GROWTH OF THE WEDGE-TAILED SHEARWATER IN THE HAWAIIAN ISLANDS

TED N. PETTIT,[1] G. VERNON BYRD,[2] G. CAUSEY WHITTOW,[1] AND MICHAEL P. SEKI[1,3]

[1]*Department of Physiology, John A. Burns School of Medicine, University of Hawaii, Honolulu, Hawaii 96822 USA, and* [2]*U.S. Fish and Wildlife Service, P.O. Box 87, Kilauea, Hawaii 96754 USA*

ABSTRACT.—Growth studies of a tropical seabird, the Wedge-tailed Shearwater (*Puffinus pacificus*), were conducted over 3 yr at three locations in Hawaii. Basic growth patterns of body dimensions are described. The range of asymptotes and maximal recorded weights suggests that feeding and the availability of food may influence growth from year to year and in different colonies within the same year. *Received 15 September 1982, accepted 1 September 1983.*

GROWTH among procellariiform chicks is characterized by slow development, a long and flexible fledging period, large deposits of lipid reserves, and achievement of a prefledging weight well above the adult's body weight, followed by a prefledging weight loss. These growth characteristics are considered to be adaptations to meager, distant, or fluctuating food resources (Lack 1967, 1968; Ricklefs 1968).

Few studies of tropical seabirds have addressed intraspecific variations in the growth of nestlings at different latitudes or in different colonies. Nelson's (1978) study of the Red-footed Booby (*Sula sula*) in the Galapagos Islands and at Christmas Island, Indian Ocean is a notable exception. We present here the results of growth studies of the Wedge-tailed Shearwater (*Puffinus pacificus*), conducted over several years at three different locations in the Hawaiian Archipelago.

METHODS

Data were collected from three locations during 1978–1980: Manana Island, Oahu (1978, 1979); Kilauea Point, Kauai (1978, 1979, 1980); and Tern Island, French Frigate Shoals (1979). Manana (Rabbit) Island (21°30′N, 157°40′W) is a small island lying approximately 1 km off the southeastern shore of the main island of Oahu. Kilauea Point (22°15′N, 159°30′W) is a peninsula rising about 45 m above sea level on the northwestern coast of Kauai. Tern Island (23°52′N, 165°18′W) is one of several small flat islands just above sea level that comprise French Frigate Shoals in the northwestern Hawaiian Islands. Data for body-weight gain in Wedge-tailed Shearwater chicks from Manana Island, Oahu during 1972 (Shallenberger 1973) have also been analyzed for comparison. Morphological and developmental notes were made throughout the growth period. Growth measurements were obtained by separate parties of observers on each island. A single person in each party was responsible for making a single set of observations (body weight or body dimensions) to assure uniform measurements. Fledging success in Wedge-tailed Shearwaters averages 80% of hatched chicks (Byrd, Moriarty, and Brady unpubl.). The following measurements were obtained from chicks of known age (±1 day) that lived either beyond 90 days or were known to have fledged successfully.

(1) *Body weight*: chicks were weighed on an Ohaus triple-beam balance to ±0.1 g (Manana Island) or with calibrated Pesola spring scales to ±1 g (Kilauea Point and Tern Island). Measurements were made either 1–3 times a week (Manana Island and Kilauea Point) or daily (Tern Island).

(2) *Culmen length*: the bill was measured with calipers or dividers (±0.5 mm) from the tip of the upper mandible to the edge of the nasal skin covering the bill.

(3) *Wing length:* wings were measured with a tapemeasure (±2 mm) either with the wing straightened and extended perpendicularly to the axis of the body, from the most anterior point of the humerus at the shoulder joint to the tip of the phalanges (Manana Island), or with the wing flattened, from the shoulder joint to the tip of the longest primary or to feather sheath if primaries had not erupted (Kilauea Point).

(4) *Tarsus length*: the length of the tibia-fibula was measured with calipers (±0.5 mm) from the distal end of the tibiotarsus to the proximal end of the tibia (Manana Island). The tarsometatarsus was measured on Kilauea Point according to Pettingill (1970).

[3] Present address: National Marine Fisheries Service, Honolulu Laboratory, Hawaii 96822 USA.

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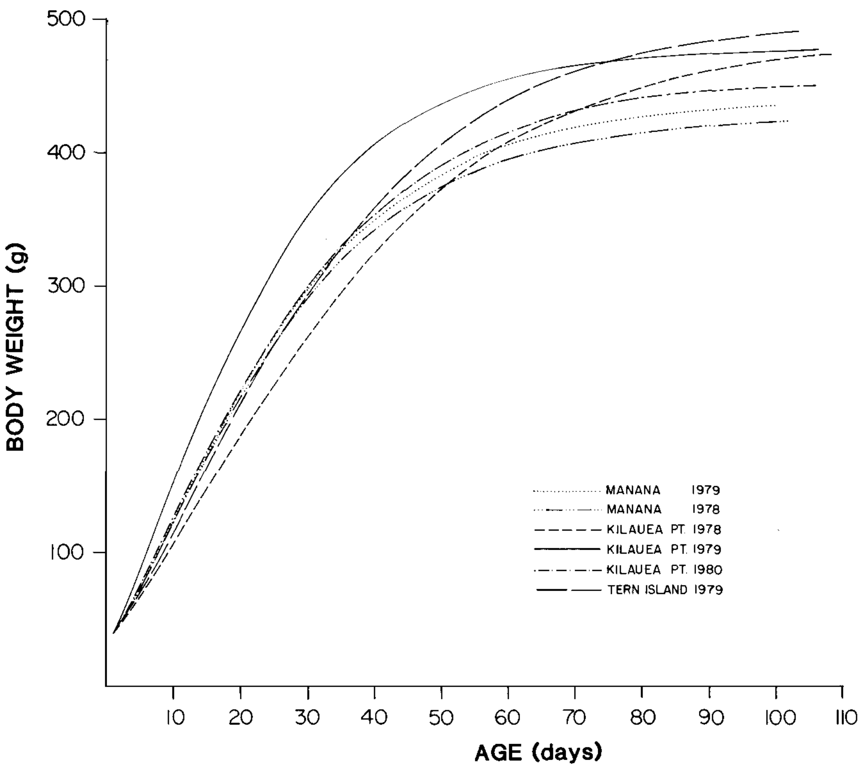

Fig. 1. Growth in body weight of Wedge-tailed Shearwaters on Manana Island, Oahu; Kilauea Point, Kauai; and Tern Island, French Frigate Shoals in 1978, 1979, and 1980.

(5) *Middle toe length*: the middle toe was measured with calipers or dividers (±0.5 mm) from the tip of the claw (Manana Island) or from the tip of the toe without the claw (Kilauea Point) to the proximal fold in the webbing between the middle and lateral toe.

(6) *Tail length*: the tail feathers were measured with dividers (±2 mm) from the tip of the longest rectrix to the point between the middle rectrices where they emerge from the skin.

Each set of body-weight data was transferred to computer cards. Body-weight data for chicks undergoing prefledging weight recession have been omitted from computer analysis. Logistic, Gompertz, and von Bertalanffy equations were fitted to the data

TABLE 1. Analysis of growth in the Wedge-tailed Shearwater.[a]

Location	Year	n	x	K	b	A	$4KA/9$	$t_{10\text{-}90}$	A/w	Fw	A/Fw	KR (100)/ 0.444
Manana Is.	1972	—	65	0.038	0.591	499	8.43	59.2	1.28	—	—	—
Manana Is.	1978	11	120	0.052	0.574	424	9.80	43.3	1.09	417	1.02	12.8
Manana Is.	1979	13	145	0.051	0.579	456	10.34	44.1	1.17	392	1.16	13.4
Kilauea Pt.	1978	37	393	0.045	0.588	440	8.80	50.0	1.25	429	1.03	12.7
Kilauea Pt.	1979	16	175	0.059	0.597	477	12.51	38.1	1.22	406	1.17	16.2
Kilauea Pt.	1980	23	346	0.049	0.583	454	9.89	45.9	1.16	426	1.07	12.8
Tern Is.	1979	14	621	0.043	0.595	503	9.61	52.3	1.29	440	1.14	12.5

[a] The von Bertalanffy growth equation is $W = [A(1 - be^{-KT})]^3$, where W is mass (g), K is the growth constant (days^{-1}), e is the base of the natural logarithms, T is time (days), A is the asymptote (g), and b is a constant that translates the time axis such that time (T) is equal to zero at the inflection point. Other growth parameters are $4KA/9$, the maximal amount of absolute growth (g·day^{-1}); $t_{10\text{-}90}$ (2.25/K), the amount of time required to grow from 10% to 90% of the asymptotic weight; w, the mean adult weight (390 g); Fw, the fledging weight (g); KR(100)/0.444, the maximal instantaneous growth rate (as a percentage of adult weight), which occurs at the inflection point of the growth curve.

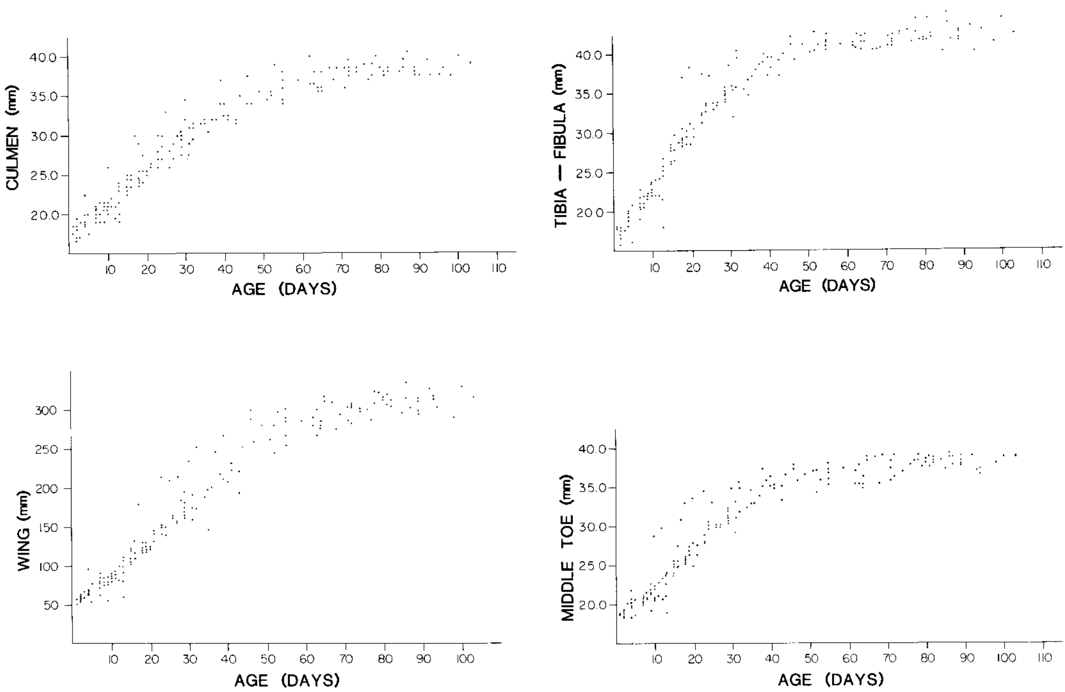

Fig. 2. Growth of body dimensions of Wedge-tailed Shearwaters on Manana Island, Oahu in 1979.

by an iterative method and analyzed for goodness-of-fit by a FORTRAN program for nonlinear least-squares regression (Smond, Pettit, and Whittow unpubl.) implemented by an IBM 370/145 computer. The von Bertalanffy equation (Fabens 1965) provided the best fit in all cases. Summary statistics of growth patterns are developed for each population as a whole.

Results

Growth analysis.—The fitted von Bertalanffy growth curves for shearwater body weight from Manana Island, Kilauea Point, and Tern Island are presented in Fig. 1. The smooth curves shown in Fig. 1 were generated by computer (Fabens 1965), and they are extended to the mean fledging period for the sample population. Thus, the smoothed growth curves do not reflect the prefledging weight recession data, which were omitted from computer analysis. Although the curves vary in slope and form, they are grouped according to the major variables, the growth rate constant (K) and the asymptotic weight (A). The von Bertalanffy growth parameters are presented in Table 1. The mean K factor ranged from 0.038/day to 0.059/day, and the asymptotes ranged from 424 g to 503 g.

Figure 2 presents the linear measurements (culmen, wing, tibia-fibula, middle toe) of Manana Island shearwaters in 1979. Figure 3 presents the linear measurements of shearwaters at Kilauea Point in 1980. The linear body dimensions cannot be compared directly (except for culmen length) due to differences in measurement techniques (see Methods). A summary of these data (Table 2) suggests that the asymptote for leg growth (tarsometatarsus and tibia-fibula length) is reached about age 50–60 days and before attainment of asymptotes for other measured body dimensions. Adult dimensions of Wedge-tailed Shearwaters (Shallenberger 1973) are presented for comparison (Table 2).

Table 3 presents the mean maximal recorded body weights of chicks and their corresponding mean ages, the mean fledging weights, and the mean fledging period for all sample populations. Analysis of variance indicated no statistical differences among the fledging periods, but several significant differences were found

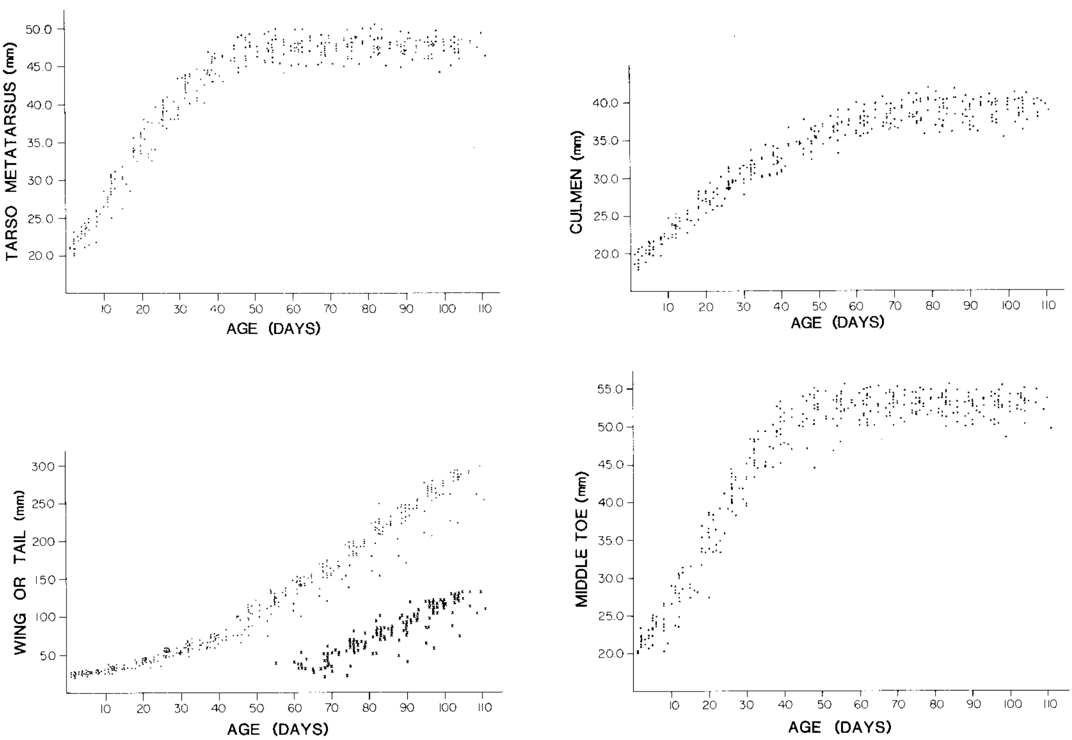

Fig. 3. Growth of body dimensions of Wedge-tailed Shearwaters at Kilauea Point, Kauai in 1980. X = tail length.

among other growth characteristics for the various populations (Table 4).

Development of the chick.—At hatching, the feet and the tarsi are flesh-colored, and the bill is a light slaty color. Hatchlings are able to support themselves and move about in the burrow nest-chamber after the first day. The primary down (protoptiles) may be quite variable but typically is a very light grey, unlike the dark grey of the secondary down (mesoptiles), which appeared at a mean age of 22.6 days ± 3.7 (SD) ($n = 23$). Chicks are hatched with eyes closed, but the eyes open generally within the first 24 h. The egg tooth disappeared at an average age of 13.6 ± 1.6 days ($n = 22$), and pin feathers of the primary and secondary flight feathers and rectrices began to appear at a mean age of 34.9 days ± 3.7 ($n = 15$). Nestlings are covered with down until age 75–85 days. After 90 days of age down may persist on the head, abdomen, and neck. It is not uncommon for fledging shearwaters to have down remaining on these areas after departure from the nesting colony.

Feeding and weight gain.—The shearwater hatchling is initially fed stomach oil by regurgitation from the adult. The stomach oil of procellariiforms is high in energy content, averaging about 10 kcal/g (Warham et al. 1976, Pettit and Whittow unpubl.). During the first 3–4

TABLE 2. Asymptotic linear body dimensions and corresponding ages of Wedge-tailed Shearwater nestlings in Hawaii.

Measurement	Length (mm)	Age (days)	Adult[a]
Tibia-Fibula	80–85	50–60	
Tarsometatarsus	45–50	50–60	50
Culmen	35–40	60–70	
Middle Toe			
With claw	50–60	60–70	
Without claw	50–55	60–70	
Wing			
Kilauea Point	275–300	100–110	297
Manana Island	310–325	80–90	
Tail	100–130	100–110	138

[a] Data from Shallenberger (1973).

TABLE 3. Growth characteristics of Wedge-tailed Shearwaters.[a]

Population	Year	Maximal weight (g)	Age (days)	Fledging weight (g)	Fledging age (days)
Manana Island	1978	497.0 ± 33.0 (11)	72.3 ± 16.1 (11)	417.0 ± 69.8 (8)	102.0 ± 6.1 (8)
Manana Island	1979	493.0 ± 87.9 (13)	79.4 ± 5.8 (13)	392.2 ± 61.8 (10)	100.0 ± 6.1 (10)
Kilauea Point	1978	565.7 ± 43.0 (37)	86.8 ± 8.9 (37)	428.8 ± 54.1 (33)	109.2 ± 3.2 (33)
Kilauea Point	1979	554.4 ± 64.0 (16)	73.9 ± 14.2 (16)	405.5 ± 24.8 (9)	107.1 ± 2.8 (9)
Kilauea Point	1980	532.5 ± 46.7 (23)	85.1 ± 11.1 (23)	426.1 ± 51.9 (23)	106.2 ± 4.6 (23)
Tern Island	1979	573.9 ± 51.3 (14)	68.4 ± 11.8 (14)	439.6 ± 32.5 (14)	104.4 ± 4.8 (14)

[a] Values are presented as mean ± SD; (n) = sample size.

days, the adult initiates the feeding process by "actually picking up the chick's bill" (Shallenberger 1973). Thereafter, the chick will peck at the bill and throat of the parent and stimulate regurgitation. Examination of regurgitated stomach contents of the chick indicated that partially digested squid and stomach oil combined and then larger pieces of whole squid and fish are fed to the chick.

Although the feeding intervals of some shearwater chicks may be quite long and variable, judging by extended weight-loss periods, the daily weight measurements of shearwater nestlings on Tern Island (1979) indicated that the mean feeding interval (the time between recorded weight gains) was 1.7 days ± 0.4 (range 1–11 days) for 432 observations of 10 chicks. Some feedings are small and result in no weight gain; therefore, this assessment is likely to be an underestimation. Among eight shearwaters at Kilauea Point (1980), which were weighed approximately every 12 h for a week before fledging and departure, feeding occurred on 66% of the days (1.3 days per feeding ± 0.4), and the average weight gain for each feeding session was 40.0 g ± 11.4 ($n = 56$). Burger (1980) has summarized data showing that a prefledging weight loss among procellariiforms occurs both in species with and without desertion periods. The 10–15% prefledging weight loss in the Wedge-tailed Shearwater is similar to that of other species of *Puffinus* (Warham 1958, Richdale 1963, Harris 1966). The absence of a desertion period has also been reported for Audubon's Shearwater (*Puffinus lherminieri*, Harris 1969).

DISCUSSION

Growth and geographical location.—Nelson (1978) reported that growth in the Red-footed Booby (*Sula sula*) is slower among chicks in the

TABLE 4. Analysis of variance: comparison of maximal recorded weight (a), age at maximal weight (b), and fledging weight (c). S = significant difference (F-test, $P < 0.05$), NS = nonsignificant difference.

	Manana 1978			Manana 1979			Kilauea 1978			Kilauea 1979			Kilauea 1980		
Population	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
Manana 1978	—	—	—												
Manana 1979	S	S	NS	—	—	—									
Kilauea 1978	S	S	NS	NS	S	NS	—	—	—						
Kilauea 1979	S	NS	NS	NS	S	NS	NS	S	NS	—	—	—			
Kilauea 1980	S	NS	NS	S	S	NS	NS	NS	NS	NS	NS	NS	—	—	—
Tern 1979	S	NS	S	S	S	S	NS	NS	NS	NS	NS	S	NS	NS	S

Galapagos Islands than at Christmas Island (Indian Ocean), and he attributed this difference to climatic conditions and food supply. If growth rate is a function of food availability, then the variations in growth parameters may reveal differences in foraging success and/or prey species (energy content) among different island breeding populations. In general, there does not appear to be a simple correlation between growth parameters and geographical location. The analysis of shearwater growth (Tables 1, 3), however, suggests that nestlings from Kilauea Point and Tern Island achieved greater maximal weights, fledging weights, asymptotic weights, and longer fledging periods than did those from Manana, although the differences were not always significant (Table 4). The fluctuation and variability of food resources are unknown for tropical Hawaiian waters, although they are currently under investigation (see Grigg and Pfund 1980). Fish (Mullidae, Carangidae) and squid (Ommastrephidae) make up the greater part of the shearwater diet (Harrison and Hida 1980). The various feeding grounds and distances to shearwater breeding colonies are unknown.

Growth and annual variation.—Harris (1966) has shown that the average growth curves for the Manx Shearwater (*P. puffinus*) during 3 yr (1955, 1963, 1964) vary little for the population residing on Skokholm Island, Wales. Data for the Wedge-tailed Shearwater over 3 years (1978–1980) at Kilauea Point, however, display considerable variation in the fitted growth curves (Fig. 1) and growth parameters (Table 1). For example, the maximum instantaneous growth rate occurs at the inflection point of the growth curve (Hussell 1972). It ranged from 12.7% in 1978 to 16.2% in 1979 for growth data from Kilauea Point. Thus, a 31% increase in this growth parameter occurred in two consecutive breeding seasons among the nestlings measured. Although the seasonal and annual variation in availability of shearwater prey species in Hawaiian waters is not well understood, the fluctuation in some prey fishes has been reported (see Grigg and Pfund 1980). Thus, variations in the observed growth patterns may be related to fluctuations in food resources. Some Hawaiian seabirds, possibly including the Wedge-tailed Shearwater, have apparently evolved breeding patterns to fit the seasonal abundance of juvenile fishes and fish larvae (Harrison and Hida 1980).

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