Ecology, 86(4), 2005, pp. 1047–1056

FOOD AVAILABILITY AFFECTS ADULT SURVIVAL AS WELL AS BREEDING SUCCESS OF PARASITIC JAEGERS

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Abstract. Long-lived species are expected to reduce their current reproductive effort in adverse conditions in order not to jeopardize their future reproduction. Parasitic Jaegers (*Stercorarius parasiticus*) breeding in Shetland, United Kingdom, have declined substantially in numbers over the last 15 years, although the causes of this decline remain unclear. By carrying out a supplementary feeding experiment during the chick-rearing period, we tested the hypothesis that food availability has contributed to this decline. Data were collected on adult territory attendance, chick growth rates, and breeding success during the experimental season, and adult return rates, body condition, and laying dates during the following season. Differences in carbon and nitrogen isotope ratios in the natural and supplementary food, analyzed in the chicks' feathers, showed that chicks received one-fifth of their protein requirements from the supplementary food, but this amount varied between broods. Compared with controls, supplemented pairs showed higher attendance on the territory, improved breeding success, and higher return rate. This emphasizes that adult return rate is more sensitive to food availability than has been assumed previously. Control birds may have maintained too high a current reproductive effort at the expense of future reproduction, perhaps due to the unpredictability of their main food source, sandeels, which seemed abundant early in the season but scarce during chick rearing. This study suggests that the consequences of poor food availability are shared between offspring and parents in this species.

Key words: activity budgets; breeding parameters; cost of reproduction; food availability; future reproductive potential; life history; Parasitic Jaeger; Stercorarius parasiticus; *supplementary feeding; survival.*

INTRODUCTION

Organisms have to decide how to allocate their resources between effort into current offspring and their future reproductive output (Roff 1992, Stearns 1992). Lifetime reproductive success primarily depends on survival rather than seasonal breeding success (Clutton-Brock 1988). Survival and longevity of parents are often thought to be inversely related to reproductive effort (Martin 1987, Boutin 1990, Newton 1998). Therefore, if the current breeding effort leads to a reduction in survival, then the optimal breeding effort is less than the effort that would maximize the number of young produced in that season (Williams 1966). Much of the research on trade-offs between current breeding effort and future reproductive output has been conducted on short-lived species (Linden and Møller 1989). In short-lived species, the probability of survival is often so low that an increased investment in current reproduction, at the expense of parental survival, would be expected (Charlesworth 1980). In contrast, long-lived organisms should only increase their current breeding effort if the gains from this outweigh the costs of possible decreased future fitness (Charlesworth 1980, Drent and Daan 1980, Stearns 1992, Erikstad et al. 1998). In order to better understand life history trade-offs, a wide range of species from different areas of the life history spectrum need to be studied, in particular more long-lived species.

The trade-off between breeding effort and future reproductive output also will be influenced by ecological factors. In long-lived birds, such as seabirds and geese, even a small reduction in adult survival greatly reduces lifetime reproductive success; therefore, it has been suggested that their breeding effort is a fixed strategy independent of offspring need (Ricklefs 1992, Sæther et al. 1993, Hamer and Hill 1994). However, recent studies suggest that long-lived birds alter their reproductive effort in response to experimental manipulation of breeding effort, even at the expense of their own survival (Reid 1987, Johnsen et al. 1994, Jacobsen et al. 1995, Tombre and Erikstad 1996, Erikstad et al. 1997). An important ecological factor that influences current breeding is food availability (Martin 1987, Boutin 1990, Stelzer 2001). The optimal response to a change in food availability may differ between species and different life history parameters are expected to be affected by increasing levels of food stress (Cairns

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Manuscript received 22 June 2004; revised 21 September 2004; accepted 24 September 2004. Corresponding Editor: T. D. Williams.

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1987). In a long-lived seabird, a reduction in food availability is expected predominantly to affect current breeding success, whereas future fitness is expected to be affected only at extremely low levels of food (Cairns 1987, Erikstad et al. 1998, Weimerskich et al. 2001). However, the effects of decreasing food availability on current breeding success may be masked by changes in the seabirds' behavior, such as increasing their foraging effort, to buffer against environmental perturbations (Cairns 1987, Uttley et al. 1994, Gill et al. 2002). Hence, adult behaviors, such as territory attendance and foraging activity, are expected to be the most sensitive parameters to food limitation (Cairns 1987). To examine how the balance between current and future reproduction is resolved in the face of food limitation, it is therefore important to study the whole range of life history parameters.

Food availability to top predators in marine environments, such as abundance, distribution, age structure, and composition of prey species, is dependent on oceanographic conditions and fisheries. Oceanographic conditions can affect food availability, influencing breeding success, recruitment, and adult survival (Romero and Wikelski 2001, Barbraud and Weimerskirch 2003, Durant et al. 2003). Fisheries can affect prey abundance for top predators both directly and indirectly, through altering the structure of marine communities (Tasker et al. 2000). In the past, fisheries made additional food available by decreasing the abundance of large predatory fish and by discarding large amounts of fish and offal, and marine top predators benefited from this (Newton 1998, Furness 2002). However, recent collapses of fish stocks due to overexploitation by fishing have markedly reduced food supplies and affected populations of marine mammals and seabirds (Yodzis 2001).

Food availability, and therefore food limitation, is often difficult to determine. Here we want to address experimentally the role of food availability in the breeding behavior and key life history traits in a declining seabird, the Parasitic Jaeger *Stercorarius parasiticus*. We manipulated current breeding effort by providing supplementary food to nests during the chick-rearing period. This allowed us to both gather a better understanding of life history trade-offs in long-lived birds and to determine the likely implications of potential anthropogenic perturbation of the marine ecosystem. Parasitic Jaegers in Shetland have declined by 42% over the last 15 years (Furness and Ratcliffe 2004). Although some Arctic breeding birds carry considerable nutrient reserves to the breeding grounds from lower latitudes, Parasitic Jaegers arrive in Shetland several weeks before they lay eggs, and courtship feeding at the colony is important in determining laying date and egg size (Phillips and Furness 1998). Thus Parasitic Jaegers in Shetland appear to depend on local food resources for breeding decisions early in the season. Sandeels *Ammodytes marinus* are the main prey of many seabird species in Shetland during the breeding season, and Parasitic Jaegers feed predominantly by stealing sandeels from Arctic Terns *Sterna paradisaea*, Black-legged Kittiwakes *Rissa tridactyla*, Atlantic Puffins *Fratercula arctica*, and Common Murres *Uria aalge*. During the 1980s, the sandeel stock around Shetland declined dramatically and was a likely cause of widespread breeding failure of many of these seabird species, probably contributing to the population decline in Parasitic Jaegers (Bailey et al. 1991, Phillips et al. 1996, Furness and Tasker 2000). Although sandeels are the target of the largest single-species fishery in the North Sea, it is far from clear what causes these dramatic declines (Furness 2002).

We examined evidence that food shortage contributed to the decline of the Parasitic Jaeger by looking at the effect of supplementary feeding of breeding adults on several life-history parameters. Stable isotope analysis of chick feathers was used to establish whether supplementary food was being fed to the chicks. We predicted that the life history traits would be affected sequentially by limited food availability, depending on the level of food shortage (Cairns 1987). We predicted that supplemented birds would show increased parental attendance, breeding success, and possibly survival in comparison to control birds.

METHODS

This study took place during the 2001 and 2002 breeding seasons on Foula (60°08′ N, 2°05′ W), a small island (~15 km^2) situated 25 km west of the Shetland mainland, United Kingdom. The population of Parasitic Jaegers nesting on Foula is one of the most important British populations. It has declined at a rate similar to that of the total Shetland population (Furness and Ratcliffe 2004). In 2001 there were 116 apparently occupied territories on Foula, with approximately two-thirds of the individuals being color banded. Parasitic Jaeger nests are shallow scrapes in the vegetation and contain one or two olive-brown eggs. Nests were located by observing the adults' behavior and were marked. Laying dates were determined by visiting territories daily early in the season. Parasitic Jaegers usually lay two eggs, with two days between each egg (Furness 1987). Nests were visited on a daily basis from the first likely hatching date. For nests found during incubation (17%, $n = 116$ nests), hatching dates were used to estimate laying dates, assuming an average incubation period (25 days for the nests with known laying dates).

Supplementary feeding experiment

A supplementary feeding experiment was carried out during the 2001 breeding season (May–July) and involved 53 pairs of Parasitic Jaegers in the main areas of the colony: 25 control pairs and 28 supplemented pairs. The pairs occupied territories surrounding their nests, which they vigorously defended against predators and conspecifics (Furness 1987). Feeding was carried out during late morning and early afternoon, the times when both parents were likely to be present on the territory to eat the food and defend it from other Parasitic Jaegers. This meant that overall there was very little chance of food stealing by control birds during this experiment (S. E. Davis, personal observation). The timing of feeding was varied slightly from day to day to decrease the likelihood of the birds learning to return to their territory to be fed, thereby increasing the attendance of the supplemented birds. The supplemented pairs were fed 100 g of tinned cat food (meat and animal derivatives, cereals, and minerals; Co-op Catfood, County Longford, Ireland) and one raw hen's egg daily. The energetic content of 100 g of cat food is 275 kJ (Kalmbach 2002) and the raw hens' eggs used in this experiment contained ~350 kJ per egg (information provided by supplier). The raw hen's egg was initially used to train the Parasitic Jaegers to take the supplementary food, and all of the supplemented birds took the supplementary food within 1–3 days. The feeding started on the first day that their eggs started to crack (usually two days before hatching) in order to give the adults a day or two to learn to take the food before having to start to provision their offspring. Supplementary feeding was stopped when chicks were 20 days old and had reached a mass close to their fledging body mass (Phillips 1995), when foraging demand on the parents should decrease (Moe et al. 2002). The territories were assigned to control or supplemented groups by alternating which group a territory was assigned to as the eggs hatched, so that laying dates would be similar in both groups.

To estimate the proportion of protein incorporated into chicks that was derived from supplementary food, feather samples were taken from 14 control and 20 supplemented 20-day-old chicks for stable isotope analysis. A sample of the supplementary food was also analyzed. Using this and the stable isotope signature of their natural food, sandeels (Bearhop et al. 1999*b*), we estimated the proportion of the chicks' protein requirements that had been made up of the supplemental food, using a two-source mixing model (Ben David et al. 1997). Feathers were ground to a homogeneous powder at liquid nitrogen temperature in a grinding mill (Spex Certiprep 6570, Glen Creston Ltd., Stanmore, Middlesex, UK) and ~0.7 mg of sample was sealed into a tin capsule for later analysis. Stable isotope analyses were carried out at the Scottish Universities Research and Reactor Centre by using continuous-flow isotope ratio mass spectrometry (CF-IRMS) using a C/N/S analyzer (Carlo Erba, Milan, Italy) coupled to a Finnigan Tracer Matt mass spectrometer (Finnigan, Bremen, Germany). Isotope ratios are expressed in the standard δ notation in parts per thousand (‰) according to the following equation: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is ^{15}N or ^{13}C and R is the corresponding ratio ^{15}N/^{14}N or ^{13}C/^{12}C. R_{standard} is PDB (Pee Dee Belemnite) for ^{13}C and atmospheric nitrogen for ^{15}N. Analytical precision was ±0.1 ppm for δ^{15}N and δ^{13}C. The δ^{15}N and δ^{13}C values for the control chicks' feathers represent the signature of Parasitic Jaegers assumed to be feeding exclusively on their natural diet.

Measurements of breeding variables

During the first 20 days of chick rearing, we recorded parental attendance using one spot check per day from outside each territory. We recorded the number of adults and also which adult(s) were present on the territory during these daily checks, which were made between 09:00 and 19:00 hours BST (British Standard Time). These spot checks provide an accurate measure of time spent foraging by the adults (Caldow and Furness 2000).

Successfully fledged chicks from nests included in the experiment were measured 7 ± 1.89 times (mean ± 1 SE; $n = 38$ chicks), with the first measurement being within a day of hatching and the last at 18–22 days. Numbers of measurements varied between chicks because their cryptic coloration and behavior make them difficult to find, and because chicks were not measured if it was raining. A pair was thought to have failed if there was no aggressive behavior by the parents and no chick had been found on the territory for five consecutive days. At 20 days of age, the chicks approached their asymptotic mass (Phillips 1995), now referred to as fledging mass, and handling after this point could increase the risk of premature fledging. At each capture, chick body mass was measured to the nearest 5 g using a 600-g Pesola balance (Pesola, Baar, Switzerland). Tarsus length was measured to the nearest 0.1 mm using callipers. Wing length was measured to the nearest 1 mm by the maximum chord method using a 30-cm wing ruler. Growth rates were calculated, only for chicks that survived until 20 days, as the slope of the linear regression of the chick measurements against age during the linear phase of growth between days 5 and 18. The final (age 18–22 days) body mass, tarsus length, and wing length measurements of the control and supplemented groups were also compared. We measured both survival of chicks up to fledging (day 20) and postfledging survival up to until the offspring left the colony (day 35–40).

In 2001 we caught 34 control birds and 32 supplemented adults by placing either a walk-in trap or a camouflaged, radio-controlled spring trap over the nest during incubation. Tarsus length and wing length measurements were taken as just described. Head plus bill was measured to the nearest 0.1 mm from the base of the skull to the bill tip using callipers. The keel length was measured to the nearest 0.1 mm using callipers (see Bolton et al. 1991). All individuals were measured by the same researcher (S. E. Davis). A subsample of birds was sexed (17 control pairs and 17 supplemented pairs) by behavioral observations of copulatory positions and courtship feeding, molecular analysis of blood samples (Griffiths et al. 1998), or by partnership with an adult sexed by one of these methods. These biometrics were used in principal component analyses to obtain an index of body size for each bird, but separate analyses were carried out for males and females. Adults were weighed and protein stores were estimated using a pectoral muscle index (Bolton et al. 1991). Pectoral muscle profiles were obtained by molding solder wire around the pectoral muscles perpendicular to the keel 3 cm from its anterior end and using method (E) from Bolton et al. (1991) to measure the area under the profile. The area under the profile provides a good measure of protein stores in Lesser Black-backed Gulls *Larus fuscus* (Bolton et al. 1991) and in Great Skuas *Catharacta skua* (Kalmbach 2002).

In the following year (2002), the colony was visited daily and returning birds and their laying dates were recorded. All but one breeding pair ($n = 84$ pairs) were checked for bands. Fifteen controls and 15 supplemented birds from 2001 were caught again during incubation to compare their condition one year after the manipulation.

Statistical analysis

Data were checked for the assumptions of parametric tests and, when necessary, appropriate nonparametric statistics were used. The daily attendance data were compared between supplemented and control territories from days 1 through 20 using a repeated-measures ANOVA and the Satterthwaite correction (PROC MIXED in SAS Version 8.2; SAS Institute 2001). ANCOVA was used to test for (1) the effects of supplementary feeding and hatching date on chick growth, controlled for chick age, and (2) the effects of supplementary feeding on parental body condition, controlled for body size. Clutch size and brood size were compared between control and supplemented pairs using a χ^2 test. Binomial regression with brood size at hatching as denominator and a logit link function was used to analyze the effects of the feeding treatment and season on breeding success. Logistic regression was used to analyze the effects of feeding treatment and fledging mass on postfledging survival. In most cases (91%, $n = 35$) only one chick survived, and chick is the appropriate unit of analysis. In the three cases in which two chicks survived to fledging (all for supplemented pairs), average values for measurements of the two chicks were used. Throughout, values are reported as mean ± 1 SE.

RESULTS

There was no difference in hatching date ($t_{51} = 1.17$, $P = 0.27$), clutch size ($\chi^2_1 = 2.21$, $P = 0.14$), or brood size at hatching ($\chi^2_1 = 0.01$, $P = 0.93$) between control and supplemented pairs. The protein condition of the control and supplemented adults during incubation (i.e., before the experiment started) did not differ: for females, $F_{1,23} = 0.17$, $P = 0.68$; for males, $F_{1,19} = 3.00$, $P = 0.10$ (control males tended to have more protein stores than the supplemented males). Similarly, there was no difference in the body mass adjusted for size: for females, $F_{1,23} = 0.05$, $P = 0.83$; for males, $F_{1,19} = 0.71$, $P = 0.41$.

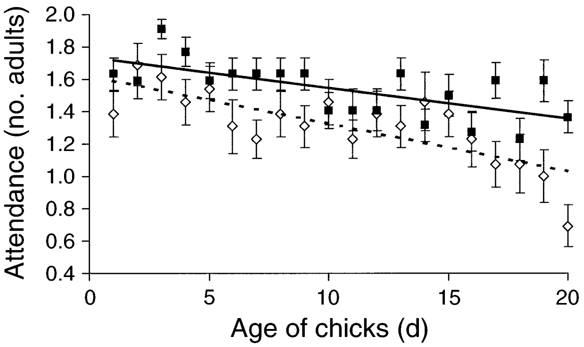

FIG. 1. Attendance (mean ± 1 SE) decreased over the 20-day chick-rearing period for supplemented (closed symbols and solid line) and control (open symbols and dashed line) territories. Attendance was always lower on control territories. The lines represent regression lines for each group to show the observed decline in attendance with chick age. The sample sizes are 13 control and 22 supplemented pairs, because only pairs that raised chicks through to 20 days were included in the attendance analysis.

Attendance

In successful nests, the daily attendance declined over the 20 days of chick rearing in both the control and supplemented groups (Fig. 1; repeated-measures ANOVA $F_{1,\,193} = 39.35$, $P < 0.0001$). Daily attendance differed between control (1.31 ± 0.07 birds present on the territory at the spot check; $n = 13$ nests) and supplemented territories (1.54 ± 0.05 birds; $n = 22$ nests; $F_{1,\,28.2} = 7.44$, $P = 0.011$). The interaction between chick age and feeding treatment was not significant ($F_{1,\,192} = 0.55$, $P = 0.46$).

Supplemented pairs tended to leave the territory unattended less often (1.6 ± 1.0%; $n = 13$) compared to the control birds (4.6 ± 1.4%; $n = 22$, $t_{33} = 1.82$, $P = 0.08$), whereas both parents were more often present (55.4 ± 4.4%, $n = 13$ vs. 35.8 ± 6.0%, $n = 22$; $t_{33} = 2.69$, $P = 0.01$). The higher attendance on supplemented territories was due to significantly higher attendance by supplemented females (86.0 ± 3.4%, $n = 7$) than by control females (69.3 ± 7.5%, $n = 15$; $t_{20} = 2.36$, $P = 0.03$). There was no difference in male attendance (68.0 ± 4.8%, $n = 7$ vs. 68.6 ± 7.7%, $n = 15$; $t_{20} = 0.65$, $P = 0.95$). Sample sizes are reduced in this analysis, as not all of the birds were of known sex.

Breeding success

Fledging success declined over the season and was higher in supplemented pairs compared to control pairs (binomial regression; for hatching date, $\chi^2_1 = 7.15$, $P = 0.01$; for supplementary feeding, $\chi^2_1 = 4.46$, $P = 0.04$; for the interaction, $\chi^2_1 = 0.002$, $P = 0.96$; Fig. 2). Supplemented pairs raised 0.89 ± 0.11 chicks (*n*

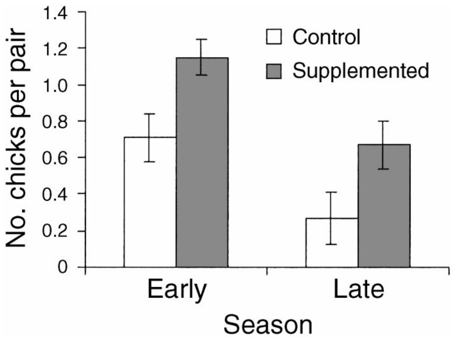

FIG. 2. Number of chicks reared to 20 days by control and supplemented parents, showing the decline of rearing success over the season. The early season is 7–17 June (control, $n = 14$; supplemented, $n = 13$); the late season is 18–24 June (control, $n = 11$; supplemented, $n = 15$). Grouping of early- and late-season nests is only done to clarify presentation.

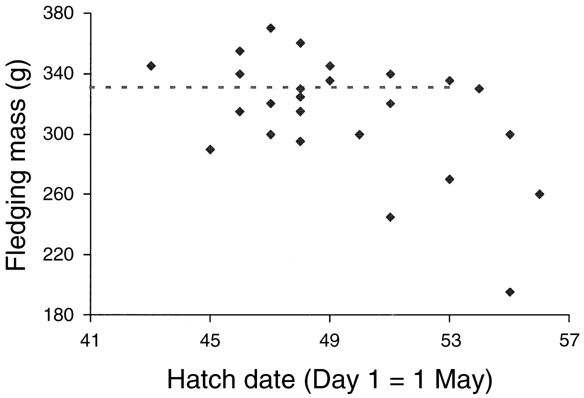

FIG. 3. Fledging mass in relation to hatching date of control chicks (dashed line; $F_{1,11} = 3.28$, $P = 0.10$) and supplemented chicks (closed symbols; $F_{1,23} = 8.04$, $P = 0.01$). No control chicks that hatched after 22 July (day 53) survived to day 20, whereas some supplemented chicks survived to day 20 but at a very poor mass, causing the interaction between supplementary feeding and hatching date in Table 1.

= 28 pairs), and control pairs raised 0.52 ± 0.10 chicks ($n = 25$). Three supplemented pairs, but no control pairs, managed to fledge both chicks.

There was no effect of supplementary feeding or hatching date on chick growth rate (Table 1). However, there was a significant interaction between supplementary feeding and hatching date on fledging mass and size. This interaction is caused by the fact that no control chicks that hatched after 22 July fledged, whereas supplemented chicks that hatched after this date survived, but achieved low fledging mass (Fig. 3) and tarsus and wing length.

Postfledging survival, after supplementary feeding had ceased, increased with increasing fledging mass, but was not significantly different between feeding treatments (logistic regression analysis, $n = 38$ chicks; for supplementary feeding, $\chi^2_1 = 0.46$, $P = 0.50$; for fledging mass, $\chi^2_1 = 9.59$, $P = 0.002$). Unsuccessful chicks only weighed 313.8 ± 6.3 g ($n = 32$) at fledging, whereas successful chicks weighed 350 ± 7.4 g ($n = 6$).

Stable isotope analysis

Comparing stable isotope signatures of control chicks' feathers and natural diet (sandeels), fractionation factors from food to feather can be estimated as 4‰ for $\delta^{15}N$ and 1.4‰ for $\delta^{13}C$ (Table 2), similar to fractionation factors found in other studies (Ben David et al. 1997, Bearhop et al. 1999*b*). There was a significant difference in the stable isotope signatures between control and supplemented chicks (for $\delta^{15}N$, $t_{32} = 7.33$, $P < 0.001$; for $\delta^{13}C$, $t_{32} = 7.24$, $P < 0.001$). From a two-source mixing model we can estimate that, in supplemented chicks, 20.3 ± 1.8% (range 5–40%) of the assimilated protein came from supplementary food. Chicks with a higher percentage of assimilated protein originating from the supplementary food grew more slowly (Fig. 4).

TABLE 1. Growth rates and fledging size compared between control chicks ($n = 13$) and supplemented chicks ($n = 25$) using ANCOVA tests to include effects of hatching date and chick age (in the case of fledging size).

Measurement	Supplementary feeding			Hatching date			Interaction (supp. feeding × hatch date)			Age		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
Growth rate ($n = 34$)												
Mass	2.89	1, 32	0.10	0.69	1, 31	0.41	0.70	1, 30	0.41		…	
Tarsus	0.36	1, 32	0.55	0.26	1, 31	0.61	0.10	1, 30	0.75		…	
Wing	4.52	1, 30	0.04	1.41	1, 30	0.24	4.38	1, 30	0.05		…	
Fledging ($n = 38$)												
Mass	**8.28**	**1, 34**	**0.01**	0.51	1, 34	0.48	**8.65**	**1, 34**	**0.01**	1.16	1, 33	0.29
Tarsus	**12.11**	**1, 34**	**0.001**	0.09	1, 34	0.76	**12.35**	**1, 34**	**0.001**	0.12	1, 33	0.73
Wing	**10.19**	**1, 33**	**0.003**	2.19	1, 33	0.15	**9.82**	**1, 33**	**0.004**	**17.82**	**1, 33**	**<0.001**

Notes: There were insufficient numbers of observations for four chicks (three supplemented and one control) to allow calculation of growth rates. The Bonferroni method was used because each chick had mass, tarsus, and wing measurements taken. Thus the data are not completely independent, leading to a significance level of $P = 0.017$. Statistically significant effects are shown in boldface type.

TABLE 2. The δ^{15}N and δ^{13}C values for the isotopic signatures of the Parasitic Jaeger chicks' diet and feathers: (a) values from Bearhop et al. (1999*b*); (b) values from this study.

Isotopic source and diet	δ^{15}N	δ^{13}C
Diet		
Natural diet	7.9 (a)	−17.5 (a)
Supplementary food	3.3 (b)	−25.8 (b)
Feathers		
Control (n = 14)	11.9 ± 0.4	−16.1 ± 0.5
Supplemented (n = 20)	11.0 ± 0.3	−17.8 ± 0.8

Note: Fractionation factors were calculated as the increase in δ^{15}N and δ^{13}C values between the natural diet signatures and the control chicks' feather signatures. Control and supplemented values are means ± 1 SE.

Between-year effects on adults

Supplemented adults showed a significantly higher local return rate in the next season (2002) than did control birds (χ^2_1 = 4.66, P = 0.03; Fig. 5). In 2002 there was no significant difference in laying dates (t_{37} = 0.53, P = 0.60) and body condition during incubation (Table 3) between pairs that were control vs. supplemented in the previous year.

DISCUSSION

Breeding Parasitic Jaegers were supplementary fed during the chick-rearing period and at least some of the supplementary food was passed on to the chicks. The food availability affected adult behavior, fledgling success, and local return rate. Parental territory attendance was affected by food availability, as control parents adjusted their activity budgets and spent increased time away from the territory compared to supplemented parents. Rearing success of supplemented pairs was also improved compared to control pairs, whereas chick growth was not improved by higher levels of food availability. Improved food availability also increased the local return rate of breeding birds in the following year. In this study we only used birds that had reached the chick-rearing stage; these were possibly among the higher quality birds, and differences could be even larger among lower quality birds. Cairns (1987) predicted that in long-lived species, such as Parasitic Jaegers, adult survival would only be affected in times of extreme food shortage. The results therefore suggest that our study population was under considerable food stress, and food limitation affected both current and future reproduction.

Current reproductive effort

Territory attendance in 2001 was lower than in any previous years when attendance was recorded, including years with poor sandeel recruitment (Phillips et al. 1996). Territory attendance was significantly higher for supplemented pairs than control pairs. Other supplementary feeding studies in seabirds only found a difference in territory attendance during the late chick-rearing period, when food demand is highest (Hamer and Hill 1994, Bukacinski et al. 1998, Gill et al. 2002). However, supplemented Parasitic Jaegers had higher attendance throughout chick rearing. In 2001, chicks on control territories, tended to be left unattended more frequently than chicks on supplemented territories and chicks in previous years were virtually never left unattended (Phillips et al. 1996). These results suggest that adult behavior is affected by food availability and that control birds suffered from extreme food stress in the 2001 breeding season. Adult attendance decreased with chick age, which may be due to the increasing food requirements of chicks as they grow, but also may be due to a seasonal decline in food abundance (Phillips et al. 1996). The similar decline in territory attendance with increasing chick age in supplemented pairs compared to control pairs suggests that their higher attendance was not the consequence of their increasing anticipation of being fed on the territory.

The higher attendance of the supplemented pairs was due to significantly higher attendance by females, whereas the attendance by males remained the same.

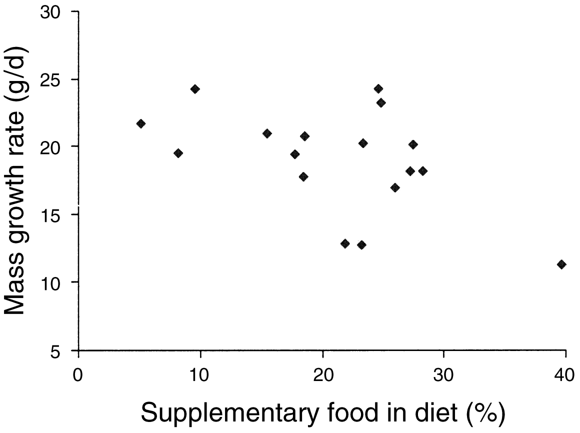

FIG. 4. Mass linear growth rate of the supplemented chicks negatively correlates with the percentage of supplementary food in the diet (r_{15} = −0.51, P = 0.038; sufficient growth data were only available for 17 supplemented chicks).

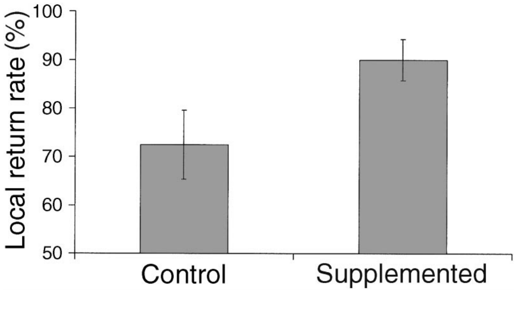

FIG. 5. Percentage of color-banded control (n = 40) and supplemented (n = 50) adults returning to Foula in the year following the supplementary feeding experiment (mean ± 1 SE).

TABLE 3. Protein stores and body mass compared between birds that were controls and supplemented in the previous season using ANCOVA tests to include body size.

	Female (n = 7 controls, 11 supplemented)						Male (n = 6 controls, 4 supplemented)					
	Feeding treatment			Body size			Feeding treatment			Body size		
Measurement	F	df	P	F	df	P	F	df	P	F	df	P
Protein stores	2.25	1, 15	0.154	7.29	1, 16	0.016	0.15	1, 8	0.706	0.001	1, 7	0.979
Mass	0.43	1, 15	0.520	11.98	1, 16	0.003	0.003	1, 7	0.957	4.58	1, 8	0.065

Note: Number of days since clutch completion was also entered as a covariate, but it had no significant effect.

In Parasitic Jaegers, males do most of the foraging, while females do most of the brooding and guarding of the chicks (Furness 1987). Several other studies on seabirds also have found that females responded to increased breeding effort, but males did not (Jacobsen et al. 1995, Hamer et al. 1998, Velando and Alonso-Alvarez 2003). This suggests that, in these species, the males have reached the maximum of their potential buffering capabilities or are unwilling to pay the costs of increased effort. Females might have a greater buffering capacity and can increase their breeding effort when necessary (Velando and Alonso-Alvarez 2003).

Fledging success for both control and supplemented groups declined over the season. This could be due to a decline in the parents' ability to raise chicks with season (Hatchwell 1991, Phillips and Furness 1998). Fledging success was significantly higher in supplemented pairs than in control pairs, as found in other supplementary feeding studies during the chick stage (Bukacinski et al. 1998, Wernham and Bryant 1998, Gill et al. 2002; but see Hamer and Hill 1994). A natural experiment with Black-legged Kittiwakes, comparing years of high and low food availability, also found that breeding success was significantly higher when food availability was high (Kitaysky et al. 2000). The higher chick survival on supplemented territories could be due to a higher rate of food provisioning such that the chicks are less likely to starve, but also could be due to increased attendance reducing predation of chicks, mainly by Great Skuas. It is very difficult to ascertain the cause of chick mortality. Because some chicks from both treatment groups were found to have died of starvation, and even those that survived to day 20 were often found with empty crops, at least some chicks died due to inadequate food provisioning. Low fledging mass had negative consequences on postfledging survival, with the heaviest fledglings having the highest chances of surviving until departure from the breeding colony, independent of the feeding treatment before fledging. A similar positive correlation between prefledging growth and postfledging survival was found in Great Skuas (Hamer et al. 1991). Postfledging survival was very low in this study (15.8%, $n = 38$ chicks); predation by Great Skuas was the main cause of postfledging mortality when parents could no longer guard their young effectively.

Experimental studies also have shown that seabird chick growth can be improved by supplementary feeding (Hamer and Hill 1994, Bucacinski et al. 1998, Wernham and Bryant 1998, Gill et al. 2002). However, in an observational study, Kitaysky et al. (2000) found no difference in growth rates of Black-legged Kittiwakes between years of high and low food availability.

In this study, we found no effect of supplementary feeding on chick growth. Fledglings in this study were lighter by an average of ~50 g than chicks reared in 1992 (Phillips 1995), suggesting that they did not grow at their optimal rate. This could be due to the tradeoff between guarding the chicks and food provisioning. Parents must provision their chicks at a minimal rate in order for the chick to survive, under food stress they may achieve this only at the expense of reduced chick guarding. Hence, both supplemented and control parents raised chicks of similar mass, but control pairs lost more chicks to predation than supplemented pairs. Especially late in the season, only a few supplemented pairs managed to adequately cover the demands of both food provisioning and chick guarding, although at the cost of reduced chick growth (which lead to the interaction between treatment and hatching date for fledging mass and size).

The absence of an effect of the supplementary food is unlikely to be due to parents not having passed it to their chicks. All chicks from supplemented territories met at least some part of their protein requirements from the supplementary food, which had a different isotope signature. However, the amount of assimilated protein originating from the supplementary food was highly variable between chicks and was negatively correlated with the chick's growth rate. This might suggest that the parents of the slower growing chicks were finding it very difficult to provision their chicks and so gave more of the supplementary food to the chicks than did parents that were managing to provision their chicks better. An alternative explanation could be that the supplementary food was missing some essential nutrients for seabird chicks to grow well, so adults that chose to feed more of the supplementary food to their young had chicks with reduced growth. Inadequate quality of the food supplement also could have contributed to the lack of a difference in chick growth rate between the treatment groups. However, our study was only designed to investigate the effect of food quantity on life history traits, but the possible effects of diet quality deserves further experiments.

Whatever the explanation of an absence of an effect of supplementary food on chick growth, it is clear that control birds had to increase their current breeding effort compared to supplemented pairs. Life history theory predicts that food limitation in short-lived species should lead to an increase in relative reproductive effort, as they may not survive to the next breeding opportunity (Charlesworth 1980, Stelzer 2001). Long-lived species, however, should not increase their reproductive effort if it is likely to decrease their survival and, therefore, future reproductive output. Did the increased breeding effort of the control birds incur costs to their future reproduction?

Future reproductive potential

The breeding season in 2002 was very poor, with low numbers of adults present, late laying dates for the whole colony, and some birds returning but not breeding. Supplemented birds had a local return rate of 90%, similar to previous survival estimates for this population (Furness 1987), but significantly higher than the control birds' local return rate of 72.5%. Differences in local return rates could be due to a combination of differences in survival, differences in resighting rates, the proportion of birds missing a breeding season, and birds permanently emigrating to other breeding colonies. Local return rate has been shown to be a good indicator of survival rate in Great Skuas (Ratcliffe et al. 2002). Because fidelity to breeding territories is extremely high and the territories on Foula are well known, jaegers and skuas in this colony have very high resighting rates (Phillips 1995, Catry and Furness 1997). Only two birds (both control birds) that were not observed on Foula in 2002 were seen in 2003. Even if we include these two birds, this gives an estimate of 77.5% return rate for control birds and is still more than double the apparent mortality rate of the supplemented birds. It is therefore unlikely that returning birds that were missed explain the differences in return rate. A small percentage of returning birds in 2002 did not breed in that year, but this is similar between treatment groups (6.7% of 45 supplemented birds and 6.9% of 29 control birds). There are no confirmed cases of birds having bred on Foula and subsequently seen breeding at another breeding colony; therefore, permanent emigration of control birds is unlikely to explain the differences in return rate. Hence the lower local return rate of control birds is most likely caused by lower survival.

Food limitation in short-lived species causes a decrease in survival but increased current breeding effort, according to life history theory (Martin 1987, Boutin 1990). In contrast, long-lived species should pass the costs of increased breeding effort to their offspring to maintain their survival rate and future reproductive potential (Cairns 1987, Stearns 1992, Cam et al. 1998). Our results do not support this hypothesis. Moreover, Reid (1987), Erikstad et al. (1995), and Oro and Furness (2002) have also found evidence of decreased survival in long-lived seabirds due to increased breeding effort. Including our study, there are six experimental studies that have looked at the consequences of manipulated parental effort on both current and future fitness components in seabirds. Five of these have found that the costs are shared between the parents and the offspring (Jacobsen et al. 1995, Golet et al. 1998, Golet and Irons 1999, Weimerskirch et al. 2000, this study). Only Wernham and Bryant (1998) found that the costs were passed on entirely to the offspring, although the large difference in survival was not significant, due to a small sample size. This sharing of increased breeding costs between parents and offspring shows that long-lived species do not necessarily have a fixed breeding effort strategy independent of offspring need, as previously thought.

There was no significant difference between the treatment groups in performance and condition one year after the experiment. Laying date, thought to be a good indicator of condition of adult birds (Bearhop et al. 1999*a*) and breeding success (Phillips and Furness 1998), did not differ between previously supplemented and control birds. Due to very poor breeding success in 2002, breeding performance could be compared more directly. There also were no differences in body condition between treatment groups. However, condition could only be estimated from birds that returned in 2002, and the lack of difference in condition between control and supplemented birds could be because birds that had not reached a certain threshold condition did not return.

It seems unclear why control Parasitic Jaegers maintained a high current reproductive effort at the expense of future reproduction under food stress. This may be because recruitment of sandeels, the main food source of seabirds in the Shetland area, is highly variable and unpredictable (Bailey et al. 1991), and Parasitic Jaegers are unable to predict whether conditions will be favorable for raising chicks when breeding starts. At the start of breeding, birds mainly rely on adult sandeels, which appeared to be numerous, and many species of seabirds return and nest in large numbers, particularly Arctic Terns, which are important kleptoparasitic hosts for Parasitic Jaegers. However, later in the season the numbers of juvenile sandeels needed for rearing chicks seemed to be very low, causing the Arctic Terns to fail and many other species to struggle (Mavor et al. 2002). The birds then could abandon their chicks, which has been reported for various seabird species as a response to poor food availability (Monaghan et al. 1992, Erikstad et al. 1997). However, this is a rare response in Parasitic Jaegers (Catry et al. 1998, this study). This suggests that predictability of food availability is an important factor in life history trade-off decisions (Erikstad et al. 1998). Therefore, more research should be carried out on species that are accustomed to different levels of food predictability, because their life history decisions may differ. The high reproductive effort of the control birds may result if this level of effort is the best trade-off possible for those birds under the limiting food conditions, with any other level of breeding effort causing even lower total reproductive success. This could be due to the importance of chick fledging mass to postfledging survival, because the adults need to get chicks to that threshold mass for breeding to have been worthwhile. However, food is clearly a limiting factor for the Parasitic Jaegers on Foula. It affects the population in two ways, through their current numbers as well as recruitment of future breeding birds, and has a significant and sustained impact on the population dynamics of this long-lived species.

ACKNOWLEDGMENTS

We are grateful to the Holbourn family for permission to work on Foula. We thank Sheila Gear and Jon Crane for their help with the fieldwork. We also thank Andrew Kelly for his help with the stable isotope analysis, Kate Orr for the molecular sexing of Parasitic Jaegers, and Pat Monaghan and two anonymous reviewers for helpful comments on the manuscript. S. E. Davis was supported by a Natural Environmental Research Council studentship, with CASE sponsorship from the Royal Society for the Protection of Birds. R. W. Furness was funded by EC contract ''DISCBIRD.''

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