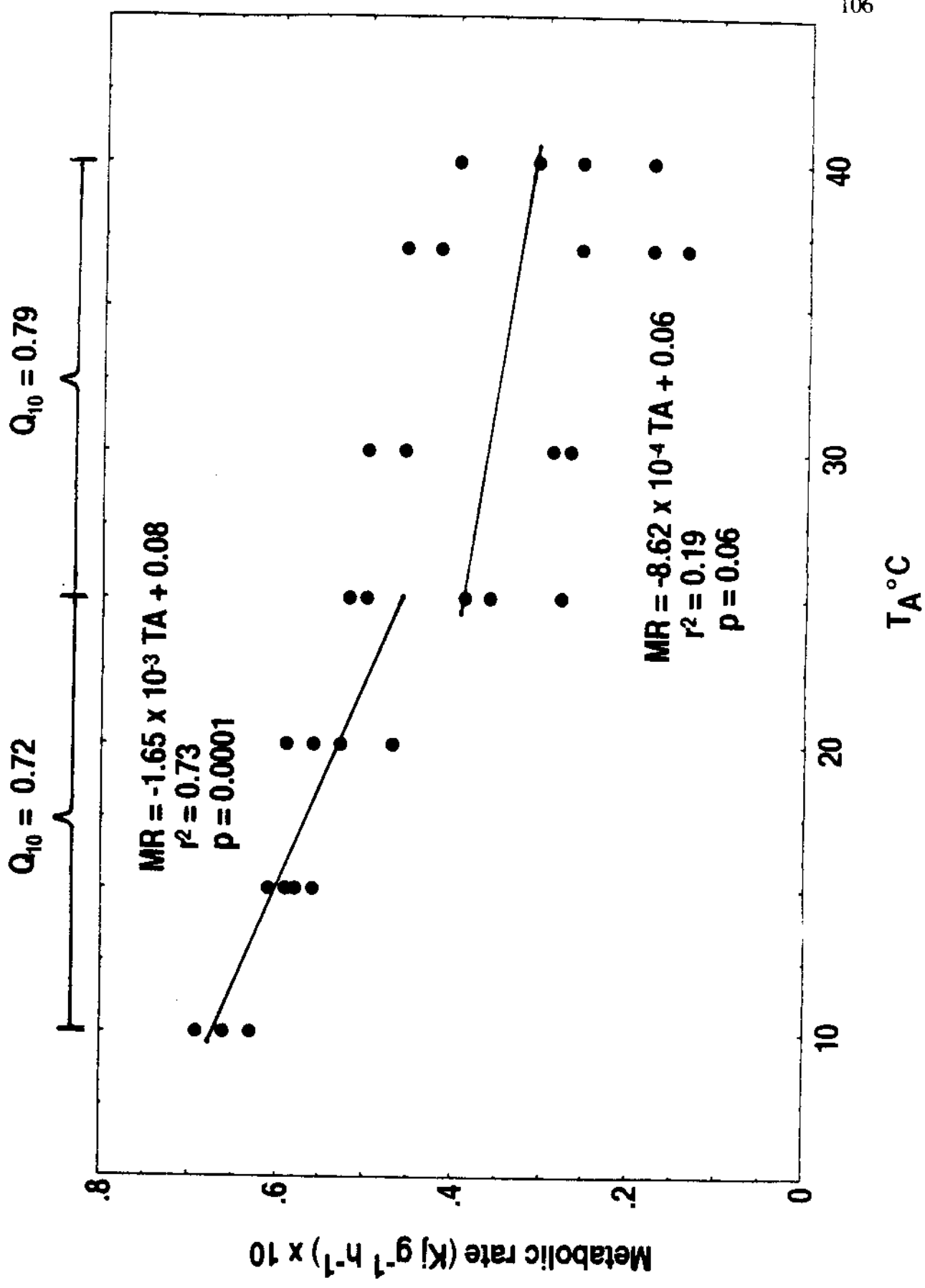
**Hypotheses 9 and 10** - To test hypotheses that chicks should have lower SMR than similar sized chicks of other species and that chicks should exhibit a wider TNZ than chicks inhabiting less extreme environments, I measured  $VO_2$ 's several time for two growing chicks at eight  $T_A$  (Figure 25). There was a significant ( $p = 0.0001$ ) decrease in  $VO_2$  with temperature increase from  $10^\circ$  to  $25^\circ$   $^\circ C$ . From  $25^\circ$   $^\circ C$ , chick metabolic rates did not change significantly ( $p = 0.06$ ) with temperature increase. The respective  $Q_{10}$ 's for these two segments of the curves ( $10^\circ$ - $25^\circ C$  and  $25^\circ$ - $40^\circ C$ ) are 0.72 and 0.79. Figure 25 shows that variance in metabolic rate increased with increasing of  $T_A$ . Since metabolic rate was so variable and only two chicks were used, the SMR and TNZ are difficult to define more narrowly than being some where within  $25^\circ$ - $40^\circ C$ . The only temperature range where the  $Q_{10}$  was 1.0 (i.e., suggesting temperature-independent metabolism or SMR) is  $37^\circ$ - $40^\circ C$ . Comparison of empirically determined  $VO_2$  within  $25^\circ$ - $40^\circ C$  for gray gull chicks of different masses, with values predicted from the equation for non-passerines ( $SMR = 327.8 Mb^{0.723}$ ) determined by Lasiewski and Dawson (1967) are given in Table 15. Experimental values were not significantly different from predicted values ( $X^2, p=0.9999$ ): mean SMR observed was  $0.033 \text{ Kj g}^{-1} \text{ h}^{-1}$  and the predicted SMR for 38.4 g (mean chick mass) is  $0.034 \text{ Kj g}^{-1} \text{ h}^{-1}$ .

TABLE 15

Empirically determined standard metabolic rate (SMR in  $\text{Kj g}^{-1} \text{h}^{-1}$ ) in gray gull *Larus modestus* chicks compared with those predicted from Lasiewski and Dawson (1967) equation ( $\text{SMR} = 327.8 \text{ Mb}^{0.723}$ ).

MASS(g)	SMR obs $\bar{X} \pm \text{SD}, (N)$	SMR predicted	Difference
33	$0.031 \pm 0.007, (4)$	0.035	- 0.004
34	$0.022 \pm 0.007, (4)$	0.035	- 0.013
38	$0.027 \pm 0.007, (4)$	0.034	- 0.007
42	$0.049 \pm 0.003, (3)$	0.033	+ 0.016
45	$0.044 \pm 0.003, (4)$	0.032	+ 0.012
$\bar{X}$	$\bar{X} \pm \text{SD}, (N)$	$\bar{X} \pm \text{SD}, (N)$	
38.4	$0.035 \pm 0.012, (5)$	$0.034 \pm 0.0013, (5)$	+ 0.001

Figure 25. Metabolic rate ( $\text{Kj g}^{-1} \text{h}^{-1}$ ;  $1 \text{ Kj} = 50 \text{ ml O}_2$ ) of two gray gull *Larus modestus* chicks (33-45 g) measured at ambient air temperature ( $T_A$ ) from 10 to 45°C. Each chick was measured at least twice at given temperature from low to high  $T_A$ , as it grew.  $Q_{10}$ 's appear above each segment of the rate-temperature curves.





## Growth Rate

**Hypotheses 11 and 12** - The hypothesis that chicks from single-egg nests should grow faster than those from two-egg nests was tested by weighing serially recaptured banded chicks and recaptured at Lealtad. Due to high mobility and ability to avoid hand-capture, I could not obtain data on chicks older than 16 days. Data in Figure 26 support the hypothesis that single chicks should grow faster than two siblings. During the first 21 days of growth, there was a significant relation between chick mass and age in both single and sibling chicks, ( $r^2 = 0.98$ ;  $p = 0.0001$ ;  $r^2 = 0.93$ ,  $p = 0.0001$ , respectively), which was significantly different between the groups (t test for slope,  $p < 0.001$ ).

For purpose of testing the hypothesis that overall growth in chicks at Lealtad should be faster than in chicks at Cerro Negro, ca. 85 km further inland, data from sibling and single chicks, although significantly different, were pooled to create a regression model ( $\text{mass} = 10.63 \text{ Age} + 23.37$ ;  $r^2 = 0.94$ ;  $p = 0.0001$ ) for comparison with pooled Cerro Negro data (Guerra et al. 1988c). These pooled age-specific growth rate data (Figure 27) support the hypothesis that chicks at Lealtad should grow faster than those growing at Cerro Negro.

Figure 26. Comparative age-specific growth rates in chicks from single and two-egg nests of gray gulls *Larus modestus* in the Lealtad nesting colony.

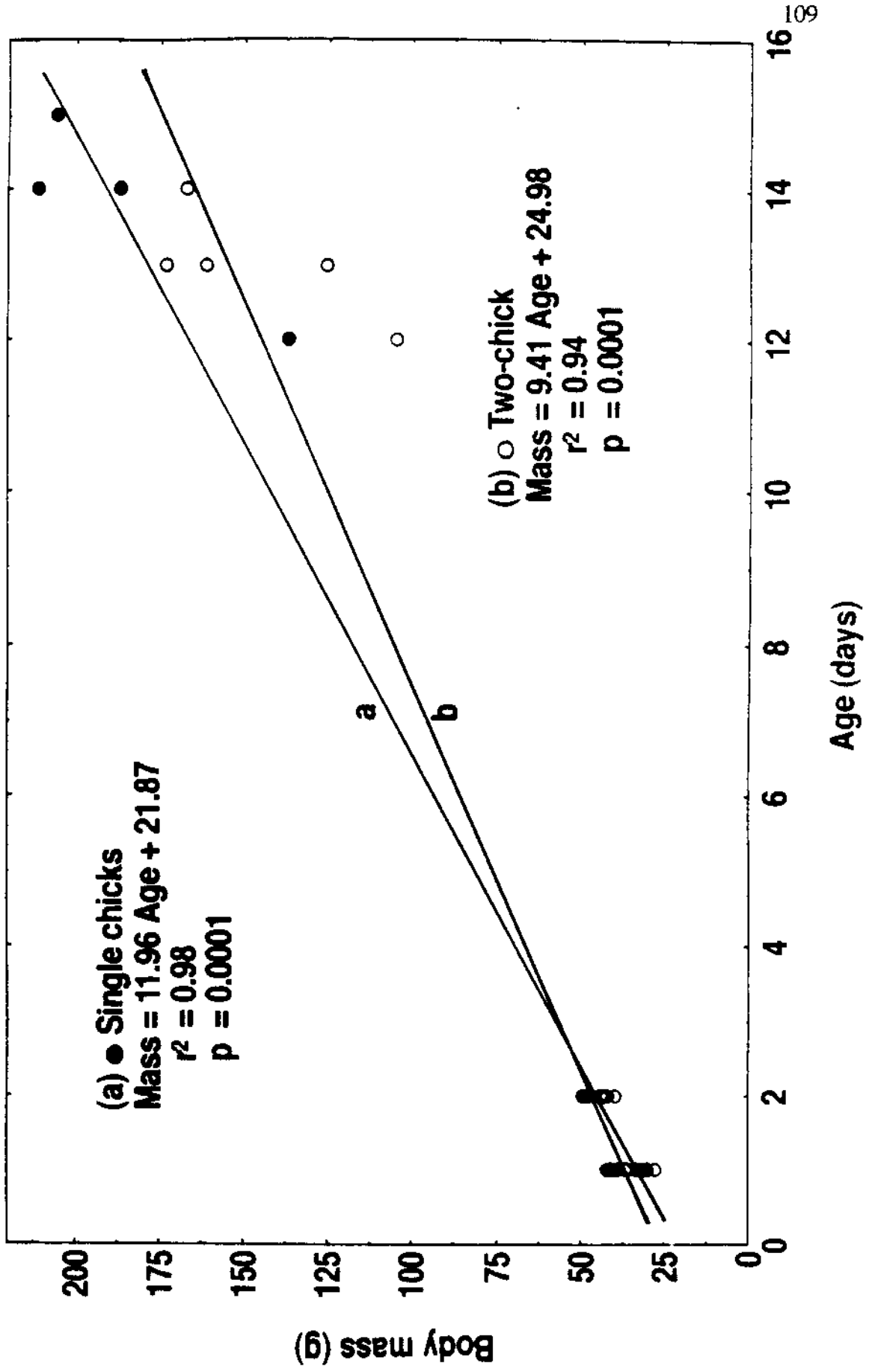
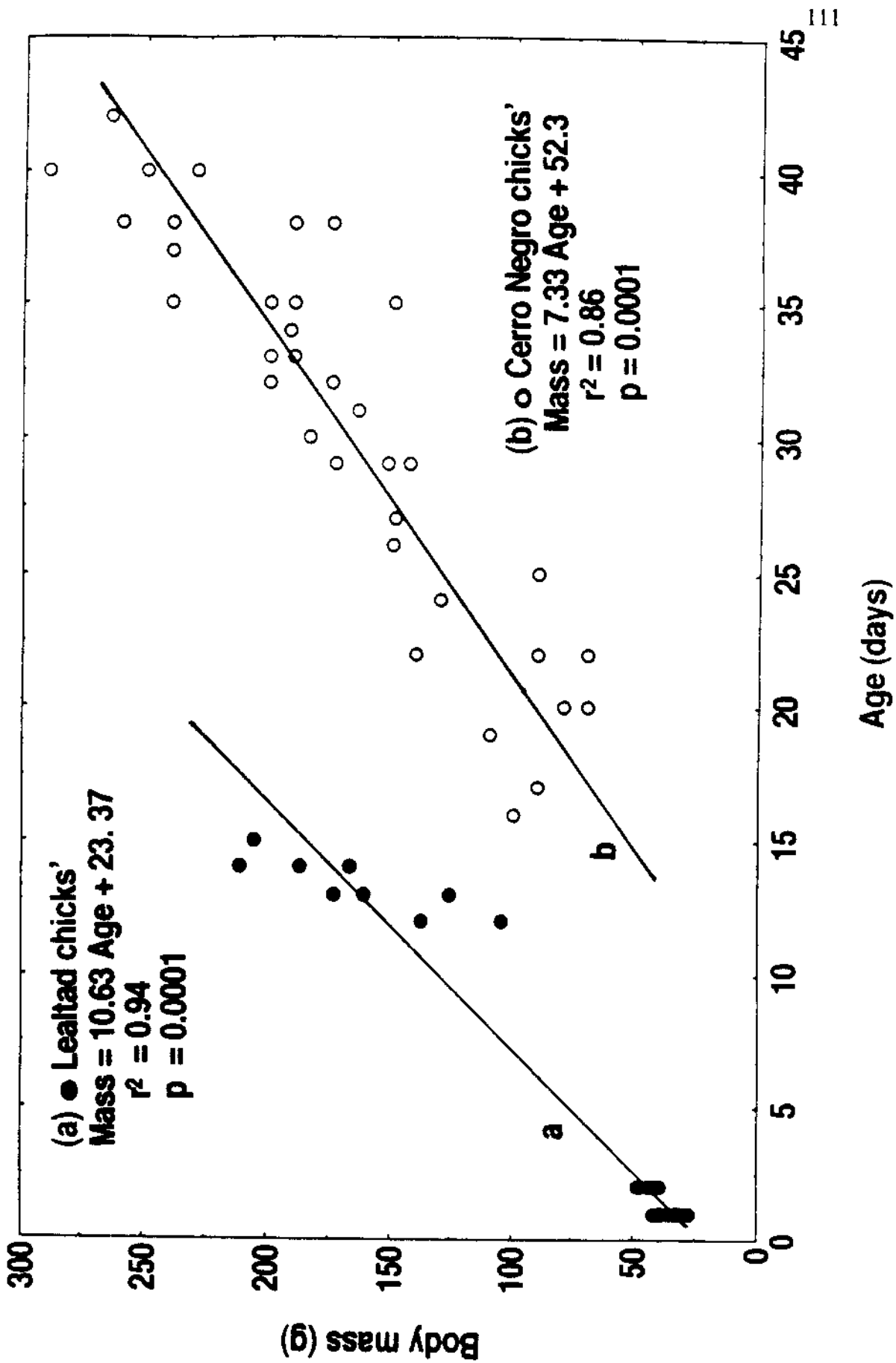


Figure 27. Comparative age-specific growth rates in gray gull *Larus modestus* chicks from Lealtad and Cerro Negro nesting sites. Data for Cerro Negro chicks were taken from Guerra et al. (1988c).



## CHAPTER IV

### DISCUSSION

#### Meteorological Conditions

Ambient conditions at the Lealtad site were similar to those reported for other nesting sites throughout the Atacama (Guerra et al. 1988c). Nights were cold with both ground ( $T_G$ ) and air ( $T_A$ ) temperatures reaching minimal daily values. After sunrise,  $T_G$  and  $T_A$  increased gradually, reaching maximal values in the afternoon. Winds at Lealtad are typical for the Atacama: calm during the night, dawn and morning, and increasing in velocity by mid-afternoon. Gray gull activities correspond to diel variations in meteorological conditions. Gulls at Lealtad showed the same activity patterns as those reported for gulls at Cerro Negro and Kimurku (Fitzpatrick et al. 1988). They arrived at Lealtad during the night when the winds had decreased (after 21:00 h) and departed for the coast ca. 04:00 h, catching a tail wind from the Andes.

#### Nest Dispersion

**Hypothesis 1.** The hypothesis that nest dispersion is clumped, which should facilitate group defense against turkey

vultures and minimize egg exposure to the dry environment when adults fly to distract or defend nest from predators, was supported, in part, by results. As pointed out by Guerra (1990), and supported by my observations, as turkey vultures approach the nesting site, small groups of 3-5 adults fly to defend the colony. Alternating this defense would divide the labor among gulls and minimize average egg exposure.

Indirect support for that contention come from my incubation temperature data: during 13:00-19:00 h, when turkey vultures normally fly above the colony and gray gulls fly for defense, the mean egg temperature recorded was 37.9°C (SD = 0.68°C; N = 37). Based on my observations and those of others (Guerra pers. comm.), it is likely that the number of turkey vultures and frequency of their nest attacks are fairly consistent throughout the breeding season. The low coefficient of variation (cv = 1.84%) in temperatures of incubated eggs indirectly suggests that if incubating adults left their nests, it was either infrequently or only for short periods of time. Although aggregated nesting should play an important role in reducing egg exposure, more data comparing egg temperature from the periphery, where nests are less dense with those from the center, are necessary to demonstrate that dense spatial dispersion actually reduces egg exposure to dessicating conditions, while reducing the probability of predation when small groups of adults fly to distract or defend their nests.

Testing the hypothesis that clumped nesting is a pattern response to avian predators is difficult because of the absence of colonies having the nest density of Lealtad in areas without predation. Comparisons with other known colonies preyed upon by turkey vultures, such as at Kimurku-Valenzuela, are not valid because nests are hyperdispersed. Density of nesting pairs differed little from that reported by Guerra (1990) for the Lealtad colony in 1989-90, suggesting that the colony is relatively stable demographically. That correspond to coastal census data which indicate that gray gull populations along the coast of northern Chile show little variation among years (Guerra 1987; 1990).

#### Clutch Size

**Hypothesis 2.** The hypothesis that clutch size of gray gulls nesting at Lealtad should be greater than for more inland sites was not supported by the results. Although data from the Colupo-Kimurku-Valenzuela area, during 1985-86 and 1986-87 (post ENSO) breeding season showed higher average (1.81 eggs) and frequency of two-egg (0.81) clutches (Guerra et al. 1988d), average clutch sizes among different nesting sites determined for different years were too similar to differentiate among locations (see Table 2). Average clutch size (1.56) and frequencies of one (0.44) and two-egg (0.55)



clutches agree with average clutch size (1.55) and relative frequencies of one and two-egg clutches of 0.47 and 0.52, respectively, reported by Howell et al. (1974) for the Colupo colony. Clutch size at Lealtad was identical to that (1.55) reported for 1989-90 breeding season at Cerro Negro (Guerra 1990). In general, clutch sizes of nesting sites (Colupo, Lealtad, Kimurku-Valenzuela) close to the coast (15-35 km; all data pooled) and Cerro Negro (all data pooled) (see Table 2) were not significantly different (Mann-Whitney U,  $p = 0.8801$ ). Differences in clutch size (e.g., 1.81 vs. 1.43) among years between 1984 and 1992, in sites located close to the coast support the statement that female gray gulls may "bet-hedge" altering their clutch size from zero to one to two according to food availability (Guerra 1987; Guerra et al. 1988d and Fitzpatrick et al. 1992). "Bet-hedging" strategies also have been observed in laughing gulls and glaucous-winged gulls associated to decrease food availability, low protein diet or incubation capacity of female gulls (Schreiber et al. 1979; Reid 1987).

Compared to most larids, *L. modestus* has a reduced average clutch size (1.56 eggs/nest). Seventeen larids have clutch sizes greater and nine lesser than gray gulls: 11 larid species have a clutch size of three eggs (*L. argentatus*, *L. atricilla*, *L. glaucescens*, *Sterna hirundo*, *L. californicus*, *L. fuscus*, *L. canus*, *L. occidentalis*, *L. delawarensis* and *L. ictchyaetus*); six (*Pagophila eburnea*, *L.*

*genei*, *Xema sabini*, *Sterna caspia*, *S. sandvicensis*, *S. dougadillii*) have two-egg clutches; and nine have a clutch size of one (*L. furcatus*, *L. tridactyla*, *L. brevirostris*, *S. maxima*, *S. fuscata*, *S. lunata*, *Anous stolidus*, *A. tenuirostris*, *Gygis alba*)(Rahn et al. 1984; Reid 1987). Among gulls with reduced clutch size, *L. furcatus* also is a long distance forager (Lack 1967). Clutch size of three in gray gulls is extremely rare; Howell et al. (1974), found only three nests in the Colupo nesting site, and I observed one nest with three eggs in Lealtad. Guerra, Fitzpatrick and collaborators never observed clutches of three. Gray gulls have three brood patches (Guerra pers. comm.).

As suggested by Lack (1968), reduced clutch size in birds that feed far from their breeding site is an adaptive response to the cost of obtaining food for their chicks. According to Guerra (1987) and Guerra et al. (1988d), clutch size in gray gulls reflects the pattern observed in long-distance foraging seabirds (i.e., pelagic). Although gray gulls nesting closest to the coast (15 km) theoretically could make more than one daily foraging trip, they do not. Thus, no matter how far from the coast gray gulls nest, they "behave" as long-distance pelagic foragers. Perhaps the cost to fly over the coastal mountains when the winds (Figure 4) are not appropriate precludes multiple foraging flights even for colonies as close to the coast as Lealtad.

### Time and Temperature of Incubation

**Hypothesis 3.** Hypotheses that average incubation time of two-egg clutches should be longer than single-egg clutches and that hatching in two-egg clutches is asynchronous were not supported by the results. There was no significant difference in overall mean incubation time between two-egg and one-egg nests (27.9 vs, 28.5 days) (one tail, t test,  $p = 0.3454$ ). Although, statistical analysis showed significant difference in mean incubation time between first and second-laid eggs (28 vs. 29 days) (one tail, t test,  $p = 0.0001$ ), the difference of only 1 day in incubation time should not have biological significance. My observations support the implications of coordinated hatching in gray gulls proposed by Guerra (1987). According to Howell et al. (1974) and Guerra (1987), eggs from two-egg clutches differ in size and color, but there are no significant differences between eggs from single-egg clutches and the first egg laid in two-egg clutches. Guerra (1987) hypothesized that the smaller second-laid egg may result from energy limitations or as a facultative response to varying food availability as has been suggested for western gull (Sydeman and Emslie 1992), and/or to insure that hatching occurs at the same time (Guerra 1987). Coordinated hatching is important for gray gulls nesting in the Atacama for two reason: (1) it would be quite difficult for parents simultaneously to incubate an egg

and tend a chick; and (2) since onset of thermoregulation in chicks determines when both adults can forage, asynchronous hatching would prolong the period when only one adult is able stay to forage. According to Guerra (1987), single-egg clutches are produced late in the breeding season by young females in their first reproductive season. That agrees with the report by Sydeman and Emslie (1992) that clutch size increases with age in western gulls. However, during years when breeding is delayed, such as in 1991-92, the nesting season is shortened, obscuring differences in clutch size between early and late laying gray gull females.

Average incubation time (29 days) at Lealtad is close to the 30 days reported by Howell et al. (1974). However, the average of 29 days for incubation in gray gulls is longer than for other gulls having the same body mass and egg size (e.g., *L. canus* = 24 days; *L. hermannii* = 26 days; *L. tridactyla* = 25 days; *L. delawarensi* = 22 days)(Lack 1967; Vermeer 1970; Ar and Rahn 1980). Guerra et al. (1988a) stated that prolonged embryonic development is a consequence of reduced functional pore area of egg shell, which results in both low water vapor conductance and exchanges of metabolic gases. Prolonged incubation has been associated with the low egg shell water vapor conductance for many species of birds (see Rahn and Ar 1974; Rahn et al. 1976; Ackerman et al. 1980; Grant 1982). Howell et al. (1974) thought that the relatively prolonged incubation in gray

gulls was associated with low temperatures reached by eggs during the night. Regardless of the causes, prolonged incubation in gray gull eggs reflects a trade off of nesting in the Atacama.

Maximal and minimal incubation temperatures of 39° and 30°C that I determined at Lealtad differed little from those reported by Howell et al. (1974) for gray gulls nesting in Colupo (38° and 33°). Variation in egg temperature during incubation reflects adult behavior. Minimal temperatures coincide with the high activity within the colony during and after the arrival of foraging adults, ca 2400 and 0200 (Guerra 1987; Fitzpatrick et al. 1988). Maximal egg temperatures occurred during periods of highest  $R_S$  and  $T_G$ , when incubating adults stood for convective cooling exposing eggs to indirect radiation and surface heat. Shading by adults prevents overheating of eggs (Howell et al. 1974). Although the minimal incubation temperature in gray gulls did not differ from the minimal temperature (30°C) reported for western gulls, the maximal incubation temperatures was higher in gray gull (39° vs. 36°C respectively). Differences in both minimal and maximal temperatures during incubation are more evident between gray gulls and their ecological equivalent, Heermann's gull (30°-39°C vs. 35°-37°C) (Rahn and Dawson 1979). Adult behavior similar to that of gray gulls has been observed during incubation in western and herring gulls (Hand et al. 1981), but not in Heermann's gulls, which

sit tightly on their eggs throughout the day, seldom directly exposing them to ambient conditions (Bartholomew and Dawson 1979). According to Rahn and Dawson (1979), periodic postural movement "ventilates" the nest by removing water vapor and CO<sub>2</sub> from the metabolizing egg by convection and/or diffusion, thereby playing a role in thermoregulation of eggs. Also, egg temperatures vary with the development stage of embryos. In many bird species, egg temperatures rise as metabolic heat production increases with embryo size (Grant 1982). I did not determine the relation between egg temperature and developmental stage of embryos.

#### Egg-Hatching Success

**Hypothesis 4.** The hypothesis that two-egg nests should have higher hatching success than single-egg nests was supported by the results. Higher hatching success in two-egg nests than one-egg nests accords with several studies that indicated lower hatching success in smaller than larger clutches of laughing gulls and western gulls (Schreiber et al. 1979; Sydeman et al. 1991). Chick survival tends to increase with hatching order in European swifts (O'Connor 1979). According to Sydeman et al. (1991) hatching success may be a complex function of quality of incubation, interspecific predation, egg infertility or damage to the egg. Additionally, young females may provision their eggs

with less energy and/or nutrients than do older females, increasing the likelihood of eggs not hatching (i.e. reduced hatchability). Young females may not be as effective in defending their nest from predators. They also may be more prone to abandon eggs than older females.

Although predation has been proposed as an important factor in determining hatching success in gray gulls (Guerra 1987), total hatching success (78.4%, N = 280 eggs) for gray gulls nesting at Lealtad, where predation is present (Guerra 1990; personal observation) is greater than those reported (66.7%, N = 60 eggs) for Cerro Negro (Guerra 1990), where predation is absent (Guerra 1987; Guerra et al 1988d; personal observation). My observations suggest that predation by turkey vultures may not be very important in the center of the colony where adults effectively defend their nest, keeping turkey vultures toward the periphery of the nesting site.

Since gray gull populations appear relatively stable along the northern coast of Chile (Guerra 1987, 1990) and the Lealtad colony exhibited adult density virtually identical to that reported by Guerra (1990) for 1989-90, actual annual recruitment must be very low. The egg-hatching success of 1.38 hatching per female suggests that mortality must be quite high during the hatchling-fledgling and/or fledgling-adult stages.

### Thermal Profile and Metabolism of Embryos

**Hypothesis 5.** The hypothesis that gray gull embryos should have a wider thermal tolerance (i.e., critical thermal maximum and minimum) than congeneric embryos, because of egg exposure during nest defense by and thermoregulatory behavior of adults (Fitzpatrick et al. 1989), was not supported by my results. The lower and upper critical temperatures (17° and 41°C) for gray gull embryos fell within those (11° and 46°C) reported for western gulls (Bennett et al. 1981), but only the upper is similar to that (41.1°C) reported for Heermann's gull; lower critical temperatures were quite different (17° vs. 7.9°C) (Bennett and Dawson 1979). Wide variation in thermal tolerance suggests that considerable fluctuation can be tolerated without interrupting embryonic development (Bennett et al. 1981). Bennett et al. (1981) argued that differences in upper temperature tolerated (46° vs. 41.1°C) between western gulls and Heermann's gulls resulted from differences in parental behavior. Since Heermann's gulls rarely expose their eggs to the environment (Bartholomew and Dawson 1979; Bennett and Dawson 1979), variation in egg temperature should be minimal. In contrast, western gulls frequently leave their nests, directly exposing eggs to ambient conditions. As such, embryos are exposed to more variable conditions and have evolved tolerance to high temperatures (eggs of western gulls resist temperatures 10°C



above the maximal incubation temperature recorded (Bennett et al. 1981). According to Bennett et al. (1981), heart rate (HR) of western gull embryos varies directly ( $Q_{10} = 1.9$ ) with temperatures over the incubation range ( $30^{\circ}$ - $35^{\circ}$ C); but below  $30^{\circ}$ C, HR decreases rapidly ( $Q_{10} = 3$ ). Bennett and Dawson (1979) reported that HR in Heermann's gull is less sensitive to temperature than other gulls species over  $30^{\circ}$ - $40^{\circ}$ C ( $Q_{10} = 1.1$ ). Over the same temperature range, 2 week-old and 3 week-old gray gull embryos exhibited a  $Q_{10}$  of 1.64 and 1.42 respectively. The maximum temperature tolerated ( $41^{\circ}$ C) by gray gull embryos is similar to that reported ( $41.1^{\circ}$ C) for Heermann's gulls (Bennett and Dawson 1979), but lower than that ( $46^{\circ}$ C) for western gulls (Bennett et al. 1981).

The slow increase in egg temperature of gray gulls at Lealtad may result from egg shell reflectance and convective heat loss, as was suggested by Bennett et al. (1981) for western gulls. My observations and those of Guerra and coworkers, indicate that gray gulls only expose their eggs to direct sunlight, when they leave to distract humans, turkey vultures or falcons. Since the highest incubation temperature ( $39.4^{\circ}$ C) recorded is lower than the highest ( $42^{\circ}$ C) temperature tolerated, gray gulls should be able to leave their eggs unattended while defending nest without their eggs reaching lethal temperatures. During the night, the lowest incubation temperature reached ( $30^{\circ}$ C) is almost twice the minimal temperature tolerated ( $17^{\circ}$ C) by embryos.

Thus, exposure to low temperatures apparently does not harm the embryos, although it may prolong their development (Bennett et al. 1981) and incubation time as proposed by Howell et al. (1974).

**Hypothesis 6.** The hypothesis that the overall metabolism of developing embryos should be lower than in other gulls, because of reduced egg shell functional pore area, was not supported by my results. All  $VO_2$  data were obtained from well-developed (4 weeks old) gray gull embryos whereas published metabolic rate/ambient temperature data for other gulls are from embryos in their early stage of development (1-2 weeks old) (e.g., Bennett and Dawson 1979; Dawson 1984). Therefore, direct comparisons with gray gull data are not appropriate.

$Q_{10}$  for  $VO_2$  vs.  $T_A$  in gray gull embryos between 30° and 34°C was 1.44, 1.39 between 34° and 40°C, and between 37° and 40°C was 1.20. This decrease in  $Q_{10}$  with increasing  $T_A$  resembles the trend reported for adult ectotherms.

#### Ontogeny of Thermoregulation and Metabolic Rates in Chicks

**Hypotheses 7 and 8.** The hypotheses that chicks should develop the capacity for thermoregulation earlier than other semi-precocial larids that nest closer to food sources and that it should coincide with the time when gray gull chicks

are first left alone in the desert was supported by my results. Body temperature ( $T_B$ ) of 0-3 day old and 6-13 day old chicks exposed to environmental conditions during the day were not significantly different, and were highly correlated to variation in ambient variables, principally  $T_A$ . Variations in  $T_B$  in hatchlings under shade were not significantly different between both groups and were correlated strongest to  $T_A$ . Differences in  $T_B$  ranges during exposure and under shade ( $5^\circ$  vs.  $1.9^\circ\text{C}$ ) suggest that direct exposure to a hot environment can stress hatchlings and that newly-hatched chicks have an incipient capacity to regulate their  $T_B$ ; which agrees with the idea that semiprecocial birds rapidly develop thermoregulatory capacity (Dawson et al. 1976; Chappell et al. 1984). Gray gull chicks thermoregulate under hot conditions principally by panting and gaping, both costly in term of water. Adults provide shade for newly hatched chicks, protecting them from intense direct radiation (Guerra et al. 1988c; Fitzpatrick et al. 1992). The same behavior has been observed in California gulls (Chappell et al. 1984). When gray gull chicks are left alone ( $\geq 5-6$  days old), they take advantage of micrometeorological conditions of areas adjacent to rocks and in dry channels (Guerra et al. 1988d). According to Guerra (1987), hyperthermia in fledging-adults gray gulls, which begins at  $T_A$   $29^\circ\text{C}$ , is an important physiological tactic for minimizing both water and energy loss by reducing  $T_B - T_A$  gradient at temperatures below

their upper TNZ limit (32°C). Chicks maintained  $T_B$  ca. 41°C at  $T_A$  22°-29°C, which is close to values observed in California gulls (70 - 500 g), 40.1°C at  $T_A$  20° -30°C. When  $T_A$  was above the maximum tolerated (39° - 41°C), California gull chicks became stressed, panted and attempted to escape. Similar behavior occurred in gray gull chicks at  $T_A$  above 41°C.

During the coldest hours, the capacity to thermoregulate differed significantly between 0-3 and 6-13 day-old chicks. Young chicks were less able to thermoregulate under changing  $T_A$  than older ones:  $T_B$  in 0-3 day-old fluctuated from 34° to 38°C, while in 6-13 day-old the range was 37.4° to 38.5°C. Poor thermoregulation in chicks under 5 days at  $T_A$  below 15°C has been reported for laughing gulls (Dawson et al. 1972), western gulls (Dawson and Bennett 1981), mew gulls, lesser black-backed gulls, greater black-backed gulls and herring gulls (Dunn 1976). Thermoregulation in chicks involves huddling, taking shelter in rocks and by metabolic heat production when they are fed by and interact with adults (Guerra et al. 1989). Since thermoregulation was assessed for chicks within, wire mesh confinements, unable to obtain protection from the cold wind or ground,  $T_B$  differences in between 0-3 and 6-13 day-old chicks indicates that thermoregulation begins ca. 5 days after hatching, coincident with the time when chicks are left alone in the desert.

**Hypothesis 9 and 10.** The hypothesis that chicks should also have lower standard metabolic rate (SMR) than similar sized chicks of other avian species was not completely supported by my results. Although the SMR, measured as  $VO_2$  ( $1.75 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) in gray gull hatchlings at  $T_A$   $25^\circ\text{-}40^\circ\text{C}$ , was lower than those reported for black-headed gulls ( $26.8 \text{ g}$ ;  $2.22 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ), laughing gulls ( $28.4 \text{ g}$ ,  $1.99 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) (Dawson et al. 1976) and California gulls (under  $200 \text{ g}$ , ca.  $2 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) (Chappell et al. 1984), it was higher to those reported for ring-billed gulls ( $34.6 \text{ g}$ , is  $1.62 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) (Dawson et al. 1976), herring gulls (0-13 day-old, under  $1.5 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) (Dunn 1976) and western gulls ( $65.4 \text{ g}$ ,  $1.35 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) (Dawson and Bennett 1980).

The thermal neutral zone (TNZ) for gray gull chicks, (estimated to be within  $25^\circ\text{-}40^\circ\text{C}$ ), extends higher than that ( $28^\circ\text{-}32^\circ\text{C}$ ) for fledgling-adults ( $200\text{-}300 \text{ g}$ ) reported by Guerra (1987).  $VO_2$  for chicks within that  $T_A$  ( $0.035 \text{ KJ g}^{-1} \text{ h}^{-1}$ ) was very close to the SMR ( $0.034 \text{ KJ g}^{-1} \text{ h}^{-1}$ ) predicted from the Lasiewski and Dawson (1967) equation for non-passerines for a  $38.4 \text{ g}$  chick (= X mass of chicks used to determine TNZ and SMR). The chick estimated SMR was 1.8 times higher than the SMR ( $0.0200 \text{ KJ g}^{-1} \text{ h}^{-1}$ ) reported by Guerra (1987) for gray gulls weighing  $200\text{-}300 \text{ g}$  and measured within their TNZ ( $28^\circ\text{-}32^\circ\text{C}$ ). Below their respective TNZ,  $VO_2/T_A$  regression slopes for both chicks and Guerra's older gulls were not different ( $p > 0.9$ ). Differences in mean  $VO_2$  within and below their

TNZ (i.e. displacement of the  $VO_2/T_A$  curves relative to the Y-intercept) resulted from at least two factors: (1) differences in integumental insulation (also reported for black-headed gulls; Palonkagas and Hissa 1971); and (2) differences in body masses (38.4 vs. 200-300 g), where mass-specific  $O_2$  consumption ( $VO_2$ ) is inversely related to body mass.

The estimated TNZ, lying within 25°-40°C, does not clearly support the hypothesis that gray gull chicks should have a wider TNZ than other congeneric chicks. TNZ for black-headed gulls, herring gulls and western gulls are (28°-30°C, 25°-35°C and 23°-35°C, respectively; Dawson et al. 1976; Dunn 1974; and Dawson and Bennett 1980). That the chick TNZ probably was within 25°-40°C accords with observation that incubation temperatures fell between 30° and 40°C.

#### Growth Rate

**Hypothesis 11.** The hypothesis that chicks from single-egg nests should grow faster than those from two-egg nests, was supported by my results. Although differences in growth rates between single and sibling chicks agree with Lack's (1968) hypothesis that siblings should share a lower amount of food. The differences disagree with the hypotheses that competition between siblings should increase growth rates and that single chicks should grow slowly. According to

Werschkul and Jackson (1979; cited in Ricklefs 1982) from the sibling competition chicks could respond more freely to selective pressures outside the nest (e.g., nest site predation) and to the food gathering abilities of adults. Ricklefs (1982), pointed out that sibling competition may be a strong selection on growth rate compared to that of external mortality factors (e.g., predation). However results of such selection would depend on the evolutionary flexibility of growth rate in response to factors causing mortality of nestlings. Gray gull sibling growth rate seems to be more influenced by factors such as food limitation than predation and/or competition.

**Hypothesis 12.** The hypothesis that overall growth rate of chicks at nesting sites close to the coast should be faster than at more inland nesting sites (e.g., Cerro Negro), was supported by my results. Differences in growth rates agree with Lack's (1968) suggestion that chick growth rate is determined by food availability and/or predation; rapid growth reduces vulnerability to predation. Thus, where predation is absent, chick growth is expected to be slower than where it occurs. However, O'connor (1984) suggested that a common predator strategy to find eggs and chicks is to follow adults during their return flights from foraging. Thus, higher growth rates which should increase frequency of foraging flights should increase the probability of predators finding nests. This scenario does not apply to gray gulls,

since they make only one daily foraging flight regardless of nest location, and it occurs after sunset, when predators are roosting. Presence of predators at Lealtad probably resulted from random searches and/or accidental discovery by turkey vultures.

In gray gulls, both of Lack's (1968) determinant factors, food availability and predation, can be identified. Assuming that food adults carry is independent of nesting site location, presence of predators should play a major role in growth rate. Guerra et al. (1988b) showed that growth rate constants ( $K_G = 0.68$ ) for chicks nesting in Cerro Negro 100 km from the coast, is lower than for other Larids except for swallow-tail gulls which are long-distance foragers. They concluded that gray gull growth is a compromise related to the long distance foraging that limits chicks to a single daily meal of approximately 67 g wet mass. Unfortunately, because of difficulties in recapturing chicks, I could not determine the asymptotic mass to calculate  $K_G$  for Lealtad chicks for comparison. Growth in gray gull chicks appears to be a complex function of limited food, foraging distances, predation and extreme ambient conditions which produce high cost of thermoregulation.

The nesting colony of gray gulls at Lealtad is closer to the coast than any known active or inactive colony reported for the Atacama. It is second in size only to the now-abandoned Colupo colony. Its location suggests that the



Lealtad colony may represent half of the old Colupo colony, which consisted of ca. 10000 nesting pairs. Coastal censuses, conducted over the years by C.G. Guerra and colleagues, indicate that the total population of gray gull in northern Chile during the breeding season has fluctuated slightly around 20000. Thus, Colupo was the principal nesting site until the early to mid 1970's. The Lealtad site, although closer to the coast and subjected to numerous attacks by turkey vultures is much more remote from humans, whose intensive egg exploitation may have caused the gulls to abandon Colupo.

At present, the other half of the gray gull population nesting in Chile appears to be represented by small colonies scattered throughout the Atacama, as much as 100 km inland. This dispersion produces differences in daily foraging flight distances and predation intensity, leading to potential variations in life history parameters and demographic patterns. Thus, studies such as mine on a colony close to the coast where predation pressure is intense provides valuable data for comparison with colonies at greater distances and without predation. Based on studies at Lealtad, Cerro Negro and Kimurku-Valenzuela by myself, Guerra and Fitzpatrick, and that on Colupo by Howell et al. (1974), there appears to be no distinct pattern relating clutch size associated with marine productivity, as influenced by ENSO's, may obscure any pattern. Intensive and extensive parallel or

within-year studies at several colony locations are necessary to determine if clutch size is a function of foraging-flight distances and/or predation intensity. Clearly, the reproductive biology of *L. modestus* reflects adaptative compromises and consequences of both food limitations and severe ambient condition in the Atacama. This study, in combination with previous ones, just begins to address the complex reproductive ecology of gray gulls.

#### Summary and Conclusion

The following is a list and status of the 12 hypotheses providing the basis for my study of gray gulls nesting 15 km from the coast of northern Chile, near Lealtad mountain in the Atacama Desert.

**Hypothesis 1.** Supported: Spatial dispersion of nests, at Lealtad during the 1991-92 breeding season was aggregated or contagious. Estimated nest density,  $3487/\text{km}^2$ , was very close to that ( $3420/\text{km}^2$ ) reported by Guerra (1990) for 1989, suggesting that the adult Lealtad population (ca. 5472) is relatively stable. Although quantitative data are unavailable, my observations suggest that egg and nestling predation by turkey vultures is more intense along the periphery of the colony than towards its center. Extensive observations are required to quantify and compare differences in predator attacks, both successful and

thwarted, at the periphery with those towards the center of the colony. Aggregated nesting allows for more effective defense of nest by incubating and tending adults. Since density appears to increase towards the center, more adults are available during any given time to be alert for and distract marauding turkey vultures, the principal nest predators of gray gulls. Efficient nest defense by small groups of adults should minimize direct exposure of egg and nestling to intense desert conditions. Theoretically,  $T_B$  of eggs and /or nestlings near the center of the colony should have lower daily variance than those closer to the edge where adults may, on the average, have to spend more time away from their nests defending against turkey vultures. Testing that would require extensive telemetry, monitoring egg temperatures in nest within and near the periphery of the colony.

**Hypothesis 2.** Not supported: Although the average clutch size (1.56 eggs) at Lealtad during 1991-92 was higher than the average (1.47) reported by Guerra et al. (1988d) for Cerro Negro, 85 km further inland, it also was higher than the average (1.47) for Lealtad in 1989-90 (Guerra 1990). The 1991-92 average was nearly identical to the average (1.55) reported by Howell et al. (1974) for the colony that nested at Colupo, only 15 km further inland, but less than the 1.81 average for 1985-87 reported by Guerra et al. (1988d) for gray gulls nesting at Kimurku-Valenzuela just 35 km from the

coast. One of the principal difficulties in making spatial comparisons of clutch sizes among gray gull colonies, in addition to the logistics of taking contemporary measurement throughout the Atacama, has been the influence of ENSO. According to Guerra et al. (1988d) and Fitzpatrick et al. (1992), gray gulls appear to "bet-hedge", varying their reproductive effort (sensu Hirshfield and Tinkle 1974) from zero to one to two in response to marine productivity which varies before, during and after ENSOs. Based on the current data base for gray gulls, among year variation in average clutch size and relative frequencies of one- vs. two-egg clutches obscures any differences associated with nesting distance from the coast.

**Hypothesis 3.** Not supported: The average incubation time of two-egg and one-egg clutches (28.5 vs. 27.9 days, respectively) was not significantly different. Although there was statistical difference in incubation time between first-and second-laid (28 vs.29 days), difference of only 1 day should not have biological significance. Coordinated hatching of both eggs is important for gray gulls nesting in the Atacama for two reasons: (1) it is difficult for a parent simultaneously to incubate an egg and tend a chick; and (2) asynchronous laying would prolong the period when only one adult is able to forage. The incubation times were close to the 30 days reported by Howell et al. (1974), but longer than other gulls having the same body mass and egg size.

Prolonged embryonic development may be a consequence of reduced functional pore area of egg shell with concomitant low exchange of metabolic gases (Guerra et al. 1988a) and/or a consequence of the low temperatures reached by eggs during the night (Howell et al. 1974). Regardless of the reason, prolonged incubation in gray gulls reflects trade offs of nesting in the Atacama.

Variations in egg temperatures reflected adult behavior during incubation. Minimal temperatures coincided with the high activity within the colony during and after the arrival of foraging adults. Maximal temperatures coincided with periods of highest  $R_S$  and  $T_G$ , when incubating adults stood for convective cooling exposing the eggs to indirect radiation and surface heat.

**Hypothesis 4.** Supported: Hatching success was higher in two-egg than one-egg nests. This agrees with several studies that indicate lower hatching success in smaller than larger clutches in laughing gull and western gulls. Hatching success may be a complex function of quality of incubation, interspecific predation, egg infertility or damage to the egg or quality and/or quantity of nutrients and energy stored in the egg. The higher frequency of failure in single-egg nests may be explained partially by Guerra's (1987) proposal that young females in their first reproductive year lay one egg. During years of normal marine productivity, older females produce two-egg clutches (recall proposed by Guerra et al.

1988d that females "bet-hedge" laying zero to one to two eggs according to level of marine productivity as influenced by ENSO). Thus, young females produce most of the one-egg nests during normal productivity years. The higher egg mortality in their nests could be explained by reduced provision (nutrients and energy) in their eggs (resulting in egg death) and/or their less effective nest defense against predators. Another possibility is that young females may abandon their egg more frequently than older females. Predation has been proposed as important in determining hatching success in gray gulls. Although quantitative data are unavailable, my observations suggest that predation by turkey vultures may not be very important in the center of the colony where more adults effectively defend their nests. Extensive observations are needed to quantitatively compare predation pressure throughout the colony.

**Hypothesis 5.** Not supported: The lower and upper critical temperatures ( $17^{\circ}$ - $41^{\circ}\text{C}$ ) for gray gull embryos were similar to those reported for western gulls. The upper, but not lower was similar to that ( $41.1^{\circ}\text{C}$ ) reported for Heermann's gull. Over  $30^{\circ}$ - $40^{\circ}\text{C}$  temperature range, gray gull embryos aged 2 and 3 weeks exhibited  $Q_{10}$  of 1.64 and 1.42, respectively, lower than that predicted by the Van't Hoff equation.

The slow increase in egg temperature of gray gull at Lealtad may result from egg shell reflectance and convective heat loss, as was suggested by Bennett et al. (1981) for

western gulls. My observations indicated that gray gulls expose their egg to direct sunlight only when they leave to distract humans, turkey vultures or falcons. The highest temperature (39.4°C) recorded during incubation was lower than the highest (42°C) temperature tolerated, suggesting that gray gulls can leave their nests to defend against predators and return before eggs reach lethal temperatures. The lowest incubation temperature (30°C) resulted be almost twice the minimal temperature tolerated (17°C) by the embryos. Exposure to low temperatures apparently does not harm the embryos , although as suggested by Howell et al. (1974) it may prolong development and incubation.

**Hypothesis 6.** Not supported: All the data were obtained from well-developed embryos (4 week-old) and published information refers only to embryos in their early stage of development (1-2 weeks-old). Therefore, direct comparisons with gray gull data are not appropriate. Observations of  $VO_2$  in embryos during early stages of development are required to test the hypothesis that, as consequence of reduced functional pore area, embryos should have lower metabolism than congeners.

**Hypotheses 7 and 8.** Supported:  $T_B$  of 0-3 and 6-13 day-old chicks during the day were not significantly different, suggesting that younger chicks have an incipient capacity to thermoregulate and endure hyperthermia as do older chicks-fledging (Guerra et al. 1989). That agrees with the idea

that semiprecocial birds rapidly develop thermoregulatory capacity (Dawson et al. 1976; Chappell et al. 1984). Gray gull chicks thermoregulate under hot conditions behaviorally by seeking refuge next to rocks or within channels and physiological by panting and gaping, both costly in term of water, while in the nest, nestling are protected from intense radiation by adults. When chicks are left alone after 5 days, they take advantage of micrometeorological conditions in areas adjacent to rocks and/or in channels. During the night, differences in capacity to thermoregulate was significantly different between 0-3 and 6-13 day-old chicks. Younger chicks were less able to thermoregulate, as has been observed in laughing gulls, western gulls, and mew gulls. Differences in capacity to thermoregulate in low temperatures indicate that parental attentiveness must plays an important role in stabilizing chicks  $T_B$  during the cold nights for at least their first 5 days. The onset of thermoregulation appears to coincide with the time when the chicks are left alone in the desert (ca. 5 days post hatching).

**Hypotheses 9 and 10.** Not supported: Although the estimated SMR in gray gulls was lower than those reported for black-headed gulls, laughing gulls and California gulls, it was higher to SMR reported for ring-billed, herring gulls, and western gulls. Although there were differences in mean  $VO_2$  average between chicks and fledglings, there were no



significant differences in  $VO_2/T_A$  slopes below TNZ. This suggests that chicks have the same capacity as older chicks (above 30 day-old) to maintain their  $T_B$ .

Estimated TNZ observed ( $25^{\circ}$ - $40^{\circ}$ C) was wider than that reported for black-headed gulls, but quite similar to those reported for herring gulls and western gulls. Since my data are based on observations of only two hatchlings which were somewhat stressed, further work on SMR in gray gull hatchlings is necessary to test the hypotheses proposed.

**Hypotheses 11.** Supported: Chicks from single-egg nests grew faster than chicks from two-egg nests, because siblings must share the same amount of food available to single chicks. This difference in growth rates disagrees with the hypotheses that competition between siblings should increase their growth rate. Gray gull sibling is more influenced by food limitation .

**Hypothesis 12.** Supported: Chicks at Lealtad grow faster than those at Cerro Negro. This agrees with the hypothesis that growth rate is determined by food availability and/or predation; rapid growth reduces vulnerability to predation. The hypothesis that rapid growth increases probability of predation because predator strategies, as proposed by O'Connor (1984), does not apply to gray gulls, since they make only daily foraging flight regardless of nest location, and it occurs after sunset when predators are in their roosts. Thus, in gray gulls both of Lack's (1968)

determinant factors can be identified. Guerra et al. (1988b) determined that the growth rate constant ( $K_G = 0.68$ ) in chicks at Cerro Negro was lower than other Larids and concluded that growth rate may be a compromise related the long distance foraging that limits the chicks to a single daily meal. However, since food carried to chicks appears to be independent of nesting site location, predators may play the major role. Growth in gray gulls chicks appears to be a complex function of food restrictions, foraging distance, predation and extreme ambient conditions.

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