INFLUENCE OF BODY CONDITION ON REPRODUCTIVE DECISION AND REPRODUCTIVE SUCCESS IN THE BLUE PETREL

OLIVIER CHASTEL, HENRI WEIMERSKIRCH, AND PIERRE JOUVENTIN

Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, 79360 Beauvoir sur Niort, France

ABSTRACT.—Following the prediction that body condition affects whether eggs are laid in birds, we examined variations in prebreeding body condition (i.e. body mass one month before laying, adjusted for structural size, breeding experience, and date of return), incidence of breeding, and reproductive success of male and female Blue Petrels (Halobaena caerulea). Condition was inversely correlated with date of return and positively related to breeding experience in males, but not in females. In both sexes, condition displayed year-to-year variations; the 1991-1992 season was distinguished by poor condition, low incidence of breeding, and low reproductive success. Condition in both males and females, and breeding experience in males had significant effects on the "decision to breed." Breeding experience also influenced the decision to breed, especially in males. Condition, but not breeding experience, had a significant influence on male incubation success. Female breeding performances were not related to condition but to breeding experience. Annual average breeding success was highly variable and significantly correlated with male condition. Prebreeding visits appeared to be critical for this pelagic seabird and may allow individuals, through their condition, to manage their reproductive investment. We suggest that condition mainly affects egg formation in females and, together with breeding experience, influences the duration and the quality of prebreeding colony attendance in males. The potential relationships of body condition, breeding experience, reproductive investment, and future survival are discussed. Received 11 November 1993, accepted 25 February 1994.

THE INFLUENCE of body mass or condition on fitness components, such as fecundity and survival, has been established for several avian species. Studies have demonstrated that heavier females produce larger clutches and that heavier males achieve greater reproductive success and higher survival rates (Aldrich and Ravelling 1983, Newton et al. 1983, Petrie 1983, Gibbons 1989). Body condition also may influence food provisioning to the chick (Weimerskirch et al. 1993, Chaurand and Weimerskirch 1994a), pair-bond status (Robb et al. 1992), and secondbrood initiation (De Laet and Dhont 1989). Longterm studies have pointed out slight but significant contributions of individual body mass to lifetime reproductive success (Gelbach 1989, Mills 1989). Additionally, brood manipulations have established relationships between female mass loss and experimentally enlarged brood size (Nur 1984). However, body mass has been shown to have no influence on fecundity or survival in some species (Naylor and Bendell 1989, Marjakangas and Aspegren 1991, Robb et al. 1992, Meathrel et al. 1993).

Most seabirds are long-lived species and have low fecundity (Lack 1968). Albatross and petrel populations typically include high proportions of nonbreeders (for review, see Warham 1990). Nonbreeding years are of regular occurrence among established breeders (Mougin et al. 1984, Wooller et al. 1989). In the order Procellariiformes, intermittent breeding has been linked to age or experience (Weimerskirch 1990, 1992), loss or change of mate (Fisher 1976, Ollason and Dunnet 1988), food availability, environmental changes, or temporary inaccessibility of breeding sites (Prince 1985, Ainley and Boekelheide 1990, Chastel et al. 1993). Only a few studies have examined the influence of individual traits, such as body condition, on reproductive decisions and recruitment in longlived seabirds (Fisher 1967, Weimerskirch 1992). In fact, the influence of body condition on reproductive success has not even been clearly established in pelagic seabirds. This is in contrast to the well documented studies of relationships between food supply, adult condition, and reproductive effort that have been conducted on inshore feeders such as terns (Monaghan et al. 1989). However, general improvement in breeding performance with age or experience has been well established (see

review in Newton 1989). Pelagic seabirds (e.g. albatrosses and petrels) are excellent subjects for studying the simultaneous effects of body condition and breeding experience on reproductive investment and breeding performance because these birds are more likely not to jeopardize their future survival (Goodman 1974, Drent and Daan 1980).

Blue Petrels (*Halobaena caeruelea*) are small seabirds (200 g) that forage over subantarctic pelagic waters (Prince 1980, Steele and Klages 1986). These colonial burrowing petrels visit their breeding grounds more than a month before a period of highly synchronous laying (Paulian 1953, Jouventin et al. 1985, Fugler et al. 1987). This prebreeding period provides a good opportunity to determine factors influencing future reproductive investment and particularly to test the prediction of Drent and Daan (1980) that the decision to breed or not is clearly related to female body condition, or that of both sexes, where the two members of the pair share breeding duties equally (Lack 1968).

In this paper we examine the variation in body condition (body mass corrected for linear dimensions, breeding experience, and date of return) of adult Blue Petrels to determine the extent to which prebreeding body condition influences the reproductive decisions and reproductive success of both males and females.

METHODS

The study was conducted on Mayes Island in the eastern part of the Kerguelen Archipelago (48°38'S, 68°38'E). The island is free of alien predators. Every year from 1986 to 1991, 150 burrows of Blue Petrels were monitored. Study burrows were fitted with a closeable observation window above the nest chamber and individuals were banded using monel bands. During the prebreeding period (8 September-6 October), petrels occupied burrows by day and, except for the 1988-1989 season, diurnal inspections of the study burrows were conducted every two days to determine dates of return and to measure prebreeding body mass for each individual. Birds were sexed using playback records (Bretagnolle 1990) and weighed to the nearest 2 g with a 300-g Pesola scale. The following measurements were taken: culmen length and tarsus length to nearest 0.1 mm; and flattened wing chord to nearest 1 mm. Burrows were checked for eggs each year in early November (range 30 October-3 November); laying of large, single eggs was highly synchronous (Jouventin et al. 1985) and, at this time, 98% of the birds are males starting their first incubation shift (T. Chaurand unpubl. data). Males were

weighed, and the presence or absence of an egg was recorded. Females were weighed at the beginning of the second incubation shift in mid-November (range 12–15 November). Hatching success was determined by inspection a few days after hatching was to occur (range 28–30 December). Chicks were banded in late January. Annual breeding success was calculated as the proportion of eggs resulting in fledged young.

Two reproductive traits (breeding decisions and breeding success) were studied and defined as follows. Breeding decision included: (1) not seen during current breeding season, but seen subsequently; (2) occupying a burrow, but not breeding; and (3) breeding. Breeding success included: (1) failure to hatch an egg; and (2) successfully rearing a chick to fledging.

Variables associated with these reproductive traits were defined as follows. (1) Prebreeding body condition (hereafter, "condition") was represented by body mass scaled by linear, structural measurements. This resulted in a condition index (Johnson et al. 1985). We combined mean body mass, culmen length, wing length, and tarsus length in a principal components analysis for 73 individuals weighed on at least three occasions (up to 13) during prebreeding visits, incubation routine, and postbreeding visits. Components scores indicated that mean body mass explained most of the variation. Loadings on principal component I were: mean body mass, 0.66; culmen length, 0.51; wing length, 0.49; and tarsus length, 0.26. Additionally, culmen length was positively correlated with mean body mass (r = 0.24, n = 73, P <0.05). Condition, therefore, was estimated using the following ratio: prebreeding body mass (g) divided by culmen length (mm). A high value for this index signifies good body condition. The date of return was the first record in the study colony (1 September = day 1, 6 October = day 36). Breeding experience was the number of previous years during which breeding was attempted. In females, the degrees of freedom for breeding experience were smaller than for males due to a smaller sample size. In the 1988-1989 season, no data were available for the prebreeding period, although burrows were checked during the breeding period. Thus, breeding experience of the birds was known. For several other calculations, birds were simply classified as inexperienced (not recorded breeding before) and experienced (at least one previous breeding attempt). Year refers to breeding seasons 1986-1987, 1987-1988, 1989-1990, 1990-1991, and 1991-1992. Return rate was the proportion of birds seen in the prebreeding period and subsequently recovered the following year.

Relationships of condition and date of return, breeding experience, previous breeding status, and year were examined using one-way analysis of variance (ANOVA). Comparisons between means were made using two-tailed *t*-tests. To evaluate the influence of these variables and noncontinuous traits (breeding decision and breeding success), we used

TABLE 1. Annual variation in mean (±SD) prebreeding body condition and date of return of Blue Petrels (males and females pooled), 1986–1991.

Breeding season	n	Prebreeding body condition	Date of return (September)
1986-1987	13	8.35 ± 0.72	12.69 ± 2.21
1987-1988	16	7.69 ± 0.70	13.62 ± 4.14
1989-1990	34	7.95 ± 1.06	13.14 ± 4.32
1990-1991	38	7.73 ± 0.99	13.50 ± 6.24
1991-1992	56	$7.11~\pm~0.53$	$22.17~\pm~6.37$

nonparametric Kruskal-Wallis tests. Statistical analyses were performed using the STATITCF and LOG-ITHEQ packages (ITCF 1988).

RESULTS

Prebreeding period.—During the prebreeding period, 75.1% of the birds occupying a burrow by day were males (n = 173). The average duration of a visit was 7.83 ± SD of 0.83 days (n = 12), during which birds lost 4.45 g per day (n = 7). Prebreeding body mass ranged from 165 to 234 g (CV = 11%) in males, and 168 to 234 g (CV = 9%) in females. No female was found twice during diurnal surveys, indicating that they spent less time ashore. Condition did not differ between males and females ($F_{1,115} =$ 0.76, P > 0.05). Condition differed significantly between years (Table 1; males and females

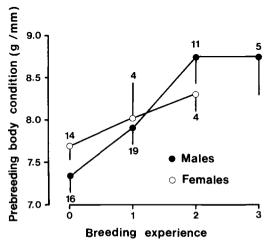


Fig. 1. Relationship between breeding experience and prebreeding body condition in male and female Blue Petrels. Samples sizes given adjacent to each point and data presented as $\bar{x} \pm$ SD. Significant difference in males only (P < 0.01).

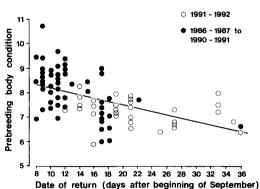


Fig. 2. Prebreeding body condition of individual male Blue Petrels in relation to date of return (r = -0.517, n = 50, P < 0.001), 1986–1991.

pooled, $F_{4,152} = 9.36$, P < 0.001) and was particularly poor in 1991–1992.

Inexperienced males had a poorer condition index than did experienced birds 7.22 \pm 0.71, n = 23, and 7.84 \pm 1.01, n = 46, respectively; t= 2.63, P = 0.01), but the difference was not significant in females (7.30 \pm 0.65, n = 11, and 7.68 \pm 0.74, n = 17, respectively; t = 1.39, P =0.17). In males, but not females, condition significantly improved with breeding experience (males, $F_{3.49} = 5.69$, P < 0.01; females, $F_{2.20} =$ 0.96, P > 0.05; year 1991–1992 excluded; Fig. 1).

There was no effect of sex ($F_{1,115} = 0.23$, P > 0.05) or breeding experience (males, $F_{3,50} = 0.29$, P > 0.05; females, $F_{4,21} = 2.28$, P > 0.05; year 1991–1992 excluded) on date of return. However, the mean date of return differed notably among years (Table 1; males and females pooled, $F_{4,152} = 23.4$, P < 0.001) due to 1991–1992, when the mean date of return was delayed by nearly 10 days. Condition and date of return were in-

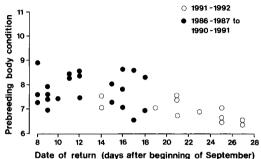


Fig. 3. Prebreeding body condition of individual female Blue Petrels in relation to date of return (r = -0.062, n = 22, P > 0.05), 1986–1991.

		Males	Females	
Source of variation	df	Н	df	Н
Bree	ding	decision		
Prebreeding body	_			
condition	2	10.20**	2	9.53**
Date of return	2	7.62*	2	0.44
Breeding experience	4	15.40**	2	7.75*
Year	4	15.54**	4	0.24
Bree	ding	success		
Prebreeding body				
condition	2	8.92**	2	2.57
Date of return	2	7.02*	2	0.57
Breeding experience	3	4.27	2	13.54***
Year	4	15.78**	4	3.04

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

versely correlated in males (r = -0.517, n = 50, P < 0.001; Fig. 2), but not in females (r = -0.062, n = 22, P > 0.05; Fig. 3).

Breeding decision .- For both males and females, the "decision to breed" was significantly influenced by condition (Table 2). Condition in the two categories of nonbreeding males (birds not present and birds present but not breeding) was similar (t = 1.06, df = 37, P > 0.05) and, therefore, data were pooled. Nonbreeding males averaged lower condition (7.34 \pm 0.68, n = 37) than breeding birds (8.04 \pm 1.05, n = 45; t =3.49, P < 0.001). Similar results were found in females; breeding birds were in better condition (7.90 \pm 0.75, n = 18) than those that did not breed (7.19 \pm 0.44, n = 16; t = 3.31, P <0.01). Breeding decision also was related significantly to date of return in males (breeding, 14.22 ± 5.89 days, n = 45; nonbreeding, 19.27 \pm 7.95, n = 37; t = 3.30, P < 0.01), but not in females (P > 0.05). More experienced males were more likely to breed; experience in females had less effect than did condition (Table 2).

Since condition and experience influenced the decision to breed, especially in males, we considered these two variables simultaneously (Table 3). Experienced males that did not breed in the current season had poorer condition than birds that bred. For inexperienced males, the same trend was not significant. Nonbreeding males showed no significant differences whether or not they were experienced (experienced, 7.46 \pm 0.66, n = 18; not experienced, 7.13 \pm 0.61, n = 17; t = 1.53, P > 0.05). In females, experienced birds that bred appeared to be in better condition than nonbreeding ones, but the difference was not statistically significant (Table 3).

The decision to breed also was influenced by year in males, but not in females (Table 2). The strong effect of year on breeding decision in males is due mainly to the poor 1991–1992 season, during which nearly 70% of the males present did not breed. If the 1991–1992 data are removed, breeding birds showed condition and were more experienced than nonbreeding ones (Table 4). However, date of return was similar, indicating that condition and experience had the most important influence on male breeding decision during most years.

Return rate in relation to breeding decision.—Birds that occupied a burrow during prebreeding, but did not breed, were mainly the inexperienced (males and females pooled, 57.1%, n = 91). Considering experienced birds, nonbreeders showed a similar return rate to breeding birds (Table 5; $X^2 = 2.29$, n = 113, P = 0.15). Nonbreeding inexperienced birds had a significantly lower rate of return (Table 5; $X^2 = 12.98$, n = 91, P < 0.001) than nonbreeding experienced birds. Many birds that were first seen in the prebreeding period, but did not breed that season, were never seen again; however, all inexperienced birds successfuly recruited into the breeding population were seen in later years.

Breeding success.-In males, condition, year,

TABLE 3. Comparisons of means (\pm SD, with *n* in parentheses) of prebreeding body condition of male and female Blue Petrels in relation to breeding decision and previous experience, 1986–1991.

Experienced				Inexperienced		
Sex	Breeding	Nonbreeding	t	Breeding	Nonbreeding	t
Males	8.08 ± 1.10 (29)	7.46 ± 0.66 (18)	2.17*	7.50 ± 0.96 (9)	7.13 ± 0.61 (17)	1.12
Females	7.87 ± 0.72 (13)	7.08 ± 0.45 (4)	2.05ª	7.68 ± 1.45 (2)	7.21 ± 0.47 (9)	0.917

*, P < 0.05.

Variable	Breeding (38)	Nonbreeding (13)	t	Successful (20)	Unsuccessful (15)	t
Prebreeding body condition	8.19 ± 1.03	7.54 ± 0.91	2.02*	8.50 ± 0.89	7.67 ± 1.09	2.48*
Date of return	$13.02~\pm~5.14$	13.38 ± 4.11	0.23	12.25 ± 3.97	14.06 ± 6.83	0.98
Breeding experience	2.29 ± 0.95	$1.54~\pm~0.77$	2.56*	2.54 ± 0.94	2.20 ± 1.01	0.75

TABLE 4. Mean (\pm SD, with *n* in parentheses in boxhead) values of prebreeding body condition, date of return (days of September) and breeding experience (years of previous breeding) relative to breeding decision and breeding success in male Blue Petrels, 1986-1990.

*, P < 0.05.

and to a lesser extent date of return had a significant effect on breeding success (Table 2), whereas breeding experience did not. Males that successfully reared a chick were in better condition (8.36 ± 0.90 , n = 23) than males that were unsuccessful at the egg stage (7.59 ± 1.03 , n =17; t = 2.43, P = 0.02). In females, breeding success was only significantly influenced by breeding experience (Table 2). In our set of data (n = 23), females recorded breeding for the first time were more likely to fail (10 of 11 breeding attempts) than females recorded breeding for the second time (2 of 7 breeding attempts; Z =3.09, P < 0.01), and for the third or more times (2 of 5 breeding attempts, Z = 2.51, P < 0.05).

Since condition influenced male reproductive performance, we examined relationships between prebreeding body mass and body mass at the onset of the first incubation shift (egg loss during this period accounted for 47% of total breeding failure; n = 125). These two categories were significantly correlated (r = 0.318, n = 47, P = 0.03) in males, but not in females (r = 0.098, n = 18, P > 0.05). Body condition of males at the start of their first incubation shift was better for birds that successfully hatched eggs than for those that failed; in females, no differences were found (Table 6). Male condition at the start of incubation was not different for experienced and inexperienced birds (experienced, 7.64 \pm 0.65, n = 56; inexperienced, 7.79 ± 0.77 , n = 21; t = 0.79, P > 0.05). The strong effect of year on breeding success in males

TABLE 5. Return rate (with n in parentheses) during year y + 1 for Blue Petrels (males and females pooled) in relation to breeding decision and breeding experience during year y, 1986–1991.

	Breeding	Nonbreeding
Experienced	0.93 (74)	0.82 (39)
Inexperienced	1.00 (10)	0.42 (52)

was related to the poor 1991–1992 season during which 72% of eggs (n = 71) failed to hatch. Because egg mortality occurred mainly during the first male incubation shift, many females were not identified (see Methods), causing the observed discrepancy in year effect. With the 1991–1992 data on males (Table 4) removed, only condition differed significantly between failed and successful males.

A significant relationship existed between mean condition of males and breeding success of the study colony (Fig. 4), while in females the relationship was not significant (r = 0.773, n = 5, P > 0.05). During 1987–1988 and particularly 1991–1992, overall breeding success was low (28 and 25%; respectively) and corresponded to the period of lowest male prebreeding body condition. However, during 1989–1990, breeding success (62%) and male condition were particularly high.

DISCUSSION

During the course of this study, body condition varied significantly among Blue Petrels. Differences were related to breeding experience, date of return, year, reproductive decision, and breeding performance.

Individual variation in body condition.—Adults exhibited great individual variation in body condition during their prebreeding visits to their

TABLE 6. Mean (\pm SD, with *n* in parentheses) hatching success in relation to body condition on the first day of first incubation shift in male and female Blue Petrels, 1986–1991.

Hatching	Males	Females
Successful Unsuccessful <i>t</i> -value	$\begin{array}{c} 7.88 \pm 0.72 \ (43) \\ 7.55 \pm 0.63 \ (43) \\ 2.30^* \end{array}$	$\begin{array}{c} 7.64 \pm 0.78 \ (46) \\ 7.66 \pm 0.78 \ (16) \\ 0.09 \end{array}$

*, P < 0.05.

colony. Males in good condition tended to arrive early. This may reflect individual differences in foraging success. Heavy males acquired reserves to visit early and stay longer. In our study, female condition was not related to date of arrival probably because they visit the colony during a more contracted period than their mate. However, the sample size for females was small.

After removing the 1991–1992 data for males, our results showed a significant improvement in condition with experience. Similar effects have been established in Manx Shearwaters (Puffinus puffinus; Brooke 1978) and Wandering Albatrosses (Diomedea exulans; Weimerskirch 1992). The observed improvement could be due to improved foraging efficiency, as established in the Herring Gull (Larus argentatus; Greig et al. 1983), thus supporting Lack's hypothesis (1968) that, in seabirds, the lower skill of young birds is responsible for the delayed onset of breeding. Among experienced breeders, male Blue Petrels continued to improve their condition with each breeding attempt. In the very long-lived Wandering Albatross, body conditions increase throughout the breeding career of males, while in females it only improves during the first 20 years, perhaps due to a progressive selection of high-quality birds at older age, rather than from an improvement in individual skill (Weimerskirch 1992). Contrary to what was found for male petrels, female condition was not related to breeding experience. In September, females visited the colony only briefly with the result that insufficient sample sizes were obtained.

Annual variation in body condition.—Condition of adult Blue Petrels varied annually. The 1991-1992 breeding season (and to a lesser extent 1987–1988) was characterized by the lowest average prebreeding condition recorded during the study. Such year-to-year variation in body condition has not been described previously in pelagic seabirds. In coastal seabirds, for example Arctic Terns (Sterna paradisea) and Common Terns (S. hirundo), poor body condition under conditions of food shortage has been detected (Monaghan et al. 1989, Monaghan et al. 1992, Uttley 1992). The low condition recorded in our study in 1987–1988 and particularly in the 1991– 1992 could be explained by a decrease in food availability.

Body condition and reproductive decision.—Our results showed that body condition of male and female Blue Petrels influenced whether an individual bred, consistent with the prediction of

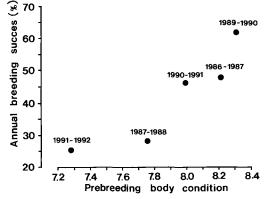


Fig. 4. Relationship between mean prebreeding body condition in male Blue Petrels and mean annual breeding success of study colony (r = 0.903, n = 5, P < 0.05).

Drent and Daan (1980). It is possible that only birds attaining a threshold condition decide to breed, as suggested by Weimerskirch (1992) for female Wandering Albatrosses. Blue Petrel populations are characterized by a significant proportion of experienced nonbreeders, as is the case for other species of Procellariiformer (Cory's Shearwater, Calonectris diomedea [Mougin et al. 1984]; Short-tailed Shearwater, Puffinus tenuirostris [Wooller et al. 1989]; Manx Shearwater [Brooke 1990]). In our study, nonbreeding but experienced birds showed a rate of return similar to their breeding counterparts. Former breeders that skip a season could have experienced low foraging success before the breeding season and may not have acquired sufficient reserves to invest in reproduction. As for the inexperienced nonbreeders, many were never recorded later in the study colony. These presumably are younger birds that may either have suffered higher mortality (as observed in Shorttailed Shearwaters; Bradley et al. 1989) or have moved to another part of the colony.

Extensive occurrence of nonbreeding during a particular year by established breeders has been related to food shortage and to large-scale environmental perturbations (Coulson 1984, Prince 1985, Ainley and Boekelheide 1990, Chastel et al. 1993). During the 1991–1992 breeding season, up to 70% of males that visited the colony refrained from breeding and showed poor condition. Breeding Blue Petrels experience severe declines in body mass during incubation and chick rearing (Chaurand and Weimerskirch 1994), as is the case in many other procellariids (Weimerskirch 1990); under adverse conditions, life-history theory (Stearns 1976) suggests a trade-off between future reproductive potential or survival. A threshold value of prebreeding body condition may allow individual Blue Petrels to "predict" the likely outcome of a reproductive decision or to abandon a breeding attempt if the "perceived" risks to their survival are too great (Drent and Daan 1980, Reznick 1985, Pugesek 1987).

Experience also played a significant role in the decision to breed, especially for males. Lower breeding incidence among young individuals is characteristic of all seabirds studied, including Black-legged Kittiwakes (Rissa tridactyla; Wooller and Coulson 1977), Short-tailed Shearwaters (Wooller et al. 1989), Adélie Penguins (Pygoscelis adeliae; Ainley et al. 1983), Antarctic Fulmars (Fulmarus glacialoïdes; Weimerskirch 1990), South Polar Skuas (Catharacta maccormicki; Ainley et al. 1990), Laysan Albatrosses (Diomedea immutabilis; Fisher 1976), and Wandering Albatrosses (Weimerskirch 1992). This general trend for less experienced birds to postpone their breeding to the next year could be explained in terms of a higher cost of reproduction (Williams 1966), especially if they show a lower body condition than more experienced breeders.

In our study, factors mediating reproductive decision differed between the sexes. In female Blue Petrels, condition was the most important factor and may influence the ability of the individual to form the egg during the prelaying exodus. However, Meathrel et al. (1993) did not find a relationship between egg size and female body condition in the Short-tailed Shearwater. In male Blue Petrels, the constraints on future reproduction are different. During prebreeding visits, males undergo a long period without feeding and they perform energy-consuming activities such as courting, digging and burrow defense. Poor condition may render them less able to perform these activities efficiently. Furthermore, condition probably determines the duration of their prebreeding attendance. Birds in poor condition may spend less time ashore, with the consequent penalties on mate retention or re-mating ability and, therefore, breeding probability (Fisher 1976, Ollasson and Dunnet 1988).

Considering both members of the pair, the ability of the male to reproduce will mainly

depend on the female's condition because, even when in good condition, a male will not breed if his mate fails to lay an egg. Moreover, in procellariiforms, mate retention is high and pair formation is a long process that is known to affect breeding frequency (Fisher 1967, Ollasson and Dunnet 1988).

Body condition and reproductive success. —In our study, condition did not play the same role in both sexes. In males, condition and not breeding experience clearly influenced breeding success and particularly hatching success. Although an improvment in breeding performance with age or experience has been well established (for review, see Newton 1989), no study on pelagic seabirds has related breeding success to body condition. Incubating Blue Petrels have a threshold mass at which they spontaneously desert the egg (Chaurand and Weimerskirch 1994), and males with lower body condition would attain this value more rapidly and particularly before the return of their mate. Consistent with this idea, nearly one-half of the total hatching failure occurred during the first incubation shift and concerned males in poor condition. The importance of male body mass on incubation success has also been demonstrated in the Moorhen (Gallinula chloropus; Gibbons 1989).

In contrast to males, breeding experience and not prebreeding body condition had a significant effect on reproductive success for females. After laying, female Blue Petrels forage at sea while their mate incubates the egg for 12 days. Breeding experience may affect the foraging efficiency of females and, consequently, the time needed to restore body condition.

Our study of Blue Petrels shows that condition in both males and females affects the reproductive decision and reproductive performance (males). The obvious linkages between breeding experience, body condition, reproductive decision, and reproductive success raise the question of the consequences for future survival or future fecundity of reproductive effort made by individuals facing poor environmental conditions.

ACKNOWLEDGMENTS

The administration of "Terres Australes and Antarctiques Françaises" provided logistic and financial support. We thank: all the successive field workers involved in banding and recovery on Mayes Island; F. Genevois for great assistance in the field; D. Besson, N. Huin, T. Micol, and D. Capdeville for help in data processing; S. Hall, D. Ainley, R. D. Wooller, and G. D. Schnell for critically commenting on the manuscript and for help with the English; and L. Ruchon for drawing the figures.

LITTERATURE CITED

- AINLEY, D. G., AND R. J. BOEKELHEIDE. 1990. Seabirds of the Farallon Islands: Dynamics of an upwelling community. Standford Univ. Press, Standford, California.
- AINLEY, D. G., R. E. LE RESCHE, AND J. C. SLADEN. 1983. Breeding biology of the Adélie Pengiun. Univ. California Press, Berkeley.
- AINLEY, D. G., C. A. RIBIC, AND R. C. WOOD. 1990. A demographic study of the South Polar Skua Catharacta maccorrmicki at Cape Crozier. J. Anim. Ecol. 59:1-20.
- ALDRICH, T. W., AND D. G. RAVELING. 1983. Effects of experience and body weight on incubation behavior of Canada Geese. Auk 100:670-679.
- BRADLEY, J. C., R. D. WOOLER, I. J. SKIRA, AND D. L. SERVENTY. 1989. Age-dependent survival of breeding Short-tailed Shearwaters (*Puffinus tenuirostris*). J. Anim. Ecol. 58:175-188.
- BRETAGNOLLE, V. 1990. Behavioural affinities of the Blue Petrel (Halobaena caerulea). Ibis 132:102–105.
- BROOKE, M. DE L., 1978. Weights and measurements of the Manx Shearwater. J. Zool. (Lond) 186:359– 374.
- BROOKE, M. DE L., 1990. The Manx Shearwater. Academic Press, London.
- CHASTEL, O., H. WEIMESKIRCH, AND P. JOUVENTIN. 1993. High annual variability in reproductive success and survival of an Antarctic seabird, the Snow Petrel *Pagodroma nivea*: A 27-year study. Oecologia 94:278-285.
- CHAURAND, T., AND H. WEIMERSKIRCH. 1994a. The regular alternation of short and long foraging trips in the Blue Petrel (*Halobaena caerulea*): A previously undescribed strategy of food provisioning in a pelagic seabird. J. Anim. Ecol. 63: 275-282.
- CHAURAND, T., AND H. WEIMERSKIRCH. 1994b. Incubation routine, body mass regulation and egg neglect in the Blue Petrel (Halobaena caerulea). Ibis 136:285-290.
- COULSON, J. C. 1984. The population dynamics of the eider duck *Somateria mollissima* and evidence of extensive non-breeding by adult duck. Ibis 126:525-543.
- DE LAET, J. F., AND A. A. DHONT. 1989. Weight of the female during first brood as a factor influencing second brood initiation in Greats Tits Parus major and Blue Tits Parus caeruleus. Ibis 131: 281-289.
- DRENT, R. H., AND S. DAAN. 1980. The prudent par-

ent: Energetic adjustments in avian breeding. Ardea 68:225–252.

- FISHER, H. I. 1967. Body weights in Laysan Albatross Diomedea immutabilis. Ibis 109:373-382.
- FISHER, H. I. 1976. Some dynamics of a breeding colony of Laysan Albatross. Wilson Bull. 88:121– 143.
- FUGLER, S. R., S. HUNTER, I. P. NEWTON, AND W. K. STEELE. 1987. Breeding biology of Blue Petrels Halobaena caerulea at the Prince Edwards Islands. Emu 87:103-110.
- GELBACH, F. R. 1989. Screech-owl. Pages 387-404 in Lifetime reproduction in birds (I. Newton, Ed.). Academic Press, London.
- GIBBONS, D. W. 1989. Seasonal reproductive success of the Moorhen *Gallinula chloropus*: The importance of male weight. Ibis 131:57-68.
- GOODMAN, D. 1974. Natural selection and cost of ceiling on reproductive effort. Am. Nat. 108:247-268.
- GREIG, S. A., J. C. COULSON, AND P. MONAGHAN. 1983. Age related differences in foraging in the Herring Gull (*Larus argentatus*). Anim. Behav 31:1237-1243.
- JOHNSON, D. H., G. L. KRAPU, K. J. REINEEKE, AND D. G. JORDE. 1985. An evaluation of condition indices for birds. J. Wildl. Manage. 49:569–575.
- JOUVENTIN, P., J. L. MOUGIN, J. C. STAHL, AND H. WEI-MERSKIRCH. 1985. Comparative biology of the burrowing petrels of the Crozet Islands. Notornis 32:157–220.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- MARJAKANGAS, A., AND H. ASPEGREN. 1990. Responses of Black Grouse (*Tetrao tetrix*) hens to supplemental winter food. Ornis Scand. 22:282– 283.
- MEATHREL, C. E., J. S. BRADLEY, R. D. WOOLLER, AND I. J. SKIRA. 1993. The effect of parental condition on egg-size and reproductive success in Shorttailed Shearwaters *Puffinus tenuirostris*. Oecologia 93:162-164.
- MILLS, J. A. 1989. Red-billed gull. Pages 387–404 in Lifetime reproduction in birds (I. Newton, Ed.). Academic Press, London.
- MONAGHAN, P., J. D. UTTLEY, AND M. D. BURNS. 1992. Effects of changes in food availability on reproductive effort in Arctic Terns Sterna paradisea. Ardea 80:71–81.
- MONAGHAN, P., J. D. UTTLEY, M. D. BURNS, C. THAINE, AND J. BLACKWOOD. 1989. The relationship between food supply, reproductive effort and breeding success in Arctic Terns Sterna paradisaea. J. Anim. Ecol. 58:261–274.
- MOUGIN, J. L., C. JOUANIN, F. ROUX, AND J. C. STAHL. 1984. Les années sabbatiques des Puffins cendrés Calonectris diomedea borealis reproducteurs de l'île Selvagem Grande, Océan Atlantique Nord Ori-

ental (30°09'N, 15°52'W). C. R. Acad. Sci. Paris 6:147-150.

- NAYLOR, B. J., AND J. F. BENDELL. 1989. Clutch size and egg size of Spruce Grouse in relation to spring diet, food supply, and endogenous reserve. Can. J. Zool. 67:969-980.
- NEWTON, I. 1989. Synthesis. Pages 441-471 in Lifetime reproduction in birds (I. Newton, Ed.). Academic Press, London.
- NEWTON, I., M. MARQUISS, AND A. VILLAGE. 1983. Weights, breeding and survival in European Sparrowhawks. Auk 100:344-354.
- NUR, N. 1984. The consequences of brood size for breeding Blue Tits. I. Adult survival, weight change and the cost of reproduction. J. Anim. Ecol. 53:479-496.
- OLLASON, J. C., AND G. M. DUNNET. 1988. Variation in success in Fulmars. Pages 268-278 in Reproductive success: Studies in individual variation in contrasting breeding systems (T. H. Clutton-Brock, Ed.). Univ. Chicago Press, Chicago.
- PAULIAN, P. 1988. Pinnipèdes, Cétacés, Oiseaux des îles Kerguelen et Amsterdam. Mem. Inst. Sci. Madas. 8:111–235.
- PETRIE, M. 1983. Female Moorhens compete for small fat males. Science 220:413–414.
- PRINCE, P. A. 1980. The food and feeding ecology of the Blue Petrel (*Halobaena caerulea*) and the Dove Prion (*Pachytila desolata*). J. Zool. (Lond) 190:59-76.
- PRINCE, P. A. 1985. Population and energetic aspects of the relationship between Black-browed and Grey-headed albatrosses and the Southern Ocean marine environment. Pages 473–477 in Antarctic nutrient and food webs (W. R. Siegfried, P. R. Condy, and W. R. Laws, Eds). Springer, Berlin.
- PUGESEK, B. H. 1987. Age specific survivorship in relation to cluth size and fledging success in California Gulls. Behav. Ecol. Sociobiol. 21:217-221.

- REZNICK, D. 1985. Cost of reproduction: An evaluation of the critical evidence. Oikos 44:257-267.
- ROBB, L. A., K. MARTIN, AND S. J. HANNON. 1992. Spring body condition, fecundity and survival in female Willow Ptarmigan. J. Anim. Ecol. 61:215– 223.
- STEARNS, S. C. 1976. Life history tactics: A review of the ideas. Q. Rev. Biol. 51:3-48.
- STEELE, W. K., AND N. T. KLAGES. 1986. Diet of the Blue Petrel at Marion islands. S. Afr. J. Zool. 21: 253-256.
- UTLEY, J. D. 1992. Food supply and allocation of parental effort in Arctic Terns Sterna paradisea. Ardea 80:83-91.
- WARHAM, J. 1990. The petrels. Their ecology and breeding systems. Academic Press, London.
- WEIMERSKIRCH, H. 1990. The influence of age and experience on breeding performance of the Antarctic Fulmar, Fulmarus glacialoides. J. Anim. Ecol. 59:867–875.
- WEIMERSKIRCH, H. 1992. Reproductive effort in longlived birds: Age-specific patterns of condition, reproduction and survival in the Wandering Albatross. Oikos 64:464-473.
- WEIMERSKIRCH, H., O. CHASTEL, L. ACKERMANN, T. CHAURAND, F. CUENOT-CHAILLET, X. HINDERMEYER, AND J. JUDAS. 1993. Alternate long and short foraging trips in pelagic seabirds parents. Anim. Behav. 47:472-476.
- WILLIAMS, G. C. 1966. Natural selection, costs of reproduction and a refinement of Lack's principle. Am. Nat. 100:687–690.
- WOOLLER, R. D., AND J. C. COULSON. 1977. Factors affecting the age at first breeding in the Kittiwake *Rissa tridactyla*. Ibis 119:339–349.
- WOOLLER, R. D., J. S. BRADLEY, I. J. SKIRA, AND D. L. SERVENTY. 1989. Short-tailed Shearwater. Pages 387-404 in Lifetime reproduction in birds (I. Newton, Ed.). Academic Press, London.