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THE INCIDENCE OF NONBREEDING BY ADULT GREAT SKUAS AND PARASITIC JAEGERS FROM FOULA, SHETLAND[1]

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Abstract. Several recent studies of seabirds have found high levels of nonbreeding by experienced adults. By contrast, just 8.9% (range 4–14%) of experienced Great Skuas (*Catharacta skua*) on Foula, Shetland Islands, deferred breeding between 1989–1996. For Parasitic Jaegers (*Stercorarius parasiticus*), a corresponding value of 5.5% (range 3–8%) was found between 1993-1994. Only 3% of the territorial pairs of Parasitic Jaegers, including new recruits, failed to lay eggs. Higher incidence of nonbreeding in Great Skuas was recorded in years when fledging production was low. Loss of mate due to death or divorce was the main direct cause of nonbreeding. Loss of territory also was important for male birds. In Great Skuas, more males missed a breeding season than females, but the same did not apply to Parasitic Jaegers. Very young and very old Great Skuas were more likely to defer breeding than mid-aged birds. Evidence is presented that the decline in breeding frequency of old birds was due to senescence as opposed to increased frequency of mate-changes resulting from a high mortality of old partners.

Key words: age effects, breeding frequency, Catharacta skua, *environmental fluctuation, Great Skuas, Parasitic Jaegers, senescence,* Stercorarius parasiticus.

INTRODUCTION

Seabirds are particularly long-lived, and several studies have reported delayed age of first breeding coupled with intermittent breeding in experienced birds (Furness and Monaghan 1987, Wooller et al. 1992). Nonbreeding can be either forced, resulting from a complete inability to nest because birds lack a breeding site, or a life-history decision whereby individuals avoid paying the costs of reproduction at a stage when costs might be potentially too high. The incidence of nonbreeding at the population level is correlated with environmental conditions, including weather and food availability (Murphy et al. 1991, Chastel et al. 1993, Crawford and Dyer 1995), and high numbers of nonbreeders are often associated with years of poor breeding performance (Coulson 1984, Boekelheide and Ainley 1989, Aebischer and Wanless 1992). The birds most likely to defer breeding tend to be young or less experienced and lower quality individuals (Wooller and Coulson 1977, Wooller et al. 1990, Calladine and Harris 1997). Nonbreeding also can be socially induced, for example resulting from loss of a mate or nest site (Harris and Wanless 1995). In species with long reproductive cycles, breeding performance in the last attempt can influence the probability of nesting in the following season (Chastel 1995). Comparatively little is known about interspecific variation in the incidence of nonbreeding, although such variation should be expected to correlate with other life-history traits.

The existence of potentially large and variable numbers of nonbreeders has important implications for population dynamics. Nonbreeders can provide a buffer against environmental stress by replacing lost breeders during periods of increased adult mortality or after periods with a reduction of breeding success (Klomp and Furness 1992). The relative incidence of nonbreeding has implications for population modeling and monitoring (O'Connell et al. 1997).

The dynamics and behavior of inexperienced Great Skuas (*Catharacta skua*) attending a colony before recruitment have been described (Klomp and Furness 1990, 1992). In this study, we investigated the incidence of nonbreeding by individually-marked adult Great Skuas and Par-

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asitic Jaegers (*Stercorarius parasiticus*) on Foula, Shetland, concentrating on birds that had at least one year of previous breeding experience. Our objectives were to (1) quantify the incidence of nonbreeding and its annual variations, (2) relate the incidence of nonbreeding to various reproductive parameters that might reflect environmental conditions, (3) identify the factors that are directly responsible for nonbreeding, and (4) examine the influence of sex and age on the probability of nonbreeding. Several of these analyses could be performed only for Great Skuas, because the Parasitic Jaeger data set was much less detailed.

METHODS

This study took place on Foula (60°08'N, 2°05'W), a small island (c. 15 km^2) situated 25 km west of Shetland Mainland. Around 2,500 Great Skua and 150 Parasitic Jaeger pairs regularly nest there. We followed the entire island population of Parasitic Jaegers, but Great Skuas were studied in a demarcated area that covered only part of the colony. Skuas and jaegers were trapped and fitted with unique combinations of color-bands allowing individual identification. Many Great Skuas had been banded as chicks and consequently were of known age. Great Skuas were sexed by observation of copulations and courtship feeding. Parasitic Jaegers were sexed by observation, by a hierarchical combination of two discriminant functions based on the prior probabilities of group membership (with an accuracy of over 91% for birds classified), by dissection of birds found dead at the colony, or by association with a partner sexed by one of these methods (Phillips and Furness 1997). Most Great Skuas were sexed only in the later years of the study.

In each year (1989–1996 for Great Skuas and 1992–1994 for Parasitic Jaegers), observers walked regularly around the study area, starting before egg laying, searching for color-banded individuals. Great Skuas rarely move territory and when they do, the distance is short (Catry and Furness 1997, Catry et al. 1997). Searches of other parts of the Great Skua colony failed to locate any of the color-banded adults at other territories. After the birds were located, visits were made daily or on alternate days until eggs were laid. The probability that clutches were initiated but depredated before detection was therefore very low. Furthermore, skuas and jaegers that lose their eggs early in incubation almost always attempt to renest. Territories where eggs were not found were checked regularly until well after the end of the laying period.

For Great Skuas between 1994 and 1996 and for Parasitic Jaegers in all years, records were kept on whether nonbreeding birds were paired or not. Clubs (aggregations of nonbreeders) were checked regularly to search for nonterritorial birds. The study areas were visited again in 1995 and 1996 (for Parasitic Jaegers) and 1997 (Great Skuas), following the end of the intensive study periods, to check for the presence of color-marked individuals that had been alive but absent (nonbreeders) in previous years. Only one Great Skua absent in 1996 was found in 1997. None of the 49 marked Parasitic Jaegers recorded on Foula in both 1992 and 1995 was absent from the colony in both the two intervening years, and just 1 of the 100 marked birds present in 1993 and 1996 was absent in both 1994 and 1995. Similarly, none of the 93 marked Great Skuas present in 1993 and 1996, nor any of the 166 marked birds present in 1994 and 1997, skipped the two intervening seasons. From this we can conclude that the probability that a Great Skua would be absent from the colony for two consecutive seasons was very low, and we are therefore confident that a further search for missing Great Skuas in 1998 would have no effect on our conclusions.

In each year, all Parasitic Jaeger territories on the island were mapped, including those with unmarked birds, and checked regularly for indication of a breeding attempt. For Great Skuas, only territories with color-marked birds were targeted. Breeding statistics, including laying dates, clutch volume of two-egg clutches, and productivity of Great Skuas were collected in a standardized fashion (Hamer et al. 1991). Number of chicks fledged per pair was recorded in six of the eight years.

DATA ANALYSIS

The annual incidence of nonbreeding in Great Skuas was compared with population mean values for breeding statistics in each year. The incidence of nonbreeding also was compared with adult survival rates calculated from resightings of color-banded birds. We tested for the effect of adult age on the probability of nonbreeding using quadratic logistic regressions. When individuals failed to breed for two or more consec-

TABLE 1. Breeding statistics and adult survival rate of Great Skuas on Foula. Sample sizes are in parentheses.

Year	Productivity (chicks per pair)	Mean clutch volume (ml)	Mean laying date (in May)	Survival from previous year
1989	0.21 (61)	165.1 (59)	19.8 (45)	0.80 (61)
1990	No data	164.7 (79)	23.6 (72)	0.91 (76)
1991	0.77 (119)	163.1 (96)	20.8 (118)	0.83 (92)
1992	0.37 (132)	164.6 (154)	19.8 (110)	0.80 (143)
1993	0.82 (135)	168.7 (221)	17.0 (159)	0.86 (160)
1994	0.86 (142)	168.0 (158)	17.0 (170)	0.90 (120)
1995	1.13 (178)	167.1 (195)	18.9 (200)	0.93 (211)
1996	No data	164.6 (213)	16.8 (222)	0.93 (361)

utive years after having bred, we defined this as chronic nonbreeding. We evaluated the influence of adult age on chronic nonbreeding by testing for the effect of age on the probability of nonbreeding for birds that had not nested in the previous season. To avoid pseudoreplication, individual nonbreeders only contributed one case to the data set. The significance of the logistic regressions was assessed by the use of likelihood-ratio tests. Means ± SE are presented.

RESULTS

GREAT SKUAS

Annual breeding statistics and adult survival rates of Great Skuas are indicated in Table 1. During this study, an average of 8.9 ± 1.4% (n = 8 years) of the Great Skuas with previous breeding experience did not breed (Table 2). The annual incidence of nonbreeding was negatively correlated with productivity ($r = -0.94$, $n = 6$, $P < 0.005$, Fig. 1). The correlations between the annual incidence of nonbreeding and clutch volume ($r = -0.63$, $n = 8$, $P = 0.10$) and laying date ($r = 0.61$, $n = 8$, $P = 0.11$) failed to reach statistical significance, but the trends were in the expected directions, given that we would predict *a priori* that a high incidence of nonbreeding would normally be associated with values reflecting poor breeding conditions (i.e., late laying and small eggs). The correlation between the incidence of nonbreeding and adult survival rates from the previous to the current breeding season just failed to reach statistical significance ($r = -0.68$, $n = 8$, $P = 0.06$).

A total of 25 males and 14 females with some breeding experience did not breed in at least one year. This is significantly different from the sex ratio of color-banded birds in the study population where 47% of the individuals sexed were males ($\chi^2_1 = 5.7$, $P < 0.05$). On a year-by-year basis, only in 1995 were males more likely not to breed than females, but samples were generally small (Table 2). During the course of the study, of 63 birds that failed to breed in any one year, 7 (11%) became chronic nonbreeders, i.e., also failed to breed in the following season. Considering birds that missed at least one breeding season, males failed to nest on average 1.4

TABLE 2. Incidence of nonbreeding by Great Skuas with previous breeding experience[a].

Year	Number of birds studied	Number of nonbreeding		Incidence of nonbreeding (%)
		Males	Females	
1989	105	—	—	14
1990	151	—	—	12
1991	80	2	2	9
1992	132	4	4	14
1993	145	1	3	5
1994	82	5	1	6
1995	140	11*	2*	4
1996	185	12	7	7
Mean ± SE				8.9 ± 1.4

[a] Few birds were of known sex in the early years of the study. Between 1994 and 1996 the sum of males and females not breeding is higher than the total number of nonbreeders as calculated from the two first columns; this results from the inclusion of known-sex birds from outside the main study plot that were known to have failed breeding in those years.

* Significantly more males than females, $P < 0.05$ (Binomial test).

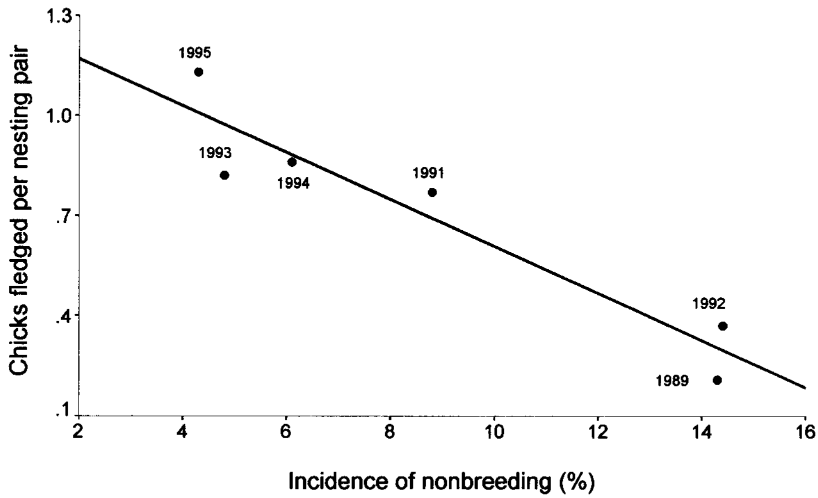

FIGURE 1. The negative relationship between the incidence of nonbreeding in experienced Great Skuas and the number of chicks raised per nesting pair.

times during the study, while the corresponding value for females was 1.3.

Among experienced Great Skuas, very young or very old birds were less likely to breed than mid-aged birds (quadratic logistic regression: $G^2_2 = 6.7$, $n = 1{,}093$, $P < 0.05$, Fig. 2). A similar effect of age was found on the incidence of chronic nonbreeding ($G^2_2 = 11.0$, $n = 63$, $P < 0.01$, Fig. 3). Both quadratic models provided a significantly better fit than linear alternatives.

Most cases (85%) of nonbreeding where the cause could be determined (all in 1994–1996) were associated with loss of partner either due to death, divorce, or loss of territory (Table 3).

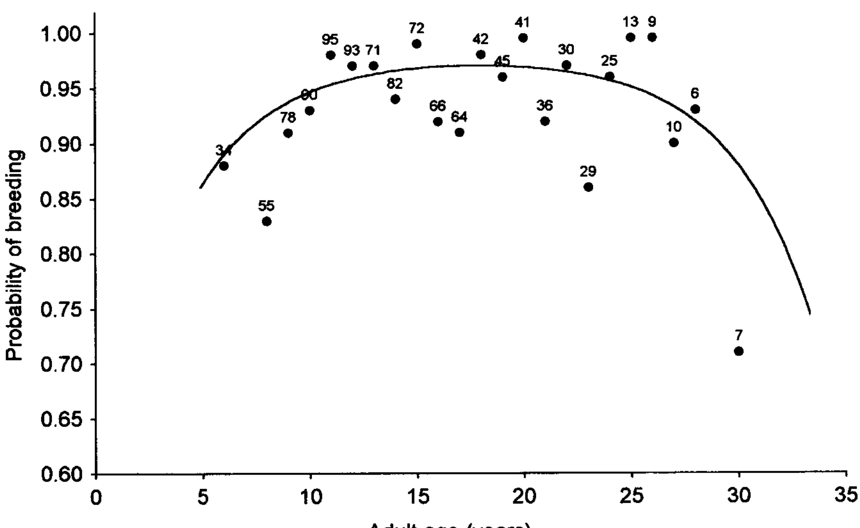

FIGURE 2. The influence of age on the probability of breeding in a particular year by Great Skuas. The line represents the best fit by a quadratic logistic regression. Dots are observed frequencies. Ages between 5 and 7, and 29 and 31 were pooled in one single dot for each group. Analysis was of the ungrouped data. Samples sizes are indicated on the figure. Note that this analysis does not presuppose that the fitted relationship will follow a quadratic equation.

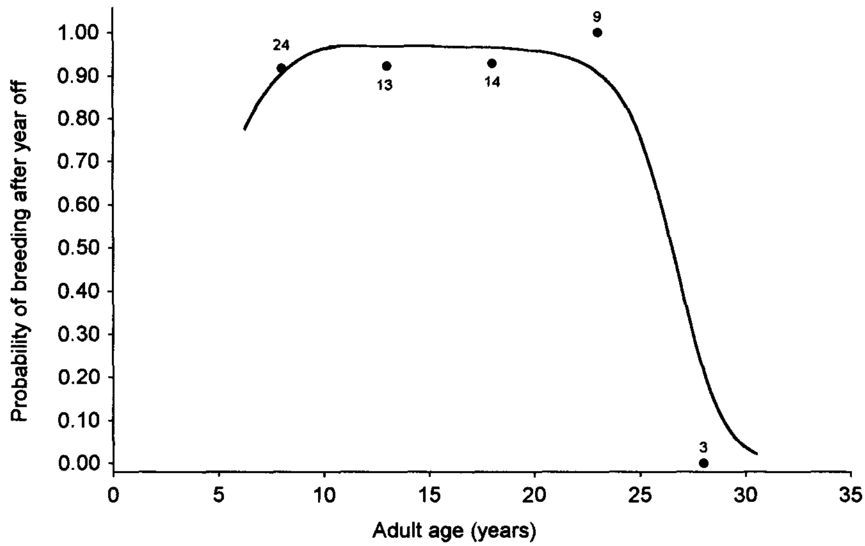

FIGURE 3. The influence of age on the probability of breeding after taking one year off in Great Skuas. Dots represent grouped data for better visual display. Line fitted on ungrouped data. Other details as in Figure 2.

PARASITIC JAEGERS

The incidence of nonbreeding by Parasitic Jaegers with previous breeding experience was 8% in 1993 and 3% in 1994. One male and 4 females out of 66 marked birds, and 4 females out of 130 birds failed to breed in 1993 and 1994, respectively. This sex ratio (eight different females and one male) was not significantly different from the sex ratio of the color-marked population ($\chi^2_1 = 2.5$), although given the small sample, the power of this test was weak. All 25 color-banded pairs that remained united from the previous year laid eggs. Out of nine cases of nonbreeding by birds known to be alive, there were only two occasions when the individual in question was not recorded at the breeding colony. Of the seven birds seen on the island, three held a territory and were paired, whereas the remaining four were only seen in clubs.

Between 1992 and 1994, all Parasitic Jaeger territories on the island were mapped. Eggs were not laid in just 3.1%, 3.4%, and 3.0%, respectively, of the total of 159, 145, and 134 occupied territories present on Foula in 1992, 1993, and 1994, respectively.

TABLE 3. Causes of nonbreeding by experienced Great Skuas on Foula in 1994–1996.

	Males	Females	Total
Loss of mate	11	5	16
Loss of territory	7	0	7
Not seen at colony	0	1	1
Unknown (paired, with territory)	2	1	3

DISCUSSION

Both Parasitic Jaegers and Great Skuas displayed a low incidence of nonbreeding during this study. In 1993 and 1994, only 3% and 8%, respectively, of Parasitic Jaegers with previous breeding experience failed to nest. Excluding years when breeding success was very low in the Great Skua, when nonbreeding reached 14%, less than 10% of experienced adults failed to breed in each season. These figures contrast with some recent studies on gulls, where around a third of experienced adult birds failed to lay eggs in any one season (Pugesek and Diem 1990, Calladine and Harris 1997), even when breeding success in the colony was not particularly low. Between 1992 and 1994, only 3% of the territorial pairs of Parasitic Jaegers on Foula, which would include new recruits, failed to lay eggs. In a similar study with Lesser Black-backed Gulls (*Larus fuscus*), 27% of pairs did not produce eggs, with no evidence that this was a result of food shortage (O'Connell et al. 1997).

Studies with auks (Alcidae) have revealed, in a similar way to skuas and jaegers, very low incidence of nonbreeding among experienced individuals (Ashcroft 1979, Harris and Wanless 1995), but most other seabirds display a higher incidence of nonbreeding, in at least some years (Boekelheide and Ainley 1989, Wooller et al. 1990, Chastel 1995). The factors responsible for large interspecific variation in nonbreeding are poorly understood. A high incidence of nonbreeding is particularly surprising in some species when environmental conditions seem to be favorable and when no simultaneous failure in breeding performance has been reported. In some years, jaegers living in the Arctic tundra, particularly the Long-tailed Jaeger (*Stercorarius longicaudus*) and the Pomarine Jaeger (*Stercorarius pomarinus*), display extensive nonbreeding, but this results from periodic crashes in lemming numbers, which are their main prey during the nesting season (Andersson 1981, Furness 1987).

The low incidence of nonbreeding among adult skuas and jaegers in the present study populations, as well as the very small number of occupied territories where breeding was not attempted, suggests that a correction factor is not necessary either when attempting to census breeding skuas or jaegers in Shetland or in estimating parameters for the purposes of population modeling.

Intraspecific variation in the annual incidence of nonbreeding in seabirds has been linked with environmental conditions. Correlations between the percentage of nonbreeders and various indices of breeding performance have been found in several seabird species (Boekelheide and Ainley 1989, Murphy et al. 1991, Chastel et al. 1993, this study). This suggests that factors such as food availability or weather might be affecting both nonbreeding and breeding birds. There is evidence for links between nonbreeding and fish stocks or weather patterns in a wide variety of seabirds, from polar regions to the tropics (Aebischer and Wanless 1992, Chastel et al. 1993, Crawford and Dyer 1995).

Increases in nonbreeding frequency in response to unfavorable environmental circumstances could result from an inability of some individuals to reach a high enough body condition prior to egg laying, by a prudent restraint by birds that are unable to make an investment in a potentially difficult breeding attempt without compromising survival and future breeding prospects, or both. An individual might have enough energy reserves to lay eggs but still refrain from nesting if body condition was below a threshold value which would indicate a minimum level of food availability. Of course, environmental conditions at the time of egg laying might not be accurate predictors of conditions later on. This might explain why so many Great Skuas nested in years when breeding success was very low. For example, in 1989, during the period of sandeel (Ammodytidae) scarcity in Shetland waters which lasted throughout the mid to late 1980s and 1990, the mean number of Great Skua chicks fledged per pair that laid eggs was 0.21, but 86% of the birds still attempted to nest (Table 1 and 2). Given that 4 to 6% of experienced Great Skua adults did not nest even in good years, less than 10% of the breeding population responded to the unusually unfavorable conditions by not laying. In a previous study applying a simple modeling approach to changes in numbers of Parasitic Jaegers on Foula, there was evidence that in the 1980s, levels of nonbreeding were slightly higher than the 3-8% we recorded during the 1990s, with at least 9–12% of experienced birds apparently absent from the colony in some years (Phillips et al. 1996). Again, this is still a comparatively small proportion of the population taking years off, even though the productivity of birds that did attempt to breed was very poor, with just 0.09–0.21 chicks fledged per pair from 1987–1990 (Phillips et al. 1996).

Annual survival rates of adult Great Skuas on Foula in the late 1980s were low, not only in comparison with other years, but also with other large *Catharacta* skuas (Ainley et al. 1990, Hamer et al. 1991). The correlation between the incidence of nonbreeding in Great Skuas and overwinter survival could be a consequence of this, as social factors, particularly mate change, have a strong influence on nonbreeding (see below), and the increased mortality would have forced more birds to find new partners during the poor years. In conclusion, the evidence suggests that comparatively few Great Skuas deferred breeding as a direct response to environmental stress. Although nonbreeding might represent a strategy in some species to maximize residual reproductive value when conditions are poor (Schaffer 1974), it seems likely that the unpredictability of the marine environment prevents this strategy being finely tuned in birds like Great Skuas.

In general, more experienced male than female Great Skuas failed to breed, suggesting that there might be a slight excess of experienced males in this population. The same does not apply to Parasitic Jaegers where no significant difference between sexes was found. Between 1994 and 1996, which were years with a low incidence of nonbreeding in Great Skuas, careful behavioral observations allowed us to determine the causes of nonbreeding, which in most cases (59%) appeared to be mate loss. One quarter of the Great Skuas that lost their mates failed to breed in the same season, but all the pairs that remained united laid eggs (Catry et al. 1997). This is similar to the situation in South Polar Skuas *Catharacta maccormicki* (Ainley et al. 1990). New mates are probably difficult to find, and experienced birds in new partnerships lay significantly later in the season than pairs that remain together (Catry et al. 1997). If a new partnership takes too long to form, breeding may simply be postponed until the following season. The second most common cause of nonbreeding in Great Skuas was loss of territory (26% of cases). After losing a territory, some males failed to establish a new one for several years. One particular male was without a territory for at least four consecutive years, not because of overcrowding (new territories were being established by other birds in empty areas in the same period) but because in each year this bird attempted to recover its former territory. In conclusion, most cases of nonbreeding were socially induced, and not simply a result of birds "deciding" to reduce their reproductive investment (see also Harris and Wanless 1995).

Nonbreeding was more prevalent among very young (but experienced) or very old Great Skuas. One potential explanation for this pattern is that these age classes have higher mortality rates, in which case mate loss is expected to be more frequent. In addition, divorce rates might be greater in young birds, which could also result in a higher incidence of nonbreeding. However, although survival prospects are poorer for the oldest Great Skuas (Catry et al., unpubl. data), we find these explanations unlikely for several reasons. Great Skuas display a poor correlation of ages within partnerships ($r = 0.28$) and there is no tendency for younger birds to have higher divorce rates (Catry et al. 1997). More importantly, very young and particularly very old birds had a greater probability of deferring breeding after one year off, in comparison to mid-aged birds in similar circumstances. This result can only be explained by some form of senescence. It is possible that very young and old birds have greater difficulty in holding territories or attracting new mates. A higher incidence of nonbreeding among younger or less experienced individuals has been described for other species (Wooller and Coulson 1977, Wooller et al. 1990). Weimerskirch (1992) also reported an increase between nesting intervals in very old Wandering Albatrosses (*Diomedea exulans*), but this was attributed to a higher probability of loss of mate among old individuals. Senescence can be difficult to demonstrate in wild birds, particularly in long-lived species (Newton and Rothery 1997). We believe that our results clearly show that very old Great Skuas experience increasing difficulties in meeting all the conditions necessary to breed. At an anecdotal level, however, it must be said that the oldest living Great Skua ever known, a female aged 34 years, was incubating a clutch in the spring of 1997.

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