

NESTLING METABOLISM AND GROWTH IN THE BLACK NODDY AND WHITE TERN

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The White Tern (*Gygis alba*) and Black Noddy (*Anous minutus*) are two tropical charadriiform seabirds characterized by prolonged incubation of their eggs, slow embryonic growth, and a high total energetic cost of embryonic development (Whittow 1980, Pettit et al. 1981, Pettit and Whittow 1983). The present study was undertaken to ascertain if post-hatching growth was also slow and if the nestling period was prolonged in the two species. A long nestling period reduces the energy requirement of the chick (Ricklefs and White 1981) but may place an energetic burden upon breeding adults. To evaluate this possible energetic constraint in the Black Noddy, the oxygen consumption of the chick was measured to estimate the total energy cost of maintenance activities.

METHODS

We studied the growth of White Terns on Midway Atoll (28°13'N, 177°23'W) January to May, 1981. Ten White Tern chicks were weighed daily with Pesola scales (± 1 g). Growth and metabolism of Black Noddies were studied on Tern Island, French Frigate Shoals (23°52'N, 165°18'W) January to April, 1982. Six noddy chicks were weighed every three days with Ohaus scales (± 0.01 g). Oxygen consumption (\dot{V}_{O_2} , l O₂ STPD·day⁻¹) of chicks was determined with a closed-system, manometric respirometer. Oxygen uptake of chicks up to nine days of age was measured at a constant temperature of 30°C. Thereafter, \dot{V}_{O_2} was measured at ambient room temperatures ranging from 22°C to 28°C. Carbon dioxide absorbant (sodasorb) and water vapor absorbant (silica gel) were placed in the chamber. After a 45-min equilibration period the metabolic chamber (volume = 38 l) was sealed, and a measured volume of oxygen was introduced into the chamber in order to maintain the pressure within the chamber at atmospheric pressure. Ambient room and chamber temperatures were determined by a Schultheis thermometer ($\pm 0.1^\circ\text{C}$) or a Yellow Springs Instruments (YSI) telethermometer and probe (#402) ($\pm 0.1^\circ\text{C}$). The body temperature of the chicks was measured before and after each experiment by inserting a YSI probe (#402) into the proventriculus; the average of the two measurements is reported to reflect body temperature during the experiment.

RESULTS

Logistic growth curves were fitted to the data (Ricklefs 1967) for mean weights of White Tern and Black Noddy chicks throughout the nestling period (Fig. 1). For the tern, $W_t = 100/1 + e^{-0.96(t-19.0)}$ where W_t is the weight of the chick at age t ; e is the base of the natural logarithms, 2.72; the numerator is the asymptote of the curve. The correlation coefficient of the linearized data is $r = .986$. For the noddy, $W_t = 115/1 + e^{-1.58(t-11.3)}$, $r = .988$.

The mean fledging period of five tern chicks was 53.2 days \pm 2.6 (SD) and the mean fledging weight was 99.8 g \pm 6.9 (SD). White Tern chicks did not lose weight before fledging as did Black Noddies. Among five noddy chicks the mean fledging period was 40.4 days \pm 1.5 (SD) and

the mean fledging weight was 100.7 g \pm 3.6 (SD). Thus, the fledging period of the noddy was 13 days shorter than that of the tern. A mean pre-fledging weight loss of 15 g occurred during the last week of development.

The O₂ uptake (l O₂ STPD·day⁻¹) of six noddy chicks suggests that \dot{V}_{O_2} reached a plateau of about 4.5 l O₂ STPD·day⁻¹ at age 25 days (Fig. 2). Mass-specific O₂ consumption (\dot{M}_{O_2} ; ml O₂·g⁻¹·h⁻¹) reached a plateau at age 12 days at a rate of approximately 2.0 cc O₂·g⁻¹·h⁻¹. Body temperature was higher from days 2-9 than any other period (Fig. 2), possibly due to the higher ambient temperature (30°C) during this period. Respiratory frequency (f , breaths·min⁻¹) ranged from 40 to 98.

DISCUSSION

The growth rate and asymptote of the growth curve in the White Tern and Black Noddy may be compared with growth characteristics in two other tropical birds without prolonged incubation periods, the Brown Noddy (*Anous stolidus*) and the Sooty Tern (*Sterna fuscata*) (Table 1). A "prolonged incubation period" is defined as an incubation time that exceeds the 95% confidence intervals for the relationship between egg mass and incubation time (Whittow 1980). A comparison of average embryonic growth rates suggests that slow embryonic growth is related to a slow "average" growth rate in the chick. Thus, the average embryonic and chick growth rates of the White Tern and Black Noddy are less than those of the Brown Noddy and Sooty Tern. Although embryonic growth rates and those of the chick may be linked pleiotropically, the constraints on growth are different in the two instances. Thus, embryonic growth may be limited by the gas conductance of the eggshell, while the growth of the chick is determined largely by the rate of delivery of food to the chick by the parent. The duration of the nestling period, however, is not necessarily correlated to the length of the incubation period among these Hawaiian larids. The Sooty Tern has the shortest incubation period and the longest nestling period of these four species (Table 1).

The mass-specific O₂ consumption (\dot{M}_{O_2}) of the Black Noddy hatchling is 1.30 ml O₂·g⁻¹·h⁻¹ and is close to the adult rate of O₂ uptake (1.28 ml O₂·g⁻¹·h⁻¹; Pettit et al., unpubl.). The metabolic rate of hatchling gulls is also close to predicted adult mass-specific metabolism (Dawson et al. 1976, Dunn 1976, Dawson and Bennett 1981). \dot{M}_{O_2} of the hatchling White Tern is 1.21 ml·O₂·g⁻¹·h⁻¹ (Pettit et al. 1981) and about 80% of measured adult \dot{M}_{O_2} (1.51 ml O₂·g⁻¹·h⁻¹; Pettit et al., unpubl.). Low rates of embryonic oxygen consumption in the Black Noddy and White Tern (Pettit et al. 1981, Pettit and Whittow 1983) do not persist into low levels of chick mass-specific oxygen uptake. Thus, prolonged incubation is not associated with a reduced metabolic level in the developing chick.

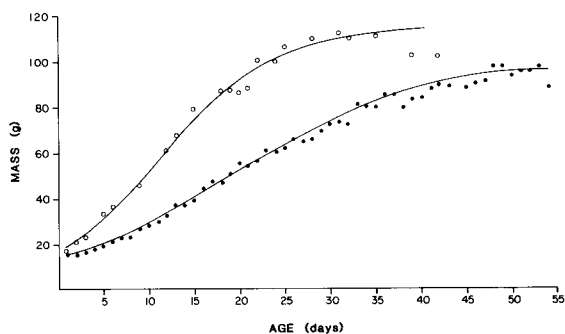


FIGURE 1. Growth of Black Noddy and White Tern chicks. Mean weights of 10 tern (black dots) and six noddy (white dots) chicks are presented along with the fitted logistic growth curves (see text).

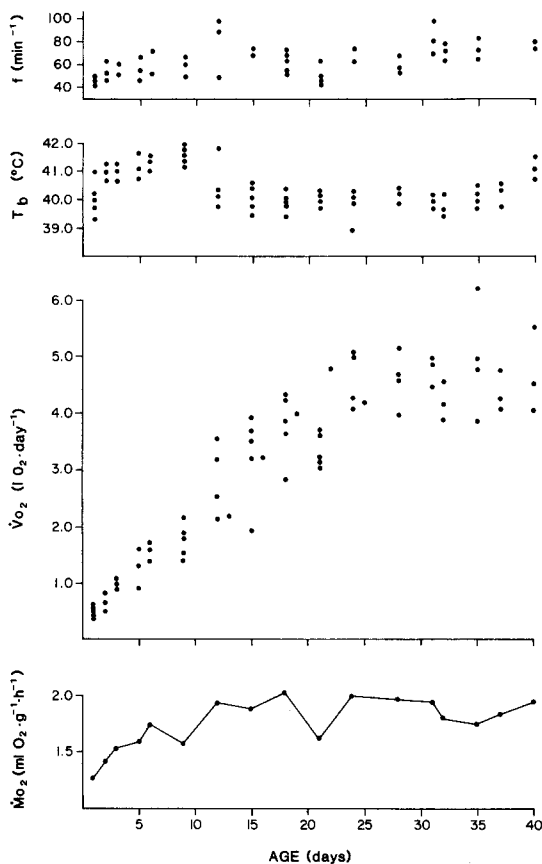


FIGURE 2. Respiratory frequency, average body temperature and oxygen consumption of Black Noddy chicks.

By measuring the total area under the curve for $\dot{V}O_2$ throughout the nestling period, the total amount of oxygen required for resting metabolism may be estimated. Black Noddy chicks consumed about 140 l of oxygen (STPD) during the 40-day nestling period. Common Tern (*Sterna hirundo*) chicks consume more oxygen (approximately 170 l; Ricklefs and White 1981) during their 30-day nestling period than Black Noddy chicks. This may be due to lower maintenance energy requirements of noddy chicks residing in a warmer environment. Sooty Tern chicks were likewise found to consume a total of approximately 280 l of oxygen

during their 60-day nestling period on the Dry Tortugas, Florida (Ricklefs and White 1981). Additional studies of the total caloric requirements and energy budget of the Black Noddy chick are required to fully assess growth efficiency or the respiration-production ratio.

In summary, the White Tern and Black Noddy have similar incubation periods and embryonic rates of growth but disparate rates of chick growth and lengths of fledging periods. The growth rate constant of the noddy chick is 65% greater and the nestling period is 12 days shorter than in the tern. Thus, in these two species, pre- and post-hatching rates of growth are not correlated.

ACKNOWLEDGMENTS

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TABLE 1. Embryonic and chick growth characteristics in four tropical terns. W = mean fresh egg weight; H = hatchling weight; I = incubation period; GR_E = average growth rate of embryo (H/I); K_E = logistic growth constant for embryo; A = asymptote of chick growth curve; NP = nestling period; GR_C = average growth rate of chick ($A-H/NP$); K_C = logistic growth constant for chick.

| Species | Embryo | | | | | Chick | | | |
|--------------------------|------------|------------|---------------|----------------------------------|-------------------------------|------------|----------------|----------------------------------|-------------------------------|
| | W (g) | H (g) | I (days) | GR_E (g·day ⁻¹) | K_E (day ⁻¹) | A (g) | NP (days) | GR_C (g·day ⁻¹) | K_C (day ⁻¹) |
| White Tern ¹ | 23.3 | 16.1 | 35.5 | .454 | .186 | 100 | 53.2 | 1.58 | .096 |
| Black Noddy ² | 24.8 | 14.8 | 34.6 | .428 | .245 | 115 | 40.2 | 2.49 | .158 |
| Brown Noddy ³ | 40.1 | 28.5 | 35.6 | .801 | .235 | 180 | 42.5 | 3.56 | .137 |
| Sooty Tern ⁴ | 36.7 | 24.2 | 30 | .807 | — | 190 | 57.3 | 2.89 | .099 |

¹ Embryonic data from Pettit et al. 1981.

² Embryonic data from Pettit and Whittow 1983.

³ Embryonic data from Pettit and Whittow 1983; chick data from Brown 1976b.

⁴ All data from Brown 1976a.

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SEX AND AGE RATIOS IN WINTERING WHITE-CROWNED SPARROWS

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Differential migration of the sexes occurs in many species of North American songbirds. The resultant asymmetry in distribution on the wintering grounds has a consistent pattern in that males tend to occur farther north than females (Ketterson and Nolan 1976). In Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) the latitudinal cline thus generated is quite marked. Populations near the northern limit of the winter range in Washington contain about 80% males whereas those to the south near the Mexican border may be only about 25% males (King et al. 1965). Major informational gaps still exist, however, concerning the winter distribution of *Z. l. gambelii*. Especially lacking are large unbiased samples from discrete locations. Herein are presented additional data on sex ratios in wintering *Z. l. gambelii* as well as evidence that they experience differential mortality with both age and sex.

METHODS

Wintering populations were sampled by mist-netting at two locations in California, one in the Owens Valley (Inyo Co.) and the other near Thousand Oaks (Ventura Co.). The Owens Valley is a deep, narrow corridor in eastern California that is bordered on its western edge by the Sierra Nevada. Birds were captured there from fence-crows and on fallow lands between Olancho and Bishop, a distance of 130 km. At Thousand Oaks, 50 km northwest of Los Angeles, *Z. l. gambelii* (and a few *Z. l. pugetensis*) were captured on agricultural lands lying 4 km or less to the west of the city. All birds were sexed by laparotomy and aged by crown color.

RESULTS AND DISCUSSION

In the Owens Valley significantly more males were captured than females (366 vs. 281, $\chi^2 = 11.17$, $P < 0.005$, Table 1). This proportion of males (57%) is considerably lower than that reported for Washington populations by King et al. 1965 (80%) and Lewis et al. 1968 (77%) (Table 2), thus supporting the putative latitudinal cline in sex ratio. It is higher, however, than ratios obtained from museum specimens also collected east of the Sierra Nevada (38%, Emlen 1943; 45%, King et al. 1965) and does not lend support to Emlen's (1943) suggestion that the mountains divide wintering populations with highly disparate sex ratios favoring males to the west and females to the east.

The small sample collected in 1969 (Table 1) has significance in that the Owens Valley had received more snow than usual. Numbers of *Z. l. gambelii* in the area appeared

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to be much lower than in other years and our netting efforts were relatively unsuccessful.

At Thousand Oaks there was a consistent yearly pattern to the sex ratio data (Table 1). Significantly fewer males were captured than females (626 vs. 897, $\chi^2 = 48.22$, $P < 0.001$). The proportion of males (41%) was lower than in the Owens Valley sample or in one netted to the north near Bakersfield (Kern Co.) by Hardy et al. (1965), again supporting the trend for fewer males to winter at lower latitude (Table 2).

Given that *Z. l. gambelii* consistently return to the same wintering area (Mewaldt 1964, 1976; Cortopassi and Mewaldt 1965), the latitudinal cline in sex ratio is maintained because immature males stop their southward migration sooner than immature females. Presumably this benefits males because it would facilitate their early return to the breeding area and procurement of a territory (King et al. 1965). In addition, they would experience a shorter, less hazardous migration. Natural selection should favor the same response in females except that they are smaller than males and may be displaced from food by them (Parsons and Baptista 1980). Intersexual behavioral dominance is probably greater in harsher (more northern) climates (Ketterson and Nolan 1979). Female *Z. l. gambelii* also cannot fast as long as males (Ketterson and King 1977) and presumably are less likely to survive severe storms.

In large netted samples the percentage of immatures in wintering flocks declines from about 70% in southern Washington, 46°N, to about 50% in southern California, 34-35°N (Table 2). Since the proportion of immatures at a given location remains unchanged throughout the winter (King et al. 1965), they apparently experience a differential increase in mortality rate over adults as migration distance increases. This seems sensible because immatures are inexperienced navigators and more are prone to go astray during migration (Stewart et al. 1974). Guidance could be provided by adults but there is no assurance that such always occurs. The first flocks that form on the breeding

TABLE 1. Sex and age of *Zonotrichia leucophrys gambelii* captured from two wintering areas in California.

| Location | Year | Adults | | Immatures | |
|---------------|-------|--------|---------|-----------|---------|
| | | Males | Females | Males | Females |
| Owens Valley | | | | | |
| | 1968 | 100 | 72 | 108 | 76 |
| | 1969 | 17 | 24 | 9 | 2 |
| | 1970 | 83 | 46 | 49 | 61 |
| | Total | 200 | 142 | 166 | 139 |
| Thousand Oaks | | | | | |
| | 1977 | 58 | 67 | 35 | 49 |
| | 1978 | 65 | 94 | 54 | 85 |
| | 1979 | 76 | 73 | 59 | 75 |
| | 1980 | 41 | 65 | 59 | 108 |
| | 1981 | 77 | 110 | 57 | 100 |
| | 1982 | 18 | 37 | 27 | 34 |
| | Total | 335 | 446 | 291 | 451 |