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Short- and long-term consequences of reproductive decisions: an experimental study in the puffin

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Abstract. The purpose of the present study was to inspect the response of the Atlantic Puffin (*Fratercula arctica*) to an experimental manipulation of the investment needed to successfully raise an offspring. We achieved this by replacing an old offspring with a younger chick, and vice versa, thereby prolonging and shortening the chick-rearing period. To examine any costs of reproduction we then followed the breeding success, the recruitment of young to the population, and the survival of parents for 11 years following the manipulation. Parents in the prolonged and shortened category had a lower breeding success than controls mainly because parents deserted their chick shortly after swapping. Among those that raised their chick, the age and body mass of foster chicks at fledging were the same in all three categories even though the parents had raised chicks for different lengths of time. The recruitment of young to the breeding population was high and independent of treatment. Likewise, the survival of adults was independent of treatment. For the 11 years after the experiment, however, the resighting rate of those that deserted their chick was clearly lower than among those that accepted their foster chick. For parents that raised their foster chick, the survival to the following year was positively related to their body mass. The results support the hypothesis that puffins have a highly flexible parental investment, which they adjust according to their own individual quality and the survival prospects of the chick.

Key words: Atlantic Puffin; cost of reproduction; Fratercula arctica; *Hornøya, Norway; individual quality; manipulation experiment; parental effort; state-dependent breeding investment.*

Introduction

An important issue in population ecology is the negative covariance among different life-history traits that contribute to fitness (reviewed in Roff [1992] and Stearns [1992]). According to life-history theory, the allocation of limited resources to various traits should result in physiological and microevolutionary trade-offs (Stearns 1992, McNamara and Houston 1996). One such important trade-off is that between the current and future reproduction, often referred to as the "cost of reproduction" (Williams 1966). If the reproductive effort in one year leads to a reduction in future reproductive output (through decreased adult survival or reduced fecundity), then the optimal effort in the current season is less than the effort that would maximize the parental effort in that season (Williams 1966, Charnov and Krebs 1974).

Costs of reproduction have for decades been the subject of a large number of both empirical and theoretical studies on various organisms. Such studies generally show that parents are able to increase their effort above their normal levels, but that this leads to a lower adult survival or future fecundity (see Lindén and Møller 1989, Jacobsen et al. 1995, Hadley et al. 2007). One topic that has been much debated is the cost of reproduction in long-lived vs. short-lived species (Lindén and Møller 1989, Wernham and Bryant 1998, Golet et al. 2004). Long-lived species can be expected to be more restrictive in their response to an increased effort than short-lived species, since even a small reduction in adult survival will reduce the number of subsequent breeding attempts and thereby greatly lower their lifetime reproductive success (Curio 1988, Wooller et al. 1992, Charlesworth 1994). However, there is empirical evidence indicating that long-lived birds are more likely to experience survival costs than short-lived species (see review by Golet et al. 1998). One explanation for this pattern, as suggested by Wernham and Bryant (1998), is that the majority of studies on short-lived birds are brood enlargements, and if such species normally work at maximum reproductive effort, increasing clutch size may not alter their effort. Long-lived species, on the other hand, may have, under average conditions, a lower-than-maximum effort and therefore more likely respond to experimentally increased effort. Therefore, an important open question in life-history evolution is why long-lived species should invest in reproduction at the cost of their own survival. Another important question is why the results from different empirical studies are

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ambiguous (reviewed in Lindén and Møller 1989, Wernham and Bryant 1998).

Fundamental to our understanding of the cost of reproduction in long-lived species is knowledge of their mechanisms to regulate parental effort. Four hypotheses, all of which have received some support, have been suggested in order to explain how individuals balance their parental effort.

1. *Stress hypothesis*.—The cost of raising young varies with season and/or the quality of the parents, while the parents always try to meet the demands of their offspring. Under such conditions, parents may suffer during bad seasons by investing too much in chicks, which results in both reduced survival of young and reduced parental survival. This hypothesis implies that costs of reproduction only may be quantifiable during bad breeding conditions (Ricklefs 1990, Wernham and Bryant 1998, Golet et al. 2004).

2. *Fixed-feeding-scheme hypothesis*.—According to this hypothesis, parents have evolved a fixed level of effort in raising young. They do not respond to the chicks' actual need; instead, the daily effort is governed by the mean expected need, based on the age of the chick (e.g., Ricklefs 1987, 1992, Weimerskirch et al. 1995, Navarro and González-Solís 2007).

3. *Fixed-breeding-period hypothesis*.—Alternatively, parents allot a fixed amount of time (or total energy) to breeding, within which a "normal" chick-rearing period can be completed (Hudson 1985, Ydenberg and Bertram 1989, Johnsen et al. 1994). According to both hypotheses 2 and 3, a fixed effort, determined by the parents' own body condition and quality, has been suggested to be an adaptation to prevent "overinvestment" at the expense of one's own survival (Sæther et al. 1993).

4. *Flexible-investment hypothesis*.—The allocation of resources should depend on the offspring's demand for energy or other essential resources. Thus, the parental provisioning should be flexible and be a result of complex behavioral parent–offspring interactions involving begging for food and its parental response (Ricklefs and Minot 1991, Bolton 1995). Among species with sexual size dimorphism, the parental investment may even vary with the sex (size) of the chick (e.g., Velando and Alonso-Alvarez 2003). Such an ability to invest and satisfy the offspring's need may be state dependent (McNamara and Houston 1996) and depend upon the body condition of the parents. According to this hypothesis, there should be a large individual variation in the parents' ability to respond to changes in the requirements (Erikstad et al. 1998).

The purpose of the present study was to inspect the response of the Atlantic Puffin (*Fratercula arctica*) to an experimental manipulation of the investment needed to successfully raise an offspring. We achieved this by replacing an old offspring with a younger chick, and vice versa, thereby prolonging and shortening the chick-rearing period. Since food provisioning is energetically expensive for the parents (Croxall 1984), this is an effective way of manipulating parental investment.

We examined (1) whether the parents are willing to increase their investment, (2) whether such a response varies among parents, and (3) whether any increase in parental investment affects the survival of chicks and adults and the recruitment rates of chicks to the population. We use data covering 12 years of observation during and after the experiment. We examine these questions in relation to the four hypotheses outlined above. To our knowledge, this is the first study on a long-lived bird to examine the relationship between parental effort, breeding success, and adult survival and at the same time estimate the survival and recruitment of young from manipulated parents.

Material and Methods

Fieldwork

The study was carried out in a seabird colony on Hornøya (72°22′ N, 31°10′ E), a small island in northeastern Norway, from May to late August 1994. For a description of the study area, see Furness and Barrett (1985). The breeding population of puffins at Hornøya was estimated to be 5000 pairs in 1980 (Barrett and Vader 1984) and has since increased to 10 000 pairs in 2007 (Lorentsen 2007).

The puffin is a boreo-panarctic North Atlantic species. It lays one egg per breeding season. Both parents incubate, and incubation usually lasts 39–44 d (Harris 1984). Both parents feed the chick three to four times per day, and the fledging period normally takes 38–44 d, but during unfavorable feeding conditions can be increased to as much as 80 d (e.g., Barrett and Rikardsen 1992). Survival of adults is generally high (>90%, Hudson 1985).

During the last part of the incubation period, the puffin burrows were checked every second day to determine hatching date. Chicks were weighed to the nearest 0.5 g using a Pesola spring balance. Adults were caught with snares fixed in the burrow entrance and weighed to the nearest 5 g using a Pesola spring balance on day 6 of the nestling period, and their head length (head + bill) and the maximum bill depth were measured to the nearest 0.1 mm using a Vernier calliper. The adults were then sexed using these two measurements according to the discriminant function presented by Barrett et al. (1985) for puffins in the study area and, where possible, intra-pair comparisons (Sandvik 2001). According to this function, 87% of the birds are classified correctly, which increases to 96% in pairs of which both birds were caught (Sandvik 2001). Both birds in a pair were captured at 58 nests. To be able to include the remaining nests, we used standardized body masses of parents at each nest when relating the body mass of adults to the growth rate and fate of chicks (i.e., body masses of either females, males, standardized to zero mean and unity variance within each sex separately, or the average of both parents).

All birds handled during the experiment, adults and chicks alike, were ringed with numbered metal rings and unique color-ring combinations. Chicks that died between ringing and fledging were excluded from the data set. In all subsequent years, the colony was searched for ringed birds using binoculars.

Experimental design and tests of hypothesis

We tested the fitness consequences (chick survival, chick recruitment, and adult survival) of reproductive decisions in the puffin by manipulating parental effort. A number of techniques have previously been used to manipulate the effort in the puffin and other long-lived seabirds (e.g., Sæther et al. 1993, Johnsen et al. 1994, Jacobsen et al. 1995, Wernham and Bryant 1998, Velando and Alonso-Alvarez 2003, Golet et al. 2004). The puffin is a single-egg seabird, making it difficult to vary their effort by means of brood size manipulation. Such a design may create a novel situation and alter the behavior of the chicks in an unexpected way, not reflecting the parent's effort (Harris 1984, Ricklefs 1987, Wernham and Bryant 1998; K. E. Erikstad, *personal observations*). Alternative treatments are to offer extra food to a subsample of birds (Wernham and Bryant 1998) or to remove entire clutches (Golet et al. 2004). However, such designs only decrease the parents' effort, and if parents normally work below their maximum capacity, any effect on the parents' residual fitness may be minimal. Additionally, such a design may also depend on the quality of the season where small and no effect on parents' residual fitness are expected if the food situation for the controls is good.

In the present study, we have adopted a design to swap chicks among burrows with known hatching dates to prolong and shorten the length of the chick-rearing period. Such treatments may alter the parent's effort in two ways. First, it may make them work for a shorter (longer) time than controls to raise an older (younger) and heavier (lighter) chick, i.e., a chick of higher (lower) fitness prospects, to independence. Second, such a design also affects the feeding scheme of the parents, in that an older chick requires more food (cf. Fig. 1). Parents may be unable to increase their food delivery fast enough, even though they face a shortened rearing period and therefore may be more willing to invest in that chick.

We swapped chicks among 120 burrows with known hatching dates to prolong ($N = 30$) and shorten ($N = 30$) the chick-rearing period by 12 d. We also swapped chicks of similar age among controls ($N = 60$). Parents in the prolonged group received a small chick of 8 d when their own chick was 20 d old, and the shortened group received a large chick of 20 d when their own chick was 8 d old. In the control group, 20-d-old chicks were swapped among parents with the same hatching date. A schematic presentation of the experimental setup is found in Fig. 1. As indicated, the pairs with reduced nestling period received a large chick at a time when its food requirement was near a maximum. A part of the experiment (intra-season effects among control birds) has been published previously (Erikstad et al. 1997). Here we present the whole experiment on parental decisions and its long-term effects on adult survival and the survival and recruitment of young to the population.

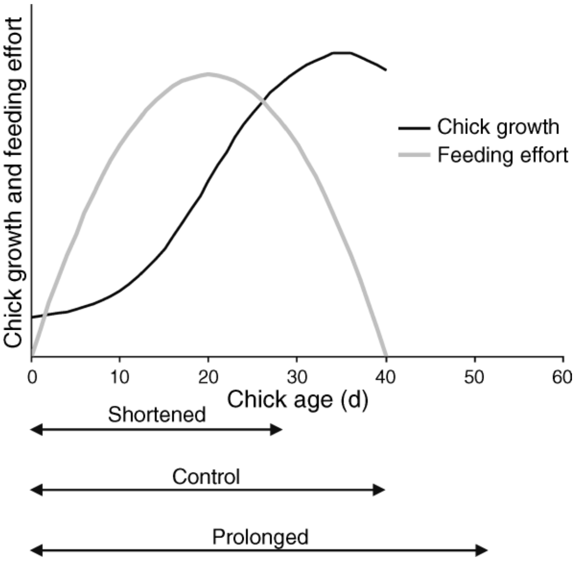

FIG. 1. Schematic presentation of the experimental rationale. The feeding effort of Atlantic Puffin (*Fratercula arctica*) (step-) parents is temporally variable and peaks when the chick growth rate is largest. The experimental swapping of chicks of different ages (8 or 20 d) resulted in nestling periods that were either shortened or prolonged in comparison to control chicks. The arrows show the length of nestling periods. The swapping also caused a potential mismatch between feeding rates and chick needs. This figure is modified after Johnsen et al. (1994).

When this experiment was carried out, there was no method to sex the newly hatched chicks. However, there is very small (~9%) sexual size dimorphism in the adult puffin (Barrett et al. 1985), so different costs to raise male and female offspring seem negligble.

We followed the fate of chicks and adults until 11 years after the experiment and examined the four hypotheses summarized in Table 1. The following testable and, in part, mutually exclusive predictions can be derived from the hypotheses.

Stress hypothesis.—According to the stress hypothesis, we expected stepparents in the prolonged group to suffer from nonbreeding or reduced adult survival the year following the experiment. Chicks will profit from shortening by reaching a higher fledging mass earlier, because stepparents are less stressed and are able to invest more in the offspring, at a lower cost to themselves. Desertion should occur late in the breeding season (if at all), when parents have exhausted their energy budget.

Fixed-breeding-period hypothesis.—According to this hypothesis, the parents should terminate the breeding period at the expected time of fledging. The chance of chick survival, their fledging mass, and recruitment rates

TABLE 1. Summary of the four hypotheses considered and the predictions derived from them.

Effect	Stress hypothesis	Fixed-breeding-period hypothesis
Fledging success	shortened ? control > prolonged	shortened ? control > prolonged
Time of chick death	late	late
Length of rearing period	shortened < control < prolonged	shortened < control = prolonged
Age at fledging	shortened < control < prolonged	shortened = control > prolonged
Fledgling body mass	shortened > control > prolonged	shortened > control > prolonged
Adult vital rates during the first year	shortened > control > prolonged	shortened = control = prolonged
Juvenile vital rates during the first six years	shortened > control > prolonged	shortened > control > prolonged

Notes: The four hypotheses (explained in more detail in *Material and methods: Experimental design and tests of hypothesis*) make different predictions as to the effects of experimental nest period manipulation on breeding parameters and the vital rates of adults and juveniles. "Vital rate" refers to apparent survival and resighting rates. Expectations are indicated by inequality and equality signs, detailing whether and in which way parameters should differ between experimental treatments (i.e., shortened, prolonged, or unchanged nest period). Question marks indicate that no a priori inequality can be derived from the hypothesis.

therefore increase from the prolonged via the control to the shortened treatment. Adult survival should be unaffected by experimental treatment.

Fixed-feeding-scheme hypothesis.—If it is feeding effort rather than the length of the breeding period that is fixed, on the other hand, control chicks may fare better than chicks in the shortened experimental treatment. This is because stepparents will not meet the age-dependent larger food requirements of larger chicks. Fledging success and mass should thus be highest, and age at fledging lowest, among control chicks. Time of chick death should be treatment dependent and happen shortly after manipulation in the shortened treatment but toward the end of the breeding period in the prolonged treatment. Adult survival should be unaffected.

Flexible-investment hypothesis.—According to the last hypothesis, if parents are unable to guarantee the chick's success, they should not accept it. Desertion should thus take place early, within a few days after manipulation. Chicks that are accepted, on the other hand, should grow and survive normally. Whether parents accept or desert their foster chicks is a function of the survival prospects of the foster chick, but also of the parents' own quality. Survival and resighting rates of "accepters" and "deserters" are therefore analyzed separately. A cost of reproduction can only be found among accepters during the first year after the experiment, although it may be masked by their higher-than-average quality. The hypothesis predicts a threshold for when reproduction occurs, however, and the costs of reproduction are expected to be most pronounced in individuals that are close to—but above—this threshold. Because individual quality may reveal itself in the long run, survival and resighting rates are also analyzed for the remaining years (2–11 yr after the experiment), where the hypothesis predicts the opposite sign: "accepters" should perform better than "deserters." Differences may be found in both survival and resighting rates, because the latter parameter is affected by intermittent breeding and therefore may mirror breeding propensity.

Capture–recapture analysis

The data were analyzed in a capture–mark–recapture framework, using program MARK (White 2004; for documentation, cf. White and Burnham 1999). This enabled us to estimate apparent survival probabilities, ϕ (survival, hereafter), and resighting probabilities, p. The analysis methods are described here; see Sandvik et al. (2005) for a more detailed account.

Initial data inspection was carried out using Test 2 and Test 3 as implemented in program Release (cf. Burnham et al. 1987). While Test 3 showed that ϕ and p were identical among individuals ($\chi^2_{27} = 12.95$, $P = 0.99$), Test 2 revealed that ϕ and p were strongly dependent on prior capture histories ($\chi^2_{144} = 700.57$, $P \ll 10^{-12}$). Because trap dependence is one of the factors that can lead to such resighting heterogeneity, we used the correction suggested by Pradel (1993). Accounting for trap dependence extending over two years was sufficient to remove the resighting heterogeneity (i.e., the overdispersion factor $\hat{c}$ was <1).

Model simplifications were guided by Akaike's Information Criterion corrected for small sample sizes ($\mathrm{AIC_c}$). The sample used in modeling included all puffins marked at Hornøya since 1990 ($N = 913$). After having arrived at the model $\{\Phi(-)\ P(t + h2)\ \phi(-)\ p(a + h2)\}$ (see Appendix: Table A1 for abbreviations used), experiment effects were included for both adult and immature survival and resighting rates. All nonexperimental birds were coded as a separate attribute group whose vital rates varied in parallel (additively) to experimental birds. The effect of their inclusion was solely to increase the precision of estimates of fully time-dependent variables (viz., resighting rates), because otherwise the interannual variation in resighting effort might have been confounded with experimental effects. Only estimates of experimental birds are discussed in the present paper. Variables considered were experimental treatment (three levels), accepters vs. deserters (two levels), sex (two levels), and adult body mass (continuously varying individual covariate). The effect of experimental treatment and of own body mass on adult survival were considered only during the first year after the experiment. Sex and the difference between accepters and deserters were considered for the entire period. The immatures considered were the birds that had been marked as chicks. Their vital rates differ from adult rates for the first six years of life (Sandvik et al. 2008). Therefore, the effect of

Table 1. Extended.

Fixed-feeding-scheme hypothesis	Flexible-investment hypothesis
shortened ? prolonged < control	shortened ? control > prolonged
shortened < control < prolonged	early (shortly after manipulation)
shortened ≤ control < prolonged	shortened < control < prolonged
shortened ? prolonged > control	shortened = control = prolonged
shortened ≤ prolonged ≤ control	shortened = control = prolonged
shortened = control = prolonged	shortened = control = prolonged
shortened ? prolonged < control	shortened = control = prolonged

experimental treatment on immature vital rates was considered for the first six years after the experiment. We refer to the cumulative survival of juveniles from fledging to six years of age as "recruitment."

Model selection based on information criteria (such as AIC$_c$) and null hypothesis testing are sometimes viewed as mutually exclusive paradigms. We agree with Stephens et al. (2005) that there is no reason not to utilize the best of both methodologies. Given that we test the effect of an experimental manipulation, the a priori hypotheses are clear-cut (cf. Table 1) and allow significance testing of the models obtained. Therefore, after model selection based on AIC$_c$, we performed likelihood ratio tests (LRT) based on twice the difference between the log-likelihoods of the models compared (deviance). Models compared were chosen so that they only differed in the presence/absence of the variable of interest, but were otherwise identical to the best model. Because such pairs of models are hierarchically nested, the corresponding LRT statistic is distributed as χ^2 and tested accordingly.

Statistical tests are two-tailed and performed using the SAS software package (SAS Institute 2008). Estimates are given as "estimated mean ± SE" or alternatively as "best estimate (95% CI)."

Results

Experimental design

The egg volume, chick body mass at hatching, female and male body size, and body mass were similar among groups at the time of manipulation (Table 2). Hatching, however, was earlier among the prolonged group than among controls and the shortened group. This result was a consequence of the experimental design. Prolonging and shortening the duration of the brood-rearing period by pairwise switching chicks required early-hatched chicks to be switched with late-hatched chicks. The body mass of both own and foster chicks at swapping were different among groups in the prolonged and in the shortened group because of the experimental design (Table 2). Own and foster chick in the control group had similar body masses.

Parental effort and chick survival

Fledging success was lower in the prolonged treatment (17%) than in the shortened (53%) and in the control treatment (72%; Table 3). Most chicks that died did so a few days after swapping, and this pattern was similar in all treatment categories (Table 3), as predicted by the flexible-investment hypothesis only. Fledging success was best explained by a model which, in addition to (and corrected for) treatment, included body mass of the parents' own chick at the time of swapping (AIC$_c$ weight of these variables, $w_+ > 0.97$; Table 4). The likelihood that parents lost their foster chick decreased with the body mass of their own chicks at swapping (Fig. 2). This was evident among controls (Wald $\chi^2 = 7.5$, $P = 0.006$) but not in the prolonged (Wald $\chi^2 = 1.5$, $P = 0.22$) and the shortened treatment (Wald $\chi^2 = 0.04$, $P = 0.98$), although this interaction with treatment was not quite significant ($w_+ = 0.23$, $P = 0.14$; Table 4). The size of the foster chick had no effect on the likelihood

Table 2. Atlantic Puffin (*Fratercula arctica*) measurements (mean ± SE) before manipulation.

	Treatment			ANOVA		
Parameter	Shortened	Control	Prolonged	*F*	df	*P*
Egg volume (cm^3)	64.1 ± 1.1 (29)	65.3 ± 0.5 (58)	65.7 ± 0.9 (25)	1.0	2, 109	0.36
Hatching date (1 = 1 June)	33.7 ± 0.7 (30)	24.4 ± 0.3 (60)	21.7 ± 0.7 (30)	109.5	2, 117	<0.001
Early chick mass (5 d old; g)	86.0 ± 2.4 (26)	91.4 ± 2.3 (60)	87.4 ± 2.7 (30)	1.2	2, 113	0.30
Female body mass (g)	451 ± 8 (8)	463 ± 11 (11)	467 ± 11 (10)	0.6	2, 26	0.56
Female head + bill size (mm)	80.5 ± 0.4 (8)	79.6 ± 0.4 (11)	81.4 ± 0.5 (10)	2.3	2, 26	0.11
Male body mass (g)	503 ± 6 (13)	516 ± 9 (18)	512 ± 14 (5)	0.7	2, 33	0.50
Male head + bill size (mm)	83.5 ± 0.4 (13)	83.4 ± 0.3 (18)	84.4 ± 0.5 (5)	0.1	2, 33	0.91
Own chick at swapping (g)	103 ± 4 (30)	226 ± 6 (60)	208 ± 8 (30)	99.0	2, 117	<0.001
Foster chick at swapping (g)	208 ± 8 (30)	226 ± 6 (60)	103 ± 4 (30)	99.0	2, 117	<0.001

Notes: Sample sizes are given in parentheses. Treatment entailed a shortening or prolongation of the chick-rearing period by 12 d by swapping chicks among different burrows with different hatching dates on Hornøya, a small island in northeastern Norway. Control nests are chicks that were swapped between nests of similar hatching date.

TABLE 3. Atlantic Puffin parameters (mean ± SE) after manipulation.

	Treatment			Test statistics†			
Parameter	Shortened	Control	Prolonged	F	df	χ^2	P
Fledging success (%)	53 (30)	72 (60)	17 (30)			20.9	<0.001
Time of chick death (d)‡	7.4 ± 1.1 (14)	6.6 ± 0.8 (17)	4.9 ± 0.7 (25)	2.5	2, 53		0.093
Length of rearing period (d)	34.5 ± 1.0 (13)	41.7 ± 0.5 (38)	54.5 ± 2.5 (4)	110.5	2, 52		<0.001
Age at fledging (d)	41.5 ± 1.0 (13)	41.7 ± 0.5 (38)	41.0 ± 2.4 (4)	0.1	2, 52		0.90
Fledgling body mass (g)	341 ± 9 (13)	348 ± 8 (38)	346 ± 28 (4)	0.1	2, 52		0.88

Notes: Sample sizes are given in parentheses. Treatment entailed a shortening or prolongation of the chick-rearing period by 12 d by swapping chicks among different burrows with different hatching dates. Control nests are chicks that were swapped between nests of similar hatching date.

† All tests except fledging success were based on two-way ANOVAs. Fledging success was analyzed using logistic models (for details, see Table 4).

‡ Expressed as days after manipulation.

that parents should desert them (Table 4), although there was a trend in the control treatment that the size of foster chick was higher among those parents that accepted to raise the chick to fledging (Fig. 2; Wald $\chi^2 = 1.7$, $P = 0.11$). None of the parental traits predicted desertion (neither head + bill length nor body mass, $w_+ < 0.18$; Table 4).

The chicks had a fledging period of 42 ± 1 d in all treatment categories (rejecting the fixed-breeding-period hypothesis), although parents had fostered chicks for 35 ± 1, 42 ± 1, and 55 ± 3 d in the shortened, control, and the prolonged categories, respectively (Table 3). In addition, the chick body mass at fledging was similar in all three treatments (Table 3). Both findings are compatible with the flexible-investment hypothesis, the latter also with the fixed-feeding-scheme hypothesis.

Resighting and survival rates of adults and fledglings

Resighting rates differed between years in adult birds, while adult survival was constant over time. The sexes did not differ with respect to survival or resighting. The best survival models and their neighborhood are listed in the Appendix (Table A1). Table 5 summarizes the effect of explanatory variables on the vital rates of the experimental birds. These observed effects can be compared to the effects predicted by different hypotheses (Table 1). While the predictions did not distinguish between survival and resighting rates, results in Table 5 are listed separately for these two vital rates.

Experimental treatment did not explain differences in vital rates the first year after the experiment (Table 5). While survival rates (derived from model I in Appendix: Table A1) were 0.896 (0.723, 0.966), 0.951 (0.837, 0.986) and 1.000 (0.994, 1.000) for the shortened, control, and prolonged experimental treatments, respectively, the corresponding resighting rates were 0.741 (0.552, 0.870), 0.834 (0.723, 0.907), and 0.855 (0.723, 0.930) (model O). Restricting the experimental effect to the group that had accepted their foster chicks did not make the pattern more pronounced. The tendency was in all cases that the shortened category had slightly lower rates than the prolonged category, thereby rejecting the stress hypothesis.

There was no significant difference between accepters and deserters in vital rates the first year after the experiment (Table 5). For instance, survival was 0.921 (0.822, 0.967) among accepters and 0.984 (0.331, 1.000) among deserters (model F). However, if the effect for all years after the experiment was considered, acceptance/desertion of the foster chick was the single most

TABLE 4. Model selection for fledging success of Atlantic Puffins after manipulation.

Model	ΔAIC_c	Dev.	df	P
Treatment + own chick	0.00	27.31	2	<0.0001
Treatment + **own chick**	0.00	7.18	1	0.0074
Treatment + own chick + **treatment × own chick**	0.46	3.92	2	0.14
Treatment + own chick + **parent head length**	1.00	1.18	1	0.28
Treatment + own chick + **foster chick**	1.32	0.86	1	0.35
Treatment + own chick + **parent body mass**	1.54	0.64	1	0.43
Treatment	5.04	25.08	2	<0.0001
Own chick	23.05	5.68	1	0.017
Null	26.66			

Notes: Models compared are binomial generalized linear models (GLMs). The information provided for each model is the Akaike's Information Criterion corrected for small sample sizes, relative to the best model (ΔAIC_c of the model), and the test statistics of the parameter in boldface (deviance, i.e., twice the negative difference of the log-likelihoods of a model with and without the respective parameter; the associated degrees of freedom; and the probability). Only the neighborhood of the best model is shown. Models are sorted by increasing ΔAIC_c. The AIC_c of the best model is 141.19. Chick body masses were standardized to zero mean and unity variance separately within each treatment.

important explanatory variable. In accordance with the individual condition-dependent strategies predicted by the flexible-investment hypothesis, long-term resighting rates of accepting birds were significantly higher than of deserting birds. The difference was 0.50 (0.19, 0.81) on a logit scale (model A). A weaker effect of the same sign was found in survival when the effect on resighting was excluded (Table 5): survival was 0.960 (0.921, 0.980) among accepters and 0.922 (0.876, 0.952) among deserters (model U). If the effect on resighting was included, however, the effect on survival disappeared (not shown, $\Delta AIC_c = 2.01$). In the best model, the difference between accepters and deserters was thus only found in resighting rates.

Body mass as an individual covariate did not explain variation in adult resighting rates. Survival during the first year after the experiment, however, increased with increasing body mass in the group of accepters (estimated slope on logit scale, +1.03 (+0.29, +1.77); model A), indicating a cost of reproduction in light birds (Fig. 3). There was no such relation among deserters (−0.58 [−1.78, +0.62]; model P). This interaction was significant (Table 5, Fig. 3).

In immatures (up to six years of age), resighting rates were a function of age, while survival was constant across ages. In contrast to all hypotheses except flexible investment, immature vital rates were not affected by experimental categories. While survival rates were 0.858 (0.702, 0.940), 0.849 (0.754, 0.911), and 0.967 (0.372, 0.999) for the shortened, control, and prolonged experimental treatments, respectively (model M), the corresponding resighting rates were −0.66 (−1.89, +0.57), −0.49 (−1.51, +0.53), and +0.07 (−1.44, +1.58) (differentials on logit scale; model N). All confidence intervals overlapped widely, but again rates in the shortened category tended to be lower than in the prolonged category.

Discussion

In the experiment described here, we manipulated the breeding effort of adult puffins by exchanging their chick with a foster chick that was 12 days older or younger than or of the same age as their own chick. Breeding performance was surveyed after the manipulation, and subsequent adult survival and resighting rates and juvenile recruitment of the experimental birds was monitored for the 11 following years.

The results allow conclusions on (1) the parental decisions underlying investment into offspring, (2) the importance of variation in individual quality, and (3) the conditions under which the occurrence of costs of reproduction can be expected.

Hypotheses about parental investment

The results show clearly that puffins have a highly flexible investment in young and that they quickly adjust to the chick's demands. Reproductive decisions are made continuously in relation to own prospects to survive and reproduce in the future and to the value of the chick. The findings reject several predictions derived from the stress and the fixed-investment hypotheses (Table 1), while all predictions based on the flexible-investment hypothesis are corroborated. In particular, desertion took place early and its timing was unaffected by experimental treatment. Those parents that accepted to raise their foster chick fed it normally regardless of experimental treatment. Independent of the time the parents spent on feeding chicks, age and body mass at fledging and recruitment rates of offspring were similar across treatments. Parents' survival to and resighting

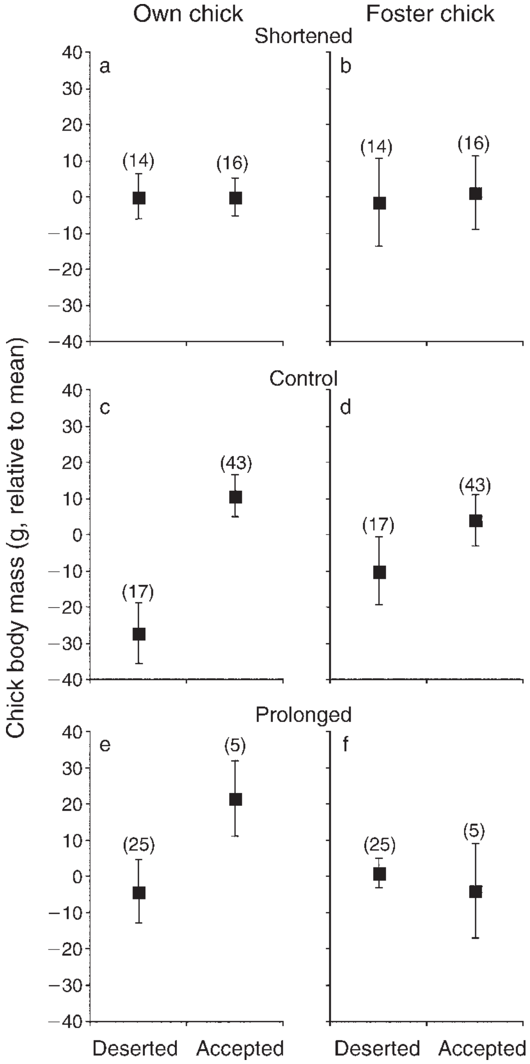

FIG. 2. Chick body mass of Atlantic Puffins at the time of experimental swapping. Variation in chick body mass is shown in relation to experimental categories and whether their own or their foster parents deserted or accepted their foster chicks. Masses are expressed as the deviation from the mean for each panel; error bars indicate standard errors. The means are provided in Table 2. The body mass of the own chick had a significant positive effect on the probability of accepting a foster chick ($\chi^2 = 7.2$, $P = 0.007$).

TABLE 5. Variables affecting vital rates of Atlantic Puffins in the years following an experiment in which nest period was manipulated.

	Observed effect on survival					
Explanatory variable	Direction	Model	Δ	Dev.	df	P
Experimental treatment						
First year	shortened $\leq$ control $\leq$ prolonged	I–A	3.11	3.03	3	0.39
Accepters only, first year	shortened $\leq$ control $\leq$ deserters $\leq$ prolonged	H–F	0.66	3.44	2	0.18
Juveniles, first six years	control $\leq$ shortened $\leq$ prolonged	M–A	4.22	1.93	3	0.59
Accepters vs. deserters						
First year	accepters $\leq$ deserters	F–A	2.44	1.66	2	0.44
All subsequent years	**accepters $>$ deserters**	**U–X**	**−1.82**	**3.87**	**1**	**0.049**
Body mass						
Accepters only, first year	**slope $>$ 0**	**A–L**	**−4.01**	**6.06**	**1**	**0.014**
Deserters only, first year	slope $\leq$ 0	P–L	1.18	0.87	1	0.35
Interaction, first year	**accepters $>$ 0 $\geq$ deserters**	**B–K**	**−2.82**	**4.87**	**1**	**0.027**
Sex, all years	female $\geq$ male	E–A	1.98	0.06	1	0.81

Notes: The explanatory variables tested (cf. Table 1) are given in the first column. The remaining columns summarize test statistics. They are reported separately for survival and resighting, while the expectations (Table 1) do not differ for these two variables. For each test, the observed direction is given (where "<" and ">" denote that the 95% CIs exclude each other's estimates; otherwise "≤" or "≥" is used). Expected directions are detailed in Table 1. The models compared can be identified by the uppercase letters used in Appendix: Table A1. The model with more parameters is given first, followed by the model with fewer parameters. The $\Delta\mathrm{AIC}_c$ values (denoted Δ) are calculated by subtracting from the AIC_c of the former model the AIC_c of the latter model (i.e., negative values indicate strong effects). The test statistic (deviance, Dev.) is twice the negative difference of the log-likelihoods of the two models compared. Because nested sets of models were tested, the latter values are distributed as χ^2. Accompanying degrees of freedom (df) and probabilities (P) are thus derived from χ^2 tests. Tests with $P < 0.05$ appear in boldface.

rates in the year after the experiment were also unaffected by treatment. Crucially, these findings were predicted by the flexible-investment hypothesis, but are in contradiction to the stress hypothesis and the fixed-investment hypotheses.

Parents that received a small foster chick deserted their nest more often than parents that received a large foster chick. This was evident across experimental treatments (prolonged vs. shortened) and, although insignificantly so, within control birds. Given that a small chick has a lower chance of survival than a large chick, this may indicate that parents respond to the chick's estimated prospects of survival and recruitment to the population. These results are in accordance with the idea that parents should balance their investment in young not only according to their own maintenance and survival (Williams 1966, Sargent and Gross 1985), but also against the value of the offspring (Dawkins and Carlisle 1976), as has been suggested in birds (e.g., Erikstad et al. 1997, 1998). The lower fledging success of "shortened" chicks than controls suggests that parents do not only respond to the size of the chicks and the length of the manipulated rearing period, but also to the chick's current food requirements. Parents in the shortened treatment received a chick that was at the top of its feeding curve (see Fig. 1), when their own chick required many fewer daily food deliveries. This may explain why more control parents perceived the work load posed by their foster chick as manageable, even though parents in the shortened treatment had reduced their overall work load over the whole rearing period.

Abandonment of the chick is thus an active choice that the parents make early after manipulation, rather than being a negative side effect of the parents' exhaustion (stress hypothesis) or of their unwillingness to prolong the time spent feeding chicks beyond the expected fledging date (fixed-investment hypothesis). This result is in contrast to several studies of procellariiforms, in which the parents have been shown not to respond to the chick's demands (e.g., Ricklefs 1987, 1992, Sæther et al. 1993). Instead, they allocate their resources according to their own maintenance, presumably in order to maximize their own survival (fixed-investment hypothesis; Sæther et al. 1993). The reason for this discrepancy between our findings and studies in procellariiforms may lie in the different behavioral strategies in these taxa: while the puffin chick is fed three to four times a day, procellariiform chicks often experience long feeding intervals of several days, and each parent feeds the chick independently of the other parent (Ricklefs 1992). As a result, the parents have fewer possibilities to assess the nutritional status of the chick. The different hypotheses may thus be valid in different taxa. However, recent studies on parental decisions in procellariiformes show that even these birds may respond to the chick's need, but that such responses are apparent only among parents in good body condition (Tveraa et al. 1998, Varpe et al. 2004). The available evidence suggests that the flexible-investment hypothesis is valid for most seabirds studied.

Individual quality and state-dependent reproductive decisions

The single most important parameter in the capture–mark–resighting models of manipulated puffins was the distinction between parents that had accepted vs. deserted

TABLE 5. Extended.

Observed effect on resighting					
Direction	Model	Δ	Dev.	df	*P*
shortened ≤ control ≤ prolonged	O–A	4.50	1.65	3	0.65
deserters ≤ shortened ≤ control ≤ prolonged	Q–A	5.53	0.62	3	0.89
shortened ≤ control ≤ prolonged	N–A	4.24	1.91	3	0.59
accepters ≥ deserters	J–A	3.97	0.13	2	0.94
accepters > deserters	**A–X**	**−8.02**	**10.07**	**1**	**0.0015**
slope ≥ 0	S–L	1.77	0.28	1	0.60
slope ≤ 0	R–L	1.72	0.33	1	0.58
accepters ≥ 0 ≥ deserters	W–T	1.45	0.60	1	0.44
female ≤ male	G–A	2.79	1.31	2	0.52

their foster chick: accepters had a higher resighting rate throughout the entire 11-year period after the experiment.

It is important to note that resighting rate can be a biologically informative measure. Besides being a function of observation effort (which of course is a nuisance parameter), resighting rates also incorporate breeding propensity. A long-term pattern in which resighting rates consistently vary in parallel with other birds, but on a higher level, as found in the present study, most likely reflects a higher proportion of birds present in each year, i.e., a lower proportion of nonbreeding. Nonbreeding seems to be a widespread phenomenon in puffins (Ashcroft 1979) and other long-lived birds (e.g., Ollason and Dunnet 1988, Golet et al. 2004).

It has been documented in a variety of animal species that lifetime reproductive success varies widely among individuals. Often, the majority of individuals do not reproduce at all, while a few individuals contribute a large proportion of the offspring in the population (Clutton-Brock 1988, Newton 1989, Reed et al. 2008). In other words, the reproductive performance of individuals tends to be highly correlated across years (and with survival), indicating that individuals consistently differ in their inherent quality. Acknowledgment of this observation has led to the development of state-dependent life-history models, in which reproductive decisions are influenced by the quality or the state of each individual (McNamara and Houston 1996). Variation in individual quality has been invoked as the reason why reproduction and survival often are positively correlated in observational studies (Nur 1988, Cam et al. 1998, Sear 2007, Weladji et al. 2008), even though the underlying trade-off would be expected to lead to a negative correlation (van Noordwijk and de Jong 1986). However, it has been hard to identify parameters that give reliable estimates of individual quality. This was also the case in our study, in which none of the measured adult parameters was able to predict whether a bird accepted or deserted its foster chick, although a close positive correlation between the parent's body condition at the time of hatching and the body mass of 20-d-old chicks has previously been shown in the same colony (Erikstad et al. 1997).

However, the long-term estimates of resighting rates and, to a lesser extent, survival rates (Table 5) document consistent differences between individuals in our study. A "side effect" of the experiment has thus been that birds sorted themselves into high-quality and low-quality individuals according to whether they accepted to raise the chick or not. Accordingly, "accepters" might have been a subsample with higher-than-average-quality birds, while "deserters" constituted a subsample with

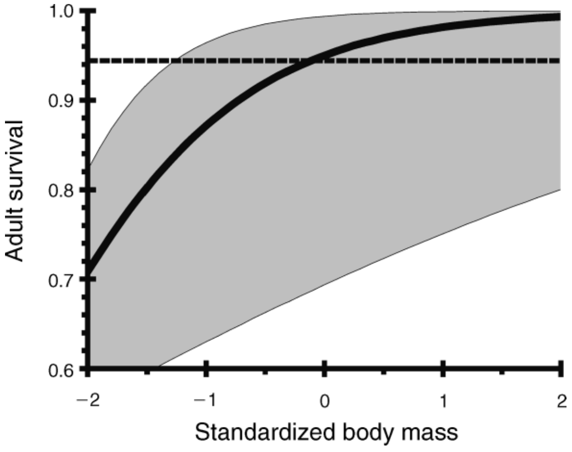

FIG. 3. Adult survival of Atlantic Puffins in relation to their body mass in the first year following the experiment. The bold line expresses the significantly positive relationship in parents that accepted their foster chick. The 95% confidence intervals are illustrated using gray shading. The dashed line shows the mean survival of parents that deserted their foster chicks. The latter relationship is not significant and is shown with a slope of zero. Body mass is standardized for each sex separately and provided in standard deviation units rather than grams. The estimates are from the best survival model (model A in Appendix: Table A1).

lower-than-average-quality birds. A similar instance of sorting was observed during an El Niño event in Nazca Boobies (*Sula granti*), in which the parents that produced fledglings under these adverse conditions survived better than less successful birds (Townsend and Anderson 2007). "Quality" may be a function of age, experience, disease, genetic quality, or a combination thereof (e.g., Clutton-Brock 1984, Reznick 1992, Erikstad et al. 1997). The results show that nonbreeding is more common among low-quality than among high-quality individuals. Such a reproductive decision may be profitable in long-lived birds in order to maximize own survival during bad breeding conditions (e.g., Cam et al. 1998, Golet et al. 2004).

The experimental protocol of swapping chicks of differing ages confounds treatments with seasonal effects. The direction of this bias rather under- than overestimates the effects of quality. High-quality parents have often been shown to initiate breeding earlier (e.g., Ezard et al. 2007). One can therefore expect that parents of higher quality are overrepresented in the prolonged treatment. Our conclusions may thus be conservative.

Costs of reproduction in a stochastic environment

Puffins are obviously prudent parents (Drent and Daan 1980) and abandon their chick if the cost of raising it becomes too high or their own quality is too low. High-quality parents, on the other hand, may adjust their effort according to the demands of the chick in order to increase its survival chances without risking their own survival too much. The cost of reproduction is highest when parents have barely crossed the quality threshold at which investment in the chick is profitable (Erikstad et al. 1997, 1998). This explains the positive relation between body mass and survival of accepters during the first winter after the manipulation experiment (Fig. 3). Heavy birds can invest in raising offspring without incurring survival costs. Lighter birds, however, pay a survival cost for their investment. Their survival is thus lower than that of low-quality birds that refrain from investing in offspring. In addition, there is a certain chance of misjudging one's own quality. Individuals that invest in reproduction although their body condition was too poor will also experience higher mortality during the first winter.

Overall, puffins succeed in protecting their own survival against reductions. This is in accordance with theoretical (Gadgil and Bossert 1970, Lebreton and Clobert 1991, Stearns 1992) and empirical findings (Gaillard et al. 2000, Stahl and Oli 2006) that adult survival is the single most important life-history trait (as measured by elasticity; Sæther and Bakke 2000). Likewise, the temporal variation in adult survival is often surprisingly low (Waugh et al. 1999, Sandvik and Erikstad 2008), suggesting that this life-history trait is canalized (Gaillard and Yoccoz 2003).

A number of studies have found evidence supporting the prediction that costs of reproduction will be visible even in long-lived species if conditions are unfavorable, although above the breeding threshold (Erikstad et al. 1998). For instance, survival of Tengmalm's Owls (*Aegolius funereus*) was reduced only in years of decreasing vole abundance and only in birds that had late laying dates (Laaksonen et al. 2002). Blue Petrels (*Halobaena caerulea*) showed a negative correlation between breeding and subsequent survival only in inexperienced breeders, while experienced breeders survived better than experienced nonbreeders (Barbraud and Weimerskirch 2005). In Common Murres (*Uria aalge*), breeding success late in life was depressed in individuals that had experienced cold winters early in life (Reed et al. 2008). Survival of breeding Soay sheep (*Ovis aries*) was depressed in relation to non-breeders only in wet and stormy winters and only in first-time breeders and old individuals (Tavecchia et al. 2005). In an historical human (*Homo sapiens*) population, longevity was negatively related to number of children only among women of the lowest social class (landless), but positively so in farmers and smallholders (Lycett et al. 2000). On the other hand, a couple of studies have actively looked for an interaction between costs of reproduction and environmental or individual conditions, without finding such effects. Weddel seals (*Leptonychotes weddellii*) paid costs of reproduction even under favorable environmental conditions (Hadley et al. 2007). In Gambian women, the positive relationship between number of children and subsequent survival held irrespective of the health status of the mother (Sear 2007).

To summarize, this paper adds to a growing body of evidence that parental investment in many long-lived species is utterly flexible (cf. Ricklefs and Minot 1991). Using a hypothesis-driven approach, we show that parents take their own quality and their offspring's prospects into account when making reproductive decisions. In accordance with predictions derived for life histories in stochastic environments (Erikstad et al. 1998), even long-lived species are willing to pay survival costs of reproduction when they are close to the threshold at which reproduction becomes profitable.

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APPENDIX

Capture–mark–resighting models (*Ecological Archives* E090-227-A1).