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SIZE-DEPENDENT VARIATION IN REPRODUCTIVE SUCCESS OF A LONG-LIVED SEABIRD, THE ANTARCTIC PETREL (*THALASSOICA ANTARCTICA*)

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ABSTRACT.—We examined how variation in parental quality influences the reproductive success of a long-lived seabird, the Antarctic Petrel (*Thalassoica antarctica*). In particular, we focused on how quality of parents can interact with and influence the effects of stochastic variation in the environment due to varying climatic conditions. Large annual variation was found in reproductive success. However, body mass of individual chicks at the end and beginning of the nestling period was strongly correlated in two of the study years, suggesting consistent variation among parents in their ability to feed offspring. Furthermore, chick mass was related both to overall body size and to body mass of their parents. Short brooding-shift intervals also were important for growth and survival of chicks. The probability of chick survival to the age of 30 days (ca. two weeks before fledging) was strongly correlated with chick mass when the chick was left unattended. However, the relative importance of different parental characteristics differed between years. These results show that reproductive success of the Antarctic Petrel is influenced by stochastic variation in the environment, probably related to climatic conditions. Effects of this stochastic variation may depend on body mass and/or body condition of the parents. *Received 29 August 1996, accepted 7 January 1997.*

LONG-TERM STUDIES of seabird populations have demonstrated large individual variation in reproductive success (Ollason and Dunnet 1988, Cairns 1992, Wooller et al. 1992). In the Short-tailed Shearwater (*Puffinus tenuirostris*), for example, only about 30% of the adults produced at least one offspring that was recruited into the breeding population (Wooller et al. 1989). Individual variation in reproductive success can be generated by two mechanisms. The first mechanism is environmental. Stochastic variation in the marine environment may affect breeding success of the adults (Croxall and Rothery 1991), causing offspring production to vary more or less randomly among individuals. For instance, food provisioning rates of petrels are thought to be strongly influenced by random variation in foraging success of parents (Ricklefs and Schew 1994), which, in turn, may be affected by weather (Boersma et al. 1980). Microgeographic variation in nest-site quality also may be important for breeding success (Birkhead and Furness 1985, Croxall and Rothery 1991), e.g. due to differences among individuals in exposure to bad weather (Potts et al. 1980). These environmental effects can cause annual changes in reproductive success, which may be counteracted by low reproductive investment and a resulting long lifespan with multiple breeding attempts (Goodman 1974, Wooller et al. 1992).

The second mechanism is individual quality. Variation in reproductive success may be related to individual differences in ability to invest in offspring (e.g. Perrins and Moss 1975, Högstedt 1980, Clutton-Brock 1988a, Pettifor 1993). For instance, if adult seabirds are constrained by the need to provision their offspring at a regular interval (Ashmole 1963), then their ability to provide sufficient amounts of the correct type of food may be related to individual quality (Chastel et al. 1995, Weimerskirch et al. 1995, Lorentsen 1996).

These two mechanisms for generating variation in reproductive success are not mutually exclusive. Effects of environmental stochasticity on breeding success, for instance, may depend on quality of parents. The relative effects of these two mechanisms on variation in repro-

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ductive success have important consequences for regulation of seabird populations and for our understanding of the adaptive significance of life-history variation in seabirds.

Many studies have documented that seabird breeding success increases with age or experience (see Sæther 1990), but the causal mechanism behind this relationship is poorly understood. Some studies have shown a positive correlation between structural body size or body mass and age or experience (e.g. Newton 1988, Thomas and Coulson 1988, Weimerskirch 1992). Thus, if the ability of the parents to provide food to their offspring is an important determinant of reproductive success, then an association between body mass or condition and reproductive performance may be expected, i.e. heavy individuals or individuals in good condition may be more efficient feeders than light individuals or individuals in poorer condition (Reid 1988).

In this paper, we evaluate the importance of these two mechanisms (i.e. stochastic environmental variation and individual quality) for individual variation in reproductive success of the Antarctic Petrel (*Thalassoica antarctica*). Because these mechanisms are not mutually exclusive, we focus on the correlations among different parental characteristics and reproductive success, and how these vary among breeding seasons in an environment with large annual variations in climatic conditions and probably also food availability. The Antarctic Petrel is a suitable study species because a large investment may be required to raise offspring due to a hostile environment and long flight distances to foraging areas in the open sea (Mehlum et al. 1988). Accordingly, experimental evidence shows that small reductions in the amount of food provided to the chicks strongly reduce their probability of survival (Andersen et al. 1993, 1995; Sæther et al. 1993). Furthermore, owing to the relatively short period with open water, we assume that offspring survival may be closely related to the size and physical development of the chick at the end of the nestling period. The probability of survival of small chicks with poorly developed flight abilities at the end of the nesting period is likely to be low because they must fly more than 200 km over the ice sheet in order to find open water where they can feed.

The Antarctic Petrel is a medium-sized petrel (500 to 675 g) that breeds only on the Antarctic continent. Both parents incubate the single egg (Lorentsen and Røv 1995), and hatching is relatively synchronously within the colony (ca. 15 January; Haftorn et al. 1991). Parents brood the chick for 9 to 13 days after hatching (Bech et al. 1988, Røv et al. 1994). Chicks are unattended after this stage, and the parents return on average every second day bringing 80 to 250 g of food (Haftorn et al. 1991, Lorentsen 1996). Both parents provision the chick.

MATERIALS AND METHODS

The study was conducted at Svarthamaren (71°53′S, 05°10′E), Mühlig-Hofmannfjella in Dronning Maud Land, Antarctica during the austral summers of 1989–90, 1991–92, and 1992–93. About 250,000 pairs of Antarctic Petrels breed in the study area on a northeast-facing slope at 1,650 m elevation, more than 200 km from the nearest open sea (Mehlum et al. 1988, Røv et al. 1994). Consequently, adults must fly more than 400 km in order to provide food to their chick. The temperature normally fluctuates between −1°C in the day and −15°C at night, when there usually is a strong katabatic wind from the Antarctic plateau. The physical features of this colony have been described in detail by Mehlum et al. (1988).

The study period differed among years due to logistic constraints. In 1990, it was from 12 January, just prior to hatching, until 18 February, when most chicks were between 30 and 40 days old. In 1991–92, the study period occurred from 1 December to 15 February, covering almost the entire incubation and nestling periods. The shortest study period was in 1992–93, from 27 December until 23 January, when the oldest chicks were about 16 days.

Weather conditions varied greatly among years. In 1989–90 and 1991–92, the weather was stable with sunshine during the day and almost no precipitation apart from minor snowfalls during 25–26 December 1991 and 13–15 February 1992. In 1992–93, the weather was more overcast with some snow flurries almost daily and temperatures rarely below −8°C during nighttime. Winds also were strong in 1992–93, and a relatively heavy snowfall covered almost the whole colony with 10 to 15 cm of snow during 9 to 12 January 1993. This resulted in a mass die-off of hatchlings (Sæther et al. unpubl. data). Different birds were used in the three study years.

After hatching, study nests were visited once a day in 1990 and twice a day in 1992. Nests were visited once a day in 1993 (once every other day during poor weather). Adults (if present) and chicks were weighed at each visit. During incubation, the body mass at departure was estimated from daily visits as the recorded body mass at arrival minus mass lost since arrival, estimated from the expression:

$$W_t = W_0 \cdot e^{-kt}, \qquad (1)$$

where W_0 is the initial mass, W_t is the mass t days later, and k is the proportion of the bird's mass lost each day (Croxall 1982), which for the Antarctic Petrel is 0.018 (Lorentsen and Røv 1995). The calculation of departure body mass during the brooding period is more difficult because adults feed chicks at regular intervals. During the brooding period it was assumed that the chick lost 14.8 ± SD of 2.2 g per day if not fed (Sæther, Andersen, and Tveraa unpubl. data). This value was estimated from the 24-h mass loss of 16 four-to-seven-day-old chicks in 1993 where the adults had been incubating and brooding for at least eight days. Thus, they were assumed to have little or no food left for the chick. The departure body mass of an adult with chick was then estimated as the recorded body mass at arrival minus the metabolic mass loss of the adult during the brooding period (which was assumed to equal that during the incubation period as estimated by the above equation) minus the sum of daily positive mass increments in the chick minus the estimated metabolic mass loss of the chick (see above).

We obtained a measure of overall body size of adults from a factor analysis (Norusis 1985) using tarsus length (± 0.1 mm), head length (± 0.1 mm; from neck to tip of bill), bill height (± 0.1 mm), and wing length (± 1 mm; maximum flattened chord). Factors were extracted by a principal components analysis, and the resulting factor score of each individual (PC1) was assumed to represent overall body size. Body condition of an individual was defined as the residuals obtained when body mass at first departure after hatching was regressed against the factor score for overall body size (see Jolicoeur and Mosimann 1960, Gilliland and Ankney 1992). Body mass at first departure after hatching was related to the factor scores in all three years ($P < 0.05$). As an index of body condition, we used the residuals from this regression of PC1 on body mass. This index was highly correlated with body mass in all three years ($P < 0.001$).

RESULTS

Chick mass at different ages.—If pairs differ consistently in food provisioning rates to their offspring, then chick masses should be positively correlated at different stages of the nestling period. In both 1990 and 1992, chick mass at 30 days of age was positively correlated with mass at 9 days of age (1990: $r = 0.52$, $n = 21$, $P < 0.05$; 1992: $r = 0.63$, $n = 32$, $P < 0.001$; Fig. 1).

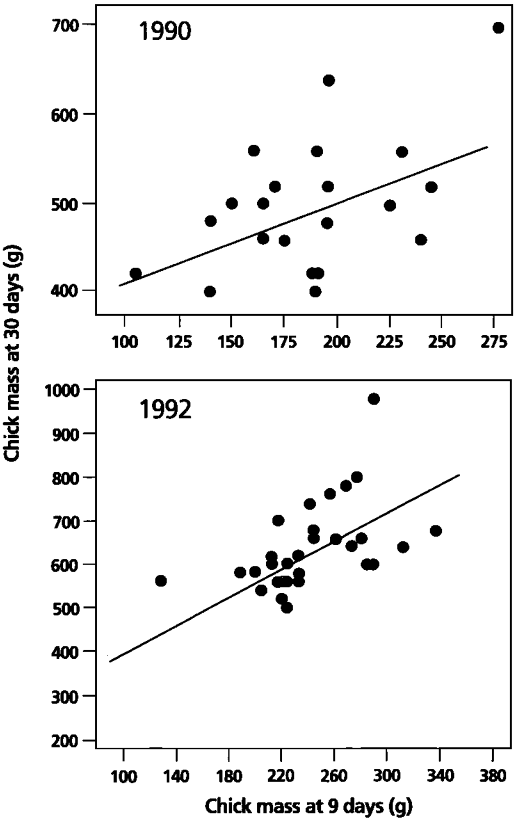

FIG. 1. The relationship between chick mass at age 9 days and 30 days in Antarctic Petrels during the austral summers of 1989–90 and 1991–92.

Correlates of chick mass.—The average factor score for the pair was positively correlated with mean body mass (computed on the basis of body mass at first departure after hatching for each of the pair members) for all years in the study period (1990: $r = 0.55$, $n = 27$, $P < 0.01$; 1992: $r = 0.39$, $n = 32$, $P < 0.05$; 1993: $r = 0.37$, $n = 31$, $P < 0.05$). These factor scores explained 14–30% of the variation in body mass, indicating that body size per se, although significantly correlated, was not a very good predictor of body mass or body condition.

The regression analyses showed that adult body mass, overall body size, and body condition explained a significant proportion of the variance recorded in chick mass at different ages. In 1990, mass of the chick when left unattended was positively related to body mass of the adult present at hatching ($r = 0.39$, $n = 28$, $P < 0.05$) and to mean body mass of the pair ($r = 0.41$, $n = 27$, $P < 0.05$). In 1992, chick mass at 30 days of age was significantly correlated

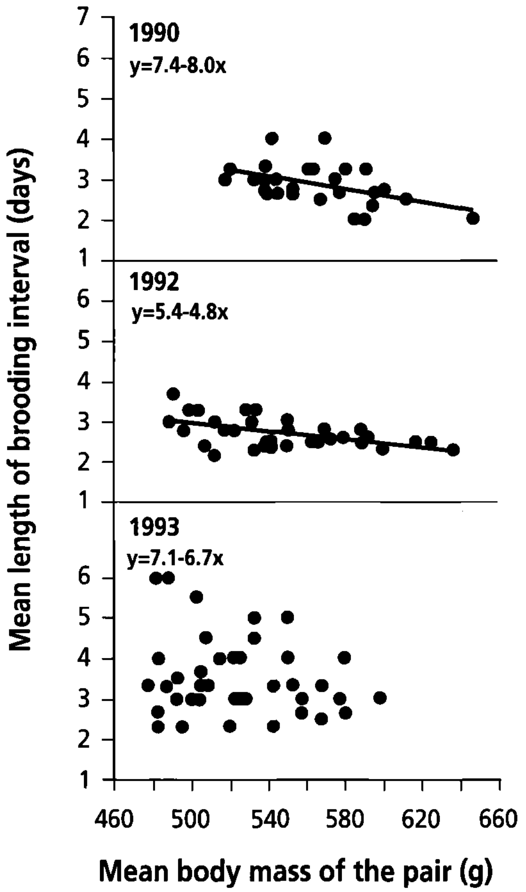

FIG. 2. The relationship between mean length of the brooding intervals and mean body mass of parents at first departure after hatching during the austral summers of 1989-90, 1991-92, and 1992-93.

with mean body mass of the parents in the beginning of the brooding period ($r = 0.42$, $n = 32$, $P < 0.05$) and with body mass of the adult not present at hatching ($r = 0.38$, $n = 32$, $P < 0.05$). Similarly, chick mass at 9 days of age was significantly correlated with the body mass of the adult present at hatching ($r = 0.39$, $n = 34$, $P < 0.05$). However, in 1993 variation in adult body mass did not explain a significant proportion of the variance ($P > 0.05$) in chick mass at any age. In this year, chick masses at age 9 days and when left unattended were related to the parents' feeding rates during the brooding period. Chick masses were higher when the mean interval between feedings was short (9 days: $r = -0.39$, $n = 44$, $P < 0.01$; unattended: $r = -0.42$, $n = 40$, $P < 0.01$).

TABLE 1. Stepwise multiple regression analysis of variables influencing the mass of Antarctic Petrel chicks at different stages of the nestling period.

Year	Variable[a]	Partial regression coefficient	R^2	n[b]
	Chick mass at 30 days			
1990	MeanPer	−0.71*	—	16
1990	BodyCond2	0.43*	0.58**	16
1992	BodyCond1	0.43*	0.19*	34
	Chick mass when first left unattended			
1990	BodyCond1+2	0.43*	0.19*	25
1992	No significant entry	—	—	37
1993	MeanPer	−0.50*	0.25*	35
	Chick mass at 9 days			
1990	No significant entry	—	—	24
1992	BodyMass1	0.42*	0.18**	34
1993	MeanPer	−0.57***	—	39
1993	BodySize1	0.46**	—	39
1993	BodyCond1	−0.35*	—	39
1993	BodyCond2	−0.29*	0.56**	39

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

[a] MeanPer: mean length of the brooding period; BodyCond: body condition of parent at first departure to sea after chick hatches; BodyMass: body mass of parent at first departure to sea after chick hatches; BodySize: PCI score describing overall size of parent; 1 = parent present at hatching, 2 = parent not present at hatching, 1+2 = mean of both parents.

[b] Number of nests.

Differences in the brooding performance and foraging rate of adults were related to body mass. Both in 1990 and 1992, pairs with low mean body mass spent on average longer time at the nests during the brooding period than did pairs with high mean body mass (1990: $r = -0.48$, $n = 27$, $P < 0.01$; 1992: $r = -0.51$, $P < 0.01$; Fig. 2). However, no such relationship appeared in 1993 ($r = -0.22$, $n = 44$, $P > 0.1$; Fig. 2). In 1993, the interval between feedings was shorter on average in pairs in which the individual present at hatching was large ($r = -0.27$, $n = 54$, $P < 0.05$).

We used stepwise multiple regression to evaluate the relative contribution of different variables to the variance in chick mass at different ages (Table 1). The relative contribution of the variables differed among years, but body mass and body condition of parents consistently were important in explaining variation in chick mass at different ages. In 1990 and 1992, the mass of 30-day-old chicks was influenced by body condition of the parents. In 1990, mean length of the brooding period ex-

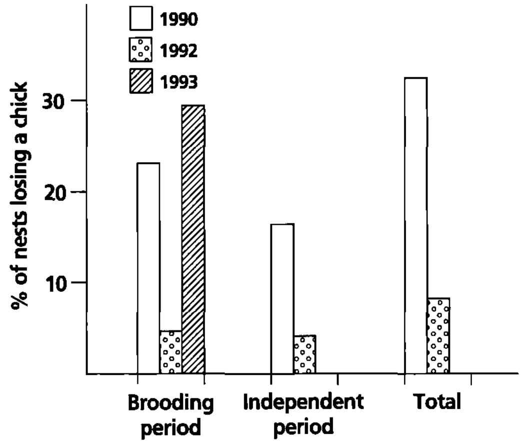

FIG. 3. Proportion of the nests where a chick was lost during the austral summers of 1989–90, 1991–92, and 1992–93 in different stages of the nestling period. In 1993 only nests where the offspring had survived to two days of age were included due to huge losses during the hatching period because of heavy snowfall.

plained significant additional variance in chick mass at 30 days. In 1992, the mass of chicks at 9 days was related to body mass of the adult present at hatching. In 1993, the mean length of the brooding interval of chicks explained the highest proportion of variance in chick mass when left unattended (Table 1). In addition, overall body size and body condition of the pair were important, i.e. larger parents produced the largest chicks although they generally were in a poor body condition, presumably due to poor weather conditions that year.

Chick loss in relation to chick mass.—Chick survival was highest in 1992 (36 out of 38 hatchlings survived to 30 days; Fig. 3). A large proportion of nests was destroyed in 1993 because of heavy snowfall during the hatching period, resulting in a greater loss during the brooding period than in 1992 ($\chi^2 = 9.41$, df = 1, $P < 0.01$). The proportion of chicks lost in 1993 was not different from that in 1990 ($\chi^2 = 3.17$, df = 1, $P > 0.05$).

Chick losses (17 out of 53 that hatched) were higher in 1990 than in 1992. The probability that a chick survived to 30 days in 1990 was closely related to its body mass at the time it was left unattended. At the time they were left unattended, the mean body mass of chicks that died ($\bar{x} = 130.5$ g, $n = 9$) was lower than that of chicks that survived the whole period ($\bar{x} = 185.0$ g, $n = 22$; $F = 16.53$, df = 1 and 29, $P < 0.001$). Thus, the implicit size-dependent differences between adults in food provisioning rates influenced nestling survival rates.

DISCUSSION

Differences among pairs of Antarctic Petrels in the rate of food provisioning to their offspring resulted in clear differences in chick masses at given ages in the nestling period (see Fig. 1). These findings are consistent with predictions of the parental-quality hypothesis. This hypothesis also is supported by two other studies on the Antarctic Petrel. First, Andersen et al. (1995) switched chicks between nests and showed that growth rate was retarded when a normally growing nestling was raised by parents whose original nestling grew slowly. Second, Lorentsen (1996) demonstrated a clear correlation between parental body condition, provisioning rate, and chick growth in the Antarctic Petrel. Amundsen et al. (1996), however, found no effect of parental quality on egg size or early nestling growth in the Antarctic Petrel, suggesting that effects of pair quality are most important from late in the brooding period onwards. Accordingly, body mass of 30-day-old chicks was not significantly correlated with chick mass at three days of age (1990: $r = 0.50$, $n = 21$, $P > 0.05$; 1992: $r = 0.19$, $n = 37$, $P > 0.1$). Similarly, in Magellanic Penguins (*Spheniscus magellanicus*), parental quality had a greater influence than egg size on fledging success and fledgling mass (Reid and Boersma 1990).

Fitness consequences of a comparatively slow chick growth resulting in low departure mass or a prolonged nestling period are difficult to evaluate for many seabird species. However, small Antarctic Petrel chicks at Svarthamaren are likely to have reduced probability of survival because the period with open shelf water is quite short (cf. Mehlum et al. 1987). Furthermore, because the distance to the nearest open water from Svarthamaren is quite far (>200 km), chicks in poor body condition would have difficulty fledging successfully. The probability of survival to 30 days of age also was closely related to chick mass at the end of the brooding period in 1990. Thus, both offspring survival during the nestling period and probably during the postfledging period seem to be closely related to parental quality (see Table 1). Yorio and Boersma (1994) found a similar effect of body condition on fledging success in Magellanic Penguins.

Our results show that the body mass of nestlings at different ages may be related both to body condition and overall body size of parents. The relative importance of these variables, however, varied between years. Chick masses were higher because parents in good body condition fed their chicks more frequently than parents in poor body condition in 1990 and 1992. However, an apparent reverse effect occurred in 1993, i.e. parents in relatively poor body condition at the end of the brooding period (compared with other parents at the same time in previous years) had the largest chicks. This result may have been related to poor weather (i.e. snowfall and strong winds) during hatching and early brooding in 1993. During the period of bad weather, few birds were flying, and the brooding intervals were longer than in previous years. In many nests in 1993, only one bird was present during the whole brooding period, whereas in 1990 and 1992 parents often replaced each other three times during this period. Consequently, adults in poor condition that were not relieved at the nest abandoned their nest before their mate returned (see Lorentsen and Røv 1995). Also, a large proportion of chicks that hatched during the period of poor weather died. Nevertheless, structurally large adults, which may have relatively more fat reserves than smaller adults, endured the bad weather for a longer period and thereby secured the survival of their chick. Similarly, when the period at sea was extended (by experimentally increasing flight costs of adults), the probability that a parent left its egg before its mate returned increased with decreasing body condition (Tveraa et al. 1997).

Patterns of brooding intervals and adult body mass revealed large interyear differences (Fig. 2). These patterns are likely to be related to interyear variation in weather conditions during the brooding period, and, possibly, to the availability of food. In 1990 and 1992, food availability apparently was good, judging from the large food loads brought to chicks (Sæther et al. 1993, Lorentsen 1996) and the relatively small variation in brooding intervals. Bad weather conditions during the brooding period in 1993 made it difficult for adults to return to the colony, resulting in a large variation in shift intervals and lower adult body masses compared with 1990 and 1992. However, the strong effect of body condition in 1993 (Table 1) suggests that the effects of stochastic variation in the environment depend on the quality of the parents. Furthermore, the positive relationship between adult body size and chick mass at nine days of age in 1993 also indicates that large size actually is an advantage. This relationship is in contrast to the suggestion that the best adults will be lightest in mass (see Witter and Cuthill 1993). Thus, good body condition may be important to seabirds for reducing the influence of stochastic environmental variation on reproductive success.

In general, petrel parents do not seem to respond to offspring need (Hamer and Hill 1993, 1994; Ricklefs 1987, 1992; Ricklefs and Schew 1994; Sæther et al. 1993; but see Bolton 1995). We have shown that individual variation in reproductive output in seabirds may depend on differences in the adults' capacity or willingness to feed their offspring (see also Johnsen et al. 1994, Lorentsen 1996). Currently, we do not know the proximate causes for these differences, but they may be related to differences in age or experience (Pugesek 1983, 1984; Thomas and Coulson 1988) or to an interaction between body condition and age (Reid 1988).

In conclusion, we suggest that the reproductive success of the Antarctic Petrel is strongly influenced by stochastic variation in climatic conditions during the breeding season. The influence of this variation on reproductive outcome may, however, depend on the quality of the parents, which, in turn, is related to body size, body mass, or body condition. The effects of individual quality on reproductive success are well known in mammals (e.g. Clutton-Brock 1988b), but such information is scarce for seabirds (but see Croxall et al. 1992, Weimerskirch 1992). Future long-term studies of seabirds can contribute much to our understanding of how differences in parental quality influence demography. Such knowledge may have a profound influence on our ability to understand and predict fluctuations in seabird populations.

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