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INFLUENCE OF PARENTAL EXPERIENCE ON THE GROWTH OF WANDERING ALBATROSS CHICKS[1]

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Abstract. The growth of the chicks and pattern of feeds to the chicks were studied for Wandering Albatross pairs (*Diomedea exulans*) with (1) no previous breeding experience, (2) a limited experience, and (3) an extensive experience. Chicks of inexperienced pairs grew more slowly than those of experienced pairs only during the first part of the fledging period and they had similar dimensions and weights when they left the colony. These differences resulted from different patterns of food delivery to the chicks during the first part of the fledging period; chicks of inexperienced pairs being fed less regularly but with larger meals than those of experienced pairs. The patterns of chick feedings were similar in the two categories during the second part of the fledging period. There was no difference between the feeding patterns for chicks of pairs with either an extensive or a limited experience and small differences in growth appeared only during the first weeks of life of the chicks, probably because of differences in egg size. These results suggest that first-time breeders are slightly less efficient at feeding the chick than experienced birds, but they attain similar skills within a few months, and pairs do not increase their efficiency after a first fledging attempt.

Key words: Seabirds; Wandering Albatross; Diomedea exulans; *breeding experience; chick growth.*

INTRODUCTION

Numerous studies have shown that in seabirds, as in other birds, the breeding success of pairs with previous breeding experience tends to be greater than that of inexperienced pairs (for a review see Ryder 1980, Nelson 1988, Gauthier 1989). The reasons for this difference have been abundantly discussed and have been interpreted as resulting either from an increasing effort with age or from an increasing skill and efficiency with age, or both (see Pugesek 1981, 1984; Curio 1983; Nur 1984; Reid 1988). Most of the authors studying the differences between experienced and inexperienced birds have concentrated only on reproductive parameters such as the size of the egg, the laying dates, or the overall breeding success (incubation and/or fledging success; see Ryder 1980, Nelson 1988). Very few studies have attempted to determine if parental experience has an influence on the parents' ability to feed the chick and on the quality of the chick produced (Nelson 1964; Ainley and Schlatter 1972; Ollason and Dunnet 1986; Weimerskirch, in press). Long-lived birds are particularly interesting for studying these questions because they are thought to require an extended learning period (foraging ability, pairing behavior) before their first breeding attempt (see Hunt 1980, Burger 1988 for a review).

The Wandering Albatross (*Diomedea exulans*) has a very extended reproductive period (12 months: Tickell 1968, Fressanges du Bost and Segonzac 1976) and high survival rate (0.968: Weimerskirch et al. 1987). Breeding maturity is delayed for 7–15 years (Weimerskirch and Jouventin 1987). As the long-deferred breeding has been interpreted as a period of increase in skills (Burger 1988), when Wandering Albatrosses first breed they will either have attained the same breeding capacities as experienced birds or, alternatively, need further years to breed as effectively as experienced birds. To test this, we have measured the efficiency of experienced and inexperienced pairs in rearing their chick. The efficiency of the parents was measured during the fledging period, when birds had to feed themselves and their chick, because the constraints of reproduction should be the highest at this time (Ricklefs 1983).

METHODS

The field study was carried out on Possession Island (Crozet Islands) in the southwestern Indian Ocean, from March 1985 to January 1986.

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TABLE 1. Volume of eggs, date of hatching, and weight at hatching of chicks ($\bar{x}$ ± SD, ns = nonsignificant). Ranges and sample sizes are given in parentheses.

Chicks	Parents			*P* (*t*-test)		
	Inexperienced	Limited experience	Extensive experience	IN-LE	IN-EE	LE-EE
Volume of eggs[a] (cm^3)	418.2 ± 31.5 (362.7–492.0) (n = 31)	437.4 ± 33.9 (381.9–541.0) (n = 51)	453.9 ± 26.4 (386.8–503.0) (n = 37)	0.01	0.001	0.01
Date of hatching	18 March ± 9.3 (7 March–6 April) (n = 10)	19 March ± 4.6 (11–24 March) (n = 13)	17 March ± 5.3 (8–28 March) (n = 31)	ns	ns	ns
Weight at hatching (g)	292 ± 58.1 (240–390) (n = 5)	331 ± 36.3 (290–400) (n = 7)	379 ± 47.3 (300–450) (n = 14)	ns	0.004	0.03

[a] The volume of eggs was measured during a different breeding season.

Wandering Albatrosses were first banded there in 1959, and since 1966 all the birds (adults and fledglings) have been banded or controlled each year (Weimerskirch and Jouventin 1987). The sex, age, and reproductive history of each individual was known from band records. Three categories of pairs were defined: (1) inexperienced pairs (IN) breeding for the first time, (2) pairs with limited experience (LE) of one or two previous breeding attempts, and (3) pairs with extensive experience (EE) having previously bred (successfully or unsuccessfully) for at least three seasons.

Fifty-three nests were checked every 3 days at the end of the incubation period (mid-March) to determine the hatching date. The volume of eggs was given by $V = L \times (0.404 \times B)^2$ where L is the length of the egg and B is the breadth (Stonehouse 1963). The body weight, and the lengths of exposed culmen, wing, and foot (= tarsus plus middle toe) were recorded every 4–8 days from hatching until the departure of the fledgling. We also noted the age of the chick when the barbs of the primaries first emerged from the sheaths, and the presence of one or both parents with the chick. To determine the frequency of visits by adults to the nest and the size of the meals delivered, chicks were weighed twice daily (1–3 hr after sunrise and 1–3 hr before sunset), between 26 May and 6 June (when 70–85 days old) and between 15 and 28 August (when 150–165 days old).

RESULTS

EGGS

Eggs laid by EE females were significantly more voluminous than those laid by LE and IN females and eggs laid by IN females were significantly less voluminous than those of LE females (Table 1). There was no significant difference between the dates of hatching by IN, LE, and EE pairs (Table 1). Chicks of EE pairs were significantly heavier than those of IN and LE pairs (Table 1).

GROWTH OF CHICKS

The growth pattern of culmen, foot, and wing length, and body weight of chicks reared by 31 experienced and 10 inexperienced pairs are shown in Figures 1–4. The data for 12 LE pairs are not presented because they were almost identical to those for EE pairs. The only significant difference between LE and EE pairs appeared when both categories of parents left their chick unattended on the nest, at 25 days old for weight (t = 2.44, df = 42, $P < 0.05$), and at 40 days old for wing, culmen, and foot (df = 42: t = 2.90, $P < 0.01$; t = 2.26, $P < 0.05$; t = 2.96, $P < 0.01$, respectively). The culmen and foot lengths of chicks reared by EE pairs were significantly longer than those from IN pairs during the first stages of growth, while the wings were longer during the entire growth period except the last 30 days before fledging (Figs. 1, 2, and 3, respectively). During these periods of significant differences, the foot length of IN chicks was on average 94% of the foot length of EE chicks, the culmen length 95.6% and the wing length 91.7%. Primaries appeared significantly sooner in the chicks of EE pairs than in those of IN pairs (Table 2). Differences between the chicks of LE and IN pairs paralleled those between EE and IN but were less pronounced (see bottom of Figs. 1–3).

The growth in weight was also significantly

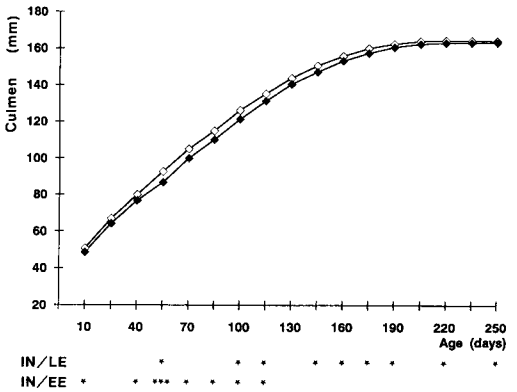

FIGURE 1. Changes with age in culmen length of Wandering Albatross chicks fledged by inexperienced parents (IN: black squares) and parents with an extensive experience (EE: white squares). Values obtained for the chicks of parents with a limited experience (LE) are virtually identical to those of the chicks of EE parents. Significant differences between chicks of IN, LE, and EE parents are indicated by asterisks at 15-day intervals (Student's t-test: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

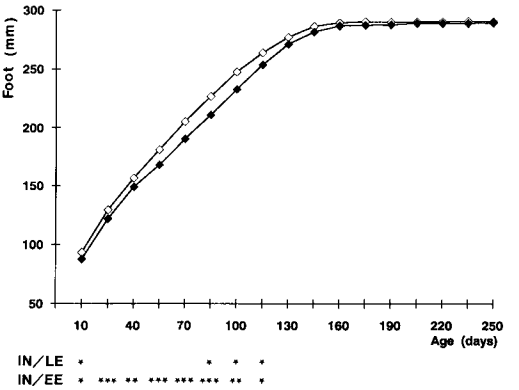

FIGURE 2. Changes with age in foot length of Wandering Albatross chicks fledged by inexperienced parents (IN: black squares) and parents with an extensive experience (EE: white squares). Values obtained for the chicks of parents with a limited experience (LE) are virtually identical to those of the chicks of EE parents. Significant differences between chicks of IN, LE, and EE parents are indicated by asterisks at 15-day intervals (Student's t-test: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

different only during the first part of the fledging period between chicks of IN pairs and chicks of both LE and EE pairs (Fig. 4, Table 2). When significantly different, the weight of IN chicks was on average 87.6% of that of EE chicks and 85.6% of that of LE chicks. Fledglings of EE, LE, and IN pairs left the colony for the sea at similar ages and with similar weight, and wing, culmen, and foot lengths (Table 2, Figs. 1–4).

PATTERN OF FEEDS TO THE CHICK

EE and LE pairs in May fed their chick significantly more frequently although with smaller meals than IN pairs (Table 3). In August, although IN pairs brought larger meals than EE pairs, they visited their chick as frequently as EE or LE pairs. We did not observe significant differences in the total amount of food brought to the chick in the three age classes (Table 3). EE parents were observed significantly more frequently near their chick than IN and LE parents during checks of the nests (Table 4). They spent more time with their chick, as EE parents were more frequently recorded with their chick on two successive nest checks (parents recorded with their chick in two successive checks on 3.2% and 650 checks of EE nests against 0% of 250 LE nests and 0.2% of 450 IN nests, Fisher's test $P < 0.001$ for EE against IN).

DISCUSSION

The extent of previous breeding experience by Wandering Albatross females had a significant influence on the volume of eggs laid and on the weight of the chick at hatching. The growth of chicks was then influenced by the breeding experience of both parents. Chicks of LE and EE pairs subsequently had similar growth patterns, except towards the end of the brooding period when chicks of LE pairs were smaller than those of EE. On the other hand, chicks of IN pairs grew more slowly than those of experienced pairs (LE and EE) during the first part of the fledging period. The body weight and the lengths of foot, wing, and culmen when leaving the colony for the sea was much the same in the three categories of pairs. These results suggest that LE and EE pairs produced chicks of similar quality, although LE females laid smaller eggs than EE females and perhaps eggs of lower quality (see Nisbet 1978), as in other seabird species (Nisbet 1978, Thomas 1983, Nisbet et al. 1984). As LE and EE pairs brought their chick meals of similar size and at similar rates, the slight difference in growth observed during the first 30–40 days might

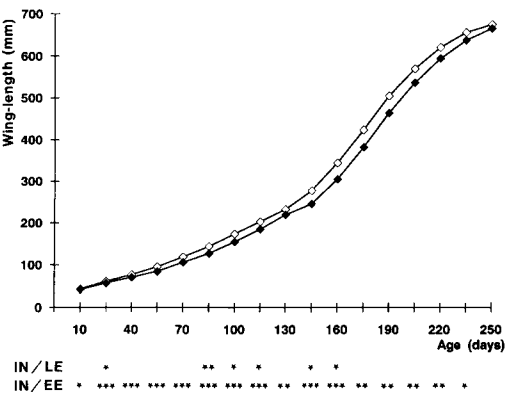

FIGURE 3. Changes with age in wing length of Wandering Albatross chicks fledged by inexperienced parents (IN: black squares) and parents with an extensive experience (EE: white squares). Values obtained for the chicks of parents with a limited experience (LE) are virtually identical to those of the chicks of EE parents. Significant differences between chicks of IN, LE, and EE parents are indicated by asterisks at 15-day intervals (Student's t-test: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

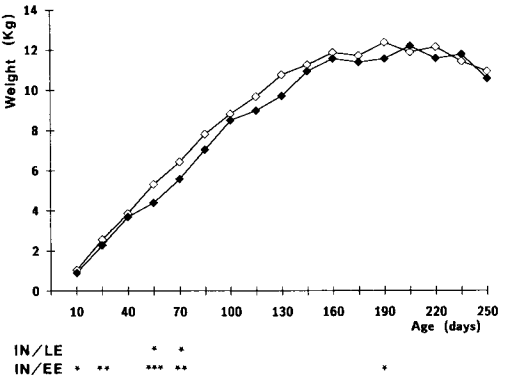

FIGURE 4. Changes with age in body weight of Wandering Albatross chicks fledged by inexperienced parents (IN: black squares) and parents with an extensive experience (EE: white squares). Values obtained for the chicks of parents with a limited experience (LE) are virtually identical to those of the chicks of EE parents. Significant differences between chicks of IN, LE, and EE parents are indicated by asterisks at 15-day intervals (Student's t-test: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

result either from the difference in the quality of the chick at hatching, or from LE pairs being slightly less efficient than EE pairs during the first weeks of the fledging period.

Chicks raised by IN pairs differed (shorter feet, culmen, and wings, and lower weight) from those of experienced pairs (LE and EE) during the first part of the fledging period, and in wing length up to 30 days before departure. This difference probably resulted from the lower frequency of chick feedings compared to experienced pairs rather than from the smaller size of the chick at hatching, assuming the chick will grow faster with frequent small meals than with large infrequent meals for the same total amount of food delivered by the pair. During the second part of the fledging period, in August, IN pairs showed the same pattern of chick feeding as experienced pairs. These changes in the pattern of chick feeding that occurred only in the IN pairs suggest that during the first part of the fledging period pairs rearing a chick for the first time were less efficient than experienced pairs but that they attained the same efficiency as experienced birds within a few months. After having reared a chick once, their efficiency probably did not increase thereafter. The difference found between IN and experi-

TABLE 2. Growth parameters of chicks ($\bar{x} \pm$ SD, ns = nonsignificant).

Chicks	Parents: Inexperienced (n = 10)	Limited experience (n = 13)	Extensive experience (n = 31)	P (t-test): IN-LE	IN-EE	LE-EE
Age when primaries appeared (days)	153.5 ± 5.2	151.4 ± 9.4	147.3 ± 7.0	ns	0.02	ns
Maximum weight (g)	13,372 ± 917	13,551 ± 874	13,395 ± 1,455	ns	ns	ns
Estimated asymptotic weight (g)	11,672 ± 791	11,880 ± 1,337	12,034 ± 1,135	ns	ns	ns
Wing length at fledging (mm)	680.5 ± 14.9	686.0 ± 10.8	684.0 ± 14.8	ns	ns	ns
Weight at fledging (g)	9,725 ± 1,028	10,056 ± 797	10,054 ± 1,216	ns	ns	ns
Age at fledging (days)	266.8 ± 7.6	266.3 ± 8.5	263.6 ± 9.9	ns	ns	ns

TABLE 3. Pattern of chick feeding by Wandering Albatross parents (percentage of days with a meal during observation periods, meal size, and total amount of food given to the chick) during May (12 days) and August (14 days) ($\bar{x} \pm$ SD, ns = nonsignificant).

Chicks		Parents: Inexperienced (n = 10)	Limited experience (n = 13)	Extensive experience (n = 31)	P (t-test): IN-LE	IN-EE	LE-EE
Feeding frequency (% days)	May	30.6 ± 22.4	61.7 ± 29.8	57.1 ± 14.8	0.05	0.01	ns
	August	53.0 ± 10.5	60.0 ± 19.9	56.2 ± 21.8	ns	ns	ns
Meal size (g)	May	1,055 ± 545	885 ± 562	810 ± 532	ns	0.03	ns
	August	929 ± 528	722 ± 531	737 ± 544	ns	0.03	ns
Total amount of food (g)	May	3,887 ± 2,439	6,546 ± 2,443	5,541 ± 2,047	ns	ns	ns
	August	6,587 ± 2,201	5,360 ± 1,932	5,282 ± 2,423	ns	ns	ns

enced pairs could, however, have been minimized by the fact that the population of Wandering Albatrosses has been reduced by fishing activities (Weimerskirch and Jouventin 1987). The competition at sea for food thus could have been reduced and reproductive performance thereby facilitated for IN pairs.

Our results suggest than when inexperienced Wandering Albatrosses first breed, they have probably already attained the same foraging skill as experienced birds during their immature life (which extends over 7–15 years; Weimerskirch and Jouventin 1987). Davis (1975) and Barret and Runde (1980) have proposed that the ability of parents to provide food and protection has a greater influence on the chick than the volume or quality of the egg. The size of the egg, and consequently the size of the chick at hatching probably have an influence on the growth of the chick only during its first weeks of life. Inexperienced birds took 3–8 months of the rearing period to adapt to the new constraints of finding food both for themselves and the chick, and bringing feeds at a high frequency (Weimerskirch, in press). But these months of initiation did not seem to limit their overall productivity, because they produced fledglings of similar quality to those of experienced birds. The cost of producing a chick may be higher for inexperienced birds, as it is for the Southern Fulmar, *Fulmarus glacialoides* (Weimerskirch, in press). In common with the Glaucous-winged Gull, *Larus glaucescens* (Reid 1988), the observation that experienced Wandering Albatrosses spent more time resting with their chick suggests that they probably need a lower investment in rearing than inexperienced birds.

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TABLE 4. Pattern of nest attendance by parent Wandering Albatrosses (percentage of nest checks with one parent or both present near the chick). Total number of checks in parentheses. ns = nonsignificant.

% parents with chicks	Parents: Inexperienced (10 pairs)	Limited experience (13 pairs)	Extensive experience (31 pairs)	P (t-test): IN-LE	IN-EE	LE-EE
May	5.1 (216)	4.2 (120)	15.4 (312)	ns	0.01	ns
August	6.0 (234)	8.5 (130)	17.2 (338)	ns	0.01	ns
Fledging period	3.2 (312)	6.0 (385)	8.1 (942)	ns	0.01	ns

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