PATTERNS AND VARIABILITY OF GROWTH IN THE YELLOW-EYED PENGUIN[1]

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Abstract. Growth of Yellow-eyed Penguin (*Megadyptes antipodes*) chicks was monitored at six breeding areas over one season, and at two breeding areas over three seasons to describe the growth pattern and determine the degree of interseasonal and interlocality variation in growth rates. Growth parameters measured were weight, bill depth, flipper area, and lengths of culmen, skull, foot, central tail feathers, wing (humerus), and flipper. Data were fitted to logistic curves which were compared using a weighted least squares technique from the Maximum Likelihood Program (Ross et al. 1980). Observed seasonal and geographical variations in growth rates were small and appeared to reflect variations in food supply. Variations in growth rates of morphometric parameters were small or absent, with few differences in final fledging size. Dimensions with invariable growth rates were those that were smaller than average at maturity. Skull and foot + claw were least variable, implying high priority in the allocation of resources during development. Foot + claw was first to reach asymptotic size, followed by wing and flipper (area and length). This pattern of growth is consistent with that of other penguin species. Feet may grow quickly to allow heat loss until the flippers can function as thermal windows. Bill dimensions did not reach adult size by the end of the fledging period.

Key words: Yellow-eyed Penguin; Megadyptes antipodes; growth; growth rates; growth pattern.

INTRODUCTION

Ricklefs (1973) hypothesized that the growth rate of a species is determined within narrow limits set by adult body size and the rate of development of mature functions, such as flight and thermoregulation. He identified a number of influences that can result in variations in growth rates within a population: variation in diet quality, quantity of food, temporal pattern of food availability, and temperature (Ricklefs 1983). Variability in these conditions may arise in relation to locality, season, habitat, weather, brood size, egg size and composition, position in hatching sequence, age and experience of the parents, and individual variability in the quality of parental care.

Few studies, particularly on penguins, have monitored growth over more than one locality or season with the purpose of identifying the extent of intraspecific variation in growth rates. The aim of this study was to examine and de-

scribe the growth pattern of the Yellow-eyed Penguin, to determine whether growth rates are variable, and if so, the magnitude of such variations. The following questions were asked: (1) Do growth rates vary according to locality and season? (2) How much do growth rates vary? (3) Are some morphometric parameters more variable than others? (4) Do variations in growth rates result in variations in fledging sizes? Relative growth rates of one- and two-chick broods, and first- and second-hatched chicks are dealt with in van Heezik and Davis (1990).

STUDY POPULATION

Yellow-eyed Penguins are the fourth largest of the penguins (Stonehouse 1976), and are endemic to the southeastern coast of South Island, New Zealand, Stewart Island, and in the sub-Antarctic region, the Auckland Islands and Campbell Island. Breeding areas are located in areas of coastal forest or scrub. Yellow-eyed Penguins are secretive nesters, with nest sites aboveground, but isolated from one another (Darby, pers. comm.). The breeding cycle on the Otago coast has been described by Richdale (1957). Two eggs are laid in September to October, and hatching occurs in the first 3 weeks of November. The duration of

the guard phase, when one adult is always present at the nest, is about 6 weeks, ending in the last week of December. Full juvenile feathering is attained in February, and chicks leave the breeding area and go to sea in the last week of February and first week of March, about 105 days after hatching. Fledging period is used here to describe the time from hatching to departure from the breeding area to the sea. Adults continue to feed chicks right up till their departure, after which parental input ceases (Richdale 1957).

METHODS

I identified variations in growth rates by measuring a number of parameters describing growth: weight (WT), bill length (BL), bill depth (BD), skull length (SK), and foot + claw (FC), tail (T), wing (W), and flipper length (FL). Although weight comparisons are most frequently used to examine intraspecific variation, either as fledging weights or as a fitted curve, body weight has been found to respond most sensitively to changes in nutritional status (LeCroy and LeCroy 1974, Schreiber 1976, Wingham 1984), making it difficult to distinguish inherent changes from strictly nutritional effects (Ricklefs 1968). A more cautious approach is the comparison of fitted curves of morphometric measurements, which appear to respond more conservatively to changes in nutritional status (Gavino and Dickerman 1972, LeCroy and LeCroy 1974, Schreiber 1976, Wingham 1984).

THE 1983–1984 BREEDING SEASON

I located nests at six breeding areas on the southeastern coast of South Island, New Zealand; Shag Point (45°20′S, 170°40′E), Alfred and Cicely Beach (45°50′S, 170°40′E), Boulder Beach (45°50′S, 170°30′E), Green Island (45°50′S, 170°20′E), and Nugget Point (46°20′S, 169°40′E) during the incubation period in October and early November. I visited each breeding area weekly except Boulder Beach, which I visited twice weekly, and Green Island, to which visits could only be made when the opportunity arose.

I made a total of seven visits to Green Island, at 2-week intervals at the beginning and the end of the breeding season, and two visits at 4-week intervals during December and January. More frequent visits to all breeding areas were not possible due to the dispersed distribution of nests and the density of the nesting habitat. For ex-

ample, monitoring chick growth at 34 nests at Nugget Point required 12–13 hr, and 14 nests at Boulder Beach required 7–8 hr. Breeding areas are small, and up to 250 km apart. In the postguard phases chicks wander from the nest site so that considerable time was spent searching for chicks in the dense scrub.

I weighed chicks with a range of Pesola balances (300 g ± 2 g, 600 g ± 10 g, 1 kg ± 20 g, 2 kg ± 50 g, 5 kg ± 100 g, 10 kg ± 100 g) and made the following measurements with Vernier calipers (accurate to ±0.5 mm): bill length (length of culmen), bill depth and flipper length (after Scolaro et al. 1983), skull length (from the bulge of the occipital condyle to the tip of the culmen), tarsus plus middle toe and claw (= foot + claw, after Warham 1972), tail (center rectrices), and wing (from the middle of the joint at the proximal end of the humerus to the elbow). Flipper area was traced out onto a card. Individual chicks in two-chick nests were marked with cotton flipper tags until their flippers had developed to the point where steel or aluminum bands could be applied.

I estimated dates of hatching (accurate to ±1 day) according to the following distinct and consistent characteristics: on the first day chicks may be wet, eyes are shut, and fragments of eggshell remain in the nest bowl. On the second day the eggshell has been removed from the nest bowl and the eyes are partially open. By the third day, the eyes are fully open, although the third eyelid is over the eye, but by the fourth day this eyelid has assumed the normal position. After 5 days, nestlings show the following behaviors; biting at nesting material, sneezing, wing stretching, tail wagging, and defecating over the nest edge (Seddon 1990), and on the seventh day secondary down first appears on the scapulars (Richdale 1957). Loss of down and development of feathering was noted, and dates of departure were recorded (accurate to ±9.3 days).

THE 1984–1985 AND 1985–1986 BREEDING SEASONS

During the 1984–1985 and 1985–1986 breeding seasons I followed growth at the two largest mainland breeding areas; Boulder Beach and Nugget Point. The measurements listed above were made at weekly intervals. Flipper area was not measured. Hatching dates, departure dates (in 1985–1986 only), and development of plumage were recorded.
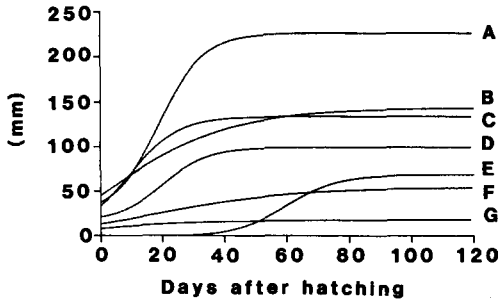
FIGURE 1. Logistic growth curves fitted to all morphometric parameters of Yellow-eyed Penguin chicks: A—flipper length; B—skull length; C—foot + claw; D—wing length; E—tail; F—bill length; G—bill depth.

CURVE FITTING

I fitted growth data to logistic and Gompertz curves and compared curves using a weighted least squares technique from the Maximum Likelihood Program, MLP (Ross et al. 1980, see also Ricketts and Prince 1981, Gales 1987). This fits curves for each data set and then pools the data to fit a single curve. The change in the residual sum of squares is then treated for significance by analysis of variance. If this test for parallelism shows nonsignificant differences between curves, then the model with common parameters should be preferred. If a significant difference is indicated, then individual curves should be used. I made single and multiple comparisons of growth curves using parallel curve analysis, comparing both the shape and the scale of the curves. If more than four curves were compared at one time, significance was set at the 1% level.

The logistic equation fitted marginally better than the Gompertz curve in the majority of comparisons, so all analyses were done using the logistic equation. Log equations were also found to best describe biomass, culmen, and flipper growth of Adelie *Pygoscelis adeliae*, Chinstrap *P. antarctica*, and Gentoo *P. papua* penguins (Volkman and Trivelpiece 1980), and Adelie Penguin biomass (Taylor and Roberts 1962), and weight, feet, flipper, culmen length, and bill depth of Blue Penguins *Eudyptula minor minor* (Gales 1987).

RESULTS

PATTERN OF GROWTH

Certain morphometric parameters developed more rapidly than others (Fig. 1). If the speed of

TABLE 1. Time taken for Yellow-eyed Penguin chicks to reach 90% of the asymptotic value.

Parameter	Time (days)		
	Minimum	Maximum	Range
Weight	55	80	25
Bill length	60	75	15
Bill depth	40	55	15
Skull	47	57	10
Foot + claw	25	35	10
Wing	28	40	12
Flipper length	30	40	10
Flipper area	45	63	18

development is expressed as the time taken to reach 90% of the asymptotic value then foot + claw was found to reach this size fastest, followed by wing and flipper lengths (Table 1). Growth rates of bill length and weight were the slowest. Variation also exists in the range of days over which all chicks reach 90% of their asymptotic value. Weight varied the most, followed by flipper area, whereas skull, foot + claw, and flipper length varied the least.

A comparison of mean adult and chick (within 2 weeks before fledging) sizes showed that bill dimensions and wing length continued to grow after fledging (Table 2). Foot + claw size of adults is significantly smaller than that of chicks. Some individuals measured as fledglings were caught again and measured as juveniles (the juvenile stage extends from departure from the natal breeding area as a fledgling until the following molt); all ($n = 14$) of these birds had longer bill dimensions than they did as chicks, 77% ($n = 13$) had longer skull and flipper lengths, 92% ($n = 12$) had longer wing lengths, whereas 62% ($n = 13$) had smaller foot + claw measurements.

The first feathers to appear were the central tail rectrices, followed by the development of feathers on the ventral flippers and rump, and finally the head and breast feathers (Table 3). Timing of plumage development in the 1983–1984 season differed between breeding areas; development of feathers on the rump, head, and breast was earlier by about 4 days, and chicks attained full feathering about a week earlier at Boulder Beach (BB) than at Nugget Point (NP) (BB: 88.1 ± 7.0 days, = 12 February 1984, $n = 14$, NP: 95.7 ± 4.1 days, = 2 February 1984, $n = 27$, $t = 4.40$, df = 39, $P < 0.001$). Since the lengths of the fledging periods were not significantly different (BB: 102.8 ± 4.3 days, = 24 Feb-

TABLE 2. Comparative morphometric parameters of adult and fledgling Yellow-eyed Penguins. Significance is as follows: $P > 0.05$ (ns), $P < 0.05$ (*), and $P < 0.001$ (***).

| | Adult | | | Chick | | | |
	n	$\bar{x}$	SD	n	$\bar{x}$	SD	P
Bill length (mm)	119	55.3	1.89	38	53.8	1.66	***
Bill depth (mm)	121	19.6	0.89	38	18.0	0.66	***
Skull length (mm)	118	142.3	4.36	37	142.9	3.97	ns
Foot + claw length (mm)	110	135.1	4.17	37	137.7	4.38	***
Wing length (mm)	112	104.0	4.07	37	101.9	2.82	*
Flipper length (mm)	115	229.1	5.84	37	227.7	6.24	ns
Flipper area (mm²)	62	93.1	4.39	28	94.1	5.22	ns

ruary 1984, $n = 14$, NP: 102.2 ± 3.7 days, $= 24$ February 1984, $n = 26$, $t = 0.462$, df $= 38$, $P > 0.05$), chicks at Boulder Beach were fully feathered 7–21 days before departure, whereas at Nugget Point chicks were feathered for only 2–10 days before leaving the breeding area.

INTRASPECIFIC VARIATION IN GROWTH RATES

Comparison of growth rates over three seasons at two breeding areas. A simultaneous comparison of growth rates over three seasons was made on growth data from Nugget Point and Boulder Beach (Fig. 2), and then paired comparisons of growth rates were made between seasons to determine whether morphometric variation was the result of one or more seasons. At Nugget Point, skull, foot + claw, and tail lengths were the only parameters not to show differences in growth rates in the three-season comparison (df $= 3, 791$, WT; $F = 14.3$, $P < 0.01$, BL; $F = 2.7$, $P < 0.05$, BD; $F = 4.2$, $P < 0.05$, SK; $F = 1.1$, ns, FC; $F = 1.4$, ns, T; $F = 1.4$, ns, W; $F = 4.7$, $P < 0.01$, FL; $F = 5.7$, $P < 0.01$). Growth rates compared between 1983–1984 and 1984–1985 did not vary for all parameters except bill length (df $= 2, 644$,

$F = 4.13$, $P < 0.05$). Only when these two seasons were compared to 1985–1986 did differences occur (1983–1984 vs. 1985–1986; df $= 2, 638$, WT; $F = 27.3$, $P < 0.001$, BL; $F = 5.84$, $P < 0.01$, BD; $F = 7.57$, $P < 0.001$, W; $F = 5.82$, $P < 0.01$, FL; $F = 11.24$, $P < 0.001$; 1984–1985 vs. 1985–1986; df $= 2, 444$, WT; $F = 12.89$, $P < 0.001$, W; $F = 6.82$, $P < 0.01$, FL; $F = 0.04$, $P < 0.01$).

No one season caused most of the variation at Boulder Beach. Only skull length did not vary in the three-season comparison of growth rates (df $= 3, 603$, WT; $F = 9.5$, $P < 0.01$, BL; $F = 5.3$, $P < 0.01$, BD; $F = 2.4$, $P < 0.05$, FC; $F = 3.2$, $P < 0.05$, T; $F = 3.5$, $P < 0.01$, W; $F = 4.0$, $P < 0.01$, FL; $F = 29.5$, $P < 0.01$). The two most different seasons were 1983–1984 and 1984–1985, from which comparison all parameters except skull showed significant differences in growth rates (df $= 2, 542$, WT; $F = 10.7$, $P < 0.001$, BL; $F = 6.2$, $P < 0.01$, BD; $F = 4.7$, $P < 0.01$, FC; $F = 5.32$, $P < 0.01$, T; $F = 5.49$, $P < 0.01$, W; $F = 4.88$, $P < 0.01$, FL; $F = 60.32$, $P < 0.001$). When growth rates from the 1985–1986 season were compared to those from 1983–1984, only weight ($F = 9.74$, $P < 0.001$), bill length (F

TABLE 3. Plumage development of Yellow-eyed Penguins at two breeding areas during the 1983–1984 season. F1 = days at which fully feathered, F2 = fledging period. ns $= P > 0.05$; ** $= P < 0.01$.

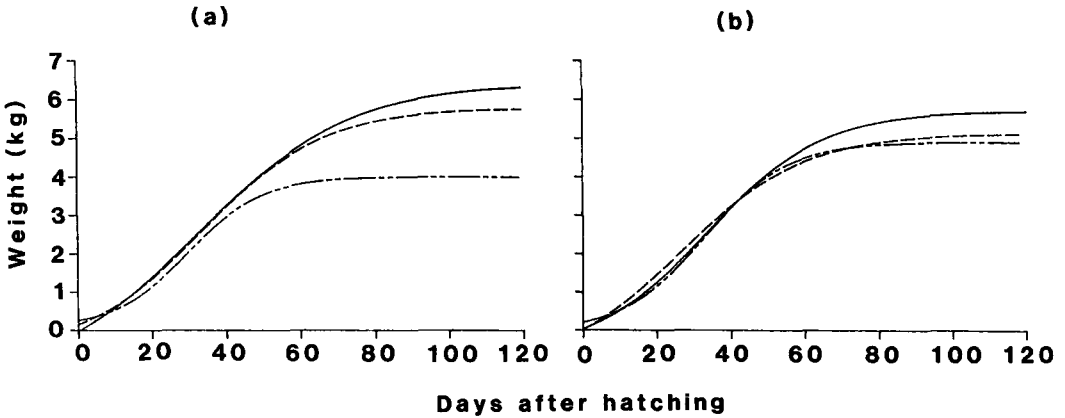| 1983–1984 | Nugget Point | | | Boulder Beach | | | |
	n	$\bar{x}$ (days)	SD	n	$\bar{x}$ (days)	SD	P
Tail	38	40.2	2.08	14	39.1	2.03	ns
Ventral flippers	36	54.6	3.52	14	52.6	4.07	ns
Rump	39	56.1	3.64	14	53.0	3.00	**
Head	35	68.9	3.85	14	65.1	4.06	**
Breast	35	68.6	2.96	14	64.7	5.59	**
F1	27	95.7	4.10	14	88.1	7.0	**
F2	26	102.2	3.70	14	102.8	4.30	ns
F2 − F1	26	6.6	4.30	14	14.6	6.10	**

FIGURE 2. Logistic weight curves fitted to all Yellow-eyed Penguin chicks during three breeding seasons: 1983–1984 (solid line); 1984–1985 (broken line); 1985–1986 (punctuated line), at two breeding areas: (a) Nugget Point and (b) Boulder Beach.

= 5.52, $P < 0.01$), and flipper length ($F = 3.43$, $P < 0.01$) differed, and when compared to those from 1984–1985, only weight ($F = 4.58$, $P < 0.01$), wing ($F = 7.63$, $P < 0.001$), and flipper length ($F = 8.33$, $P < 0.001$) varied.

At Nugget Point and Boulder Beach there was a significant difference between fledging weights and recovery rates as juveniles over the three seasons (Table 4). Fledgling sizes were compared between the first and third seasons at both breeding areas (final fledging size data were not collected during the 1984–1985 season). At Boulder Beach no differences were found between final sizes of all parameters (df = 30, BL; $t = 0.154$, BD; $t = 0.338$, SK; $t = 0.915$, FC; $t = 0.639$, T;

$t = 1.396$, W; $t = 1.201$, FL; $t = 1.572, P > 0.05$). At Nugget Point SK, FC, and W were significantly smaller in the 1985–1986 season (df = 51, SK; $t = 3.590$, FC; $t = 2.270$, W; $t = 4.535, P < 0.05$), but there was no difference between the other parameters (df = 51, BL; $t = 1.727$, BD; $t = 1.177$, T; $t = 0.793$, FL; $t = 1.456, P > 0.05$).

Interlocality comparison during the 1983–1984 breeding season. A two-by-two comparison of growth in weight at five breeding areas showed no significant differences in growth rates except between Nugget Point and Shag Point (df = 2, 572, $F = 7.8$, $P < 0.01$) and Nugget Point and Boulder Beach (df = 2, 877, $F = 10.9, P < 0.01$). Fledging weights differed between breeding areas

TABLE 4. Fledging weights, recovery of juveniles, and number of nests for two Yellow-eyed Penguin breeding areas over three seasons. χ^2 statistic calculated following multiple comparison for proportions (Zar 1984).

	1983–1984	1984–1985	1985–1986	P
Nugget Point				
Fledging weights $\bar{x}$ (kg)	6.2	5.6	4.1	<0.001
SD	0.7	0.6	1.0	$F = 46.4$
n	41	24	15	
Recovery as juveniles	59%	26%	<1%	<0.001
				$\chi^2 = 16.5$
Number of nests	38	47	39	
Boulder Beach				
Fledging weights $\bar{x}$ (kg)	5.5	4.9	4.8	<0.01
SD	0.5	0.4	0.7	$F = 6.1$
n	15	11	18	
Recovery as juveniles	61%	18%	<1%	<0.001
				$\chi^2 = 14.6$
Number of nests	14	17	11	

(SP; $\bar{x}$ = 5.33, n = 3, AC; $\bar{x}$ = 5.70, n = 6, BB; $\bar{x}$ = 5.5, n = 15, GI; $\bar{x}$ = 5.65, n = 16, NP; $\bar{x}$ = 6.2, n = 41; ANOVA: f = 4.88, df = 79, P < 0.01). Growth rates at all five breeding areas were also compared simultaneously (Fig. 3). Those breeding areas with chicks of unusually high or low fledging weights were suspected of contributing more to overall variation in growth rates, and were removed in a stepwise fashion in order to determine where the variation lay. The comparison of all five localities resulted in the largest number of parameters showing significant differences (6/8) (df = 8, 1,058, WT; F = 4.4, P < 0.01, BD; F = 4.2, P < 0.01, SK; F = 3.1, P < 0.01, T; F = 9.4, P < 0.01, W; F = 7.4, P < 0.01, FL; F = 6.6, P < 0.01). Removing Nugget Point from the comparison of growth rates reduced the number of parameters showing significant differences to only three (df = 6, 565, SK; F = 2.9, P < 0.01, W; F = 5.4, P < 0.01, FL; F = 6.6, P < 0.01). Removing Nugget Point as well as either Alfred and Cicely Beach, Green Island, or Boulder Beach did not result in a reduction in the number of parameters showing significant differences. However, removal of a combination of Nugget Point and Shag Point resulted in only flipper length showing a difference in growth rate (df = 4, 488, F = 6.6, P < 0.01). Therefore, most of the variation in growth rates was contributed by birds from Nugget Point and Shag Point.

DISCUSSION

Intraspecific annual and geographical variations in the growth pattern are not necessarily related to nutrition only (Ricklefs 1968). In this study, breeding areas of Yellow-eyed Penguins were tested for differences in growth rates because areas varied in several respects: (1) Species composition of the diet varies between areas (van Heezik 1990). (2) Mean and maximum summer temperatures show a 2° difference between Shag Point and Nugget Point (Maunder 1971). At nest-site level, potential thermoregulatory stress for this large-bodied temperate penguin is exaggerated by the lack of vegetative cover at the northern localities (due to farming practices) compared to the more natural coastal forest at Nugget Point (Seddon and Davis 1989). (3) Lack of adequate cover at the northern areas may result in additional stress due to social interference from a lack of lateral concealment and disturbance by
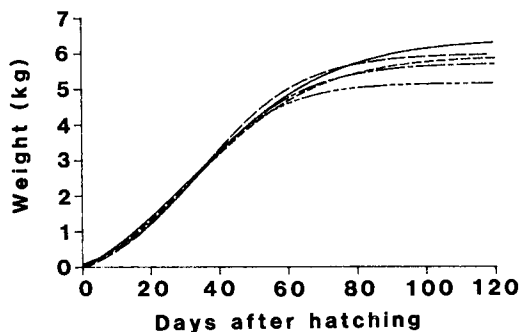

FIGURE 3.   Logistic weight curves fitted to all Yellow-eyed Penguin chicks from five breeding areas during the 1983–1984 season: Nugget Point—(solid); Alfred and Cicely Beach—(long broken); Green Island—(short broken); Boulder Beach—(punctuated once); Shag Point—(punctuated three times).

farm stock and the general public (Seddon 1988; Darby, pers. comm.).

In this study, variations in growth rate appeared to occur together with either very high or very low fledging weights, suggesting that variable food supply, rather than climatic or disturbance factors, was the proximate factor causing annual and geographical variations in growth rates. Seasonal changes in the composition of samples, in terms of the frequency of first, second, and singleton chicks, were unlikely to have resulted in different growth rates between areas and years. Although most eggs (94%) hatch on the same day (Richdale 1957), those that could be divided into first- and second-hatched chicks showed no significant differences in growth rates (van Heezik and Davis 1990). The ratio of numbers of chicks from one- and two-chick nests in a sample varied, but appeared unrelated to growth rates, and chicks from two-chick nests outnumbered singletons in all samples. Moreover, growth rates of chicks from two-chick nests and singletons did not vary in most instances (van Heezik and Davis 1990). Fledging weights varied significantly between breeding areas during the first season, but there were few differences in growth rates of morphometric parameters. Chicks from Nugget Point contributed most to the variation, and unusually high fledging weights there indicated that this may have been the result of a diet of superior quality, i.e., a higher proportion of oil-rich species such as sprat *Sprattus antipodum* (van Heezik 1990). Gales (1987) also found intraspecific differences in growth rates of weight

and bill dimensions in Blue Penguins, although bill dimensions only varied when significant differences in weight growth occurred, indicating food supply as a proximate factor. Availability of food was reflected in more rapid growth of Galapagos Penguins *Spheniscus mendiculus* (Boersma 1976) and Black-naped Terns *Sterna sumatrana* (Hulsman and Smith 1988) at some locations, and was responsible for considerable differences in all aspects of chick growth among four colonies of Thick-billed Murres *Uria lomvia* (Gaston et al. 1983). Lack of intraspecific differences in growth rates of pygoscelids was treated as being indicative of an abundant food supply (Volkman and Trivelpiece 1980). Variation in growth rates of birds from Shag Point may have been due to a diet consisting mainly of fish with low oil content (van Heezik 1990), although the sample size was low during the second half of the growth period because all but three chicks were killed by predators at about 6 weeks of age. The similarity of growth rates of most parameters from chicks at other breeding areas suggests that although characteristics of these areas may differ, they do not vary enough to have an effect on growth rates.

Rates of many developmental processes in birds are closely linked to each other, but are largely independent of the nutritional state of the young (Ricklefs 1968). In Yellow-eyed Penguins, growth rates of most morphometric parameters varied when all three seasons were compared simultaneously but not as much as weight. Weight also varied more than development of other parameters in Jackass Penguins *Spheniscus demersus* (Williams and Cooper 1984), Brown Pelicans *Pelecanus occidentalis* (Schreiber 1976), and Common Terns *Sterna hirundo* (LeCroy and LeCroy 1974). Growth rates of biomass of puffins (*Fratercula cirrhata* and *F. corniculata*) varied in response to feeding conditions (Wehle 1983), and in gannets (*Morus serrator*), weight plus certain morphometric measurements varied much more than others (Wingham 1984). Fastest growing dimensions were feet, wing, and flipper lengths, followed by bill depth, flipper area, skull, weight, and bill length in that order. The three fastest growing parameters, as well as skull length, also showed least variability in time taken to reach 90% of the asymptote, indicating priority in the allocation of resources. Maximum flipper length was achieved before flipper area. This pattern of growth is consistent with that of other

penguin species, with feet and flipper growing fastest in Jackass (Cooper 1977), Galapagos (Boersma 1976), Adelie, Chinstrap, Gentoo (Volkman and Trivelpiece 1980), and Blue penguins (Gales 1987).

Growth rates of some dimensions of Yellow-eyed Penguins varied more than others. Resources in growing birds are allocated at any one time to the growth of the components with the currently highest functional priority, with due regard for future needs (O'Connor 1977). Hence, differences in the degree to which biomass influenced growth rates of dimensions, as well as the speed at which some parts of the body attain their asymptotic value, may be interpreted in light of functional priority, with some features having a function that contributes proportionately more towards determining the successful outcome of growth and development, and therefore varying less in response to differing nutritional conditions.

The most consistently invariable parameters of Yellow-eyed Penguin growth were skull length and foot + claw. At Nugget Point, tail growth also remained invariable and at Boulder Beach, bill depth and tail. At Nugget Point final fledging sizes of skull, foot + claw, and tail measurements were smaller in the 1985–1986 season, when chicks were starving (van Heezik and Davis 1990). Therefore, parameters showing invariant growth rates were those with most variable final dimensions, suggesting that the pattern of development of these parameters is more important than their final size.

Skull growth is likely to be closely related to brain development, and should develop relatively independently of fluctuations in body weight. The foot of the developing chick has two functions; the locomotory function enables young chicks to orientate themselves towards their source of food, and when older, engage in begging chases. Rapid foot and flipper growth in pygoscelid penguins was attributed to the need to escape predators and begin begging chases upon reaching creche age (Volkman and Trivelpiece 1980), although Gales (1987) suggests that in less colonial noncreching temperate species, such as Blue Penguins, fast foot and flipper growth results from the need to maintain thermal balance.

In the large-bodied temperate-nesting Yellow-eyed Penguin, the feet showed the fastest growth of all measured parameters, with maximum size attained at the same time that chicks achieve

homeothermy (about 28 days), and soon after chicks are first observed to seek shade (about 21 days) (Richdale 1957). Large corpulent chicks covered with thick down have been observed to become heat stressed, seeking out streams or marshy ground to stand in (P. Seddon 1990). The ventral flipper is unlikely to function effectively as a heat window until it acquires feathers rather than down, since premolt down is very thick and has been shown to be a better insulator in still air or a gentle wind than feathers in both Gentoo and Chinstrap penguins (Taylor 1986). Feather development on the ventral surface of the flipper in the Yellow-eyed Penguin begins when the chick is about 55 days old. Until then feet may have an important function as heat dissipators. Both Galapagos (Boerma 1975) and Jackass penguins (Frost et al. 1975) also gain or lose heat by regulating the blood flow to the feet and underside of the flippers.

Variations in biomass and final size affected survival of fledglings after leaving the natal colony. Data on diet collected during the years spanning the 1984–1985 and 1985–1986 seasons showed diet quality differed significantly between these two seasons, the difference being most pronounced at Nugget Point (van Heezik and Davis 1990). The 1985–1986 season of poor growth in biomass resulted in lower growth rates of some morphometric parameters which reached a normal final size but took longer to do so, and unchanged growth rates of other parameters, that ended up slightly smaller in size, i.e., fledglings with smaller heads and feet, and lower body weights. The figure of 21% given by Richdale (1942) as an average expected rate of recovery of first-year birds, was achieved only by birds from the first two seasons at Nugget Point and the first season only at Boulder Beach (Table 4). Almost negligible recovery of birds from the 1985–1986 season indicated chicks fledging at less than 5 kg have little chance of survival, although it is difficult to assess the importance of small size and weight relative to the impact of fledging during a season of poor food supply.

ACKNOWLEDGMENTS

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