Experimental evidence that age-specific reproductive success is independent of environmental effects

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An age-specific improvement in reproductive performance has been reported in many iteroparous breeders. However, whether this is a consequence of intrinsic differences in competence amongst age classes or extrinsic differences in the environment they experience is unclear since the timing of breeding within a season generally also differs with age. To disentangle these effects, we experimentally manipulated the timing of breeding in shags, *Phalacrocorax aristotelis*. Old and young individuals thus reared their chicks at the same time both early and late in the breeding season. When breeding in the same environmental conditions, old pairs performed consistently better than young pairs. These data clearly demonstrate that the age-related differences in reproductive performance are not a result of environmental effects, but rather a consequence of intrinsic differences in brood rearing capacity.

Keywords: shag; parental age; timing of breeding; reproductive success

1. INTRODUCTION

In species which breed episodically, there is generally a close interaction between reproductive performance and age, with younger individuals typically performing less well (Clutton-Brock 1988). There are a number of different hypotheses to explain the pattern of age-specific reproductive success observed at the population level. These encompass both changes in the spectrum of phenotypic quality represented in different age groups and age-related changes in the competence of individuals and the associated costs of reproduction (Stearns 1992; Forslund & Pärt 1995). At the individual level, much of the observed intraspecific variation in reproductive performance with age is likely to be state dependent. Variation in condition between and within individuals will affect their capacity to produce and rear offspring and thereby influence the scheduling of various life-history events such as the age of first reproduction and, in seasonally breeding species, the relative timing of breeding within a season (McNamara & Houston 1996).

Studies of long-lived birds have provided a large amount of the empirical data on age-specific reproductive success (Clutton-Brock 1988; Newton 1989; Sæther 1990; Forslund & Pärt 1995). However, generally, there is also an age-related difference in the timing of breeding associated with the observed differences in breeding success. Younger individuals tend to breed later in the season than older birds and may experience different environmental conditions as a result (Perdeck & Cavé 1992). Therefore, in correlative studies in which reproductive success is

examined in relation to age, the potentially independent effects of the time of year and age are confounded. This makes it very difficult to identify age-related differences in performance which are independent of seasonal changes in the environment. In order to tease apart these intrinsic and extrinsic effects, it is necessary to alter the timing of breeding in relation to age experimentally and thereby examine the performance of individuals of differing ages experiencing the same environmental conditions.

While there have been numerous experimental studies investigating the effect of timing of breeding on avian reproductive success (e.g. Parsons 1975; Hatchwell 1991; Brinkhof *et al.* 1993; Norris 1993; Verhulst *et al.* 1995; Aparicio 1998), there has been surprisingly little experimental work on age-specific reproductive performance (Forslund & Pärt 1995). Only one study has specifically manipulated the timing of breeding in relation to age: by removing first clutches, de Forest & Gaston (1996) forced older common guillemots (*Uria aalge*) to breed, in this case, not at the same time as younger birds, but later in the season. No studies have manipulated the timing of breeding such that old and young birds breed at the same time or manipulated the timing of breeding of younger pairs. Furthermore, comparisons of breeding performance generally span the whole breeding event and the capacity to rear chicks has not been separated from the capacity to produce and hatch eggs. Therefore, using the shag (*Phalacrocorax aristotelis*), a seasonally breeding bird with marked differences in reproductive success and timing of breeding in relation to age (Potts *et al.* 1980; Aebischer 1993; Aebischer *et al.* 1995), we (i) manipulated young birds so that the hatching date of the chicks they reared was

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brought forward in the season to coincide with those of control older pairs, and (ii) manipulated older birds so that they reared chicks hatching late in the season at the same time as control younger pairs. Our protocol allowed us to test whether, when breeding in the same environmental conditions, young parents perform less well during chick rearing than do older pairs.

2. METHODS

The work was carried out during the summer of 1998 at a colony of 600 pairs of shags on the Isle of May, south-east Scotland (56°11' N, 02°33' W). Approximately 25% of the breeding birds at this colony had been ringed as chicks, so were of known age. A further 25% had been ringed as breeding adults and, thus, their minimum ages were known. In addition, two-year-old shags, the youngest recorded breeding age, can be recognized from plumage characteristics (Potts 1971). Previous correlative work on shags has suggested that the major difference in age-specific reproductive success occurs between two-year-old and older males and that there is no independent effect of female age (Potts *et al.* 1980; Aebischer 1993). However, pairs involving two-year-old males also breed significantly later in the season than older males (Potts *et al.* 1980). Thus, as is generally the case, age and seasonal effects are confounded. In light of this, we identified two age groups of parents from a combination of ringing and plumage information: 'young' pairs were those containing a two-year-old male, while 'old' pairs consisted of those in which the male was at least three years old (mean $\pm$ s.e. age where exact age known 6.95 ± 0.63 years, $n=19$). Although pairs were defined in terms of the age of the male, male and female age within a pair were significantly and positively correlated (among all pairs in 1998 where the precise age of both pair members was known; Spearman's rank correlation $r_s=0.56$, $n=65$ and $p<0.001$). The female is generally older than the male and there was no difference in the age gap in pairs where the male was two years old and pairs in which he was older (older males, female 2.50 ± 0.74 years older than the male and two-year-old males, female 2.59 ± 0.71 years older than the male; $t_{57}=0.09$ and $p>0.9$, no significance (n.s.)).

On average the old pairs laid 12 days earlier than young pairs (old pairs' laying date, 7 May ± 1 day, $n=33$ and young pairs' laying date, 19 May ± 1 day, $n=34$; $t_{65}=6.89$ and $p<0.001$). In order to separate the confounding effects of age and season on reproductive performance, hatching dates were manipulated by extending (old pairs) or reducing (young pairs) the incubation period through a cross-fostering protocol. This involved exchanging clutches between groups of four pairs that comprised two old pairs matched for their laying date and two young pairs laying on average 12 ± 1 days later. All nests contained three eggs, the modal clutch size in the shag irrespective of age (Coulson *et al.* 1969; Stockland & Amundsen 1988). One of the old pairs was given the clutch of a young pair, thereby becoming an 'old experimental', with its hatching date delayed by 12 days. The hatching date of one of the young pairs was advanced by 12 days by replacing its clutch with that of the second old pair in the group, thereby becoming a 'young experimental'. This old pair and the remaining young pair were given the clutches from the same age experimentals and formed control pairs of each age class. This procedure gave a matched design in which old controls and young experimentals were both given eggs laid by old pairs, which hatched early in the season, and young controls

Figure 1. Diagrammatic representation of the experimental procedure in which half the old pairs (O) were delayed and half the young pairs (Y) were advanced. Dotted circles illustrate the predicted outcome where the difference in breeding performance is a consequence of parental age.

and old experimentals had eggs laid by young pairs, which hatched late in the season. The clutch exchanges were carried out within ten days of the hatching of the old eggs and, thus, at least one-third of the way through incubation in all cases (total incubation period 36 days; Potts *et al.* 1980). The experimental protocol ensured that (i) there was the same spread of laying dates for birds in all treatment groups, (ii) no pairs reared their own brood, and (iii) pairs hatching chicks at the same time had eggs of a similar quality (i.e. both old and young pairs had eggs produced by old pairs in the early hatching groups and by young pairs in the late hatching groups; older pairs tend to produce larger eggs; Coulson *et al.* 1969). The overall experimental design is illustrated in figure 1, which also shows the predicted outcome if the age-related difference in performance is not due to environmental effects.

The clutch exchanges were carried out within 17 groups of four pairs. Of the 68 nests in the experiment, one was subsequently found to be attended by three adults, an occasional occurrence in shags (Harris 1982) and was excluded from all analyses. Three nests were lost to human disturbance in the period after the clutch exchanges had been completed and were excluded from all analyses except laying date. The remaining 64 nests comprised 15 old controls, 16 old experimentals, 17 young controls and 16 young experimentals.

We used generalized linear models (GLMs) to investigate the effects of parental age (young or old parents rearing the chicks) and time of hatching (early or late hatching date) on fledging success (the proportion of hatched eggs giving rise to fledged chicks per nest) with a binomial distribution and logit link function corrected for overdispersion (ANODEV; see Crawley 1993). All means are given ± 1 s.e.

As expected given the experimental protocol, there was no difference in hatching date between old controls and young experimentals (old pairs' hatching date, 11 June ± 2 days, $n=15$ and young pairs' hatching date, 10 June ± 1 day, $n=13$; $t_{26}=0.39$ and $p>0.5$, n.s.) or between old experimentals and young controls (old pairs' hatching date, 21 June ± 2 days, $n=14$ and young pairs' hatching date, 20 June ± 2 days, $n=14$; $t_{26}=0.43$, and $p>0.6$, n.s.). There was also no difference in male

Figure 2. The effects of parental age and time of hatching on fledging success in control and experimental old and young pairs. The two arrows indicate the direction of the manipulation of hatching date. Fledging success was significantly higher in the old pairs and there was no significant effect of time of hatching (GLM: age, $F_{1,55} = 7.11$ and $p < 0.025$, time of hatching, $F_{1,54} = 3.10$ and $p > 0.09$, n.s. and interaction term, $F_{1,53} = 0.02$ and $p > 0.75$, n.s.).

age between old controls and old experimentals, where the exact age was known (old controls, 7.29 ± 1.34 years, $n = 7$ and old experimentals, 6.75 ± 0.68 years, $n = 12$; Mann-Whitney $U = 38$ and $p > 0.2$, n.s.). Since the timing of the clutch exchanges was part way through the incubation periods, pairs that lost eggs early in incubation were not included in the experiment and hatching success (proportion of eggs hatching per nest) was high in all groups (old controls, 0.87 ± 0.05 , $n = 15$; old experimentals, 0.73 ± 0.10 , $n = 16$; young controls, 0.70 ± 0.09 , $n = 17$; young experimentals, 0.81 ± 0.09 , $n = 16$; GLM: age, $F_{1,61} = 0.39$ and $p > 0.5$, n.s., time of hatching, $F_{1,62} = 2.36$ and $p > 0.1$, n.s. and interaction term, $F_{1,60} = 0.29$ and $p > 0.5$, n.s.). The majority of chick mortality occurs in shags during the first ten days of life (Snow 1960), the period when chicks are unable to produce their own body heat and rely on brooding by the adults (Østnes & Bech 1997). Young chicks also receive partly digested food from their parents. We therefore split chick rearing into two periods to examine the pattern of chick mortality: zero to ten days and ten days to fledging (50 days).

To examine effects on chick growth, chicks were weighed (initially to the nearest 0.1g, then the nearest 2.5g when between 200 and 1000g and thereafter to the nearest 10g) approximately every four days until close to fledging. Asymptotic masses of surviving chicks were calculated by fitting logistic growth curves to the data (Ricklefs 1967). Growth rates at the point of inflection derived from these curves are misleading because they depend on the estimate for the asymptote (Krebs 1999). Therefore, we took the gradient of the linear phase of growth (chick age eight to 30 days) as a measure of growth rate. Both asymptotic masses and growth rates were summed for the whole brood, with the number of chicks included in analyses as a covariate to account for the effects of differences in brood size.

3. RESULTS

As expected from previous studies (Potts *et al.* 1980; Aebischer 1993), in the control groups the old pairs hatching chicks early in the season had a higher reproductive performance than did young pairs hatching chicks late in the season (figure 2). However, when

Figure 3. Proportion of hatched eggs surviving in relation to chick age, age of parents and hatching date. Filled circles, old pairs in the early hatching group; filled squares, old pairs in the late hatching group; open circles, young pairs in the early hatching group; open squares, young pairs in the late hatching group. There was a significant effect of parental age on chick survival during the first ten days after hatching; chick survival during this period was not affected by time of hatching (GLM: age, $F_{1,55} = 9.30$ and $p < 0.01$, time of hatching, $F_{1,54} = 0.08$ and $p > 0.75$, ns and interaction term, $F_{1,53} = 3.90$ and $p > 0.05$, n.s.). There was a significant effect of time of hatching but no effect of parental age in the period from chick age ten days to fledging (GLM: age, $F_{1,48} = 1.72$ and $p > 0.2$, n.s., time of hatching, $F_{1,49} = 4.87$ and $p < 0.05$ and interaction term, $F_{1,47} = 2.53$ and $p > 0.1$, n.s.).

breeding at the same time, old pairs consistently outperformed young pairs. Early in the season, old controls reared 48% more hatched eggs to fledging than young experimentals and late in the season old experimentals raised 79% more hatched eggs to fledging than young controls (figure 2).

The effect of parental age on chick survival was most marked during the first ten days after hatching. During this early period, there was a significantly higher survival rate in chicks reared by old pairs and this did not differ with respect to time of hatching (figure 3). For chicks older than ten days, survival was not related to parental age. While the survival of these older chicks was significantly poorer in the later hatching groups (figure 3), this effect was not sufficient to produce any difference in overall fledging success in relation to season (figure 2).

There was no effect of parental age or time of hatching on the growth of chicks surviving in broods (ANCOVA of brood growth with number in brood as the covariate: brood number, $F_{1,45} = 626.13$ and $p < 0.001$, age, $F_{1,43} = 0.20$ and $p > 0.5$, n.s. and time of hatching, $F_{1,44} = 0.46$ and $p > 0.5$, n.s.; all interactions n.s.). There was also no effect of parental age or time of hatching on total asymptotic mass of chicks surviving in broods (ANCOVA of brood asymptotic mass with number in brood as covariate: brood number, $F_{1,45} = 560.17$ and $p < 0.001$, age, $F_{1,44} = 0.36$ and $p > 0.5$, n.s. and time of hatching, $F_{1,43} = 0.24$ and $p > 0.5$, n.s.; all interactions n.s.).

4. DISCUSSION

The results of this experiment clearly demonstrate an effect of parental age on breeding performance that is independent of the time of season. Young birds hatching chicks early in the season and thereby experiencing the same environment as the old birds that normally breed at this time reared significantly fewer young than old birds. Similarly, old birds hatching their chicks later in the season, in the same environment as that normally experienced by young birds, did better than the young birds. This consistently higher performance of the older birds was not due to any differences in clutch size or hatching success (these were the same for all pairs) or egg quality (both young and old pairs breeding at the same time had eggs from the same age group—old bird eggs for the early hatching pairs and young bird eggs for the late hatching pairs).

Experiments of this kind can only be achieved by manipulations, in this case by exchanging clutches. Our protocol ensured that both experimental and control pairs experienced a clutch exchange but, in the case of the experimental pairs, the duration of the incubation period was also altered, being increased in the old experimentals and reduced in the young experimentals. This was necessary in order to achieve the changes in hatching date. It is possible that this influenced the amount of time available for females to recover from the demands of egg laying. If this recovery time effect was important enough to influence reproductive performance during chick rearing to an appreciable extent, we would expect to see evidence of an improvement in breeding success in pairs with extended incubation in comparison with controls of the same age (i.e. in the late-hatching old pairs compared with control old pairs) and a corresponding impairment in those with reduced incubation time (i.e. the early-hatching young pairs compared with control young pairs). In fact, there were no significant differences between these groups and the trends actually went in the opposite direction (figure 2). On the other hand, incubation itself can be relatively demanding, particularly when, as in this study, birds are incubating at temperatures outside the thermoneutral zone (Williams 1996; Thomson *et al.* 1998). Experimental changes in incubation costs alone can have fitness consequences (Heaney & Monaghan 1996; Monaghan & Nager 1997; Bryan & Bryant 1999). However, in this case the possible fitness costs associated with the changes in incubation would be expected to produce the opposite results from those that we observed. The experimental old birds had an increased incubation demand, which would be expected to reduce their breeding success. Despite this, they still performed better than young birds hatching at the same time having experienced normal incubation demands. Conversely, the experimental young birds had a reduced incubation demand, but still performed less well than normally incubating older birds breeding at the same time. Thus, our observed differences between the adult and young birds may in fact have been greater had incubation demand not also been altered. Furthermore, the experimental protocol was such that clutches were exchanged part way through incubation. This meant that any birds that lost all or some of their eggs very soon after laying, and thereby did

not have a three-egg clutch when the manipulations were performed were not included in the experiment. Such early egg loss tends to be more common in young birds (Potts *et al.* 1980) which may have resulted in the sample of young pairs being somewhat biased towards relatively high-quality individuals. Nonetheless, they still performed less well than older pairs.

Our experiment was specifically designed to examine differences in chick rearing abilities. Thus, we largely excluded the effects of differences between young and old pairs in egg loss during incubation which, rather than differences in chick rearing capability, have been considered to be where the main age-specific effects occur in a number of studies (Reid 1988; Boekelheide & Ainley 1989; Weimerskirch 1992; de Forest & Gaston 1996). It is possible that the apparent lack of parental age effects during chick rearing reported in these studies may be because only the highest quality young birds remain in the sample by this stage.

The difference between the parental age groups in our study was largely due to differences in early chick survival and these were not related to the time of the season. For chicks older than ten days, survival was poorer in the later hatching groups. It is not possible to say to what extent this was due to the experimental alteration in incubation demand, differences in environmental conditions or egg quality differences, each of which could have enhanced chick survival in the early young pairs and reduced it in the late old pairs. In any event, the seasonal effect on the survival of chicks over ten days old was not strong and the overall chick survival from hatching to fledging was not significantly influenced by time of season in either old or young pairs.

There are a number of potential mechanisms that could give rise to the poorer chick rearing performance of young birds observed in this study, relating to differences in competence and/or effort. Differences in the foraging abilities of young and old birds may be a contributory factor. The lack of any detectable effect of parental age on growth rates and asymptotic masses of surviving chicks might imply that the young birds are reducing their brood to a size that they can raise successfully. Loss of chicks in the first ten days of life is well known in the shag (Snow 1960) and an alternative explanation to the brood reduction hypothesis is that young breeders may have difficulty adjusting to the new feeding requirements. In the first few days after hatching, shag chicks are too small to eat intact fish and instead receive partly digested food from their parents. Snow (1960) reported breeding shags experiencing extreme difficulties feeding young at this time, in some cases failing completely to feed a chick successfully. It is also possible that young birds are less effective at brooding chicks during the period of thermal dependency or cannot sustain the energetic requirements of the brooding period. The age effects we observed might also operate through other aspects of breeding experience, such as intrapair coordination of activities (Bradley *et al.* 1990; Cézilly & Nager 1996). Individual state and its effect on breeding performance is likely to be involved; this may show age-related changes within the individual itself and there may also be a higher proportion of good quality phenotypes in old age classes through differential survival rates (Forslund & Pärt 1995;

McNamara & Houston 1996). Previous studies in shags have suggested that age effects operate primarily through the males (Potts *et al.* 1980; Aebischer 1993). However, given that the male and female ages within pairs were closely correlated, in the absence of experimental manipulations, it is not possible to attribute age effects unequivocally to one or other sex. Whatever the mechanism, even when faced with the same environmental conditions either early or late in the season, this study clearly demonstrates that young birds are less able to rear chicks successfully than older pairs, irrespective of the time of the season. Thus, the relatively poor reproductive performance of young pairs is not primarily a consequence of extrinsic factors such as environmental quality at the time of chick rearing, which could be forced upon them by, for example, a longer period being required for egg formation. Even if they did breed earlier in the season they would apparently gain little by way of fitness benefits, since intrinsic differences in chick rearing capacity are involved.

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