The effects of parental age on reproductive performance in the shag *Phalacrocorax aristotelis*

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ABSTRACT

An improvement in reproductive performance over the first few breeding attempts is widespread among iteroparous breeders. A number of mechanisms have been suggested to explain this pattern, including age-related changes in competence and effort, improvements in average quality with age, and extrinsic effects. In this study, I aimed to investigate some of the mechanisms underlying age-specific changes in reproductive performance in the shag *Phalacrocorax aristotelis*.

As well as having a lower breeding success, in most species young breeders also breed later in the season than older birds. Therefore, age-related improvements in breeding performance may be due to differences in environmental conditions experienced by young and older breeders, rather than intrinsic differences in breeding capacity. Experimental manipulations are therefore required to separate the confounding effects of age and timing of breeding on reproductive performance. In this study, hatching date was manipulated in young and older shags using a clutch cross-fostering protocol, such that both age classes reared their chicks at the same time, both early and late in the season, from eggs of a similar quality. Older pairs performed consistently better, rearing significantly more chicks both early and late in the season. Thus, the age-specific improvement in breeding success in the shag is not a result of extrinsic factors, but is due to intrinsic differences in brood-rearing capacity.

A key hypothesis proposed to explain underlying intrinsic differences in breeding success is an age-related improvement in foraging performance. This theory proposes that young breeders are unable to meet the extra demands of rearing offspring because of their reduced foraging capabilities. The consequences in sexually size dimorphic species may be that young pairs will have particular problems rearing offspring of the more expensive sex. Most studies of sexually size dimorphic species have found that the larger sex is more expensive to rear in absolute terms. In the shag, the male is 20% heavier than the female, and sons and daughters fledge at a similar size disparity. When breeding in the same environmental conditions, and from eggs of the same quality, this study demonstrated that sons reared by young pairs grew more slowly and reached a lower peak mass than sons reared by older pairs, whereas there was no equivalent difference for daughters. This suggests a difference in young and older

pairs' provisioning capacity, such that young pairs can provide sufficient food to daughters, but are not able to deliver the additional food required for sons. This has important implications for optimal age-specific sex ratios.

The cross-fostering protocol provided two opportunities to compare the foraging behaviour of young and older pairs rearing their chicks at the same time, using radio telemetry. Each individual was followed for a single, complete feeding trip. Early in the season, birds were flying short distances, and making few dives. Late in the season, birds were flying greater distances, and making many more dives. This latter period was also characterised by many broods in the colony being left unattended, a previously undocumented occurrence in shags. Overall, therefore, there was strong circumstantial evidence that feeding conditions were considerably poorer late in the season. There were no differences with respect to age in mean dive duration or mean foraging depth either early or late in the season. However, at the end of the season, older birds had a significantly lower surface to dive duration ratio compared with younger breeders. Older birds were therefore spending less time resting between dives, thereby increasing the time spent foraging. There was no difference between the two age groups when foraging conditions were better early in the season. Thus, there was an interaction between age and environmental conditions on foraging behaviour. Older breeders appear to be adjusting their behaviour to the prevailing conditions, increasing their foraging effort to safeguard offspring fitness when feeding is poor, whereas young pairs do not seem to have the capacity to do this, which could be an important component of their reduced breeding success.

Older individuals may be able to invest more in the current breeding attempt because they are more efficient foragers. Foraging efficiency was measured directly by comparing energy gained (energetic content of food loads) to energy expended (time-energy budgets) during foraging trips of young and older pairs breeding at the same time. There was a tendency for older males to bring back larger food loads than young pairs. However, there was no strong evidence for a difference in foraging efficiency. Older individuals may have improved breeding success through increased food provisioning, achieved through a combination of increased foraging effort and higher foraging efficiency.

Individual ectoparasite load is likely to have an important age component. Young breeding individuals may carry higher loads themselves, through age-related changes in infection rate, behaviour or resistance. There could be important consequences for their offspring, if adult and offspring loads are correlated, or if adults are less proficient at grooming ectoparasites. Loads of the chewing louse *Eidemanniella pellucida* were counted on the broods of young and older parents. Broods of young parents carried significantly more lice, independent of environmental effects.

Sexual selection in species where both sexes have evolved a sexual ornament has been little studied, and the role of age is almost unknown. Young breeders may display a poorer quality ornament, if they are of lower genetic or phenotypic quality, and thus attract a lower quality mate. Shags grow a crest of feathers prior to pair formation, which is lost during incubation. Crest size was quantified in both sexes across a range of ages. There was no evidence of an effect of age on crest size. Rather, variation in crest size was strongly related to aspects of breeding performance, notably if, and when, birds bred. In addition, there was assortative pairing on ornament size. Thus, crests are likely to be play an important role in mutual mate choice.

Chapter 1

General introduction

AGE-SPECIFIC REPRODUCTIVE PERFORMANCE

Among iteroparous breeders, numerous studies have shown that average reproductive performance improves with parental age over the first few breeding attempts (Clutton-Brock 1988; Newton 1989). The majority of such studies have been carried out on birds (e.g. Coulson & White 1958; Ollason & Dunnet 1978; Nisbet *et al.* 1984; Coulson & Thomas; 1985; Nol & Smith 1987; Boekelheide & Ainley 1989; Wooller *et al.* 1990; Hamer & Furness 1991; Sydeman *et al.* 1991; Croxall *et al.* 1992; Komdeur 1996b), and together provide a compelling body of evidence that young individuals perform less well than older individuals in all aspects of the breeding process, including egg volume and mass, clutch size, hatching success and fledging success (review in Sæther 1990). Generally, reproductive success levels off after the first few breeding attempts, and may decrease again in old age (e.g. Newton *et al.* 1981; Reid 1988; Gustafsson & Pärt 1990; Hamer & Furness 1991; Weimerskirch 1992; Clum 1995; Komdeur 1996b; Møller & de Lope 1999). Thus, age-specific reproductive performance has four possible stages: I) delayed breeding; II) improving performance after onset of breeding; III) experienced adulthood; IV) decrease in performance in old age (senescence) (figure 1.1).

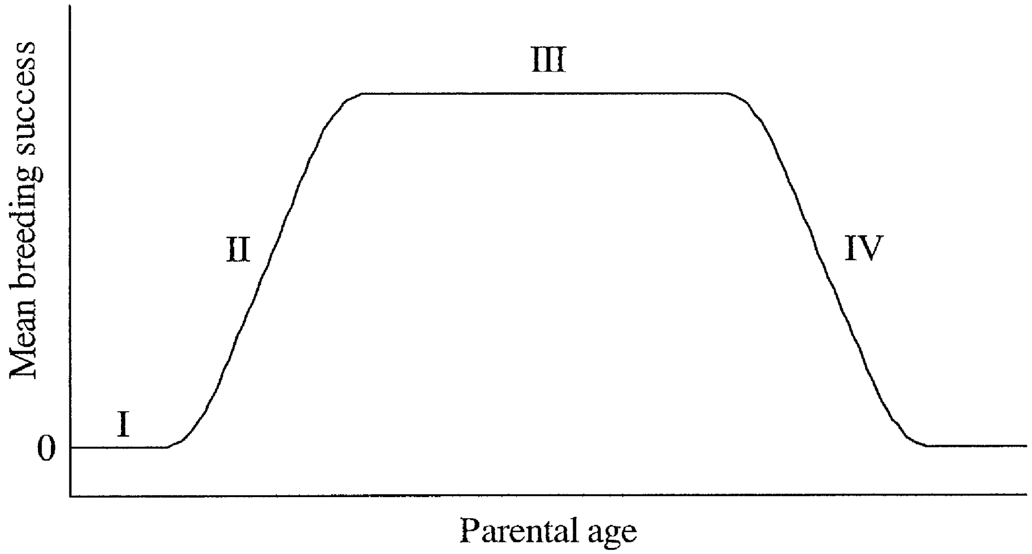

Figure 1.1: Stages of age-specific breeding success (from Fowler 1995; see text).

MECHANISMS OF AGE-SPECIFIC REPRODUCTIVE PERFORMANCE

A number of mechanisms have been proposed to explain the variation in reproductive performance with age (Forslund & Pärt 1995; Fowler 1995; Martin 1995; Nisbet & Nager in press).

1. Reproductive effort

In iteroparous species, life history theory predicts that individuals will adjust the effort they put into the present reproductive event in order to maximise the prospect of future survival and reproduction (Residual Reproductive Value - RRV) (Williams 1966; Roff 1992; Stearns 1992). Therefore, there is a trade-off between current reproduction and future survival and reproduction, because of 'costs of reproduction' in terms of reduced subsequent fitness associated with current breeding (Clutton-Brock 1991; Ylönen *et al.* 1998). Older individuals with a low RRV may improve their fitness by putting more effort into present reproduction than do young individuals with a high RRV, because older individuals are likely to have fewer reproductive attempts in the future. Young individuals are said to be showing 'restraint' (Curio 1983). However, RRV only begins to decrease when survival rate decreases, and in many species this only occurs among the oldest individuals, presumably due to senescence (Forslund & Pärt 1995). Therefore, this mechanism is not predicted to explain the improvement in performance among the youngest breeders. An alternative explanation is that older individuals are more efficient, and as a result incur a lower cost of reproduction, and can thus invest more in the present reproductive attempt without incurring extra costs (young individuals are less efficient – 'constraint' hypothesis, Curio 1983 – see below). Studies based on indirect measures of costs of reproduction, such as mass loss during the current breeding attempt (Pugasek 1981, 1983, 1984; Hamer & Furness 1991), cannot separate these two potential effects. Experimental demonstration of costs, i.e. future survival and reproduction, is needed to show an effect of reproductive effort

(Clutton-Brock 1984; Partridge 1992; Pärt *et al.* 1992; Pärt & Forslund 1996; Galbraith *et al.* 1999). In addition, with reproductive effort only predicted to increase amongst the oldest individuals, such effects may be masked by senescence. Moreover, most studies have reported a decrease in breeding performance towards the end of reproductive life, rather than an increase that would be expected with an increase in effort (e.g. Newton *et al.* 1981).

2. Improvements of competence

i) Foraging efficiency

It is well established that juveniles are often less efficient foragers than adults (reviewed in Wunderle 1991). Young breeders may also forage less efficiently than older breeding individuals (Curio 1983; Burger 1988). There is growing support for this mechanism explaining much of the variation in age-specific reproductive performance over the first few breeding attempts (Nur 1984; Reid 1988; Desrochers 1992a; Forslund & Pärt 1995; Catry & Furness 1999; Galbraith *et al.* 1999). There may be consequences on the individuals themselves (e.g. inability to attain breeding condition, inability to attract a high quality mate – Weimerskirch 1992; Andersson 1994), or on the survival and growth of their offspring. The constraint on young individuals could be due to them not being fully mature (Marchetti & Price 1989), or requiring time to learn the necessary skills (Martin 1995). However, only two studies have measured foraging efficiency of young and old breeders directly, and both have shown that efficiency improves significantly with age (Jansen 1990; Desrochers 1992b).

Amongst the oldest individuals, senescence may be caused by a reduction in foraging efficiency through ‘wear and tear’ (Clum 1995).

ii) Breeding experience

Individuals will improve their performance as they age through increased experience, if there is a strong learned component to successful breeding. This experience could refer to any aspect of the breeding process (e.g. guarding a nest site, fighting off predators, finding nest material, allocation of food between competing offspring, preening ectoparasites from offspring), although when it is examined it is invariably measured simply as number of years of breeding experience. Age and experience are very closely linked, because individuals breed in most years after recruitment. Some studies have shown there to be a strong influence of experience independent of age (e.g. Ainley & Schlatter 1972; Pyle *et al.* 1991; Croxall *et al.* 1992; Forslund & Larsson 1992; Komdeur 1996a; for a review see Pärt 1995), while other studies have found no such effect (e.g. Newton *et al.* 1981; Nol & Smith 1987; Boekelheide & Ainley 1989). The only experimental evidence comes from a study by Pärt (1995), who separated the effects of age and experience by manipulating age at first breeding, by preventing recruiting individuals from breeding. Manipulated birds returned the following season, and he found that they were more successful than unmanipulated birds of the same age with one year of breeding experience, concluding that experience was much less important than other factors, such as individual quality, in determining patterns of age-specific breeding success.

iii) Duration of the pair bond

A number of studies have found that an improvement in reproductive success has been associated with the length of the pair bond (e.g. Ollason & Dunnet 1988; Bradley *et al.* 1990, 1995; Ens *et al.* 1996; Cézilly & Nager 1996). This is thought to occur because pairs become more skilled at co-ordinating activities with each breeding attempt together (Catry & Furness 1999; Ratcliffe & Furness 1999; Weimerskirch 2000), although this mechanism has been measured purely in terms of the number of years a pair has been together. Divorce is most frequent among younger individuals, and often occurs after breeding failure (Aebischer *et al.* 1995).

However, in some species with improvements in breeding performance with age, mate retention even among older individuals is either very low or zero (Shaw 1986; Boekelheide & Ainley 1989; Cézilly & Johnson 1995).

iv) Access to resources

Older individuals may have better access to resources (mates, nest sites, territories) through a number of mechanisms, such as early arrival, social dominance and local familiarity (Potts *et al.* 1980; Nelson 1988), and may limit access of younger individuals to such resources.

3. Mutations

This is an alternative hypothesis to that of 'wear and tear' to explain the phenomenon of senescence. A reduction in reproductive success among the oldest individuals might occur if there are mutations that only affect this age group (Partridge 1989). Natural selection acts more strongly earlier in the lifespan, since the proportion of the population exposed to selection pressures decreases with age, so that mutations affecting survival and reproduction of young individuals will be more strongly selected against. As individuals get older, there may be an accumulation of mutations affecting fertility, leading to a decline in fertility with age. Alternatively, genes with beneficial effects early in the lifespan may have deleterious effects late in the lifespan. Pleiotropy of this kind could be maintained because the beneficial effect is acting on many more individuals (Partridge 1989).

4. Selection hypothesis

This hypothesis states that individuals do not vary in reproductive performance as they age, but average individual quality at the population level increases with age.

This can occur in two ways. First, individuals with high breeding quality may also have improved survival rates. Some studies have found that average quality increases with age due to differential survival rates of good and poor breeders (e.g. van Noordwijk *et al.* 1981; Nol & Smith 1987; Wooller 1990; Ratcliffe *et al.* 1998; Cam *et al.* 2000; Espie *et al.* 2000). However, some studies have shown that age-specific variation is entirely explained by improvements with age within individuals (e.g. Hamann & Cooke 1987; Newton & Rothery 1998). Secondly, high quality individuals may delay breeding (Nol & Smith 1987; Gustafsson & Pärt 1990), but most studies have shown the converse i.e. a higher breeding performance was recorded among individuals with a young age of first breeding (Newton *et al.* 1981; Boekelheide & Ainley 1989; Pyle *et al.* 1991; Forslund & Larsson 1992). The selection hypothesis cannot explain the breeding performance among the oldest individuals, because the observed reduction in reproductive success is opposite to that predicted by the high average quality among these age classes, but this mechanism may be superseded by others at these ages.

5. Extrinsic factors

In the majority of species, younger individuals breed later in the season than older individuals, and thus may encounter different environmental conditions (Perdeck & Cavé 1992; de Forest & Gaston 1996). The reasons for this are unclear, but the role of body condition, operating through foraging performance (Weimerskirch 1992; Desrochers 1992a) and competition (Potts *et al.* 1980) is likely to be important. Alternatively, young individuals may need more time to carry out activities such as courtship and site selection. Therefore, the patterns of age-specific reproductive performance observed in these species may be due entirely to extrinsic rather than intrinsic factors. Table 1.1 summarizes mechanisms underlying age-specific breeding performance that have been proposed.

Mechanism	Explanation
Reproductive effort	decreasing Residual Reproductive Value with age
Competence	foraging efficiency breeding experience duration of pair bond access to resources
Selection	differential survival delayed breeding
Mutation	senescence pleiotropy
Extrinsic factors	experiencing different environmental conditions

Table 1.1: Proposed mechanisms for age-specific breeding success (Forslund & Pärt 1995; Fowler 1995; Martin 1995; Nisbet & Nager in press).

BACKGROUND TO THIS THESIS

1. The study species

The shag *Phalacrocorax aristotelis* is a pursuit-diving piscivorous marine bird that breeds in colonies of up to 7,000 pairs on the coasts of north-eastern Europe, the Mediterranean and North Africa (Wanless & Harris 1997). 90% of male and 17% of female shags recruit to the breeding population at age two, the remainder thought to recruit at age three (Aebischer 1986), and live for up to 20 years (Wanless & Harris 1997). Timing of breeding within a season is very variable. Shags have an elaborate courtship during pair formation (Snow 1963). A large nest is built, and the female usually lays 2 to 4 eggs (modal clutch size is 3 in all colonies recorded, Snow 1960; Coulson *et al.* 1969; Aebischer 1985; Stokland & Amundsen 1988). Shags are socially monogamous, with both sexes taking part in incubation and chick-rearing, although extra-pair paternity is 18% (Graves *et al.* 1992). Incubation lasts approximately five weeks. Hatching is asynchronous (Amundsen & Stokland 1988;

Stokland & Amundsen 1988), often leading to a marked size hierarchy in the brood. Chicks fledge from the nest at seven weeks of age (Snow 1960).

2. Age-specific reproductive performance in the shag

Three main studies have investigated age-specific breeding biology in shags. Coulson *et al.* (1969) measured egg size in relation to age, laying sequence and laying date, of birds of known age on the Farne Islands, north-east England (55°37'N, 01°37'W) from 1963-67. Breadth, length, volume and shape all showed a marked increase with age. Young birds also showed more variability in egg breadth. Volume showed the most pronounced change with age. However, there was no independent effect of age on clutch size after controlling for laying date (laying date declined with age).

Potts (1966) and Potts *et al.* (1969, 1980) followed the same population in the Farne Islands from 1961-71. Reproductive success was mainly accounted for by quality of the nest site (based on four factors found to be important determinants of breeding success, Potts *et al.* 1980) and to a lesser extent breeding experience. It was not affected by age after the first breeding attempt. Overall, first time breeders were 30% less successful than established breeders were. The effect of age was accounted for by experience i.e. whether they had bred before or not.

The third major study on age-specific breeding performance in shags was carried out by Aebischer (1985, 1986, 1993) on the Isle of May, south-east Scotland (56°11'N, 02°33'W) from 1981-83. The effects of age, timing of breeding and nest site quality on reproductive performance were examined. Two-year old males performed half as well as older males. The effects of female age were not found to be significant, although age within pairs was positively correlated. Pairs containing a two-year-old male bred later in the season, occupied lower quality nest sites (based on four factors found to affect breeding success, Aebischer 1985) and fledged fewer chicks. They also showed lower mate retention in the following season than experienced breeders (Aebischer *et al.* 1995). There was no effect of age on clutch size.

In summary, egg volume, fledging success and overall breeding success in shags have been found to increase with age, although in the Isle of May study this was only true in pairs containing two-year-old males. In both populations, there appeared to be no significant improvement past the first breeding attempt. First-time breeders bred much later in the season, and had a lower nest site quality.

3. The study colony

Fieldwork took place on the Isle of May, at the same colony used by Aebischer. Counts of shags have been made there since 1921 (annually since 1973), and ringing of chicks and adults has occurred every year since 1962 (Aebischer 1986). Numbers increased from one pair in 1921 to a peak of 1,916 pairs in 1987. This rise was interrupted on two occasions (1974-6 and 1985-6), when the drop in breeding numbers was attributed to substantial non-breeding by adults, rather than mortality (Aebischer 1986, Aebischer & Wanless 1992). From 1987, numbers fluctuated until another non-breeding event in 1993. In early 1994, there was a dramatic wreck of adults (Harris & Wanless 1996). This was the most severe mortality of shags recorded in the last 30 years. The population dropped to 403 pairs in 1994, and has increased to 541 pairs in 2000. Currently, approximately half of the adults in the colony are ringed, of which half were ringed as chicks so are of known age.

4. Age-specific breeding performance in 1997

In 1997, prior to the main experimental part of this study, I recorded a number of breeding parameters on shags of known age. Age was largely derived from ringing information. In addition, two-year-olds, the youngest breeding age, can be distinguished on plumage (Potts 1971). Reproductive success (number of chicks fledged per nest) of known age male and female shags are shown in figure 1.2. Among males, there is a marked improvement in breeding performance between the ages of two and three, after which success levels off (figure 1.2a). Sample sizes were considerably lower among young female breeders, due to their lower recruitment rate at that age (Aebischer 1986), but there appears to be a lower breeding performance among two and three year olds (figure 1.2b). Given the high sample sizes of two-year-old males, and previous research at this colony suggesting that there was no independent effect of female age (Aebischer 1985), I concentrated my research on the comparison between pairs containing two-year-old males ('young') and males aged at least three ('older'). It is important to note, however, that age of the male and female within pairs was correlated (Spearman's Rank: $r_s = 0.34$, $n = 53$, $p < 0.05$). Table 1.2 shows that pairs containing two-year-old ('young') males had lower clutch volume, chick peak mass, fledging success and reproductive success than pairs containing a male aged at least three ('older'), but there was no effect of age on nest site quality (scored in the same way as Aebischer, 1985), clutch size, hatching success or chick growth rates. These results accorded well with previous findings, with the exception of nest site quality, which was no different between the two age groups. This may well have been due to the population crash in 1994, reducing the colony size by 75% (Harris & Wanless 1996) enabling young breeders to obtain nest sites that were equally good as those used by older breeders. This result parallels the findings of Potts *et al.* (1980), who recorded an improvement in nest site quality among young breeders after a population crash.

Young males also bred significantly later in the season (see table 1.2). As mentioned previously, this can have important consequences for the study of age-specific breeding success because the effects of age and season are confounded. Figure 1.3 illustrates this effect. In 1997, the two variables were so tightly correlated that when parental age and laying date were entered into an analysis of breeding success, there was no independent effect of parental age (Generalized Linear Model with logit link function corrected for overdispersion (ANODEV – Crawley 1993): parental age: $F_{1,113} = 0.12$, ns; laying date: $F_{1,114} = 22.76$, $p < 0.001$; interaction term: $F_{1,112} = 1.76$, ns).

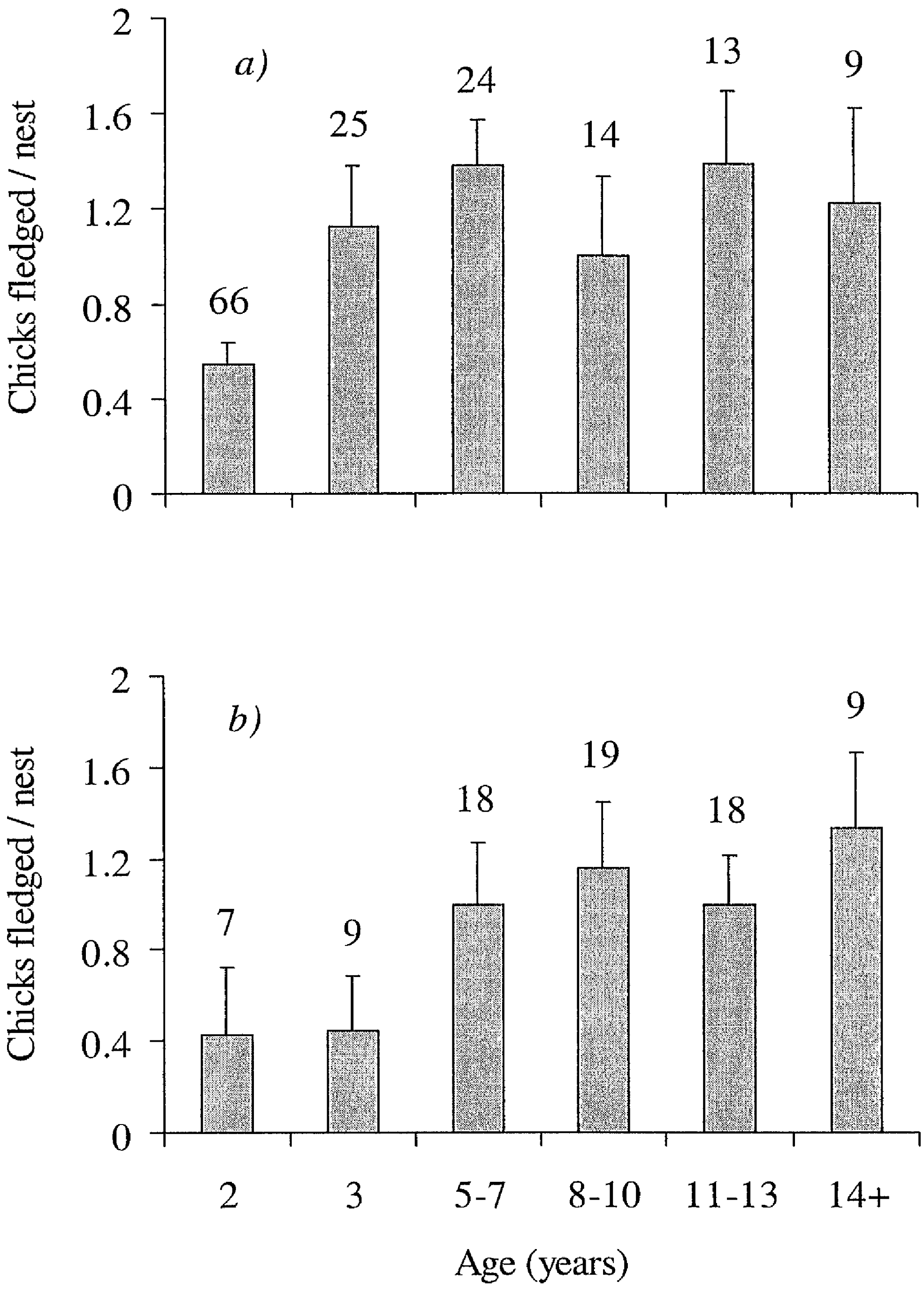

Figure 1.2: The effects of a) male age and b) female age on reproductive success (mean ± s.e.); sample sizes are shown above the bars.

Breeding parameter	Males 2 yrs	Males 3+ yrs	Statistic	p
Nest site quality rating *	2.11 ± 0.02	2.12 ± 0.02	$t_{143} = 0.31$	ns
Laying date (days after Mar 1st)	60.31 ± 1.97	40.55 ± 1.51	$t_{114} = 7.96$	< 0.001 †
Clutch size	2.94	3.04	$\chi^2_3 = 2.38$	ns
Clutch volume (cm^3)	133.77 ± 2.58	140.18 ± 1.70	$t_{38} = 2.38$	< 0.05 †
Hatching success	0.35	0.55	$F_{1,101} = 3.10$ **	ns
Chick growth rate (g/day) ***	50.38 ± 1.77	54.00 ± 1.00	$t_{40} = 1.68$	ns
Chick peak mass (g) ****	1513.69 ± 38.22	1620.61 ± 29.77	$t_{38} = 2.18$	< 0.05 †
Fledging success	0.35	0.65	$F_{1,50} = 6.28$ **	< 0.05 †
Reproductive success	0.55	1.22	$F_{1,149} = 13.40$ **	< 0.001 †

Table 1.2: Breeding performance (mean ± s.e.) of the two male age groups in 1997.

* Rating based on multiple regression analysis of 25 characteristics of the nest site by Aebischer (1985), which derived the following equation:

rating = 0.259 (ledge size) + 0.166 (risk of flooding after rain) - 0.042 (risk of level attack by other shags) + 0.230 (wave reach)

** Generalized linear model with logit link function corrected for overdispersion (ANODEV – Crawley 1993).

*** Gradient of the linear phase of growth (chick age 8-30 days); mean taken for each brood

**** Logistic curves fitted to the growth data (Ricklefs 1967); mean taken for each brood

† significance retained after sequential Bonferroni analysis (Rice 1989)

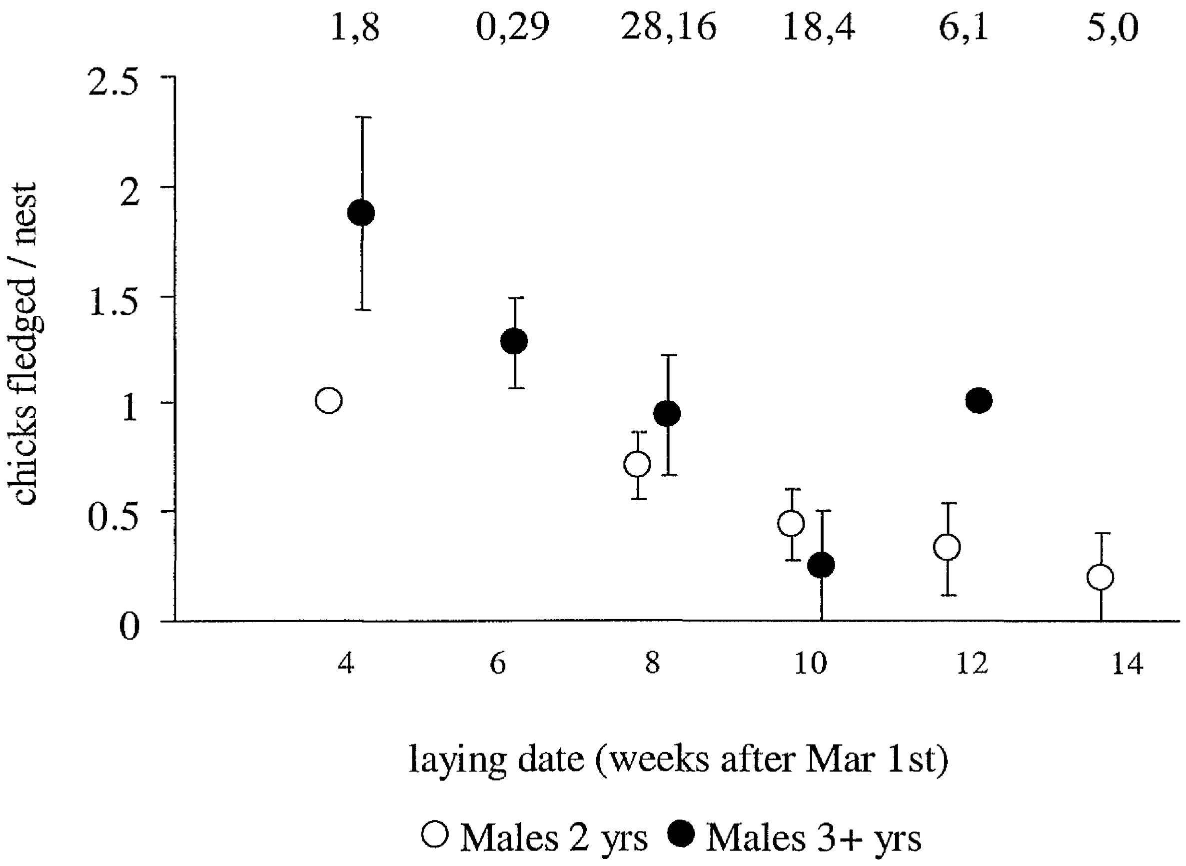

Figure 1.3: The confounding effects of parental age and laying date on reproductive success (number of chicks fledged/nest) in 1997. Sample sizes are shown above each fortnightly mean (males 2 yrs, males 3+ yrs).

5. Outline of the thesis

This chapter has attempted to summarise the mechanisms that have been proposed to explain age-specific patterns of variation in breeding success. However, they remain very poorly understood. Therefore, the aim of this thesis was to investigate some of these mechanisms in a species where marked improvements in breeding performance with age have been recorded. Previous work on shags, including my own findings in my first field season, have found that a) the main source of variation with age lies between pairs containing a two-year-old male and pairs containing an older male, but that b) both extrinsic and intrinsic differences could explain this pattern, due to differences in the timing of breeding. These two findings formed the background to the thesis.

I firstly investigated the role of timing of breeding, by separating the effects of age and season. This was achieved by a cross-fostering experiment carried out in the 1998 season between young and older breeders. By manipulating the length of incubation, I forced young and older breeders to rear their chicks at the same time. I describe this experiment in chapter 2. Once I had controlled for the confounding effects of age and season, I was able to investigate some of the other mechanisms that may be operating on age-specific breeding performance. In chapter 3, I describe the consequences of offspring sex on age-specific offspring fitness. The shag is sexually size dimorphic, with males 20% heavier than females, and I predicted that young pairs would have difficulties in rearing sons because of the increased demands in raising them. In chapter 4, I examine the interaction between age and environmental conditions, by comparing the foraging behaviour of young and older breeders in two periods of contrasting feeding conditions. I assessed whether older individuals are increasing their breeding performance by adjusting their foraging behaviour to the prevailing environmental conditions, increasing foraging effort when conditions are poor. In chapter 5, I assess the evidence for the constraint hypothesis in explaining patterns of age-specific breeding performance, by calculating the foraging efficiency (ratio of energy gained to energy expended) of young and older birds. I investigate the role ectoparasite load plays in age-specific breeding performance in chapter 6.

Finally, in chapter 7, I diverge from a study purely of the difference between pairs containing two-year-old and older males, and examine the effects of age and condition on a little studied subject: the role of sexual selection in the evolution of ornaments in both females and males, a study I carried out in the 1999 season. This chapter is followed by a general discussion in chapter 8. Finally, an experiment carried out in 1997 manipulating incubation demands is presented in Appendix 1.

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Chapter 2

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

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ABSTRACT

An age-specific improvement in reproductive performance has been reported in many iteroparous breeders. However, whether this is a consequence of intrinsic differences in performance 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*. Older 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, older 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.

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 (Roff 1992; 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, associated with the observed differences in breeding success, there is generally also an age-related difference in the timing of breeding. Younger individuals tend to breed later in the season than older birds, and may experience different environmental conditions as a result (Perdeck and Cavé 1992). Therefore, in correlative studies in which reproductive success is examined in relation to age, the potentially independent effects of time of year and age are confounded. This makes it very difficult to identify age-related differences in performance that 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;

Moreno *et al.* 1997; Moreno 1998), there has been surprisingly little experimental work on age-specific reproductive performance (Forslund & Pärt 1995). Only two studies have specifically manipulated the timing of breeding in relation to age. Reid (1988) cross-fostered broods for a three day period to assess territory attendance among old and young glaucous-winged gulls *Larus glaucescens* with chicks of the same 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 for the entire chick-rearing period. 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. This is particularly relevant when there is an improvement in egg quality with parental age (Coulson *et al.* 1969). Therefore, using the shag, *Phalacrocorax aristotelis*, a seasonally breeding bird with marked differences in reproductive success, timing of breeding and egg quality in relation to age (Coulson *et al.* 1969; Potts *et al.* 1980; Aebischer 1993; Aebischer *et al.* 1995), we (1) manipulated young birds such that the hatching date of the chicks they reared was brought forward in the season to coincide with those of control older pairs, and (2) manipulated older birds such that they reared chicks hatching late in the season, at the same time as control young pairs. Our protocol allowed us to test if, when rearing chicks in the same environmental conditions, from eggs of a similar quality, young parents perform less well during chick rearing than do older pairs.

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 recognised 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 the 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; 'older' pairs consisted of those in which the male was at least three years old (mean age where exact age known: 6.95 ± 0.63 s.e. years, range 3-12 years, $n = 19$). Although pairs were defined in terms of the age of the male, male and female age within a pair are significantly and positively correlated (among all pairs in 1998 where the precise age of both pair members was known: Spearman rank correlation: $r_s = 0.56$, $n = 65$, $p < 0.001$). 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 s.e. years older than the male; two-year-old males: female 2.59 ± 0.71 s.e. years older than the male; $t_{57} = 0.09$, ns).

The older pairs laid on average 12 days earlier than young pairs (older laying date: 6 May ± 1 s.e. days, $n = 37$; young laying date: 18 May ± 1 s.e. days, $n = 38$ – see figure 2.1), and also laid larger eggs (see figure 2.2). In order to separate the confounding effects of age and seasonal and egg quality effects on reproductive performance, hatching dates were manipulated by extending (older pairs) or reducing (young pairs) the incubation period through a cross-fostering protocol. This involved exchanging clutches between groups of four pairs with identical clutch size that comprised two older pairs matched for laying date, and two young pairs laying on average 12 days ± 1 s.e. day later. One of the older pairs was given the clutch of a young pair, thereby becoming an 'older experimental', with its hatching date delayed by 12 ± 1 s.e. days. The hatching date of one of the young pairs was advanced by 12 ± 1 s.e. days by replacing its clutch with that of the second older pair in the group, thereby becoming a 'young experimental'. This older 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 older controls and young experimentals were both given eggs laid by older pairs that hatched early in the season, and young controls and older experimentals had eggs laid by young pairs that hatched late in the season. The clutch exchanges were carried out within 10 days of the hatching of the older 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 (1) there was the same spread of laying dates for birds in all treatment groups, (2) no pairs reared their own brood, and (3) pairs hatching chicks at the same time had eggs of a similar quality (i.e. both older and young pairs had eggs produced by older pairs in the early hatching period, and by young pairs in the late hatching period). The overall experimental design is illustrated in figure 2.3, 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 amongst 17 groups of four nests that all laid three eggs (the modal clutch size in the shag, Coulson *et al.* 1969; Stockland & Amundsen 1988), and two groups that all laid two eggs. Of the 76 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 72 nests comprised 17 older controls, 18 older experimentals, 19 young controls and 18 young experimentals.

We used Generalized Linear Models (GLM) to investigate the effects of parental age (young or older parents rearing the chicks) and hatching period (early or late) 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).

As expected given the experimental protocol, there was no difference in hatching date between older controls and young experimentals (older hatch date: 11th June ± 2 s.e. days, n = 17; young hatch date: 12th June ± 1 s.e. days, n = 16; $t_{31} = 0.44$, ns) nor between older experimentals and young controls (older hatch date: 21st June ± 2 s.e. days, n = 16; young hatch date: 20th June ± 2 s.e. days, n = 16; $t_{30} = 0.53$, ns). There was also no difference in male age between older controls and older experimentals, where the exact age was known (older controls: 7.29 ± 1.34 s.e years, n = 7; older experimentals 6.75 ± 0.68 s.e. years, n = 12; Mann Whitney $U = 38$, $p > 0.2$, ns). 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 (older controls: 0.88 ± 0.05 s.e., n = 17; older experimentals: 0.69 ± 0.09 s.e., n = 18; young controls: 0.68 ± 0.09 s.e., n = 19; young experimentals: 0.80 ± 0.08 s.e., n = 18; GLM: age: $F_{1,69} = 0.27$, ns; hatching period: $F_{1,70} = 3.58$, ns; interaction term: $F_{1,68} = 0.45$, ns). The majority of chick mortality occurs in shags during the first 10 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 and 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: 0-10 days and 10 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 200-1000g, and thereafter to the nearest 10g) approximately every 4 days until close to fledging. Chick peak masses were calculated by fitting logistic growth curves to the data (following Ricklefs 1967), using the equation:

$$w_t = \frac{a}{1 + [(\frac{a-i}{i}) * (e^{-kt})]}$$

where w = mass, t = age, a = peak mass, i = mean hatching mass of shag chicks (37.0g, unpublished data) and k = the rate constant.

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 8-30 days) as a measure of growth rate. For both peak masses and growth rates, a mean was taken for the whole brood, and parental age (young vs older) and hatching period (early vs late) entered as factors. All means are given ± 1 s.e.

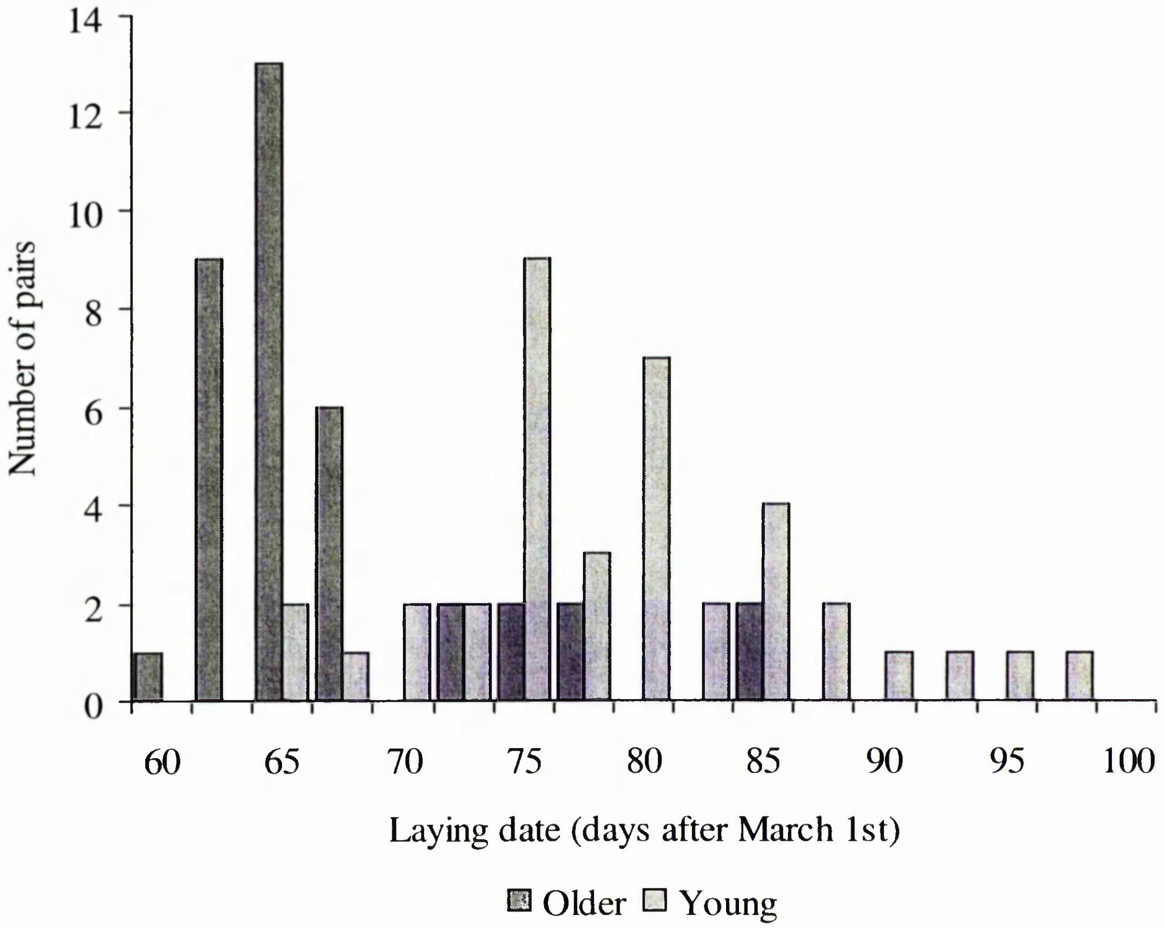

Figure 2.1: Laying dates of young and older breeders. There was a significant difference between the two age groups ($t_{73} = 7.54$, $p < 0.001$), with older pairs laying 12 days earlier on average.

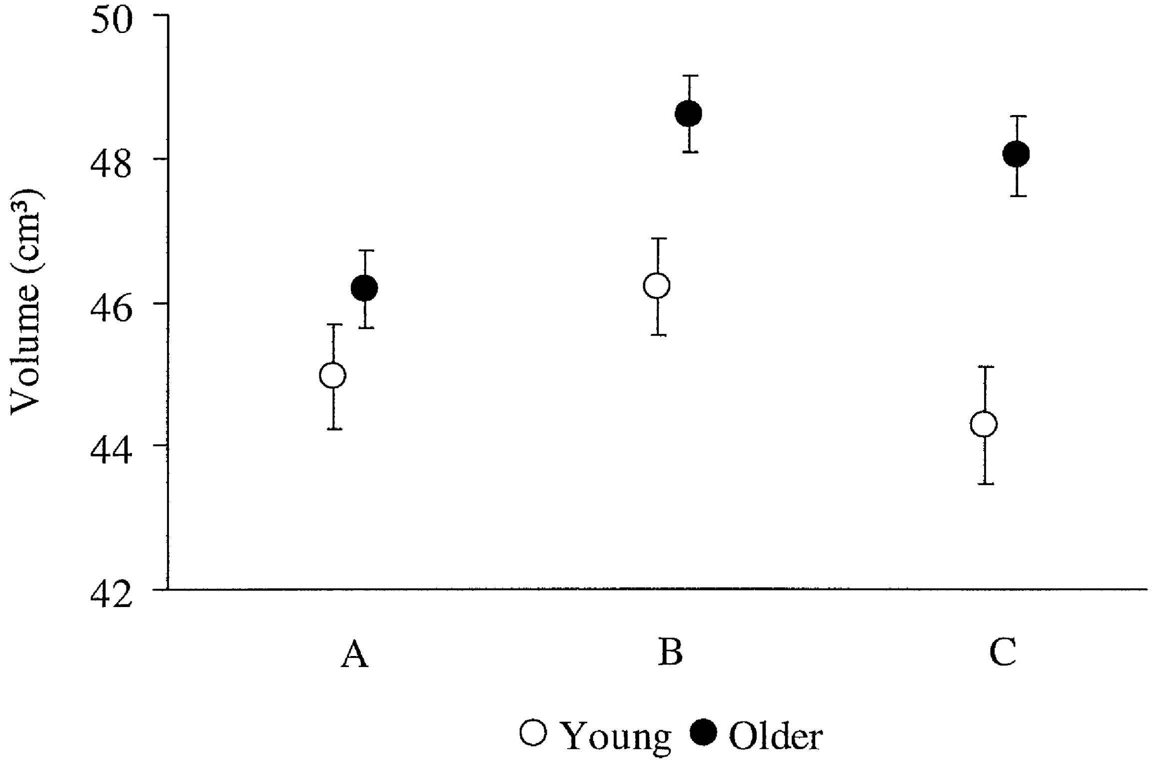

Figure 2.2: Egg volume of A (first laid), B (second laid) and C (third laid) eggs from three-egg clutches of young and older pairs where laying sequence was known. Young pairs produced significantly smaller eggs than older pairs (repeated measures ANOVA: parental age: $F_{1,49} = 9.05$, $p < 0.01$; laying sequence: $F_{2,48} = 36.02$, $p < 0.001$; interaction term: $F_{2,48} = 4.75$, $p < 0.05$). Clutch size does not differ with parental age (Coulson *et al.* 1969).

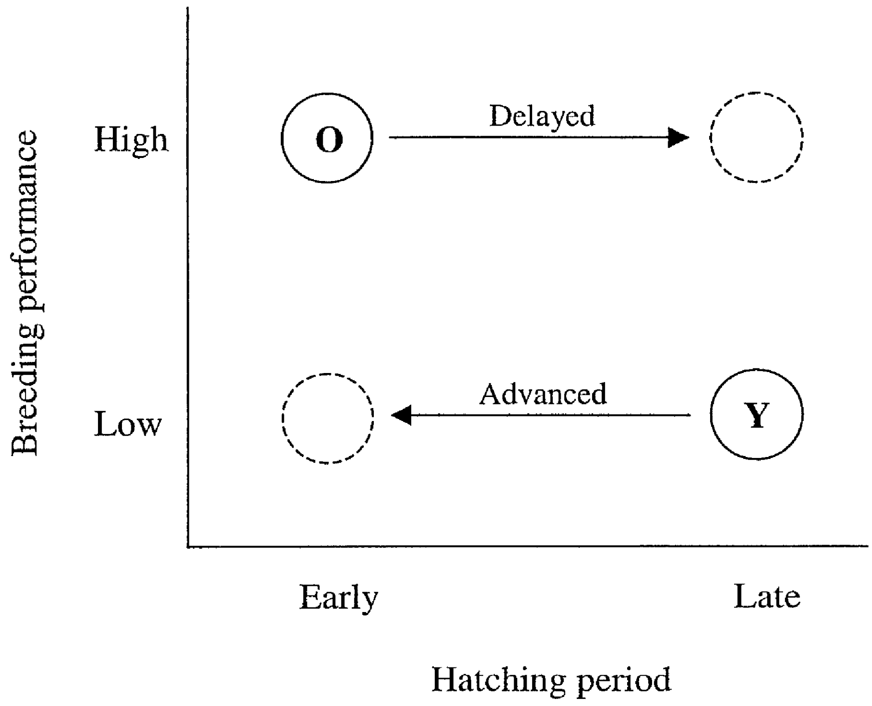

Figure 2.3: Diagrammatic representation of the experimental procedure, in which half the older pairs (O) were delayed and half the young pairs (Y) were advanced. Dotted circles illustrate the predicted outcome of the difference in breeding performance as a consequence of parental age.

RESULTS

As expected from previous studies (Potts *et al.* 1980; Aebischer 1993), in the control groups the older pairs hatching chicks early in the season had a higher reproductive performance than did young pairs hatching chicks late in the season (figure 2.4). However, when breeding at the same time, older pairs consistently out-performed young pairs. Early in the season, older controls reared 39% more hatched eggs to fledging than young experimentals, and late in the season older experimentals raised 54% more hatched eggs to fledging than young controls (figure 2.4).

The effect of parental age on chick survival was most marked during the first 10 days after hatching. At this young chick age, there was a significantly higher survival rate in chicks reared by older pairs and this did not differ with respect to hatching period (figure 2.5). For chicks older than 10 days, survival was not related to parental age. While the survival of these older chicks was significantly poorer in the late hatching period (figure 2.5), this effect was not sufficient to produce any difference in overall fledging success in relation to season (figure 2.4).

There was no effect of parental age or hatching period on the growth rate or peak mass of surviving chicks in broods (table 2.1).

	Mean (s.e.)		Parental age		Hatching period		Interaction	
	Young	Older	F	*p*	F	*p*	*F*	*p*
Growth rate (g/day)	54.2 (1.3)	56.6 (1.1)	1.96	ns	0.03	ns	1.13	ns
Peak mass (g)	1506.4 (30.2)	1557.4 (25.9)	1.64	ns	0.52	ns	0.19	ns

Table 2.1: Mean (s.e. below) growth rates and peak masses of surviving chicks for two parental age groups. Parental age and hatching period were entered as factors.

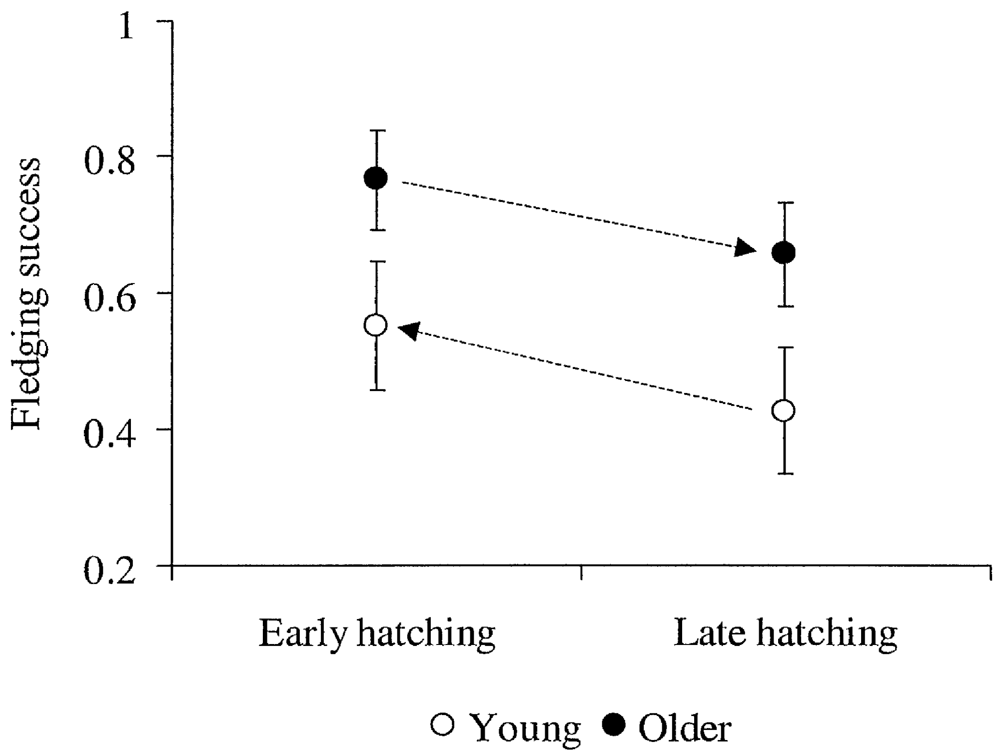

Figure 2.4: The effects of parental age and hatching period on fledging success in control and experimental older and young pairs. The two arrows indicate the direction of the manipulation of hatching date. Fledging success was significantly higher in the older pairs, and there was no effect of hatching period (GLM: age: $F_{1,63} = 6.34$; $p < 0.05$; hatching period: $F_{1,62} = 3.41$, ns; interaction term: $F_{1,61} = 0.03$, ns).

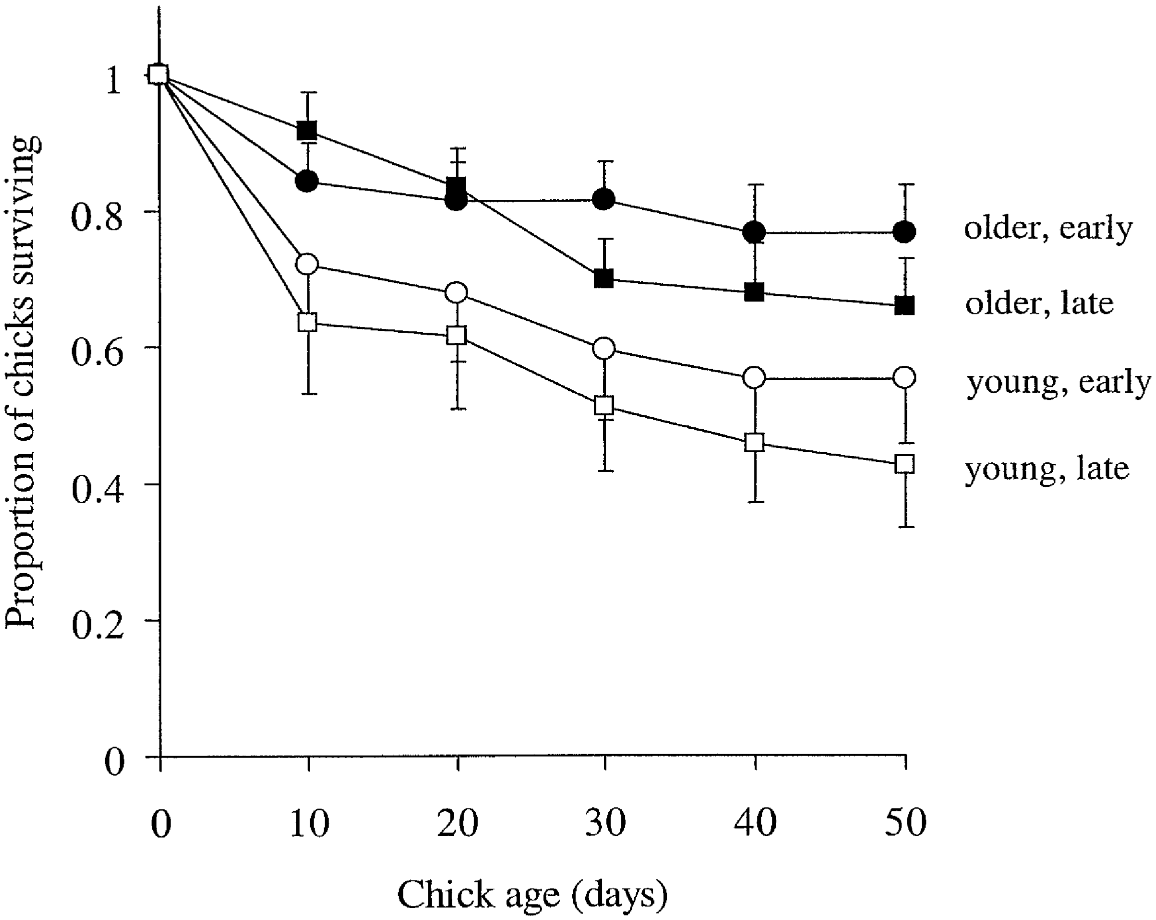

Figure 2.5: Proportion of chicks surviving in relation to chick age, age of parents and hatching period. There was a significant effect of parental age on chick survival during the first 10 days after hatching; chick survival during this period was not affected by hatching period (GLM: age: $F_{1,63}$ = 7.35, $p < 0.01$; hatching period: $F_{1,62}$ = 0.04, ns; interaction term: $F_{1,61}$ = 2.58, ns). There was a significant effect of hatching period but no effect of parental age in the period from chick age 10 to fledging (GLM: age: $F_{1,55}$ = 1.73, ns; hatching period: $F_{1,56}$ = 6.28, $p < 0.05$; interaction term: $F_{1,54}$ = 2.49, ns).

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 older birds that normally breed at this time, reared significantly fewer young than older birds. Similarly, older 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 older pairs breeding at the same time had eggs from the same age group - older 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 older 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 were 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 older pairs compared with control older pairs), and a corresponding impairment in those with reduced incubation time (i.e. the early 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 2.4). 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). Appendix 1 describes an experiment carried out in the summer of 1997 in which the incubation demand was manipulated. No effect of incubation cost was found, but sample sizes were small. Other studies have shown that experimental changes in incubation costs alone can have fitness consequences (Heaney & Monaghan 1996; Monaghan & Nager 1997; Bryan & Bryant 1999; Reid *et al.* 2000). 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 older 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 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 effects of differences between young and older 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 and 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 time of season. For chicks older than 10 days, survival was poorer in the late hatching period. 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 older pairs. In any event, the seasonal effect on the survival of chicks over 10 days old was not strong, and the overall chick survival from hatching to fledging was not significantly influenced by time of season in either older 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 (Curio 1983; Roff 1992; Stearns 1992). Differences in the foraging abilities of young and older birds may be a contributory factor (Nur 1984; Reid 1988; Desrochers 1992; Martin 1995). The lack of any detectable effect of parental age on growth rates and peak 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 aspects of breeding experience, such as intra-pair co-ordination of activities (Bradley *et al.* 1990; Cézilly and Nager 1996; Black 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 and 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 males and female age are closely correlated, in the absence of experimental manipulations, it is not possible to unequivocally attribute age effects 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. 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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Chapter 3

Sons and daughters: age-specific differences in parental rearing capacities

In press as:

F. Daunt, P. Monaghan, S. Wanless, M. P. Harris & R. Griffiths: Sons and daughters: age-specific differences in parental rearing capacities

Functional Ecology

ABSTRACT

Numerous studies of iteroparous breeders have demonstrated an increase in average breeding success with parental age. One of the most widely suggested mechanisms to explain this pattern is that the foraging performance of young breeders is relatively poor. Where this is coupled to differences in the costs of rearing male and female offspring, for example due to sexual size dimorphism, young breeders may have difficulties rearing the more expensive sex. We investigated this in the shag, a monogamous seabird in which adult males are on average 20% heavier than adult females. Young pairs breed later in the season than older pairs, and lay smaller eggs. We controlled for differences in timing of breeding and egg quality in a cross-fostering experiment in which older and young individuals reared chicks simultaneously from eggs of similar quality. Male chicks raised by young parents grew more slowly and attained a lower peak mass than those raised by older parents, whereas there was no equivalent difference for female chicks. These results suggest that sons are energetically more demanding on their parents than daughters, and the more expensive sex fledges in significantly poorer condition when the parents are young. Therefore, we predict that optimal offspring sex ratio will vary with parental age.

INTRODUCTION

In most sexually size-dimorphic species, offspring of the larger sex not only grow faster, but in addition are usually more expensive to rear (Clutton-Brock *et al.* 1981; Fiala & Congdon 1983; Slagsvold *et al.* 1986; Teather & Weatherhead 1988; Clutton-Brock 1991; Anderson *et al.* 1993; Ono and Boness 1996; Riedstra *et al.* 1998; Krijgsveld *et al.* 1998; but see Newton 1978; Torres & Drummond 1999). In the absence of any behavioural changes in the parents or the offspring that bias food allocation to the larger sex, in situations where parents have difficulties provisioning their young one would expect the effects to be most manifest in offspring of the sex with the higher food requirement. Numerous studies of iteroparous breeders have found that parental age is an important factor influencing reproductive performance; average breeding success usually improves with age over the first few breeding events (reviewed in Sæther 1990; Forslund & Pärt 1995). One of the most widely suggested mechanisms to explain this pattern is an age-related improvement in foraging performance (Martin 1995). Accordingly, we would expect young breeders to experience more difficulties in provisioning offspring of the larger sex (Weimerskirch, Barbaud & Lys 2000).

Seabirds are generally long-lived and tend to show pronounced improvements in reproductive success with age (e.g. Coulson & White 1958; Ollason & Dunnet 1978; Nisbet *et al.* 1984; Reid 1988; Boekelheide & Ainley 1989; Hamer & Furness 1991). We investigated the relationship between offspring sex and age-specific breeding performance in a sexually dimorphic seabird, the shag (*Phalacrocorax aristotelis* Linnaeus). Adult males of this species weigh 1,900g on average and adult females 1,600g (approx. 20% lighter), and marked differences in fledging masses between male and female chicks were inferred by Snow (1960) and have been recorded by Velando (2000). In shags, young pairs breed later in the season on average than older pairs (Potts *et al.* 1980; Aebischer 1993; Daunt *et al.* 1999) and lay smaller eggs (Coulson *et al.* 1969). Thus, both seasonal changes in the environment and differences in egg quality could also influence the growth and survival of offspring, in addition to age-specific parental provisioning capacity. In an investigation of the effects of parental age on breeding performance in shags, we used a cross-fostering experimental protocol to remove the effects of environmental conditions and egg quality (Daunt *et al.* 1999). Irrespective of time of season, and for a given clutch size and quality, young pairs fledged fewer chicks than older pairs. Here we examine whether there is any evidence of a differential capacity of young and older pairs to rear male and female chicks from eggs of the same quality, hatching at the same time. Specifically, we test the prediction that male offspring of young shags will grow less well than those being reared by older pairs.

METHODS

The study was carried out in 1998 on the Isle of May (56°11'N, 02°33'W). Full details of the choice of age categories and the experimental protocol are contained in chapter 2. In brief, two parental age groups were defined: 'young' pairs contained a two-year-old male breeding for the first time; 'older' pairs contained a male that was at least three years old. As expected from previous research (Potts *et al.* 1980; Aebischer 1993), young pairs laid on average 12 days later than older pairs (older laying date: 6 May ± 1 s.e. days, $n = 37$; young laying date: 18 May ± 1 s.e. days, $n = 38$; $t_{73} = 7.54$, $P < 0.001$), and laid significantly smaller eggs (repeated measures ANOVA on three-egg clutches: parental age: $F_{1,49} = 9.05$, $p < 0.01$; laying sequence: $F_{2,48} = 36.02$, $p < 0.001$; interaction term: $F_{2,48} = 4.75$, $p < 0.05$). The timing of hatching in young and older pairs was manipulated using a cross-fostering protocol. Clutches were exchanged within tetrads comprising two older and two young pairs; clutch size was constant for all four pairs, and within each age class the two pairs were matched for initial laying date. Clutch exchanges were such that no pairs, whether controls or experimentals, reared their own eggs. Control pairs received a clutch from the same age class; experimental young pairs were given the clutches of older pairs, and experimental older pairs were given clutches laid by young pairs. As a consequence, experimental young and control older pairs hatched eggs early in the season (all rearing eggs from older pairs), while experimental older and control young pairs hatched eggs late in the season (all rearing eggs from young pairs). The clutch exchanges were carried out amongst 17 tetrads that all laid three eggs, and two tetrads that all laid two eggs.

Of the nests from which at least one young fledged (16 older controls, 15 older delayed, 13 young controls, 13 young advanced), surviving chicks were weighed (to the nearest 0.1g up to 200 g; to the nearest 2.5g from 200 - 1,000 g; to the nearest 10g over 1,000g) approximately every four days from hatching to close to fledging (mean age of final weighing: 39.59 ± 0.58 days; shags fledge at age c50 days). Chick growth rate was taken as the gradient during the linear phase of growth (chick age 8-30 days). Chick peak masses were calculated by fitting logistic growth curves to the data (following Ricklefs 1967) with a fixed intercept.

A blood sample was taken (under licence) from the leg of each chick, from which the DNA was extracted and the chicks sexed using two *CHD I* genes (Griffiths *et al.* 1996). Blood samples could not be taken from chicks at hatching due to logistical difficulties, and thus it was not possible to examine differential survival of male and female chicks because the initial sex ratios in the broods were not known.

General Linear Models were used to examine the effects of parental age (young vs older) and hatching period (early vs late) on growth rate and peak mass on two categories of chicks for which there were sufficient sample sizes: the oldest (broods of one, two or three) and second oldest (broods of two or three) surviving chicks. In almost all cases the two categories represented the first- and second-hatched chicks (and these terms will be used hereafter). However, in six cases a senior chick in a brood died (in every case prior to the linear phase of growth), and consequently chicks junior to it in the brood had their seniority increased accordingly in the analyses, to match their improved competitive status in the brood. None of the young pairs reared three chicks so it was not possible to carry out the same analysis on third-hatched chicks.

Brood sex composition can have important implications for an individual offspring's growth (Gowaty 1991). Therefore, in broods of two and three, the effect of sibling sex on the relationship between parental age and the growth rate and peak mass of sons and daughters was analysed. For first-hatched chicks, the sex of the second-hatched chick was entered as a factor in a General Linear Model, as well as parental age and hatching period. For the second-hatched chick, the sex of the first-hatched chick, parental age and hatching period were entered into a General Linear Model. Sample sizes again prevented the inclusion of the sex of third-hatched chicks.

RESULTS

There was no difference in the volume of the eggs from which male and female chicks hatched (three-egg clutches: A egg: $t_{33} = 0.70$, ns; B-egg: $t_{32} = 0.30$, ns; C-egg: $t_{25} = 0.78$, ns; analysis includes non-surviving as well as surviving chicks). However, male chicks grew faster and attained a higher peak mass than female chicks, when parental age was not taken into account. Figure 3.1 shows overall mean growth curves for male and female first-hatched chicks; the curves for second-hatched chicks show a similar difference.

When the sex of chicks is not considered, there is no overall difference in chick growth rates or peak masses with respect to parental age in shags (Daunt *et al.* 1999). However, when chick sex is identified and taken into account, it is clear that parental age does influence chick growth patterns. Both first-hatched and second-hatched male chicks reared by young pairs grew significantly more slowly than those reared by older pairs; there was no equivalent effect of parental age on either first-hatched or second-hatched female chicks (figure 3.2a). Similarly, first-hatched and second-hatched male chicks reared by young pairs had a lower peak mass than those reared by older parents, but there was no difference with respect to parental age in female chick peak masses (figure 3.2b). Moreover, young parents' sons did not grow faster or fledge heavier than their daughters, whereas there was a highly significant difference between older parents' sons and daughters (table 3.1).

The inclusion of sibling sex in the analysis did not alter the differential effects of parental age on the growth rates and peak masses of male and female chicks, and the sex of the sibling was found to be unimportant in all cases.

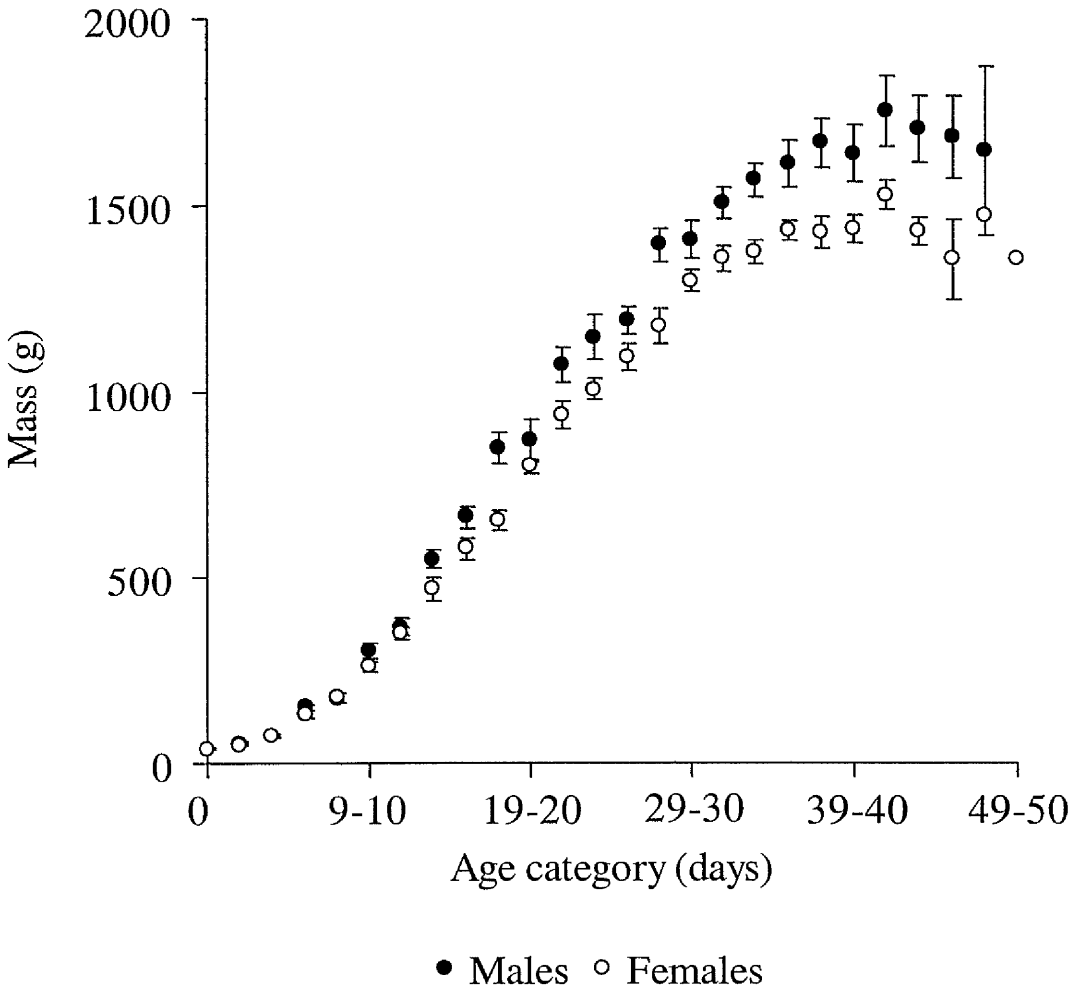

Figure 3.1. Mean (± s.e) growth curves for first-hatched male and female chicks. Age categories follow the pattern 0 days, 1-2 days, 3-4 days etc, with no chick appearing more than once in each category. Male chicks grew significantly faster during the linear phase, and reached a significantly higher peak mass (First-hatched chicks: growth rate: male chicks: 58.31 ± 1.28 g/day, $n = 27$; female chicks: 52.67 ± 0.81 g/day, $n = 30$; $t_{55} = 3.80$, $p < 0.001$; peak mass: male chicks: 1,592.2 ± 33.6 g, $n = 27$; female chicks 1,454.0 ± 17.1 g, $n = 30$; $t_{38.8} = 3.67$, $p < 0.01$. Second-hatched chicks: growth rate: male chicks: 58.82 ± 1.37 g, $n = 16$; female chicks: 52.12 ± 1.45 g, $n = 18$; $t_{32} = 3.34$, $p < 0.005$; peak mass: male chicks: 1,612.5 ± 42.3 g, $n = 16$; female chicks 1,415.5 ± 26.0 g, $n = 18$; $t_{32} = 4.07$, $p < 0.001$).

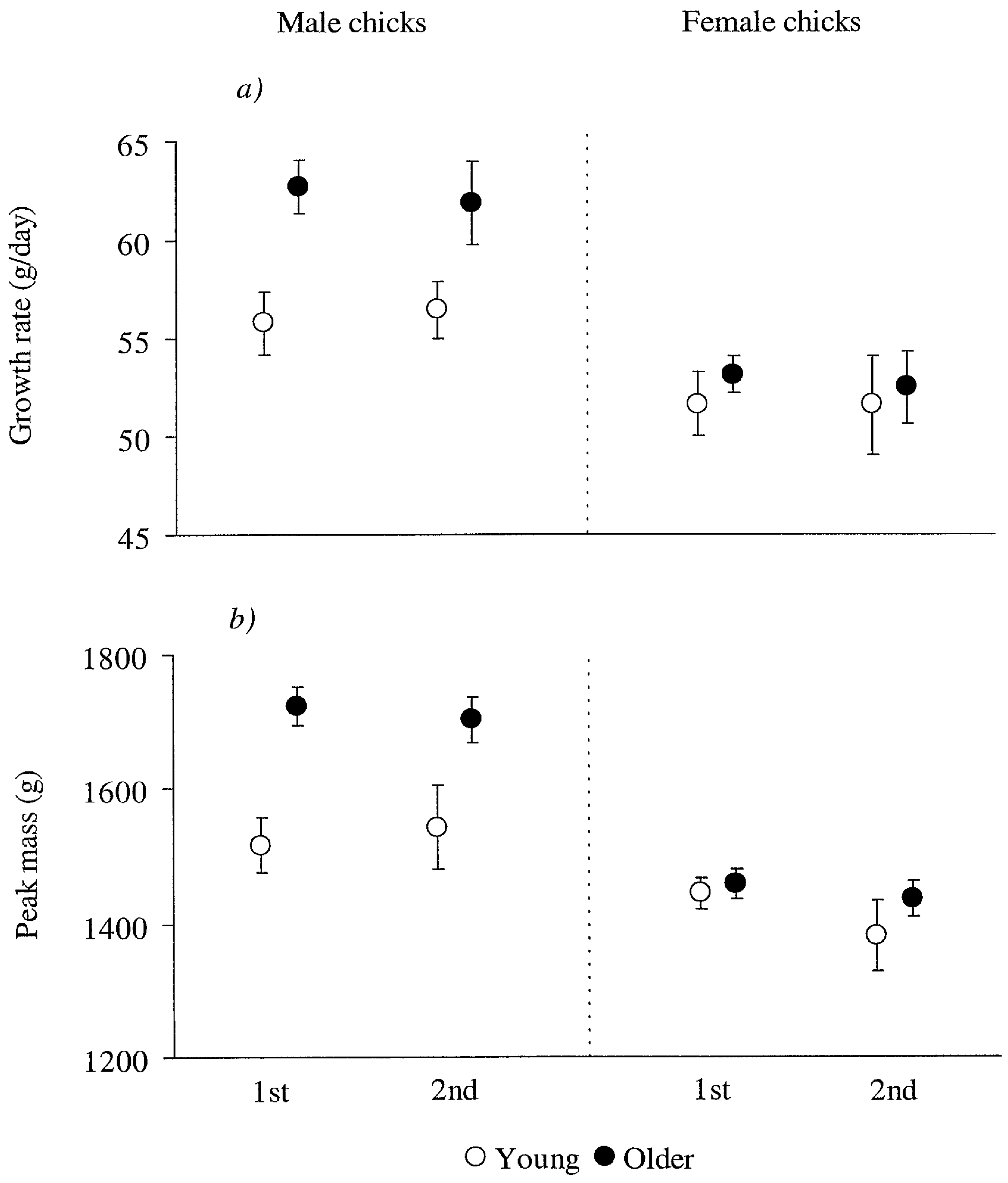

Figure 3.2. (legend over page)

Figure 3.2 a) Growth rates during the linear phase (age 8-30 days) of male and female first- and second-hatched chicks raised by young and older pairs. There was no significant effect of hatching period on growth, so the two older groups (older controls; older delayed) and two young groups (young controls; young advanced) have been pooled in this figure. Male chicks reared by young parents grew significantly more slowly than those reared by older parents, but there was no age-specific effect on the growth of female chicks (General Linear Model of parental age and hatching period on growth rate: first-hatched male chicks: parental age: $F_{1,25} = 8.87$, $p < 0.01$; hatching period: $F_{1,24} = 1.22$, ns; interaction term: $F_{1,23} = 1.14$, ns; second-hatched male chicks: parental age: $F_{1,14} = 4.87$, $p < 0.05$; hatching period: $F_{1,13} = 0.01$, ns; interaction term: $F_{1,12} = 1.14$, ns; first-hatched female chicks: parental age: $F_{1,27} = 0.38$, ns; hatching period: $F_{1,28} = 2.14$, ns; interaction term: $F_{1,26} = 0.10$, ns; second-hatched female chicks: parental age: $F_{1,15} = 0.00$, ns; hatching period: $F_{1,16} = 2.14$, ns; interaction term: $F_{1,14} = 0.45$, ns)

b) Peak masses of male and female chicks raised by young and older pairs. This figure follows the same convention as figure 3.2a). Male chicks raised by young parents had a lower peak mass than those raised by older parents (although the result for second-hatched chicks was marginally non-significant), but there was no equivalent difference for female chicks (General Linear Model of parental age and hatching period on peak mass: first-hatched male chicks: parental age: $F_{1,25} = 12.99$, $p < 0.01$; hatching period: $F_{1,24} = 3.08$, ns; interaction term: $F_{1,23} = 2.23$, ns; second-hatched male chicks: parental age: $F_{1,14} = 4.32$, $p = 0.057$; hatching period: $F_{1,13} = 0.02$, ns; interaction term: $F_{1,12} = 0.30$, ns; first-hatched female chicks: parental age: $F_{1,28} = 0.13$, ns; hatching period: $F_{1,27} = 0.13$, ns; interaction term: $F_{1,26} = 2.50$, ns; second-hatched female chicks: parental age: $F_{1,16} = 1.07$, ns; hatching period: $F_{1,15} = 0.02$, ns; interaction term: $F_{1,14} = 0.96$, ns).

age	factor	growth rate						peak mass					
		1st hatched			2nd hatched			1st hatched			2nd hatched		
		F	df	*p*	F	df	*p*	F	df	*p*	F	df	*p*
older	sex	33.89	29	***	10.81	16	**	47.87	29	***	37.70	16	***
	period	0.88	28	ns	1.77	15	ns	0.67	28	ns	0.36	15	ns
	int.	0.13	27	ns	0.99	14	ns	0.49	27	ns	0.42	14	ns
young	sex	2.75	24	ns	3.16	14	ns	2.00	23	ns	3.61	14	ns
	period	0.64	23	ns	0.03	13	ns	1.52	24	ns	0.02	13	ns
	int.	2.03	22	ns	0.06	12	ns	4.22	22	ns	0.05	12	ns

** $p < 0.01$ *** $p < 0.001$

Table 3.1: Effects of offspring sex and hatching period on growth rates and fledging masses. Separate analyses on first-hatched and second-hatched chicks of older and of young pairs. The sons of older pairs grew significantly faster and reached a significantly higher peak mass than their daughters, but there was no significant effect of offspring sex on growth and peak mass of young pairs' chicks.

DISCUSSION

Given that the shag is a sexually dimorphic species, in which adult males are approximately 20% heavier than adult females, we predicted that male offspring reared by young pairs would grow less well. This prediction was upheld. We found evidence for a differential effect of parental age on the condition of male and female offspring, independent of seasonal and egg quality effects. In a non-experimental study of wandering albatrosses, which could not therefore control for egg or seasonal effects (which are known to differ with age in this species – Weimerskirch 1992), Weimerskirch *et al.* (2000) found that male chicks of young parents grew less well. In our study, young and older pairs reared chicks from the same egg quality and at the same time of year. Nonetheless, males reared by young pairs grew less well and reached a lower peak mass, demonstrating that difficulties in rearing the larger sex can be caused entirely by intrinsic differences in the brood rearing capacities of young and older parents. Furthermore, this poorer growth of sons occurred despite the fact that the reproductive demands on young birds were lessened relative to older birds, since the experimental protocol was such that incubation periods of young experimental pairs were shortened and those of older experimental pairs lengthened to advance and delay hatching date respectively. This difference in peak mass between sons reared by young and older shags is likely to have had important implications for their fitness, as a number of studies have found a significant relationship between mass at fledging and post-fledging survival (reviewed in Magrath 1991). We were unable to weigh chicks right up to fledging, due to the dangers of causing premature departure from the nest (shag chicks become very mobile at this time). However, it is unlikely that the patterns we found would change in the few days to fledging. There is no evidence for mass recession in this species; parents do not abandon their chicks prior to fledging, but continue to feed their chicks for several weeks after leaving the nest (Snow 1960; Velando 2000).

There are a number of reasons why young pairs might be having difficulty meeting the demands of sons. At the individual level, much of the variation in rearing capacity between parents is likely to be state dependent (McNamara & Houston 1996). Young birds may have a lower foraging efficiency, which may have particularly marked consequences during the energetically demanding chick-rearing period (Curio 1983). Alternatively, they may be showing reproductive restraint, putting less effort into the present reproductive attempt due to their higher Residual Reproductive Value (RRV) (Roff 1992; Stearns 1992). The young pairs were all first-time breeders, and a lack of experience or experience with their mate may be a component of the age effect (Pärt 1995; Black 1996). At the population level, average quality may increase with age if higher quality individuals have improved survival rates, or show delayed first breeding (Forslund & Pärt 1995). In addition, the magnitude of the difference between the performance of young and older breeders may vary with prevailing environmental conditions. One might expect age-specific differences in the growth rates of sons to be most apparent only in years of low food abundance. However, conditions were in fact not particularly poor during this study; overall breeding success was typical for the colony, and the difference between the age groups was apparent both early and late in the season. However, it would be interesting to know whether young pairs would be able to meet the demands of both sons and daughters in years of very high food abundance.

A number of theories have been put forward to explain the differences in growth dynamics between sons and daughters. These include alternative allocation patterns in growth and development, differences in activity levels and the influence of competitive interactions between siblings (Richter 1983; Stamps 1990; Richner 1991; Clutton-Brock 1991; Krijgsveld *et al.* 1998; Torres & Drummond 1999). Most studies on birds where males are the larger sex have found that sons, although cheaper to rear per unit mass than daughters, are nonetheless more expensive in absolute terms (reviewed in Krijgsveld *et al.* 1998). In species where the female is larger the evidence that they are more expensive to rear is absent or, at best, equivocal (Newton 1978; Collopy 1986; Torres & Drummond 1999). However, our results support the view that the heavier sex is more expensive to raise energetically. The possibility that sons are achieving enhanced growth on the same amount of food as daughters, and are thus no more demanding to raise, seems unlikely. The sons and daughters of young parents were observed to grow at similar rates. If sons in fact grew faster on the same amount of food as daughters, then these similar growth rates would only come about if young parents selectively provision their female chicks, or if female chicks are more competitive. This seems unlikely, since we found no effect of sibling sex on the differential effect of parental age on growth of sons and daughters, but warrants further investigation.

Given our results, young pairs might be expected to show a bias in the fledging sex ratio towards females, either by manipulating the primary sex ratio or through differential mortality (Trivers & Willard 1973). In this study, we were not able to obtain sufficient information on the primary sex ratio in the clutches laid by young and older birds. Furthermore, in our experiment, none of the pairs actually reared their own chicks. Since females may have tailored their clutches to suit the pair's rearing capacity, it is not meaningful for us in any event to examine differences in the overall production of sons and daughters from these data. Our study has established that young pairs do have more difficulty than older pairs in raising sons. This suggests that optimal sex ratios will differ in relation to parental age.

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Chapter 4

The interactive effects of age and feeding conditions on the foraging behaviour of breeding shags

ABSTRACT

Age-specific improvements in breeding success are often attributed to improved foraging performance in older individuals. There is likely to be an interaction between age and feeding conditions, such that age-specific foraging performance will be more manifest when conditions are poor. Typically, the timing of breeding in younger and older birds differs, so it is not possible to examine the relationship between age and environmental effects because of a temporal segregation in chick-rearing. Using a cross-fostering procedure, I experimentally manipulated the timing of chick-rearing in young (first-time) breeding and older breeding shags *Phalacrocorax aristotelis*, such that the two age classes reared their chicks at the same time both early and late in the season. The two hatching periods differed profoundly with respect to many aspects of the foraging behaviour of the birds, providing strong circumstantial evidence that foraging conditions differed. Late in the season, foraging trips were much longer, with birds flying further from the colony and making many more dives suggesting that feeding conditions were relatively poor; during this period, older birds spent less time recovering between dives than young birds, spending more time under water as a result. There was no equivalent difference early in the season. At this time, birds of both age classes were feeding closer to the colony and making many fewer dives, suggesting better foraging conditions overall. The time spent on the sea surface at the end of a diving bout, prior to the return flight to the colony, was significantly longer in young pairs compared with older birds during both hatching periods. These results suggest that older individuals are able to spend more time actively foraging and less time resting than younger individuals when the environmental conditions are poor, which may give them an enhanced capacity to acquire resources.

INTRODUCTION

An improvement in breeding performance with age has been widely reported among iteroparous breeders during the first few breeding attempts (Clutton-Brock 1988; Newton 1989). One potential mechanism to explain this improvement is that older individuals have a greater capacity to find food due to age-related improvements in foraging efficiency or effort (Curio 1983; Martin 1995; Forslund & Pärt 1995). The prevailing environmental conditions may have an important impact on such a relationship. An interaction between age and foraging conditions will occur if age-related differences in foraging performance are more apparent when feeding conditions are poor (Ratcliffe *et al.* 1998). This could occur if older individuals are able to increase their foraging effort during poor feeding conditions without incurring undue costs, because they are more efficient foragers (Forslund & Pärt 1995). During good feeding conditions, the level of effort required to obtain sufficient food will be within the limits of young as well as older individuals. However, in seasonally breeding species, there is often a difference in the timing of breeding between young and older breeders (Perdeck & Cavé 1992). Comparative studies are therefore unable to assess the interactions between age and foraging conditions, because the two age groups are not breeding in the same environmental conditions. Experimental manipulations are required to force young and old individuals to breed at the same time (Daunt *et al.* 1999).

Seabirds tend to show pronounced age differences in reproductive success and timing of breeding (Potts *et al.* 1980; Shaw 1986; Reid 1988; Boekelheide & Ainley 1989; Hamer & Furness 1991; de Forest & Gaston 1996; Moreno 1998). They are also subject to highly variable intra- and inter-seasonal variation in environmental conditions. Collection of data on foraging behaviour of diving seabirds at sea involves considerable logistical difficulties. While direct observation is possible in some cases, most studies have obtained information from transmitting or recording devices attached to the bird, and there have been considerable technological advances in such techniques (Dewar 1924; Stonehouse 1967; Kooyman *et al.* 1971; 1982; Trivelpiece *et al.* 1986; Cairns *et al.* 1987; Wanless *et al.* 1988, 1993a, 1998; Wilson & Wilson 1988; Ydenberg & Forbes 1988; Burger & Piatt 1990; Croxall *et* *al.* 1988; 1991; Ydenberg & Guillemette 1991; Croll *et al.* 1992; Williams *et al.* 1992; Uttley *et al.* 1994; Monaghan *et al.* 1994; Grémillet 1997). I equipped first-time and experienced breedings shags *Phalacrocorax aristotelis* with radio transmitters (Wanless & Harris 1992) and time-at-depth (Wilson *et al.* 1989) gauges to record detailed information on diving behaviour. The shag is a pursuit-diving piscivorous seabird in which first-time breeders are much less successful and breed much later in the season than experienced breeders (Potts *et al.* 1980; Aebischer 1993; Daunt *et al.* 1999). To investigate the interaction between age and environmental conditions on foraging behaviour, I carried out a cross-fostering experiment between young and older breeders (Daunt *et al.* 1999). The two age groups were also matched for brood size, because it can have profound effects on foraging behaviour (Wanless *et al.* 1993b). The protocol enabled me to compare the foraging behaviour of the two age classes breeding at the same time in two separate periods in the season, namely when the older pairs would normally feed their chicks and when the young pairs would normally feed their chicks.

METHODS

The effect of parental age on breeding performance in this species is manifest largely in differences between pairs containing a two-year-old male and pairs containing an older male. Accordingly, foraging performance was measured in males from these two age classes. These males were from nests used in the experiment described in chapter 2. Therefore, the cross-fostering procedure is as in that chapter, with four experimental groups (two age classes: 'young' and 'older'; two hatching periods: 'early' and 'late').

Of the 76 nests in the experiment, a single foraging trip of 18 older males (10 from the early hatching period, eight from the late hatching period) and 20 young males (10 from the early hatching period, 10 from the late hatching period) was radiotracked during chick-rearing. Young and older birds were monitored at the same time by alternating radiotracking (on a day-to-day basis where possible) between the two age classes through the season. Thus, the two age classes did not differ in the date that radiotracking took place; birds from the late hatching period were radiotracked significantly later in the season (Older early: 30th June ± 3 s.e. days; young early: 30th June ± 3 s.e. days; Older late: 15th July ± 4 s.e. days; young late: 17th July ± 3 s.e. days; Two-way ANOVA: age: $F_{1,35} = 0.21$, ns; hatching period: $F_{1,36} = 30.56$, $p < 0.001$; interaction term: $F_{1,34} = 0.06$, ns). The manipulation of hatching dates also ensured that there was no difference between the parental age groups in chick age at the time of radiotracking (range 14-31 days). However, the average chick age of birds from the late hatching period was greater (Two-way ANOVA: parental age: $F_{1,35} = 0.63$, ns; hatching period: $F_{1,36} = 23.70$, $p < 0.001$; interaction term: $F_{1,34} = 0.59$, ns), because the initial spread of laying was tighter than the spread of radiotracking.

Brood biomass (total mass of the brood at time of radiotracking) is correlated with trip length and food load (Wanless *et al.* 1993b). Therefore, although young pairs had significantly fewer chicks overall (see chapter 2), the offspring demands of young and older males whose foraging behaviour was studied were approximately equal, due to close matching of the two age classes for brood size. This was carried out on a day-to-day basis where possible (e.g. older male with brood of two on day 1;

young male with brood of two on day 2), although occasionally I was not able to catch the target bird, or a bird with the correct brood size and brood age was not available. Therefore, brood sizes were not identical between age groups, but were similar to the extent that there was no significant effect of parental age on brood biomass (older early: 1744.62 ± 223.61; young early: 1388.33 ± 151.97; older late: 1967.76 ± 265.93; young late: 1683.43 ± 241.99; Two-way ANOVA: parental age: $F_{1,36} = 1.96$, ns; hatching period: $F_{1,35} = 1.43$, ns; interaction term: $F_{1,34} = 0.03$, ns). Brood biomass was not significantly higher in the late hatching period, despite the increase in chick age (see above). This was because the need for effective sample sizes forced me, in my attempt to match brood size between the two age groups, to use the full range of available brood sizes (one, two or three) from the outset, and maintaining this range became impossible because the number of broods of three declined significantly among young pairs as the season wore on. Brood size matching was continued, but the lack of broods of three among late hatching pairs resulted in brood size declining significantly with hatching period (Generalized Linear Model with binomial errors and a logit link function: parental age: $\chi^2 = 0.45$, ns; hatching period: $\chi^2 = 3.96$, $p < 0.05$; interaction term: $\chi^2 = 0.03$, ns). Therefore, the combination of fewer, but older, chicks in the late hatching period resulted in there being no seasonal effect on brood biomass. Matching the two age classes for brood size resulted in the sample of young birds having a higher than average brood size for their age class. As such, there was a bias towards higher quality young birds, which was likely to have made differences between the two age classes harder to detect.

Birds were caught and fitted with two devices. A radio transmitter (Biotrack, mass 20g) was attached below two central tail feathers with Tesa tape and two cable ties. A time-at-depth gauge (Wilson *et al.* 1989, mass 11g) was attached to the bird at the same time, above the tail and attached with two cable ties to the same two feathers as the radio transmitter. The combined mass of the two devices represented < 2% of body mass. Handling time for the complete procedure was less than 10 minutes.

Birds were radiotracked from a station near the highest point on the island (73m a.s.l.). The receiving system consisted of two parallel eight-element Yagi aerials joined by a 2m crosspiece, attached to a vertical 5m mast which allowed the aerials to rotate freely through 360°. The aerials were connected to an ATS R4000 scanning receiver, operating in the 173MHz band. A typical foraging trip consisted of a flight out to the feeding site, a number of dives with periods between dives on the sea surface, and a return flight to the colony. The outward flight was often preceded by a small number of dives near the colony, and the bird occasionally made short flights between foraging areas and had periods of rest on land away from the colony between diving bouts. The method by which information on foraging activity is obtained from radio-tracking is well-established in shags. From the strength and consistency of the signal, it is possible to determine a precise time-activity budget, namely whether the bird is flying (strong, continuous signal), on the water surface (unsteady, continuous signal) or diving (signal disappears) (Wanless *et al.* 1991a, 1991b; Wanless & Harris 1992; Wanless *et al.* 1993a, 1993b, 1998), and no adverse effects on behaviour resulting from handling or device attachment have been recorded (Wanless *et al.* 1991a, 1991b). Foraging locations were estimated by dead-reckoning, using the bearing of the bird, the flight time to the foraging site, and an average flying speed of 15.4 ms^{-1} (Pennycuick 1997); shags generally fly directly between the colony and the feeding site (Wanless 1991b).

The time-at-depth devices contained a light-emitting diode attached to a bung that moved up and down inside a cylinder in response to changes in hydrostatic pressure. A strip of photographic film was wrapped round the cylinder and recorded the movements of the diode (Wilson *et al.* 1989). This device was used to calculate the mean foraging depth and the proportion of the total underwater time spent foraging ('bottom time' - see Wanless *et al.* 1997), assuming a swim speed of 1.8 ms^{-1}. To ensure that the depth and time-activity data corresponded, it was essential that no foraging occurred between device deployment and radiotracking. Therefore, deployment took place at dusk each day and the first trip after dawn the next day was followed (shags on the Isle of May do not feed at night – Wanless *et al.* 1999). One bird was followed each day. Birds were caught on their return to the nest after the foraging trip, to ensure that the data from the two devices corresponded exactly. This was successful with eight older early, seven young early, six older late and four young late males.

I compared the mean individual dive durations and mean foraging depths of young and older males. Bottom time was examined in the two age groups, with mean foraging depth included as a covariate (bottom time is heavily dependent on this variable - Wanless *et al.* 1993b; 1997). I examined the dive duration to succeeding surface duration relationship. There is a significant, non-linear relationship between these two parameters (Wanless *et al.* 1993, 1998; Walton *et al.* 1998). All surface times were included in this analysis except those immediately succeeding or preceding flights and those deemed longer than the bout criterion surface recovery interval, calculated by a two-process model on log frequency plots of surface periods (Sibly *et al.* 1990). The analysis was repeated using preceding ('anticipatory') surface time instead of succeeding ('recovery') surface time (after Lea *et al.* 1996). I compared number of dives, total time under water and total trip duration. Finally, the final period on the sea surface prior to the return flight to the colony was also compared. This is generally much longer than recovery periods between dives (unpublished data), and is highly variable between individuals. Thus, it may indicate the current physical state of the bird at the end of the diving bout.

Age (young vs older) and hatching period (early v late) were entered as factors in all analyses.

RESULTS

Foraging locations for the two age classes in the early hatching period are shown on figure 4.1a), and for the two age classes in the late hatching period on figure 4.1b). Birds tended to feed either just off the island or close to the mainland coast, which is typical of this colony (Wanless *et al.* 1991b, 1998). Accordingly, we analysed differences in the distribution of birds feeding chicks early and late in the season by dividing the foraging area into two sectors (after Wanless *et al.* 1991b), one sector represented the area within 4km of the island and the second sector represented the area between the 4km circle and the mainland (see figure 4.1a). There was a significant effect of hatching period on foraging location (age groups combined; $\chi^2 = 4.95$, $p < 0.05$), with many more birds from the early hatching period feeding close to the colony. There was no significant difference in the proportion of young and older males in the two foraging locations, either early (figure 4.1a) or late (figure 4.1b) in the season (early: $\chi^2 = 1.8$, ns; late: $\chi^2 = 0.35$, ns). However, there was a tendency in the late hatching period for the two age classes to use different areas close to the mainland, with older birds operating towards the south-west.

Birds from the late hatching period were making shorter dives, and diving to shallower depths, but there was no difference between the age classes (figure 4.2). Bottom time (proportion of time underwater spent foraging) was heavily dependent on average foraging depth, but there were no effects attributable to differences in age or hatching period (figure 4.3a, b).

Figure 4.4 shows that surface duration was highly dependent on dive duration, as documented by Wanless *et al.* (1993a; 1998), and is best explained by an exponential fit to the data. There was a significant interaction between age and hatching period, with older males in the late hatching period spending shorter periods on the surface between dives (figure 4.4b). This resulted in late, older males making more dives and spending more total time under water, but there was no difference in total length of trip (figure 4.5a - c).

The duration of the final period of recovery on the surface prior to the return flight to the colony was significantly longer among young males during both hatching periods (figure 4.6).

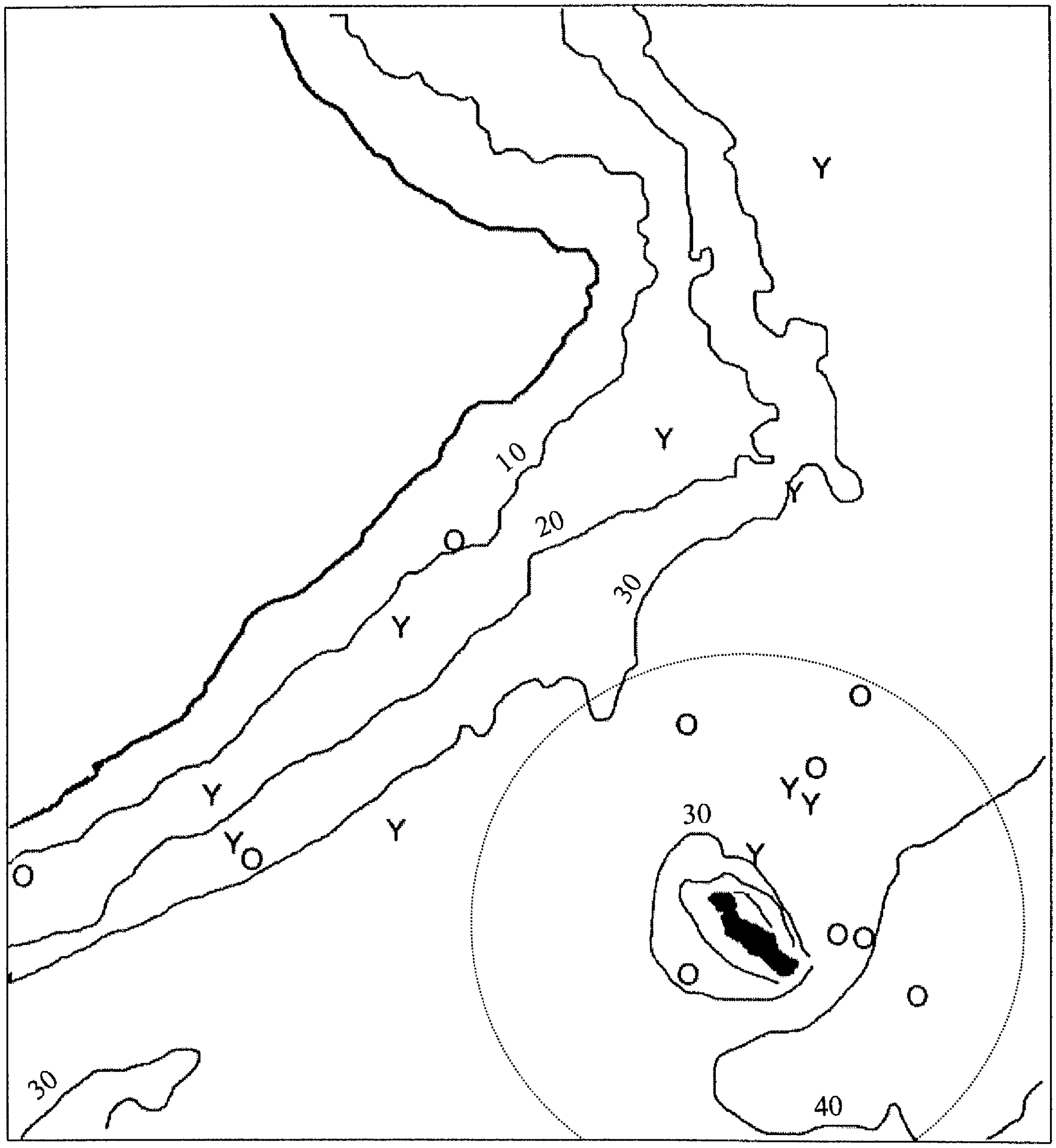

Figure 4.1 a): Foraging locations of young (Y) and older (O) males in the early hatching period. Map shows the Isle of May in solid black, the mainland coastline (thick line), 10m bathymetric contours (thin lines) and sector boundary (dotted line – see text). Scale 1cm = 1km.

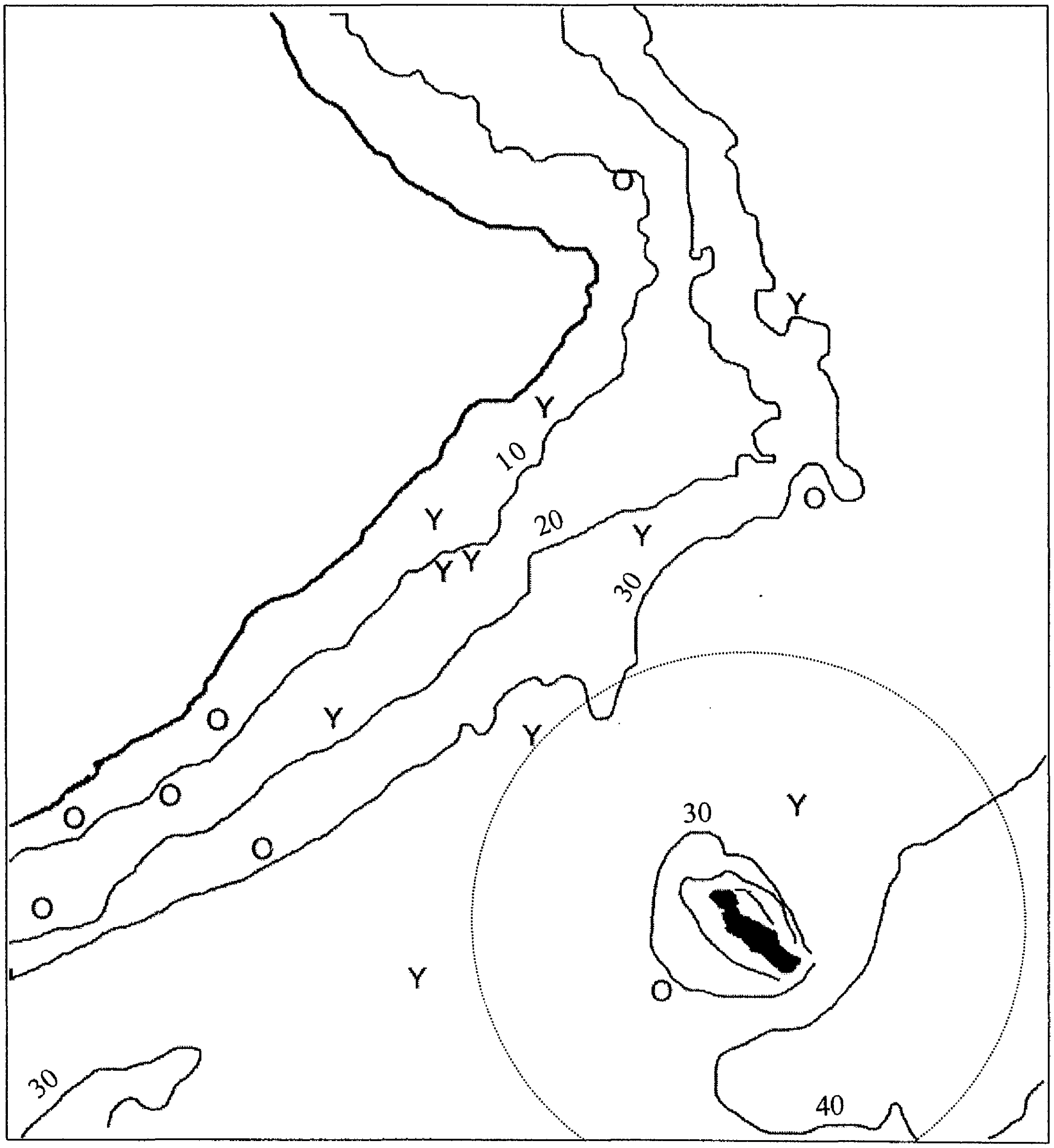

Figure 4.1 b): Foraging locations of young (Y) and older (O) males in the late hatching period. Map shows the Isle of May in solid black, the mainland coastline (thick line), 10m bathymetric contours (thin lines) and sector boundary (dotted line – see text). Scale 1cm = 1km.

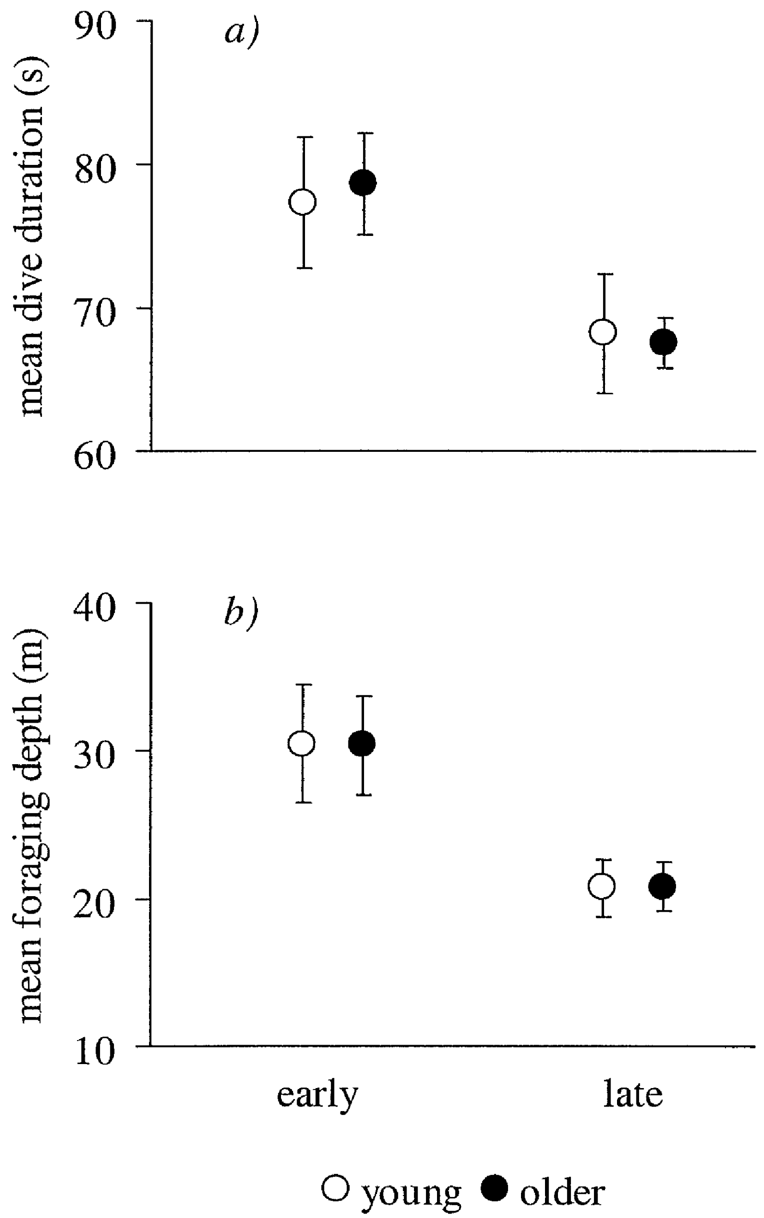

Figure 4.2: The effects of age and hatching period on **a)** mean dive duration (from radio telemetry) and **b)** mean foraging depth (from time-at-depth gauges). There was no effect of age on either parameter, but there was a significant effect of hatching period, with dives shorter and dive depths shallower in the late hatching period (ANOVA on mean dive duration: age: $F_{1,35} = 0.00$, ns; hatching period: $F_{1,36} = 7.19$, $p < 0.05$; interaction term: $F_{1,34} = 0.06$, ns; ANOVA on mean foraging depth: age: $F_{1,22} = 0.00$, ns; hatching period: $F_{1,23} = 8.89$, $p < 0.01$; interaction term: $F_{1,21} = 0.00$, ns).

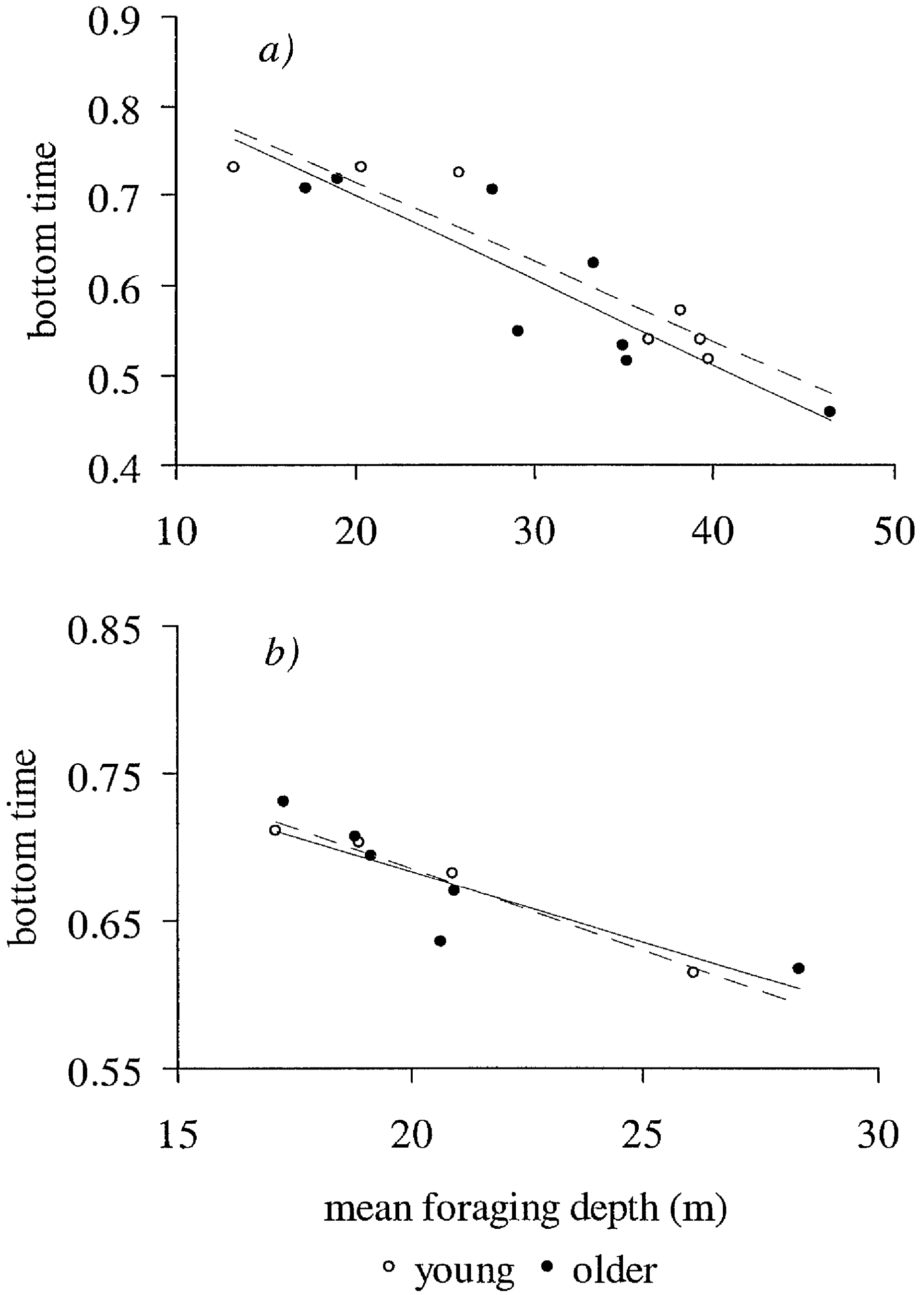

Figure 4.3: Bottom time (proportion of time underwater spent foraging) in relation to age and mean foraging depth **a)** early and **b)** late in the season from time-at-depth gauges. Dotted line = young males; solid line = older males. The hatching periods are plotted separately for clarification, but all nests were analysed together, with age and hatching period as factors. There was a significant effect of foraging depth on bottom time, but no effect of age and hatching period (ANCOVA on arcsine-transformed bottom time: foraging depth: $F_{1,23} = 107.87$, $p < 0.001$; age: $F_{1,22} = 0.90$, ns; hatching period: $F_{1,21} = 2.10$, ns; all interaction terms ns).

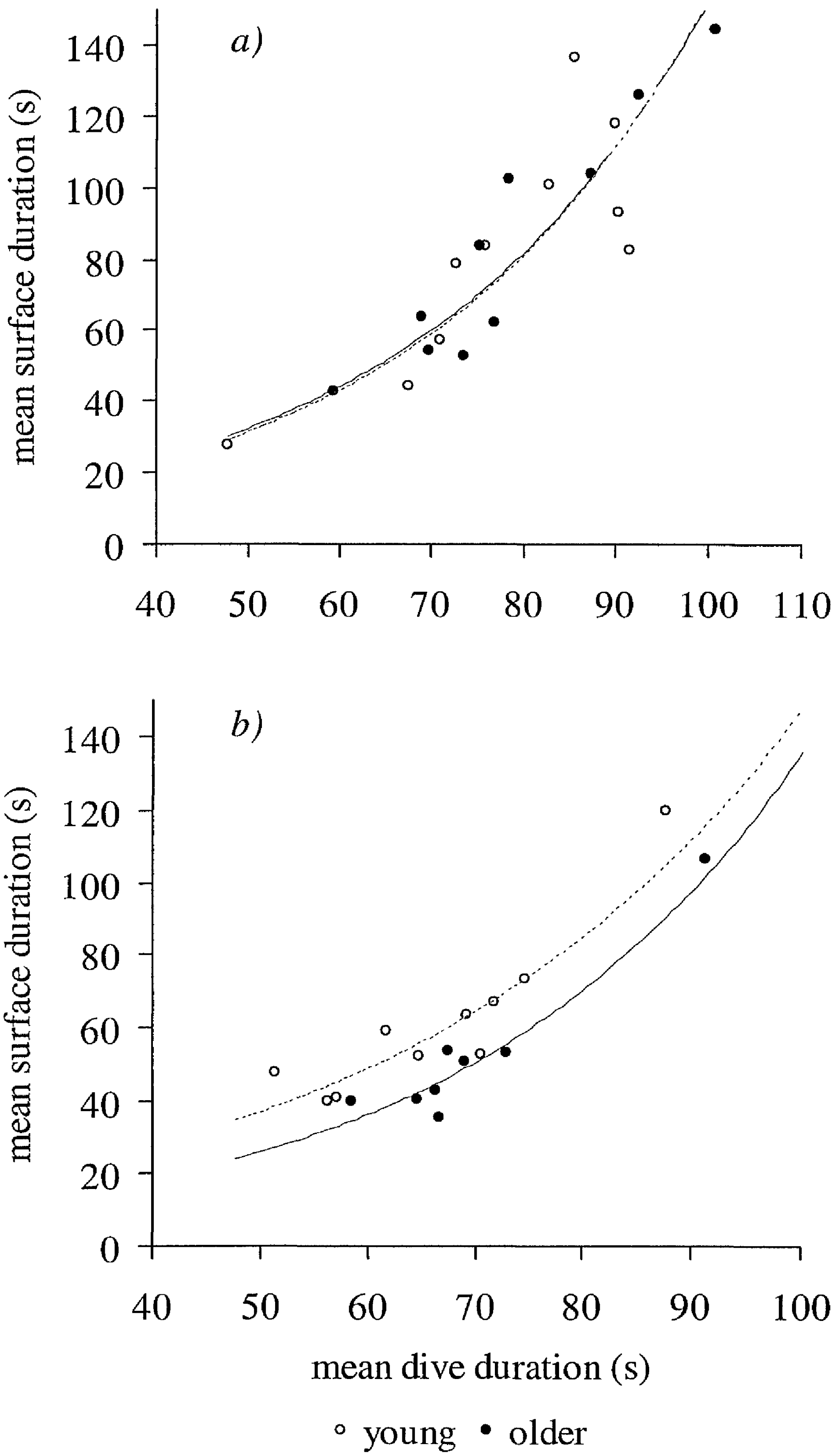

Figure 4.4: (legend over page)

Figure 4.4: Surface duration in relation to age and mean dive duration **a)** early and **b)** late in the season. Regression lines are exponential functions. Dotted line = young males; solid line = older males. The hatching periods are plotted separately for clarification, but all nests were analysed together, with age and hatching period as factors. There was a significant effect of dive duration on succeeding surface duration, and a significant interaction between age and hatching period (ANCOVA on ln(surface duration): dive duration: $F_{1,33} = 144.27$, $p < 0.001$; age: $F_{1,33} = 3.02$, ns; hatching period: $F_{1,33} = 0.71$, ns; age x hatching period: $F_{1,33} = 5.44$, $p < 0.05$; all other interaction terms ns). The result was similar replacing succeeding dive with preceding dive in the analysis, after Lea *et al.* 1996 (ANCOVA on ln(surface duration): dive duration: $F_{1,33} = 151.56$, $p < 0.001$; age: $F_{1,33} = 2.13$, ns; hatching period: $F_{1,33} = 0.90$, ns; age x hatching period: $F_{1,33} = 5.38$, $p < 0.05$; all other interaction terms ns).

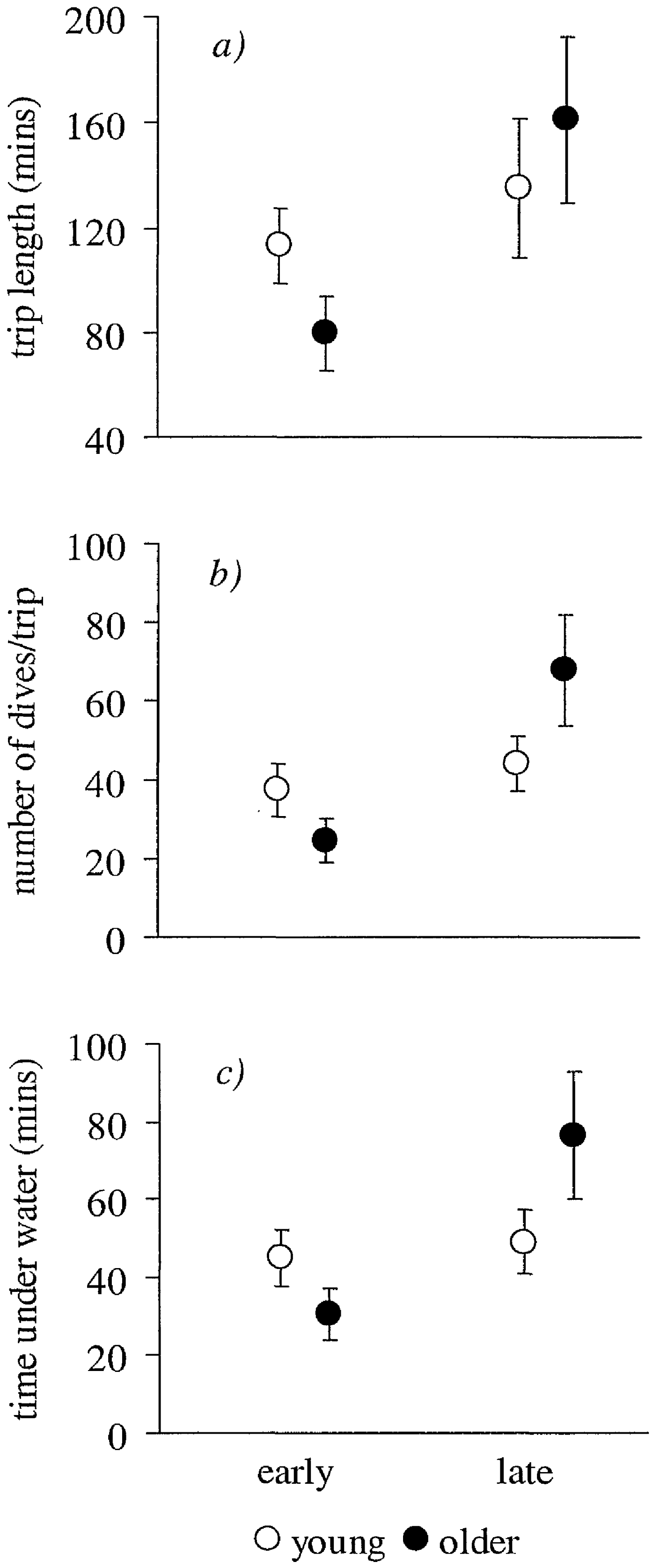

Figure 4.5: (legend over page)

Figure 4.5: The effects of age and hatching period on a) trip length (mins), b) number of dives per trip and c) total time under water (mins). There was a significant effect of hatching period on all three variables, and there was an interaction between age and hatching period in the number of dives per trip and total time under water, but not trip length (ANOVA on trip length: age: $F_{1,35} = 0.06$, ns; hatching period: $F_{1,36} = 5.24$, $p < 0.05$; interaction term: $F_{1,34} = 1.82$, ns; ANOVA on number of dives per trip: age: $F_{1,34} = 0.43$, ns; hatching period: $F_{1,34} = 6.77$, $p < 0.05$; interaction term: $F_{1,34} = 4.86$, $p < 0.05$; ANOVA on total time under water: age: $F_{1,34} = 0.48$, ns; hatching period: $F_{1,34} = 5.25$, $p < 0.05$; interaction term: $F_{1,34} = 4.79$, $p < 0.05$).

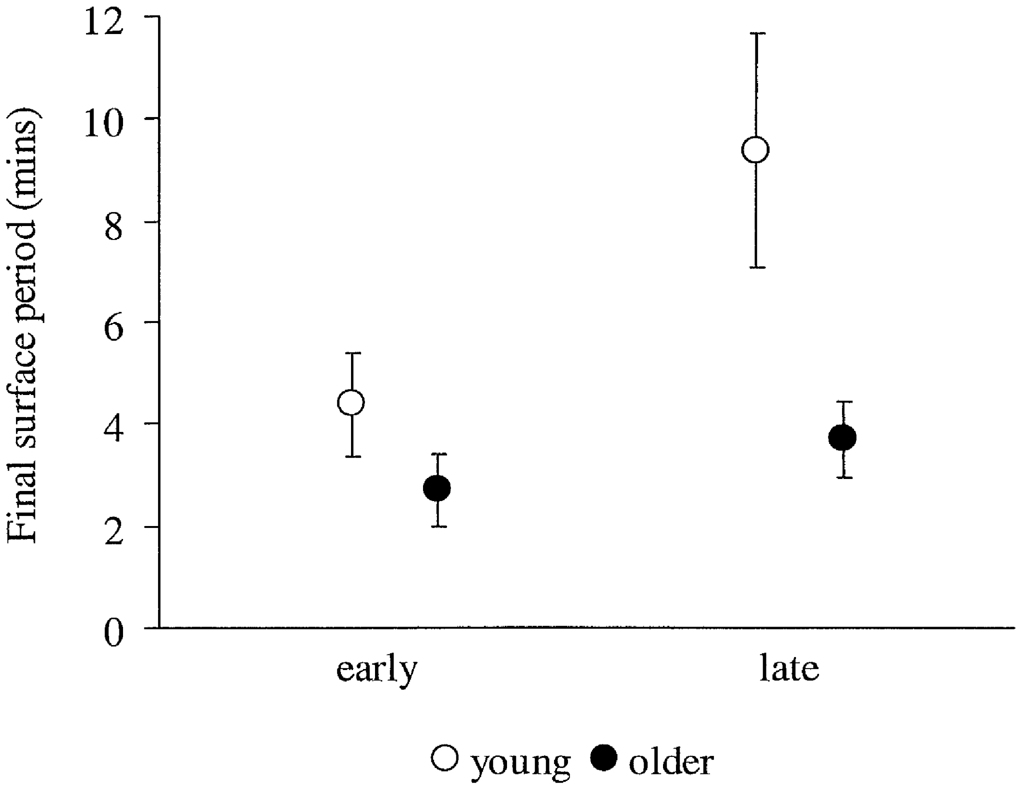

Figure 4.6: Duration of the final surface period in relation to age and hatching period. There was a significant effect of age and hatching period on final surface period, with young and late males spending more time on the sea surface before the return flight to the colony (ANOVA: age: $F_{1,35} = 5.32$, $p < 0.05$; hatching period: $F_{1,35} = 4.23$, $p < 0.05$; interaction term: $F_{1,34} = 1.62$, ns).

DISCUSSION

Overall, the two hatching periods differed markedly in almost every aspect of the feeding activity of the radiotracked birds, including location, dive duration, foraging depth and foraging effort. In addition, unattendance of chicks was widespread throughout the colony (previously unrecorded on the Isle of May). This provides convincing circumstantial evidence that there was a significant difference in feeding conditions early and late in the season. It would appear that there was a shift in prey from close to the colony to close to the mainland. Dramatic changes in local food abundance within a season have been recorded previously at this colony by Wanless *et al.* (1998), in their case the shift occurring in the opposite direction, from close to the mainland early in the season to close to the colony later in the season.

The cross-fostering protocol enabled me to compare young and older birds rearing chicks at the same time in contrasting feeding conditions. The prediction that there would be an interaction between age and the external environment on foraging behaviour was upheld. Late in the season, when feeding conditions appeared to be poorer, older males spent a greater proportion of their time underwater than young males. They did not achieve this by altering the length or depth of dives. Moreover, bottom time was very similar between the two age groups both early and late in the season. Rather, older individuals in the late hatching period spent less time resting between dives, resulting in a greater number of dives and more overall time spent underwater in a foraging trip. There was no equivalent difference early in the season, when foraging conditions were apparently better. Older males may have achieved this improved diving efficiency because they are more efficient foragers (Curio 1983; Nur 1984; Reid 1988; Jansen 1990; Desrochers 1992). This would enable them to increase foraging effort without incurring costs. One theory that has been suggested to explain improvements in foraging efficiency with age is that young breeders may not be physically mature (Marchetti & Price 1989), putting them at a physiological or competitive disadvantage. Alternatively, they may be inexperienced at locating food (Martin 1995). The tendency for there to be a difference in foraging location between the two age classes in the late hatching period suggests that there may be an important learned component of age-specific foraging performance, thus enabling older individuals to fly to the few profitable feeding areas when conditions are poor, improve their prey capture rates, and increase diving efficiency as a result. An improvement in average foraging efficiency with age may also occur through selective effects, if high quality individuals have a higher survival rate (Forslund & Pärt 1995).

In addition, the last recovery period, prior to the flight back to the colony, was significantly longer among young males. One possibility is that young males are physically constrained, requiring longer to recover from diving or to prepare for the energetically costly return flight. Last recovery duration was also longer in the late hatching period, when foraging trips were significantly longer, suggesting that the length of time spent on the sea surface before returning to the colony is indeed an index of the current physical state of the bird. Alternatively, young males may be inexperienced and still be learning to optimise their time budget to maximise food provisioning to the chicks, which would be achieved by returning to the nest rapidly to reduce digestion time. Conversely, they may be deliberately spending longer on the water at the end of feeding to allow more time for digestion. However, a better strategy would be to do this back at the colony, rather than in the water, because of the increased cost of the latter (Schmid *et al.* 1995), and a period of time spent on the sea rocks after a foraging trip before returning to the nest is a common feature in shags and has been interpreted as time allocated to digesting food for self-maintenance (Wanless *et al.* 1993b).

Matching the two age groups for brood size resulted in the young males that were selected for radiotracking having a larger average brood size than the mean brood size for all young males persisting to this stage in chick-rearing, whereas the older males followed in this study represented average quality individuals for their age class. Thus, the age effects may be even more marked than those observed.

The capacity of older individuals to adjust their foraging behaviour to the prevailing environmental conditions could be an important factor determining their improved breeding performance (Potts *et al.* 1980; Aebischer 1993; Daunt *et al.* 1999; Daunt *et al.* in press). Young males may not have the capacity to work harder when foraging conditions are poor because they are constrained (Curio 1983), possibly through a lower mean foraging performance. Alternatively, the reduced diving efficiency of young birds in poor conditions could be a result of reproductive restraint, because of their higher Residual Reproductive Value; the harder working older individuals may carry longer term costs, even if in the short term their greater foraging effort is associated with increased breeding performance (Curio 1983; Roff 1992; Stearns 1992). However, the longer period of recovery on the sea surface prior to the return to the colony among young males suggests that they are physiologically constrained. Young males do not appear to be able to increase their foraging effort when conditions are poor, and, in species such as seabirds that live in unpredictable environments, this is likely to have profound consequences on the fitness of their offspring. To establish whether the increased foraging effort among older breeders during poor foraging conditions results in higher food loads being brought to the chicks, data on food acquisition during foraging trips are required.

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Chapter 5

The effects of foraging efficiency on age-specific breeding performance

ABSTRACT

Improvements in breeding performance have been recorded in many species over the first few breeding attempts. Such patterns may occur if older individuals are more efficient foragers. I compared the overall foraging efficiency of young first-time breeding and older breeding shags *Phalacrocorax aristotelis.* Efficiency was calculated by comparing energy gained (from food loads on return from foraging trips) to energy expended (from time-energy budgets during the foraging trip). Hatching dates were manipulated experimentally to ensure the two age classes were foraging in the same environmental conditions, and young and older adults were also matched for brood size. Irrespective of the time of season, there was a strong tendency for older breeders to bring back more food to their chicks than young breeders. There was no difference in overall energy expended, but older males expended more energy on diving later in the season, a period when foraging conditions appeared to be relatively poor. No significant difference in foraging efficiency was detected between the two age groups. Body condition was the same for the two age classes, suggesting older breeders can provision themselves and their offspring successfully, whereas young breeders may safeguard their own body condition at the expense of the fitness of their offspring. Older individuals achieve improved breeding performance probably through a combination of increased foraging efficiency and more efficient time allocation during poor foraging conditions.

INTRODUCTION

An improvement in breeding performance with parental age is widespread among iteroparous breeders (Clutton-Brock 1988; Newton 1989). A key mechanism likely to explain this pattern is foraging efficiency (Curio 1983; Reid 1988; Nur 1984; Desrochers 1992a; Forslund & Pärt 1995; Catry & Furness 1999; Galbraith *et al.* 2000). Two main theories have been suggested to explain individual improvements in foraging efficiency with age. First, young breeders may not be physically mature (Marchetti & Willard 1989), which may put them at a physiological and/or competitive disadvantage. Second, the greater experience of older breeders will be significant if there is an important learned component to foraging, which may be particularly apparent during the reproductive period when demands are higher (Martin 1995). Cross-sectional comparisons will also find an age-specific improvement in foraging efficiency if, at the population level, older age classes comprise birds of a higher average quality (Forslund & Pärt 1995). This occurs if more efficient foragers also have a higher survival rate (Nol & Smith 1987; Ratcliffe *et al.* 1998; Cam *et al.* 2000), or if high quality foragers delay age at first breeding (Nol & Smith 1987; Gustaffson & Pärt 1990). Despite the strong theoretical support, there has been surprisingly little work on the role foraging efficiency plays in age-specific breeding performance. While a number of studies have shown that juveniles are less competent foragers (reviewed in Wunderle 1991), only two studies have compared the foraging efficiency of young and older breeders (Jansen 1990; Desrochers 1992b), both reporting an age-specific improvement.

Here I describe the first study among non-passerine birds that measures age-specific foraging efficiency directly among breeding individuals, using the shag *Phalacrocorax aristotelis*, a pursuit diving seabird which feeds almost exclusively on small fish, notably sandeels *Ammodytes marinus* (Harris & Wanless 1991). Previous research on this species has shown marked improvements in offspring growth and survival between pairs containing a two-year-old male breeding for the first time and pairs containing older, experienced males (Potts *et al.* 1980; Aebischer 1993; Daunt *et al.* 1999; Daunt *et al.* in press). Differences in foraging performance are a possible cause of these patterns. Foraging efficiency of the two age classes is defined as the energy gained, derived from food loads obtained from birds on their return to the nest after foraging trips, to the energy expended on foraging trips, derived from time-activity budgets (from radio telemetry – Wanless & Harris 1992) converted into energy budgets from activity-specific costs available in the literature ('gross foraging efficiency', after Weathers & Sullivan 1991). To examine the allocation of energy gained between themselves and their offspring, adults were weighed and a range of morphometrics measured to assess their body condition (mass corrected for size). Young breeders lay later in the season than older breeders (Potts *et al.* 1980; Aebischer 1993; Daunt *et al.* 1999), so a cross-fostering experiment was carried out to ensure that young and older individuals were foraging at the same time of season. Brood size was also matched between the two age groups because it can have important effects on foraging behaviour (Wanless *et al.* 1993b).

METHODS

Details of the brood hatching date manipulation protocol, male age categories and matching of brood size are given in chapters 2 and 4. Data on one complete foraging trip was obtained for 18 older males (10 from the early hatching period, eight from the late hatching period) and 20 young males (10 from the early hatching period, 10 from the late hatching period). One bird was tracked each day. Deployment of the radio transmitter took place at dusk. The bird was weighed (to the nearest 10g) and wing length (maximum flattened chord, to the nearest mm), tarsus length (to the nearest 0.1mm) and head and bill length (to the nearest mm) were measured. Handling time for the complete procedure was less than 10 minutes. The first foraging trip the next day was followed. A detailed time-activity budget was obtained from the strength and consistency of the signal (Wanless & Harris 1992; chapter 4).

Energy expended

The total energy expended on each foraging trip was estimated for all birds that were radiotracked, including those that were not recaught on their return to the nest, by converting the time-activity budget to a time-energy budget using activity-specific energy costs taken from the literature.

Flight costs were calculated from Pennycuick (1989, using the updated BASIC program available from http://detritus.inhs.uiuc.edu/wes/pennycuick.html). This program requires the mass, wing span, aspect ratio and air pressure. For birds that were captured on return to the nest, the mass at capture was used for the inward flight ('loaded' mass i.e. bird + food in gut) and the mass at capture minus the mass of the food load for the outward flight ('empty' mass i.e. bird's gut is empty, although this estimate of empty mass did not account for food in the intestine). For any flights taken during the foraging trip between feeding areas (<8% of flying time on average), the mean of the empty and loaded masses was used. For those birds not caught on return to the nest, no estimate for empty or loaded masses was available, so the mass taken the evening before was used (i.e. when the devices were deployed) for all flights. Wing span was calculated from wing length, which was measured for all birds, from the equation $y = 2.752x + 0.360$, where y = wing span and x = wing length. This equation was obtained by taking both measurements from a sample of breeding adult male shags in 1999 ($n = 18$, $r^2 = 0.71$) using the methods outlined in Pennycuick (1989). Aspect ratio was set at 6.85 (Pennycuick 1997), and air pressure was 1.23 kg m^{-3} (0.5m a.s.l, the approximate flying height for shags). From the output from Pennycuick's program, the chemical power expended at a speed of 15.4 ms^{-1} (Pennycuick 1997) was used.

Data on great cormorants *Phalacrocorax carbo sinsensis* from Schmid *et al.* (1995) were used for the costs of diving underwater (36.7 W kg^{-1}) and resting on the sea surface (14.1 W kg^{-1}). For all swimming calculations, the mean of the empty and loaded masses was used for birds that were captured on return to the nest, and the previous evening's mass was used for all other birds.

For the costs of resting on land during a foraging trip, a figure of 6.06 W $kg^{-0.723}$ from data on great cormorants *Phalacrocorax carbo carbo* (Storch *et al.* 1999) was used. The same mass data were used as with swimming costs.

All activity costs are presented in kJh^{-1}.

Energy gained

The load was drained and the wet mass taken. Each prey item was identified, and its length measured (see Wanless *et al.* 1993b). Individual prey masses were calculated from species-specific length/mass equations (D.A.D. Grant, unpublished data). This information was used to derive the mass of each prey species in the load. From this, the energy content (kJ) of the load was estimated by multiplying each prey species' mass by the following estimates of energy density of prey species recorded: 1-group lesser sandeel 7kJ/g (*Ammodytes marinus*); butterfish (*Pholis gunnellus*) 5kJ/g; dragonet (*Callionymus lyra*) 5 kJ/g; unidentified wrasse (Labridae sp.) 5kJ/g; unidentified crustacea 5kJ/g; unknown species 5kJ/g (Harris & Hislop 1978; Hislop *et al.* 1991).

The load present in the stomach at the time of capture represented the maximum food available for the brood. However, it did not represent the true amount of food caught on the trip, due to digestion that will have taken place between prey capture and flushing (Jackson 1992; Grémillet *et al.* 1996; Wanless *et al.* 1997; Hilton *et al.*

2000b). A mean stomach retention time of 171 minutes has been derived for captive shags fed on sandeels (Hilton *et al.* 2000a). From this, the amount of food consumed (g/min) was calculated from the following equation:

$$x = \frac{q_{return} * e^{\frac{t_{notfeed} + t_{feed}}{171}}}{171 * [e^{\frac{t_{feed}}{171}} - 1]}$$

where x = amount of food consumed per minute, q_{return} = food load obtained at the nest, $t_{notfeed}$ = time between the end of the feeding bout and capture at the nest and t_{feed} = duration of feeding bout (G. Hilton & D. Hilton pers. comm.). The correction assumes a constant rate of food acquisition throughout the foraging bout. The corrected food load is obtained by multiplying x by the duration of the feeding bout (t_{feed}).

The energy content of food loads corrected for digestion was calculated by multiplying the mass by the prey species proportions observed in the uncorrected loads, converting the individual species' masses into energy content (Harris & Hislop 1978; Hislop *et al.* 1991), and summing the energy contents.

Foraging efficiency

Foraging efficiency was calculated as the ratio of energy gained, in kJ, to the energy expended, in kJ ('gross foraging efficiency - Weathers & Sullivan 1991; Grémillet 1997), multiplied by the assimilation efficiency (77% - Grémillet *et al.* 1995). A value of 1 indicates a balance of gain and expenditure, a value greater than one a relative gain and a value less than one a relative loss.

Body condition

An index of body size was generated from the morphometric measurements taken (wing length, tarsus length, head and bill length), after Golet & Irons (1999), for all except one young and two older individuals (whose tarsus was not taken in error). The three measurements were entered into a prinicipal components analysis. The first principal component explained 51% of the variance (loadings: wing length = 0.649, tarsus = 0.865, head and bill = 0.601). The original measurements were standardised, multiplied by the loadings and summed to produce the body size index. Body mass for all birds was regressed against body size, using the mean of the empty and loaded masses of birds that were retrapped, which represented the most consistent estimate with respect to gut content, and the masses from the previous evening for the birds that were not retrapped (i.e. the only mass measure available for those individuals). The analysis was repeated on retrapped birds only using the 'empty' mass.

Statistical analysis

Normality was tested with Kolmogorov-Smirnov goodness-of-fit tests, and parametric statistics were employed where appropriate. Age (older vs young) and hatching period (early vs late) were entered as factors in all analyses, and brood mass at the time of tracking was entered in the analysis on energy expended and energy gained (parents work harder and bring back heavier loads as chicks get larger – see e.g. Wanless *et al.* 1993b; Catry & Furness 1999; Ratcliffe & Furness 1999). All analyses were carried out at the level of the nest.

RESULTS

Energy expended

There was a significant difference in energetic cost per unit time for all foraging activities between young and older birds (see table 5.1). This was due to older males being significantly heavier than young males ($t_{36} = 2.10$, $p < 0.05$), and the activity calculations are completely or largely dependent on mass (see methods). Despite this, there was no significant difference in total energy expended on foraging trips with respect to age. However, energy expended increased significantly in the late hatching period (figure 5.1). Comparisons of total energy spent on different activities showed no effect of age, but an effect of hatching period on flight and diving. There was an interaction between age and hatching period with respect to energy expended on diving, with older males in the late hatching period expending more energy underwater (table 5.2). There was no effect of brood mass.

	Relative energy expenditure (kJh^{-1})		Age		Hatching period		Interaction	
	Young	Older	*F*	*p*	*F*	*p*	*F*	*p*
Flight (‘empty’)	541.4 ± 10.7	564.7 ± 10.4	2.40	ns	1.08	ns	0.67	ns
Flight (‘loaded’)	550.3 ± 11.7	593.8 ± 11.2	7.12	< 0.05 *	0.73	ns	0.13	ns
Flight (between foraging areas)	545.8 ± 11.1	579.1 ± 10.2	4.80	< 0.05 *	0.98	ns	0.38	ns
Land	33.9 ± 0.3	34.9 ± 0.3	4.63	< 0.05 *	0.48	ns	1.22	ns
Sea surface	92.9 ± 1.3	97.3 ± 1.2	6.18	< 0.05 *	1.24	ns	0.47	ns
Diving	241.8 ± 3.4	253.3 ± 3.1	6.18	< 0.05 *	1.24	ns	0.48	ns

Table 5.1: Mean ± s.e. energetic cost per unit time of each activity for two age classes of breeding shags. Age and hatching period (early vs late) were entered as factors in the analysis.

* significance retained after sequential Bonferroni analysis (Rice 1989).

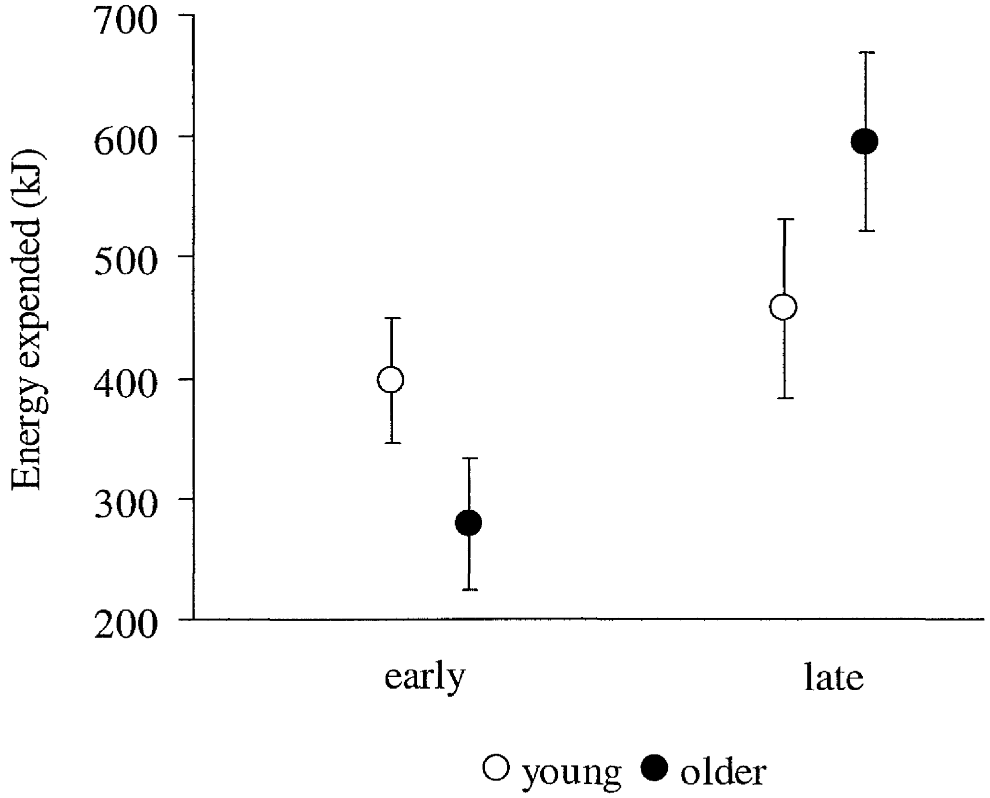

Figure 5.1: The effects of age and hatching period on overall energy expended per foraging trip (ANOVA: age: $F_{1,35} = 0.00$, ns; hatching period: $F_{1,36} = 6.28$, $p < 0.05$; interaction term: $F_{1,34} = 3.29$, ns).

	Energy expended (kJ)		Age		Hatching period		Brood mass		Interactions
	young	old	*F*	*p*	*F*	*p*	*F*	*p*	(summary)
Flight empty	61.8 (7.6)	52.4 (8.4)	1.04	ns	8.50	< 0.01 *	0.86	ns	all ns
Flight full	63.0 (6.6)	66.3 (10.4)	0.18	ns	5.35	< 0.05	1.91	ns	all ns
Flight other	15.2 (7.8)	8.2 (4.9)	0.03	ns	0.02	ns	0.00	ns	all ns
Land	1.2 (1.2)	1.6 (1.6)	0.26	ns	0.03	ns	1.42	ns	all ns
Surface	94.1 (14.2)	78.8 (12.1)	0.54	ns	3.15	ns	0.30	ns	all ns
Underwater	191.8 (23.5)	212.8 (38.9)	0.61	ns	6.43	< 0.05 *	2.00	ns	age * time of hatching: $F_{1,34} = 4.59$, $p < 0.05$; rest ns
Total	427.1 (44.4)	420.2 (66.3)	0.06	ns	6.28	< 0.05 *	1.49	ns	all ns

Table 5.2: Mean (s.e. below) total energy expended on each activity for two age classes of breeding shags. Age, hatching period and brood mass were entered as factors in the analysis.

* significance retained after sequential Bonferroni analysis (Rice 1989).

Energy gained

There was a tendency, though not statistically significant, for food loads delivered by older males to contain more energy on average than the loads of young males (111% more energy early in the season; 90% more energy late in the season; figure 5.2a). There was no significant effect of hatching period or brood mass (figure 5.2a). There was also a tendency for corrected loads i.e. that allowed for digestion to be more energy rich among older males (figure 5.2b).

Foraging efficiency

There was no significant difference in foraging efficiency between the two age groups, although older males tended to have higher efficiency both early and late in the season (figure 5.3).

Body condition

Older birds were heavier (see above; figure 5.4a), but this was largely explained by a strong tendency for them to be structurally larger (size index: $t_{33} = 1.90$, $p = 0.067$; figure 5.4b). Thus, there was no significant difference in body condition (mass corrected for size) between young and older birds (figure 5.4c). There was also no difference when the analysis was repeated using the empty mass of those birds retrapped on return to the nest.

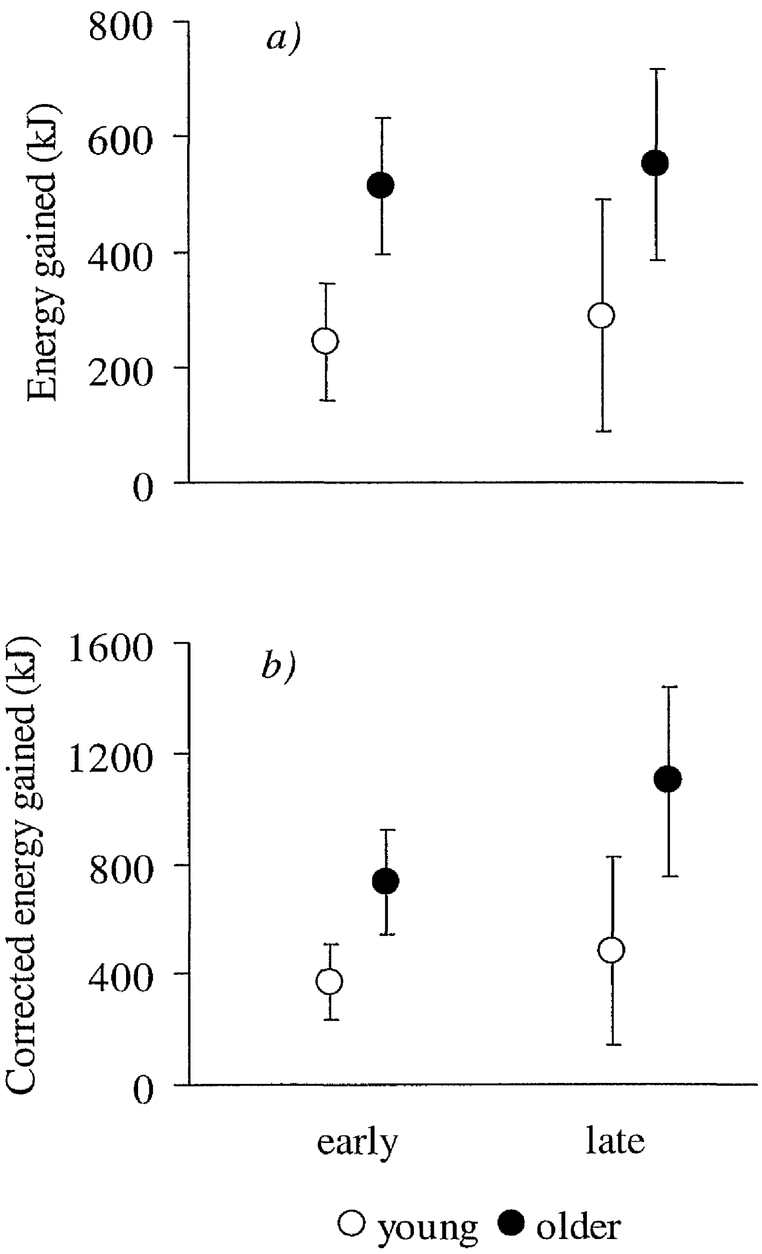

Figure 5.2: The effects of age and hatching period on energy gained during foraging trips: **a)** uncorrected loads; **b)** loads corrected for digestion between prey capture and water off-loading. There was a tendency for an effect of age, and no effect of hatching period and brood biomass, for both uncorrected and corrected loads (ANCOVA on uncorrected loads: age: $F_{1,20} = 4.01$, $p = 0.059$; hatching period: $F_{1,18} = 0.00$, ns; brood mass: $F_{1,19} = 0.76$, ns; ANCOVA on corrected loads: age: $F_{1,20} = 3.85$, $p = 0.064$; hatching period: $F_{1,19} = 1.10$, ns; brood mass: $F_{1,18} = 0.30$, ns).

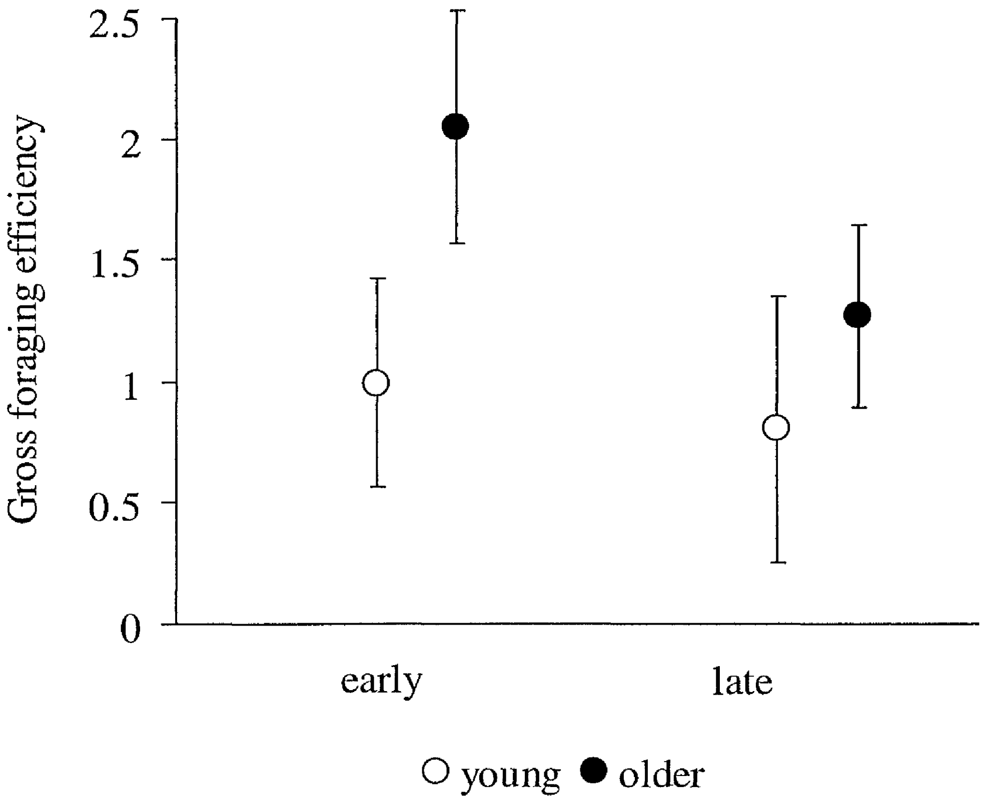

Figure 5.3: The effects of age and hatching period on foraging efficiency (ANOVA: age: $F_{1,20} = 2.66$, ns; hatching period: $F_{1,19} = 1.40$, ns; interaction term: $F_{1,18} = 0.36$, ns).

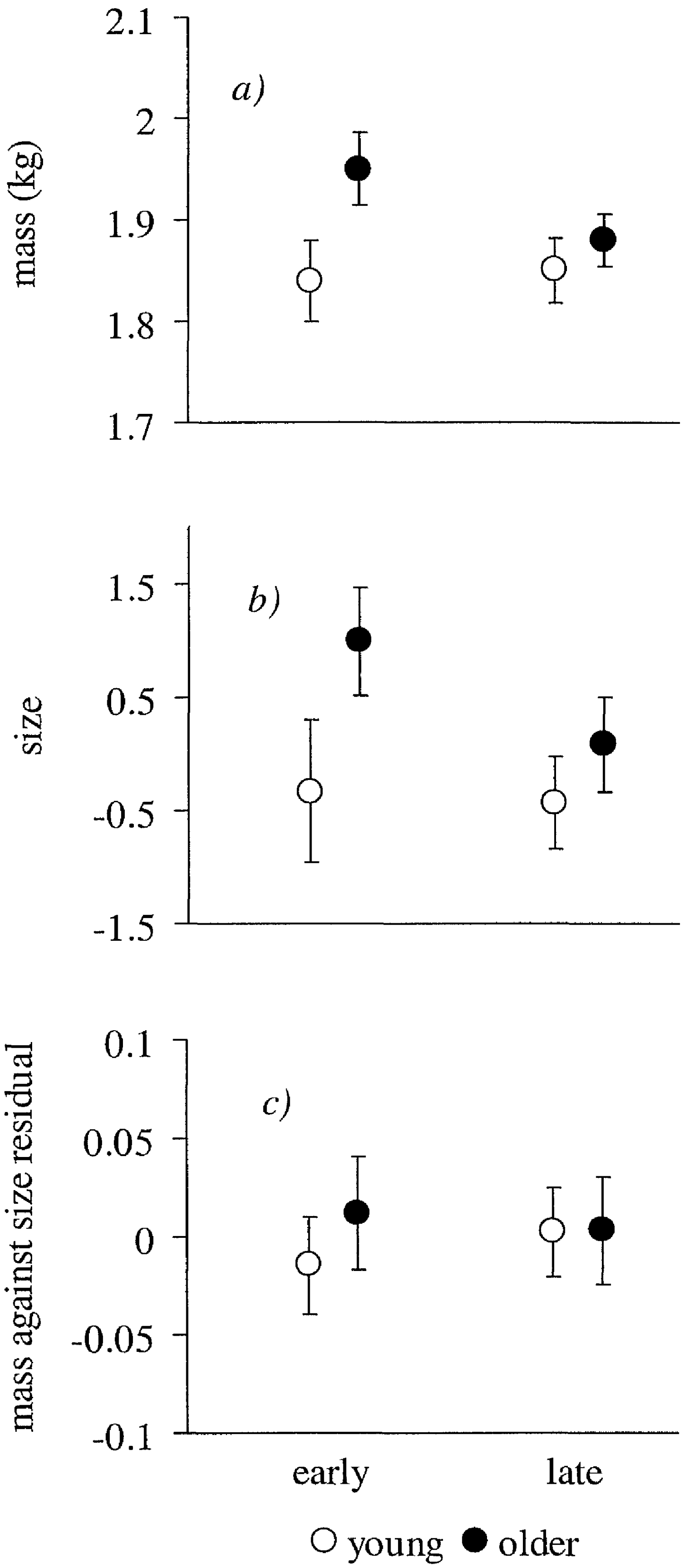

Figure 5.4: (legend over page)

Figure 5.4 a) Mass of young and older males in the early and late hatching periods. Older males were significantly heavier, and there was no effect of hatching period (ANOVA: age: $F_{1,36} = 4.41$, $p < 0.05$; hatching period: $F_{1,35} = 0.51$, ns; interaction term: $F_{1,34} = 1.21$, ns).

b) Size of young and older males in the early and late hatching periods. There was a tendency for older males to be larger, but no effect of hatching period (ANOVA: age: $F_{1,33} = 3.60$, $p = 0.067$; hatching period: $F_{1,32} = 0.94$, ns; interaction term: $F_{1,31} = 0.67$, ns).

c) Condition (residual of mass/size regression) of young and older males in the early and late hatching periods. There was no effect of age or hatching period (ANOVA: age: $F_{1,33} = 0.27$, ns; hatching period: $F_{1,32} = 0.04$, ns; interaction term: $F_{1,31} = 0.24$, ns). The same result was obtained using pre-flushing masses, on birds that were caught on return to the nest after a foraging trip (ANOVA: age: $F_{1,17} = 0.23$, ns; hatching period: $F_{1,18} = 0.39$, ns; interaction term: $F_{1,16} = 0.00$, ns).

DISCUSSION

Older males brought back food loads to their offspring that tended to have a higher energy content on average than those delivered by younger males, although the result was not statistically significant. This tendency may suggest that a poorer foraging performance is a significant component explaining the reduced overall fledging success (Daunt *et al.* 1999) and condition of sons (Daunt *et al.* in press) of young breeders, independent of seasonal effects.

There was no difference in overall energy expenditure (i.e. foraging effort) during single trips between the two age classes, in either hatching period, despite the increased activity-specific costs per unit time of older males due to their higher mass. However, no information was available on the number of foraging trips made per day, which can vary considerably between and within individuals (Wanless *et al.* 1993a). Either age group may adjust patterns of foraging effort across the day that can not be detected from following a single trip.

Older males from the late hatching period spent more energy on diving. This was at a time when foraging conditions appeared to be considerably more difficult than early in the season, with birds expending significantly more energy on flight and diving (chapter 4; table 5.2). Thus, when feeding conditions were poor, older males appeared to be allocating their time more efficiently, by increasing the proportion of time spent feeding.

I could detect no patterns of age-specific foraging efficiency. This may have been due in large part to the small sample sizes, with only 13 loads from older males and 9 from young males obtained. In addition, the young males that were studied were likely to have a high average quality for their age class. The majority of chick mortality among young pairs occurs in the first 10 days after hatching (Daunt *et al.* 1999), so many young nests had failed by the time radiotracking commenced (chick age 14-31 days). Also, matching the two age groups for brood size resulted in the young males having a larger than average brood size for their age class persisting to this stage in chick-rearing. Therefore, my study was conservative. In addition, a number of trips would probably be required for each bird, spread over the entire chick-rearing period, to account for the considerable intra-individual variation in foraging performance that is typical of seabird species such as shags (Wanless *et al.* 1993b, 1998).

Improvements in foraging efficiency within individuals could occur for two reasons. First, if there is a significant learnt component to foraging, older breeders will benefit from greater experience in locating and catching prey (Martin 1995). Second, young breeders may not be physically mature (Marchetti & Price 1989) which could put them at a physiological disadvantage. The difference in size between young and older males in this study lends some support to the maturation hypothesis. Alternatively, the size difference between young and older males may be due to differential survival of low and high quality individuals (Forslund & Pärt 1995).

With the exception of the older males from the early hatching period, mean gross foraging efficiency was approximately equal to one i.e. these individuals were not making an energetic profit from their foraging trips. In addition, the energy gained is partitioned between themselves and their offspring, making the need for a high foraging efficiency even more apparent. The low rate measured among young and late older males may be an accurate reflection of age and/or environmental effects. However, it is unlikely that such a low efficiency could be maintained for long without adverse effects on the offspring, and there was very little chick mortality between radiotracking and fledging in either age class. Birds could have been underperforming because of stress induced by the previous evening's capture and handling. Alternatively, there may be inaccuracies in the water off-loading technique, or the estimates for the prey mass to energy conversion, activity-specific energy costs, assimilation efficiency, or digestion. The correction for digestion was achieved by assuming a mean stomach retention time of 171 minutes (after Hilton *et al.* 2000a). However, strategies could exist that the captive data from which the correction was derived could not detect. Birds may be able to inhibit digestion during chick-rearing to maximise food availability to their offspring. However, Grémillet *et al.* (2000) have shown from work on great cormorants that stomach pH fluctuates during foraging trips, suggesting that some digestion appears to be taking place, although in their study they believed that the birds were foraging prinicipally for themselves, and not their chicks. In addition, the assumption that there was constant food acquisition during the foraging bout may not be realistic. Birds making longer trips may be doing so because the first part of the trip was not successful, causing them to continue diving until food is found, or until other cues become important e.g. exhaustion, the need to take over duties at the nest, or physiological constraints due to their wettable plumage (Grémillet *et al.* 1998). Clearly, more work is required to ascertain digestion strategies and feeding rates during foraging trips.

In many cases, the errors associated with the calculations made to obtain foraging efficiency would impact on the two age groups similarly. However, it is possible that there are age-specific biases that may have made it especially hard to find an effect of foraging efficiency. First, blanket conversion of time-activity budgets into time-energy budgets, irrespective of age or state, will potentially be problematic. A heavy bird may be able to carry out activities more economically than a light bird, but the energy conversion calculations, largely or exclusively dependent on mass, give the opposite effect. Older birds had a higher energy expenditure per unit time for all activities because they were heavier, but they may have a higher foraging efficiency than we could detect because they are more economical. Second, if older males are bringing back larger loads on average, this may be in part due to age-specific digestion strategies, with young males not inhibiting digestion during foraging to safeguard their body condition. However, there was no significant difference in the condition of young and older males, suggesting that both age groups are allocating a similar amount of food to themselves. Older males are probably more successful in foraging, and can thus maintain their offspring's condition as well as their own.

Larger sample sizes may confirm that poorer foraging performance is an important component of the lower breeding success of young males. The improved survival of chicks and growth of sons of older pairs (Potts *et al.* 1980; Aebischer 1993; Daunt *et al.* 1999; Daunt *et al.* in press) is probably achieved through a combination of higher foraging efficiency per se and more efficient use of time at sea during poor feeding conditions. Such patterns may be a result of constraint, or restraint among young males due to their improved Residual Reproductive Value (Williams 1966; Curio

1983; Clutton-Brock 1984; Roff 1992; Stearns 1992; Ylönen *et al.* 1998). Cross-sectional studies such as this can also not exclude the possibility that any differences in foraging performance are caused by the older male age groups containing birds of a higher average breeding quality, which could occur if high quality breeders delay breeding, or have improved survival (Forslund & Pärt 1995).

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Chapter 6

Parental age and offspring ectoparasite load in shags

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F. Daunt, P. Monaghan, S. Wanless & M. P. Harris: Parental age and offspring ectoparasite load in shags

ABSTRACT

Ectoparasite load can have a significant deleterious effect on many aspects of host fitness. Improvements in breeding success with parental age have been reported in a number of avian species. If younger breeders carry high parasite loads and, if effects of this are reflected in their chicks, this could contribute to their poorer breeding success. We measured loads of the louse *Eidemanniella pellucida* (Phthiraptera: Amblycera) on chicks reared by young and older breeding shags *Stictocarbo aristotelis*. Since young shags breed relatively late in the season, and lay smaller eggs, we used a cross-fostering procedure to control for environmental and egg quality effects on chick louse loads. We found that, independent of breeding period and whether the chicks hatched from eggs laid by young or older birds, broods raised by young pairs carried a significantly higher louse load than those raised by older pairs. However, we could not detect an effect of louse load on offspring growth and survival independent of parental age.

INTRODUCTION

Many studies of iteroparous breeders have shown that average reproductive performance improves with parental age (Clutton-Brock 1988; Newton 1989). Ectoparasites can have a significant deleterious effect on offspring growth and survival, so could play a crucial role in this pattern (Loye & Zuk 1991; Lehmann 1993; Møller 1997; Clayton *et al.* 1999). Mean parasite load is sometimes higher in younger age classes, the decline with age either being due to poorer survival of heavily parasitized individuals, or to declines in parasites within individuals as a consequence of age-related changes in infection rate, behaviour, exposure or resistance (Anderson & Gordon 1982; Thomas *et al.* 1995; Rousset *et al.* 1996; Hudson & Dobson 1997). Differences in ectoparasite load could influence the patterns of age-related breeding success by affecting the performance of breeding adults. They may also influence offspring directly if adult and offspring infestations are correlated (Clayton & Tompkins 1995; Wakelin & Apanius 1997), or if young breeders are less efficient at removing ectoparasites from their young (Clayton 1991; Hart 1997).

There is a distinct lack of empirical data to support these ideas. We examined the extent to which offspring ectoparasite load varies in relation to parental age, by measuring infestations of the louse *Eidemanniella pellucida* (Phthiraptera: Amblycera) on the chicks of shags *Stictocarbo aristotelis.* Amblyceran lice feed on feathers, debris and blood, and spend their entire life cycle on the host (Marshall 1981). They are transmitted primarily from parent to offspring (Clayton & Tompkins 1994), and can be present on shag chicks from hatching onwards. There is some evidence that lice time their breeding to coincide with the peak reproductive period in their host (Foster 1969; Marshall 1981). In the shag, younger individuals breed later in the season than older birds (Potts *et al.* 1980; Aebischer 1993). Therefore, in correlative studies in which chick louse load is examined in relation to parental age, the effects of time of year and parental age are confounded. Egg quality may also be an important factor influencing the susceptibility of chicks to ectoparasites. Clutch size does not differ with parental age, but young females lay smaller eggs (Coulson *et al.* 1969), which may give rise to chicks in poorer phenotypic condition and thus more susceptible to infestation. On average, offspring of young parents may also inherit reduced parasite resistance, if more susceptible individuals show reduced survival rates (Wakelin & Apanius 1997). Therefore, we used a cross-fostering experiment to examine the extent to which chicks that hatched from eggs of the same quality, at the same time of year, but were reared by parents of different ages, differed in their louse load, and the effect louse load had on offspring fitness.

METHODS

The parental age categories and experimental protocol are as described in chapter 2, with the exception that the original experiment comprised tetrads of nests with clutch sizes of two and three, whereas lice loads were only monitored from nests with a clutch size of three. We obtained a louse count for 11 older controls, 12 older experimentals, 13 young controls and 12 young experimentals. All chicks in each of these nests were searched over their entire body for adult lice when the first hatched chick was 6-9 days older. This was the oldest age at which an accurate visual count was possible prior to the growth of the down feathers. Although the person counting the lice was aware of the experimental group of the nest, observer expectancy bias (Balph & Balph 1983) was unlikely because lice were very visible, and present in numbers low enough to ensure that counting was straightforward. There was no difference with respect to parental age (older vs young) and hatching period (early vs late) in the age of first hatched chick when the count was taken (Older parents; early hatching period; count taken when first hatched chick was: 7.81 ± 1.33 s.d. days; older parents; late hatching period: 7.33 ± 1.30 s.d. days; young parents; early hatching period: 7.83 ± 1.03 s.d. days; young parents; late hatching period: 7.46 ± 1.27 s.d. days; Two-way ANOVA: parental age: $F_{1,45} = 0.04$, n.s.; hatching period: $F_{1,46} = 1.49$, n.s.; interaction term: $F_{1,44} = 0.03$, n.s.).

Brood louse loads showed a frequency distribution that is typical of parasite abundance on hosts, with many carrying few lice and a smaller number carrying many lice (Anderson & Gordon 1982; Wilson *et al.* 1996 – see figure 6.1). Therefore, to compare infestation rates we entered brood louse count into a Generalized Linear Model (GLM) with a poisson distribution and log link function corrected for overdispersion (ANODEV – see Crawley 1993) with parental age (older versus young), hatching period (early versus late) and brood size (one, two or three) entered as factors and brood age (age of first hatched chick in days) entered as a covariate.

Young shags generally rear fewer chicks than older pairs, independent of seasonal effects (Daunt *et al.* 1999). To examine offspring survival in relation to brood louse load independent of parental age, we entered the fledging success (the proportion of hatched eggs giving rise to fledged chicks per nest) into a GLM, with parental age, hatching period and louse load category (low: 0-2 lice, *n* = 16; medium 3-13 lice, *n* = 17; high: 14+ lice, *n* = 15) as factors, with a binomial distribution and logit link function corrected for overdispersion (ANODEV – see Crawley 1993). To examine relationships between brood louse load and chick growth, surviving chicks were weighed approximately every four days until close to fledging. We took the gradient of the linear phase of growth (chick age 8-30 days) as the measure of growth rate of surviving chicks. A mean growth rate for surviving chicks in each brood was entered into an ANOVA, with parental age, hatching period and louse load category included as factors.

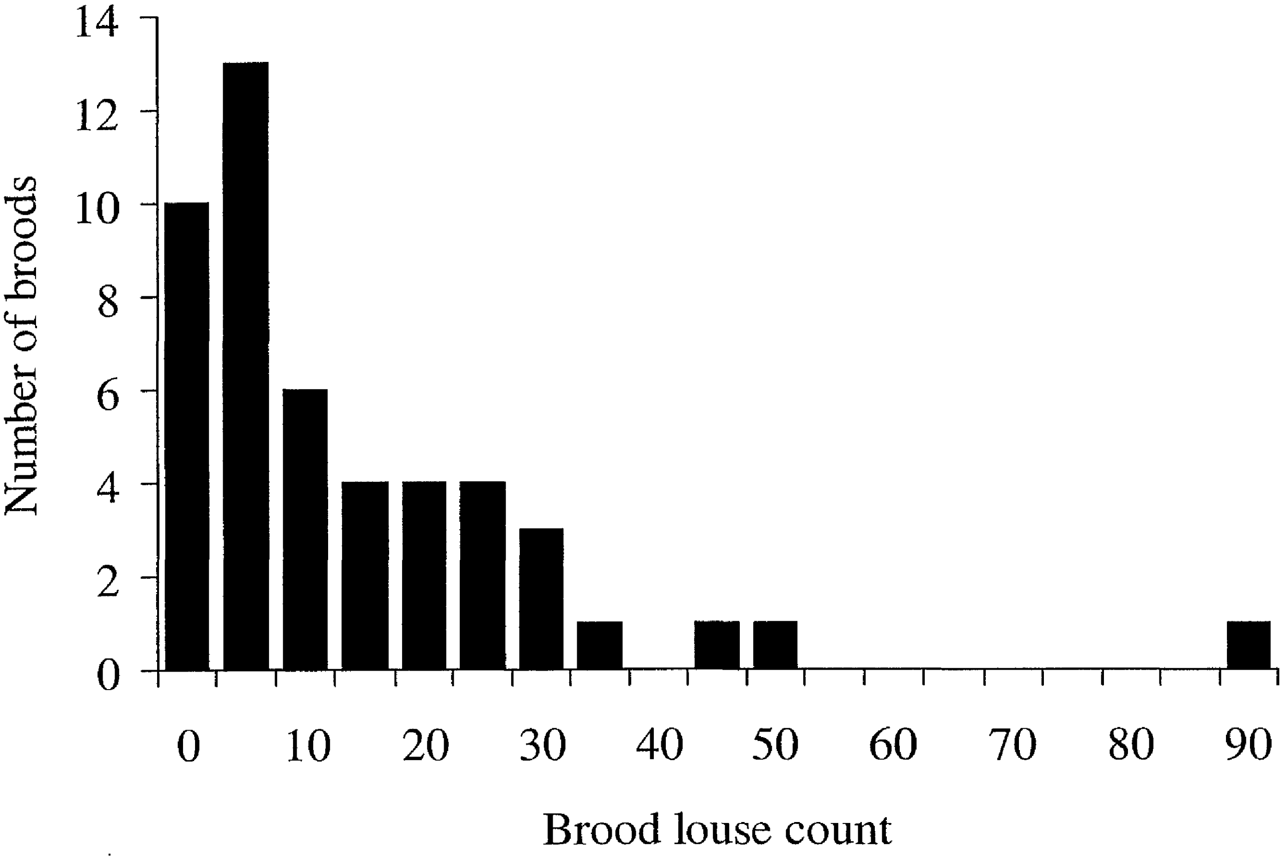

Figure 6.1: Frequency distributions of lice on broods.

RESULTS

Young pairs' broods carried 4.1 times more lice than broods reared by older pairs early in the season (young: 22.00 ± 14.34 s.d., range 2-47; older: 5.35 ± 6.52 s.d., range 0-20; figure 6.2), and young pairs' broods carried 2.8 times more lice than broods reared by older pairs late in the season (young: 16.31 ± 24.17 s.d., range 0-90; older: 5.83 ± 8.44 s.d., range 0-30; figure 6.2). This difference was highly significant; there was no effect of hatching period or brood size, and a significant positive relationship between brood age and louse load (table 6.1).

We found no statistical evidence of an effect of louse load on fledging success independent of parental age (GLM: louse load: $F_{1,44} = 0.30$, n.s.; parental age: $F_{1,46} = 4.15$, $P < 0.05$; hatching period: $F_{1,45} = 2.21$, n.s.; all interactions n.s.). Nor was there any significant independent effect of louse load on chick growth rate (ANOVA: louse load: $F_{1,36} = 0.46$, n.s.; parental age: $F_{1,35} = 0.03$, n.s.; hatching period: $F_{1,38} = 0.64$, n.s.; all interactions n.s.).

	Deviance	df	*F*	*p*
Null model	38.21	47		
Final model	20.08	45		
Brood age	9.56	1	21.42	< 0.001
Parental age	8.66	1	19.41	< 0.001
Brood size	0.26	2	0.28	n.s.
Hatching period	0.01	1	0.02	n.s.
Period x brood size	2.11	2	2.38	n.s.
Parental age x period	0.23	1	0.51	n.s.
Brood size x brood age	2.10	2	2.53	n.s.
Period x brood age	0.05	1	0.12	n.s.
Parental age x brood age	0.06	1	0.14	n.s.
Parental age x brood size	0.64	2	0.72	n.s.
Parental age x period x brood age	0.07	1	0.15	n.s.
Parental age x period x brood size	0.89	2	0.98	n.s.
Parental age x brood size x brood age	0.00	2	0.00	n.s.
Period x brood size x brood age	0.00	2	0.00	n.s.
Age x period x brood size x brood age	0.00	2	0.00	n.s.

Table 6.1: Results of the ANODEV to correct for overdispersed louse count data in the GLM with a poisson distribution and log link function on the effects of parental age, hatching period, brood size and brood age on brood louse load (Crawley 1993).

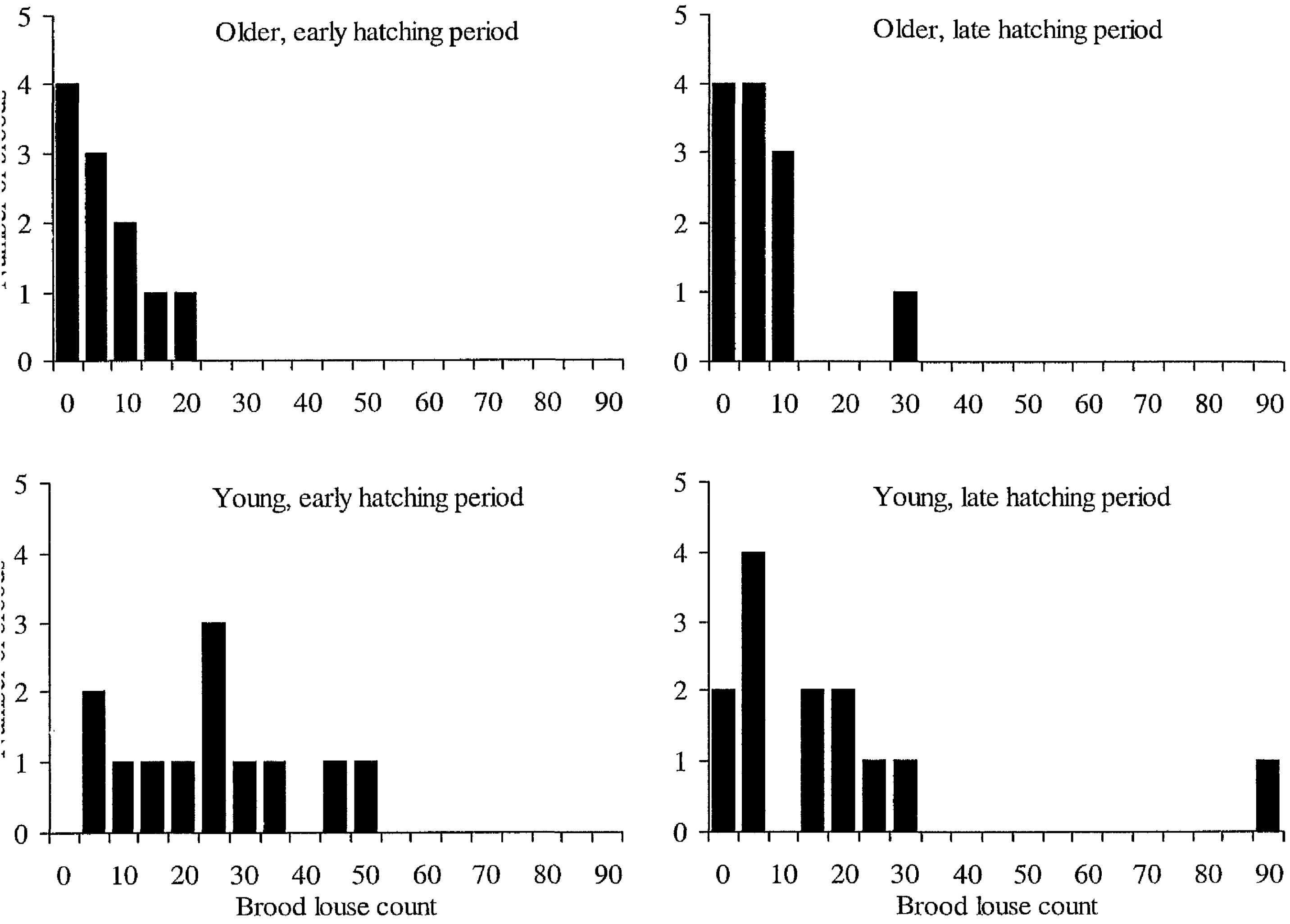

Figure 6.2: The effects of parental age (older vs young) and hatching period (early vs late) on brood louse load. Number of lice carried by broods was significantly higher in young parents, and increased with brood age, but there was no significant effect of hatching period or brood size (table 6.1).

DISCUSSION

There was a difference in louse load between the offspring of young and older breeders which was independent both of the time of season, egg quality and brood size. Broods hatching from eggs laid by older pairs, but reared by young birds early in the season, under conditions normally experienced by older pairs, carried significantly more lice than those reared by older birds breeding at the same time. Similarly, broods from eggs laid by young pairs and reared by young pairs late in the season carried more lice than those of older pairs at that time.

There are several reasons why offspring infestation levels could differ so markedly with respect to parental age. One of these, namely the effects of time of season on louse abundance was precluded by our experimental design. The cross-fostering protocol was also designed to control for the effect of chick quality on infestation levels operating through heritable immune response or phenotypic hatchling quality. However, it is possible that the age at which lice were counted was too young for the louse load to reflect the quality of the offspring, because the lice were all new colonisers. Rather, the higher louse loads found on young parents' broods may indicate a higher louse load on the adults themselves. The vertical mode of transmission (parent to offspring) exhibited by lice would predict such a correlation. There is some empirical evidence that this is so (Clayton & Tompkins 1994, 1995; Lee & Clayton 1994), and the positive relationship that we found between brood age and louse load supports this hypothesis. Infestation levels may peak in the younger age classes (Anderson & Gordon 1982), either through differential host mortality (Rousset *et al.* 1996) or age-related changes in infestation (Thomas *et al.* 1995).

A fourth possibility is that young birds are not grooming their chicks as effectively as older birds. In shags, chicks of the age that we measured louse load are unable to groom themselves and are groomed by their parents (Snow 1963). No ticks, mites or other louse species were observed on the chicks that we examined. However, even if older pairs are grooming their naked chicks more than young pairs, there may be reasons for doing so other than the removal of louse e.g. the removal of more deleterious ectoparasites invisible to the naked eye, or skin debris.

After controlling for parental age, we detected no independent effect of louse load on chick growth or survival. Other studies have also found no effect of louse load on offspring fitness (Clayton & Tompkins 1994, 1995; Lee & Clayton 1995; Tompkins *et al.* 1996; Clayton *et al.* 1999). Booth *et al.* (1993) warned of the difficulties of assessing the effects of unmanipulated infestation levels, due to the aggregated distribution of ectoparasites leading to very small sample sizes of hosts with high loads (see figure 1). With louse load tightly linked with parental age in our data set, variation in louse load within the parental age classes was probably insufficient for us to detect any direct effect on offspring fitness by statistically controlling for parental age in our analyses. The apparent lack of any effect on chick growth or survival in this study may also be due to the louse load on naked chicks not adequately reflecting louse load during the remainder of the pre-fledging phase.

Early studies also found no effect of lice on adult host survival (Ash 1960; Clayton & Tompkins 1994; 1995; Lee & Tompkins 1995). However, a recent paper demonstrated that birds with a high louse load showed lower recapture rates the following summer (Clayton *et al.* 1999), the authors arguing that experiments need to be long-term, because of the chronic impact lice have on their hosts. The effects may also be more apparent under certain environmental conditions. Furthermore, the patterns we have observed may be exacerbated if the abundance of one ectoparasite is positively correlated with that of other parasites (Marshall 1981, Borgia & Collis 1989). Older, feathered shag chicks also carry mites and the Ischnoceran louse *Pectinopygus brevicornis* (pers obs.). Amblyceran lice are carriers of endoparasites (Clayton 1990; Bartlett 1993), and transmission could occur by injestion of infected lice during grooming (Clayton & Tompkins 1995). If the ectoparasite loads measured in this study are a reflection of post-fledging infestation rates, then we might expect effects on post-fledging survival and recruitment rate of offspring.

It is clear from this study that offspring parasite load and parental age are negatively related. There are likely to be several mechanisms contributing to age-specific differences in breeding performance (Sæther 1990; Forslund & Pärt 1995). Clearly, data on ectoparasite loads on the adults themselves are required, coupled with the manipulation of ectoparasite numbers, before we can fully elucidate the role ectoparasites play in age-specific reproductive success.

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Chapter 7

Sexual ornament size, individual quality and age in male and female shags

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F. Daunt, P.Monaghan, S. Wanless & M. P. Harris: Sexual ornament size, individual quality and mating preferences in male and female shags.

ABSTRACT

Research into sexual selection and animal ornamentation has been largely directed at males in sexually dimorphic species. In contrast, there is relatively little empirical information on the link between ornament size and female quality. Using the shag *Phalacrocorax aristotelis*, a species in which both sexes have an ornamental crest during pair formation, we investigated the evidence for 1) assortative pairing on crest size and 2) a correlation between crest size and breeding performance. Crest size was unaffected by age in either sex, though our sample of males did not include first time breeders. Individuals were paired assortatively with respect to crest size. The year of study was one in which overall breeding performance at the colony was poor. Females that did not produce a clutch had significantly smaller crests than those which did, suggesting a link between ornament size and current condition. This relationship was also significant in males. Among those birds that did manage to lay eggs, there was a significant relationship between ornament size and laying date, again significant in both sexes, with early breeders having larger crests. Early breeding is generally associated with relatively high breeding performance in shags. Given that males and females contribute substantially to parental care and that there will be intra-sexual differences in quality, choosiness is likely to be favoured in both sexes. Our results suggest that ornament size is an indicator of phenotypic quality in shags. Ornamental crests have been shown experimentally to be important in mate choice in both sexes in other seabirds, and our data suggest that crest size is subject to sexual selection in male and female shags.

INTRODUCTION

It is now well established that sexual selection is a major force underlying the evolution of male ornamental traits (Darwin 1871; Andersson 1994; Cunningham & Birkhead 1998). However, until recently, female ornamentation had received relatively little attention (Amundsen 2000a, b). A number of theories have been put forward to explain the occurrence of female ornamentation. These include non-adaptive genetic correlation between the sexes (Lande 1980), selection for sexual indistinguishability (Burley 1981), and direct selection on females (Darwin 1871; West-Eberhard 1983; Johnstone *et al.* 1996). Sexual selection on female ornamentation, as with the evolution of male ornaments, can operate through two mechanisms. First, female ornaments may be subject to male mate choice, and thereby influence the quality of male with whom the female pairs. Mutual mate preferences are expected in species with biparental care (Burley 1977), and there is evidence in such species that males do show active choice for females (e.g. Monaghan *et al.* 1996; Hansen *et al.* 1999). Males have been reported to choose females on the basis of their ornamental trait (Jones & Hunter 1993; 1999; Hill 1993; Amundsen *et al.* 1997; Hunt *et al.* 1999), from which they may derive fitness benefits if attributes of the ornament signal higher genetic and/or phenotypic quality (Andersson 1994). Second, female ornaments may signal dominance status (Johnstone & Norris 1993), and there is some evidence that female ornaments can be maintained by female-female competition (Johnson 1988; Jones & Hunter 1999). Using a combination of observations of agonistic interactions and responses to models with differing crest lengths, Jones & Hunter (1993; 1999) demonstrated in crested auklets *Aethia cristatella* that crest length is related to dominance and mating preferences in both sexes. However, while a number of additional studies have also found evidence for sexual selection acting on female ornamental traits (Hill *et al.* 1993; Amundsen *et al.* 1997; Hunt *et al.* 1999), other studies have not found any supporting evidence (Muma & Weatherhead 1989; Cuervo *et al.* 1996). Relationships between ornament size and measures of individual quality have been found in a number of bird species (Jones & Montgomerie 1992; Møller 1993; Johnsen *et al.* 1996; Potti & Merino 1996; Amundsen *et al.* 1997; Linville *et al.*

1998; but see Cuervo *et al.* 1996; Rohde *et al.* 1999; Tella *et al.* 1997; Smiseth & Amundsen 2000). If ornament quality is a signal of individual quality in both sexes, then in species where both females and males are ornamented and both contribute parental care, we would expect to find 1) assortative mating with respect to ornament quality and 2) a positive relationship between breeding performance and ornament quality.

In the shag *Phalacrocorax aristotelis*, both females and males grow a crest of feathers on the head prior to pair formation, which is retained until incubation (Snow 1963; Wanless & Harris 1997). The breeding system is based on social monogamy, and both sexes participate in the incubation and rearing of the brood (Snow 1963; Wanless & Harris 1997). Crest size varies considerably in both sexes. This, together with the timing of the appearance and disappearance of crests relative to pair formation, and the lack of any obvious alternative function, implies that shag crests are the product of sexual selection acting on both sexes (Andersson 1994; Jones *et al.* 2000). To test the two predictions outlined above, we examined the relationship between crest size within mated pairs of shags, and the relationship between crest size and breeding performance. An improvement in breeding performance with age has been shown in many bird species, particularly long lived seabirds such as shags (reviewed in Sæther 1990; Forslund & Pärt 1995). If ornament size is related to current reproductive potential, we would expect to see some relationship between crest size and breeding age mediated either through an age-specific improvement in foraging performance leading to improved breeding condition, or as a consequence of older age classes containing individuals of higher average genetic quality (Andersson 1994; Kokko & Lindström 1996; Kokko 1997). We therefore also examined the relationship between crest size and age in a sample of known age individuals.

METHODS

The work was carried out in the summer of 1999 on the Isle of May, south-east Scotland (56°11'N, 02°33'W). Shag crests are grown very early in the breeding season, many weeks before egg-laying, and remain throughout the pre-laying period during which courtship and pair formation takes place. Photographs were preferred to direct measurement, because it is very difficult to catch adults prior to egg laying, and the high level of disturbance that this would involve could invalidate the data on breeding performance. Accordingly, at the beginning of the 1999 breeding season, prior to any egg-laying, the colony was visited on six days when conditions were suitable for photography. Photographs were taken of the profile of birds (n = 85) with a Canon F1 camera with 80-200 mm lens and 2X converter from varying distances (2 – 6 m), using Ilford FP4 black and white film. Birds were sexed from vocalisations, size and behaviour (Snow 1963). The exact age of 36 birds was known because they had been ringed as chicks. Age of first breeding in shags is on average two for males and three for females (Aebischer 1986). However, we had no two-year-old males in our sample of known age birds and none were present at the colony in the year of study (ages ranged from 3-17 in males, and 3-15 in females). For 20 pairs we had photographs of both birds.

After the photographs were taken, the colony was visited regularly throughout the season and the subsequent laying date and outcome of the breeding event were recorded without disturbing the birds. However, in 1999, a substantial proportion of mature adult shags did not produce a clutch. The photographed birds could therefore be classified into those that bred and those that did not. A bird was defined as a non-breeder if it occupied a nest site throughout the colony pre-laying period but did not actually produce a clutch. A small number of individually marked birds were seen at the colony but did not occupy a nest site, and these were included as non-breeders. Breeders were defined as those in a pair that produced at least one egg, and their laying date and breeding success were recorded.

Photographic prints of the head and crest of each bird were scanned into Adobe® Photoshop® 4.0. The resulting image was printed at A4 size, each image having the same dimensions. Therefore, the heads were approximately to scale, thus giving relative rather than absolute crest size (females are smaller than males: head and bill length taken from a sample of adults: females: 135.40 ± 0.82mm, $n = 40$; males: 138.71 ± 0.48mm, $n = 59$, $t_{97} = 3.73$; $p < 0.01$). Eight observers, unconnected with the project, were asked to rank each crest on overall size, essentially a combination of height and thickness, from 1 ('smallest') to 5 ('biggest'), and to exclude any they could not rank if they considered the quality of the photograph not good enough. Four photographs were ranked by fewer than four people, and excluded from all analyses. For the remaining crests, there was very strong agreement between observers (Kendall's W = 0.90; $n = 8$; $p < 0.001$). Therefore, we used the average rank as a measure of crest size for each bird. Figure 7.1 gives an example of four crests of differing sizes. Non-parametric tests were used in all analyses.

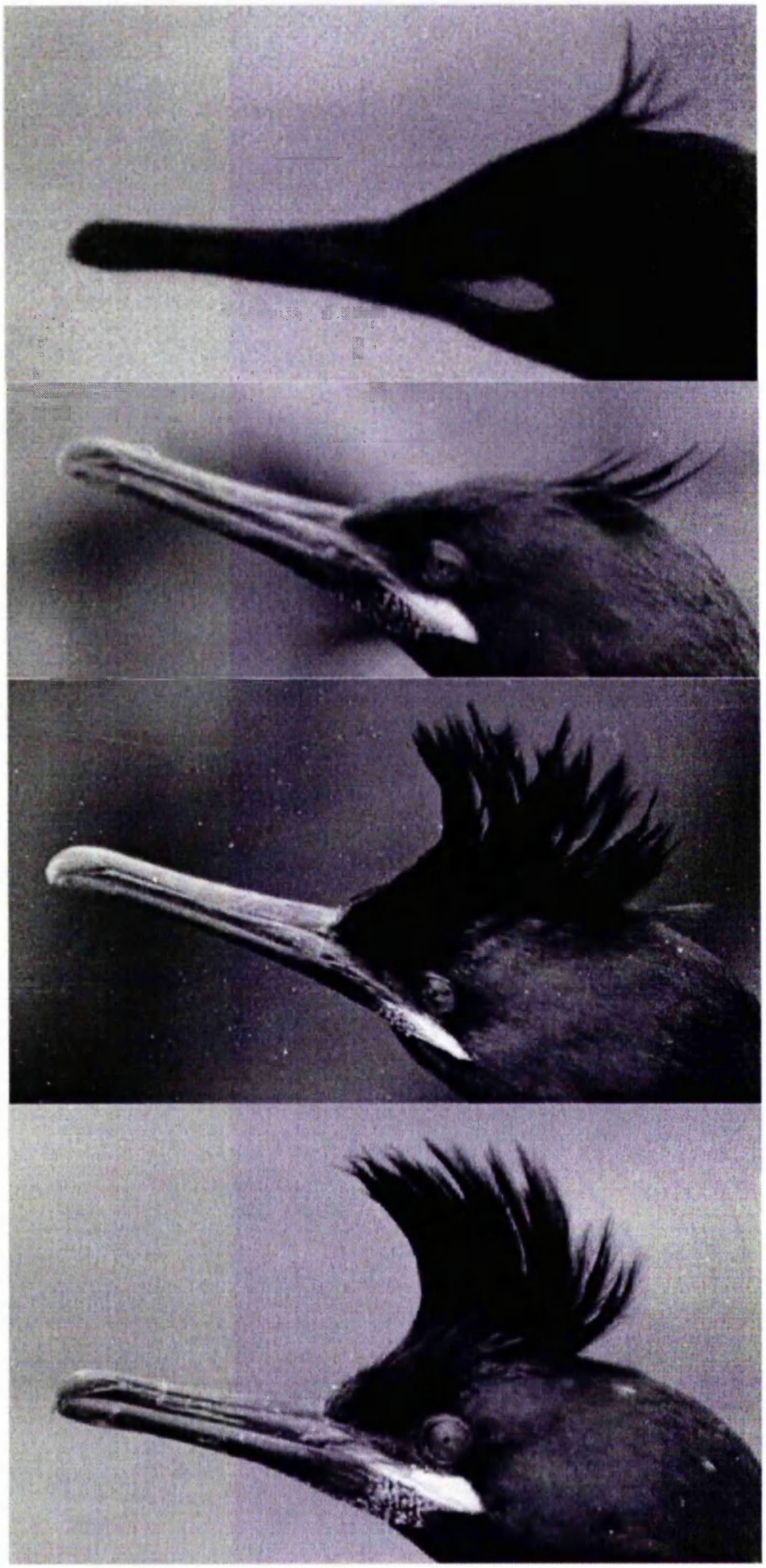

Figure 7.1: Extremes in crest size among shags in this study (from the top: small-crested female, rank 1; small-crested male, rank 1; large-crested female, rank 4.88; large-crested male, rank 5).

RESULTS

There was no significant difference in relative crest size between females and males, (median female crest score: 3.50, n = 43; median male crest score: 3.00; n = 38; Mann Whitney: U = 765.50, n = 81, ns). Both sexes showed considerable variation in relative crest size (female range: 1 - 4.88; male range: 1 - 5) and the frequency distributions of crest sizes did not differ between them (figure 7.2). There was evidence of significant positive assortative pairing with respect to crest size (figure 7.3).

Crest size was not correlated with age in either sex over a range of 3-17 years (Figure 7.4). The majority of the birds in our study, both breeders and non-breeders were marked and known to be experienced breeders (n = 30 females and 23 males). The remainder (n = 13 females and 15 males) were unmarked, and so their previous breeding histories were unknown. Unmarked individuals are likely to be younger on average, because a large number of breeding adults are ringed every year at the Isle of May colony and so the likelihood of an individual remaining unringed decreases with each breeding attempt. However, unmarked birds did not differ significantly in crest size from the marked birds, (Mann-Whitney: females: U = 165.50, ns; males: U = 112.50, ns), and were distributed equally among breeders and non-breeders in both sexes.

Birds that did not produce eggs had significantly smaller crests than those that did for both sexes (Figure 7.5). Among those that did breed, there was a strong correlation between laying date and relative crest size in both females and males, with early layers having significantly larger crests (Figure 7.6). Overall breeding performance in the study colony was poor in 1999, with only 0.34 chicks fledged per pair that laid compared with a mean of 0.77 from the 14 previous years (unpublished data). We found no significant difference in crest size between breeders that were unsuccessful and breeders that were successful i.e. that fledged at least one young (Figure 7.7).

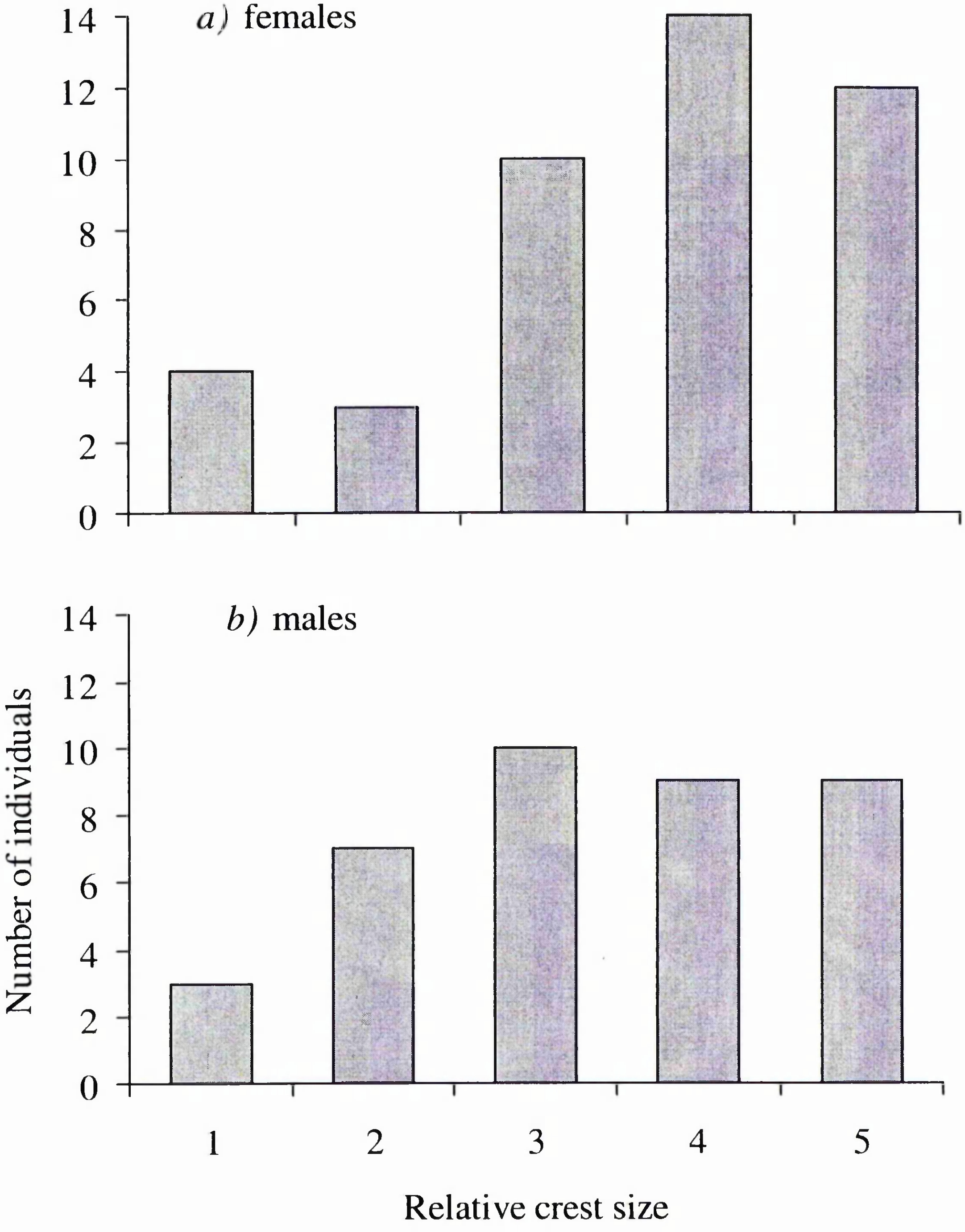

Figure 7.2: Frequency distributions of relative crest size for females (a) and males (b); there was no significant difference in the frequency distributions of the two sexes (Kolmogorov-Smirnov: $Z = 0.94$; ns).

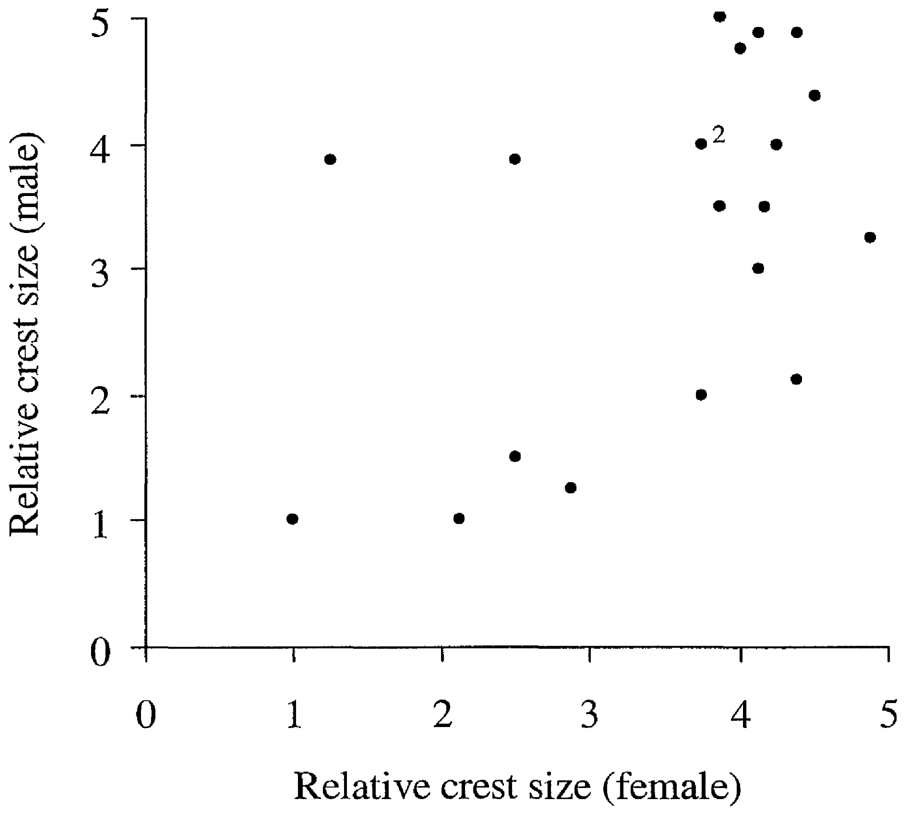

Figure 7.3: Relationship between relative female and male crest size within pairs (Spearman's rank correlation, $r_S = 0.44$, $n = 20$, $p = 0.05$).

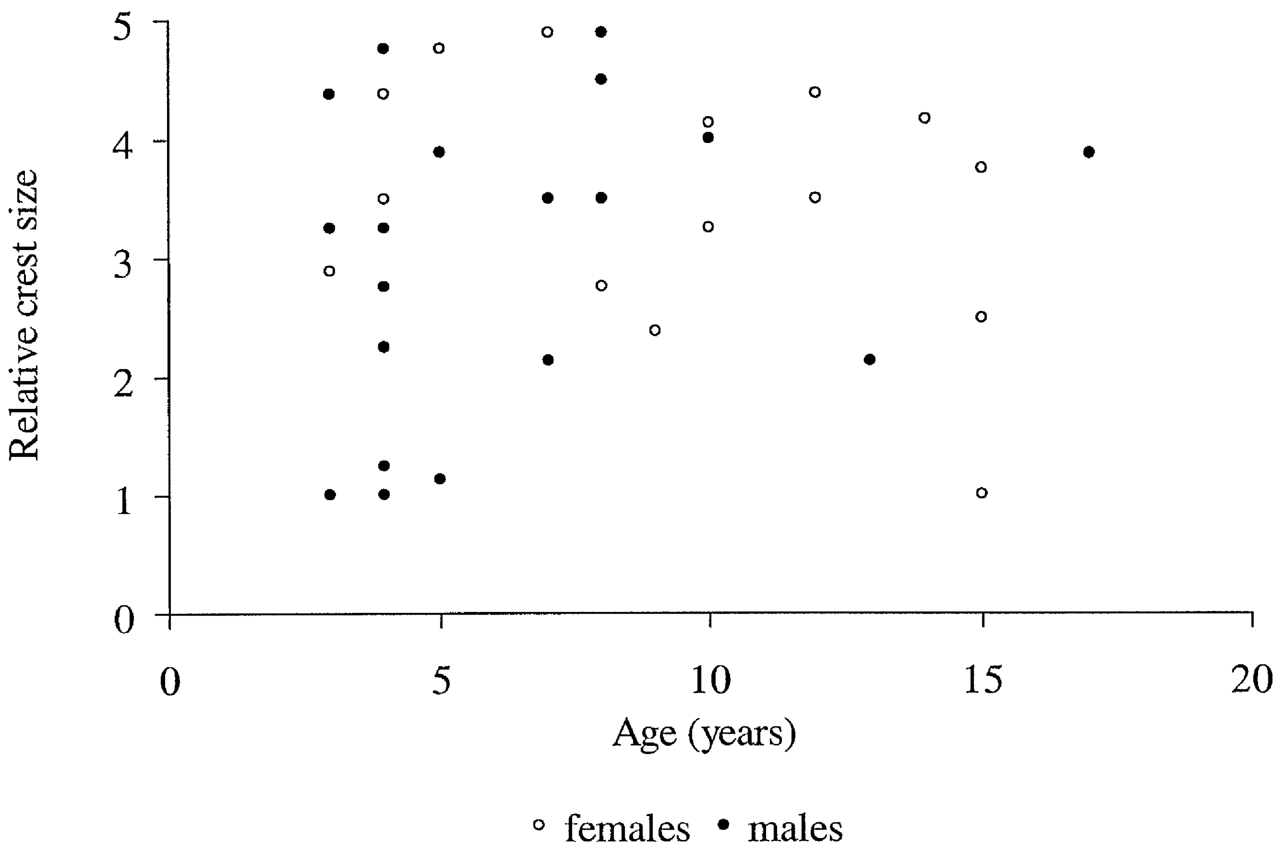

Figure 7.4: Relationship between relative crest size and parental age. There was no effect of parental age (Spearman's rank correlation: females: $r_S = 0.05$, $n = 17$, ns; males: $r_S = 0.31$, $n = 19$, ns).

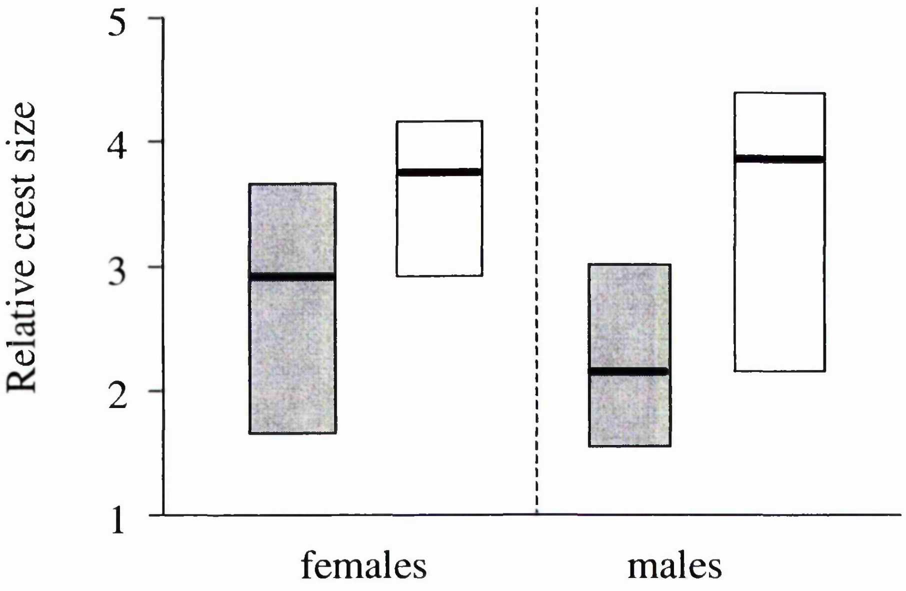

Figure 7.5: Relative crest size (median and interquartile range) of female and male breeders (open boxes) and non-breeders (shaded boxes). Non-breeders had significantly smaller crests than breeders among females and males (Mann-Whitney: females: $U = 145.50$, $n = 43$, $p < 0.05$; males: $U = 98.00$, $n = 38$, $p < 0.05$).

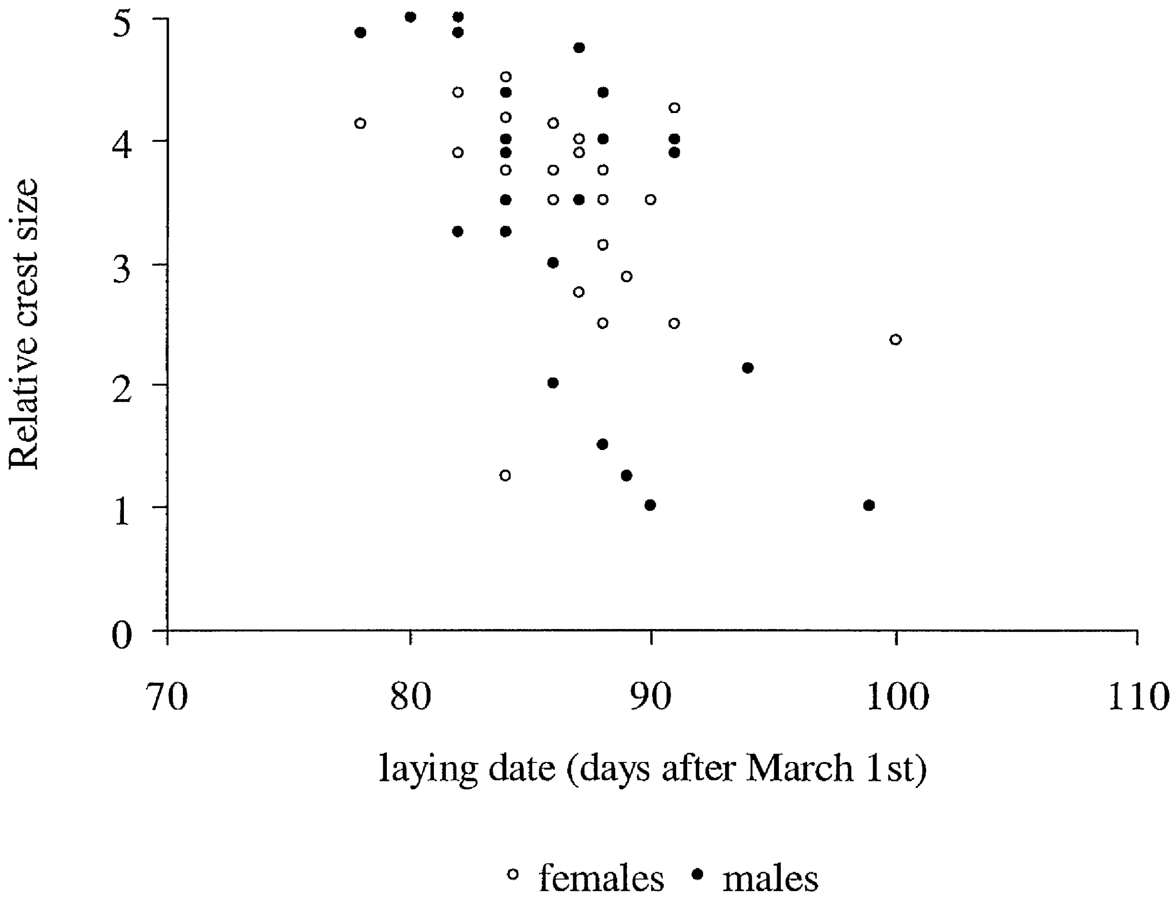

Figure 7.6: The relationship between laying date and relative crest size. There was a significant correlation between the two variables for both sexes, with crest size declining through the season (Spearman's rank correlation: females: $r_S = -0.57$, $n = 25$, $p < 0.01$; males: $r_S = -0.60$, $n = 23$, $p < 0.01$).

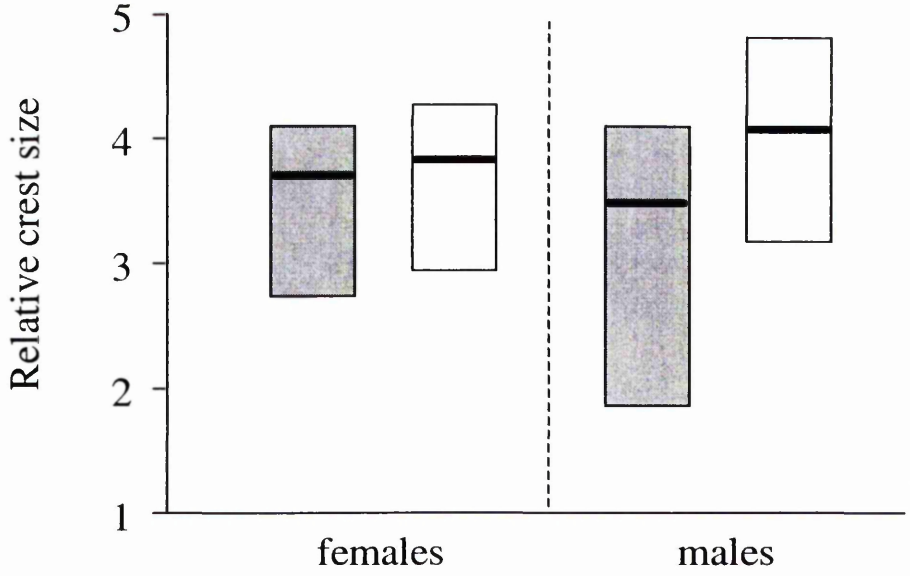

Figure 7.7: Relative crest size (median and interquartile range) of female and male failed (shaded boxes) and successful (open boxes) breeders. There was no relationship between breeding success and crest size (Mann-Whitney: females: U = 51.00, n = 25, ns; males: U = 34.50, n = 23, ns).

DISCUSSION

Several studies have found that sexual ornaments in birds increase with breeding age, the larger ornament thus signalling an individual with greater breeding experience (most studies on males, reviewed in Andersson 1994, but see Jones *et al.* 2000). However, we found no effect of age on relative crest size in shags of either sex. This may reflect the relative lack of age-specific variation in breeding performance in shags after the first breeding year. Male shags usually recruit at age two years, in contrast to females who do not usually breed until at least the age of three (Aebischer 1986). The principal difference in age-specific reproductive success occurs between two-year-old and older males (Potts *et al.* 1980; Aebischer 1993; Daunt *et al.* 1999), with no independent effect of female age, and from the age of three there is no subsequent improvement in breeding performance. There was a complete absence of two-year old males in the colony in 1999, so we did not obtain crest measurements for these birds. It thus remains possible that in males there may be a difference in crest size between two year old and older males.

There was positive assortative mating with respect to crest size, which may be a consequence of mutual mate choice. Females that did not subsequently manage to produce eggs had significantly smaller crests early in the season than those that did. As would be expected given the assortative pairing, this was also the case for males, but it is unlikely that the females' capacity to produce eggs is simply a consequence of the quality of her mate. Crest size was measured during the pair formation and courtship period, several weeks prior to egg laying, and there is no courtship feeding in shags. This strongly suggests that crest size reflects the current condition of the female, probably her nutritional state or capacity to subsequently obtain resources for egg production. This would therefore accord with nutritional effects encompassed in the Darwin-Fisher theory of sexual selection in monogamous birds (Kirkpatrick *et al.* 1990), but in this case applied to both sexes. This result is unlikely to be due to any difference in breeding experience between those that did and did not lay eggs, because both groups comprised mainly marked birds known to have bred on previous occasions, and the proportion of unmarked birds was similar in both groups. In a sample of birds of unknown breeding experience, Jones *et al.* (2000) reported a similar difference between breeders and non-breeders among female crested auklets, but no effect in males.

Among those adult shags that did produce eggs, we found a strong negative relationship between laying date and relative crest size, again significant in both females and males. Individuals were photographed once only, and the precise timing of crest growth and disappearance is not known in shags. However, crest size appears to peak early in the season co-incident with pair formation and decline gradually, through wear and tear or moult, following egg laying. Hence, given that early laying individuals were photographed closer to egg laying, the crest may in fact already have begun to decline in size since the pair bond would have been well established. If so, then the relationship between crest size and laying date may be even more pronounced than our data suggest.

Laying date is very often an important predictor of reproductive performance (Spear & Nur 1994; Sydeman & Eddy 1995; Catry *et al.* 1998). However, we did not find a correlation between crest size and breeding success among those birds that did breed. This may, in part at least, have been due to the exceptionally low breeding success in 1999, with few pairs successfully rearing young. While laying date and breeding success were not related in shags on the Isle of May in 1999, this is not generally the case; in most years early laying birds have significantly higher breeding success (Potts *et al.* 1980; Aebischer 1993; Harris *et al.* 1994; Daunt *et al.* 1999; Harris *et al.* unpublished data). Therefore, in a more typical breeding year, a positive relationship between breeding success and crest size in shags would most probably occur.

Overall, our data suggest that ornament size and phenotypic quality are linked in both sexes in shags. To what extent the ornament in females is a correlated character related to paternal quality or has evolved as a direct consequence of sexual selection with a signalling function requires further experimental investigation. Furthermore, in our study we focussed on crest size, which could be measured reasonably accurately from photographs. Other qualities of the crest, such as its colour and irridescence, may also be important.

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Chapter 8

General discussion

With the widespread finding among wild populations of iteroparous species that there is an improvement in breeding performance with age over the first few breeding attempts (Clutton-Brock 1988; Newton 1989), evidence for the mechanisms that have been suggested to explain this pattern is now required. There remain comparatively few studies that have addressed this issue, and there is an almost complete lack of experimental work. In this thesis I have attempted to investigate some of the mechanisms explaining improvements in breeding performance, and my aim here is to place my findings in a wider context and suggest directions for future research.

In the majority of species studied, young individuals breed later in the season, and are therefore likely to experience different environmental conditions (Perdeck and Cavé 1992). In shags, the results of this study demonstrate that young breeders are less successful not primarily because of extrinsic factors caused by differences in the timing of breeding, but due to intrinsic differences in breeding performance that are manifest both early and late in the season. Two obvious questions arise from this finding. First, why is there normally a temporal difference between young and older birds in the onset of breeding within a season? Much of the variation in timing of breeding is likely to be state dependent (McNamara & Houston 1996). Young individuals may require longer to reach breeding condition, or have to invest more time to carry out certain functions such as selecting a mate or a nest site. Other factors may also be important; for example, young individuals may not be able to compete for resources (mates, nest sites, nest material) with older breeders, and are thus unable to commence breeding at the same time (Potts *et al.* 1980). In shags, there is overt competition at the beginning of the breeding season, and young individuals may not be able to compete effectively. They come into the colony to breed at a time when competition among the older breeders appears to be much less intense.

Second, what mechanisms might explain the intrinsic differences in breeding success? Such a difference could either arise from improvements within individuals, or at the population level (Forslund & Pärt 1995). Two main theories have been proposed to explain age-specific breeding performance at the individual level, namely restraint and constraint (Curio 1983). Distinguishing between these is very difficult. There are very good reasons for this. To truly understand whether a young individual performs less well because it is unwilling to do so, or because it is unable to do so, requires a full understanding of the determinants of individual capacity. However, it is important to clarify the predictions of these two hypotheses. Life history theory, which predicts a trade-off between current reproductive investment and future survival and reproduction, because of costs in terms of future fitness associated with current breeding, cannot explain the improvement in breeding with age over the first breeding attempts. Residual Reproductive Value (RRV – Williams 1966) does not decrease over this time period, because survival rates do not decrease, and in many cases actually increase during the first few years (reviewed in Cam & Monnat 2000). It is only amongst the oldest age classes, when RRV is decreasing, that increases in reproductive effort in the current breeding attempt are predicted. However, at these ages, the effects of senescence may mask any impact of increased current investment.

Thus, investigating the constraint hypothesis in explaining improvements in breeding success over the first few breeding attempts was considered a key priority for future research by Curio (1983). Patterns of offspring growth point strongly to the possibility that foraging performance is an important component of age effects. Therefore, it seems extraordinary that only three studies have measured age-specific foraging efficiency among breeding individuals, all on birds (Jansen 1990; Desrochers 1992a; chapter 5). Using data on individual foraging behaviour in male shags, I was unable to find conclusive evidence of a difference in foraging efficiency between young and older individuals. However, the sample size was relatively small and calculations of efficiency required a number of assumptions to be made. The differential condition of the two sexes of offspring in broods reared by young pairs reported in this study suggests strongly that young breeders are energetically constrained. In addition, the interaction that I demonstrated between age and environmental conditions suggests that foraging capacity is depressed in first-time breeders, which becomes apparent during poor feeding conditions. Future studies on foraging performance should concentrate on manipulations of, for example, foraging costs (Sæther *et al.* 1993), parental condition (e.g. supplementary feeding, Desrochers 1992b) or offspring demands (Ratcliffe & Furness 1999). There is also a need to distinguish whether individual-based foraging efficiency improvements are caused by maturation or learning effects. I found some evidence in shags that young breeders were on average physically smaller, suggesting that they may not be physically mature. However, another possibility is that there is a size related mortality pattern, with the smaller individuals having a higher mortality rate. This may point to an increase in the average quality of individuals with age, essentially the selection hypothesis. This posits that an individual does not improve its breeding performance as it ages, but that younger age classes have a higher proportion of low quality individuals, either due to quality-related age of first breeding, or because high quality breeders also survive better (Charlesworth 1980; Newton 1989). Therefore, in shags, first-time breeders may be smaller on average because they contain a higher proportion of low quality individuals that subsequently survive less well and as a consequence are less well represented in the older age classes. Understanding the relationship between quality and age is an important priority for the future. There have been advances in this area of research, with some studies demonstrating improvements in average quality with age (e.g. Nol & Smith 1987; Cam & Monnat 2000; Espie *et al.* 2000). An interesting approach is that adopted by Newton & Rothery (1998), who examined the selection hypothesis indirectly by comparing changes in age-specific breeding performance at the individual level and at the population level. They found that the two patterns matched one another closely. In other words, in their study, individuals improved their breeding performance with age and the selection hypothesis was probably unimportant.

Age at first breeding is another area of research that is attracting interest (Pyle *et al.* 1997). The selection hypothesis may operate through delayed age at first breeding of high quality individuals (Gustaffson & Pärt 1990). Alternatively, age at first breeding may be dictated by breeding condition, with high quality individuals being more likely to begin breeding at a younger age (Newton *et al.* 1981; Pyle *et al.* 1991). There is growing evidence that recruitment age can have profound consequences for Lifetime Reproductive Success (LRS – Lunn *et al.* 1994; Pyle *et al.* 1997; Cam & Monnat 2000). Individuals recruiting at a young age suffer higher costs than those that delay breeding, possibly due to their reduced foraging competence. The majority of male shags recruit at the age of two, but interestingly only a small proportion of females do so. This difference may arise from the energetic costs of producing the clutch. Are most two-year-old female shags unable to obtain sufficient reserves to lay a clutch? Young females lay smaller eggs, suggesting that they are constrained. However, I have little information on structural size of young females, and they may be smaller than older females (i.e. female and egg size may be correlated), mirroring the situation in males.

Another important consideration is the significance of low reproductive success in the early breeding years, irrespective of age at first breeding. In long-lived species such as shags, one or two 'bad' years may have little effect on LRS. Other aspects of state dependence, notably individual quality, are likely to be much more significant. However, recent research suggests that success in the first breeding attempt can have profound consequences on subsequent survival and thus LRS (Clutton-Brock *et al.* 1996; Cam & Monnat 2000). If shags become successful on average from the second breeding attempt onwards, then the impact of the first attempt might not be severe, because shags can live for 20 years and breed in most years after recruitment. However, first-time breeding male shags may not only have a very low reproductive performance, but may also suffer greater costs from the breeding attempt, through constraint or selection mechanisms, compared to experienced breeders.

In this thesis, I have explored other avenues of age-specific breeding performance that have been rarely studied but have considerable future potential. First, having established that young breeders have difficulty raising the more expensive sex, it is now important to obtain hatching sex ratios of young and old parents, to determine whether young and older pairs are biasing the sex ratio as has been reported in other species (Sheldon 1998, Nager *et al.* 1999) and, if so, how they do this. Second, parasites may play an important role in age-specific breeding performance, but the relationship has been little studied (Thomas *et al.* 1995; Rousset *et al.* 1996; chapter 6). Future research is needed to understand whether young individuals are carrying fewer ecto- and endo parasites, and if so whether this is as a result of infection rate, behaviour, exposure or resistance, and most importantly what the implications are for fitness. Third, the role of parental age in the study of sexual selection is another avenue of research that remains almost completely unexplored (Andersson 1994; chapter 7), particularly in species where both sexes have evolved sexual ornaments

(Amundsen 2000; Jones *et al.* 2000). If young breeders have lower quality ornaments, this may affect their chances of obtaining high quality mates, and may partly explain why young breeders have little choice but to breed with each other later in the season, after high quality individuals have paired up and laid much earlier.

I was unable to investigate the role of breeding experience and pair bond duration, which are both frequently cited as mechanisms underlying age-specific breeding performance. The older breeders in my study were all experienced, and many of them will have spent a number of years with their current partner. Previous investigations that have quantified experience and experience with the mate simply by counting the number of years do not help us understand the mechanisms. A number of suggestions have been put forward, such as the need to acquire skills (e.g. choosing a good breeding site, foraging) or the coordination of activities of mates, but these remain largely untested (Coulson & Woller 1984; Catry & Furness 1999; Ratcliffe & Furness 1999). However, they may be very relevant to many studies including this one. I found that, in shags, much of the variation in breeding success between young and older breeders is due to chick mortality in the first 10 days after hatching, at a time when differences in foraging performance are less likely to be the cause. Other aspects of breeding experience may be important, such as the ability to brood small nestlings effectively, and the ability to feed them food of the right consistency.

Understanding senescence among the oldest age classes was also outwith the scope of this thesis, but is virtually unstudied among wild populations. One problem is that sample sizes of very old birds are usually low. However, a number of studies have now shown a decrease in breeding performance towards the end of reproductive life (Promislow 1991; Clum 1995). This pattern is opposite to that predicted by the restraint hypothesis, which states that as Residual Reproductive Value decreases, investment in the current breeding attempt will increase (Williams 1966; Roff 1992; Stearns 1992; Ylönen *et al.* 1998). The reason for this is presumably because other mechanisms have a more profound impact on breeding performance.

In this thesis, I have attempted to take the subject further by examining the mechanisms using a combination of experimental and observational techniques.

Intrinsic differences in breeding performance largely explain age-specific improvement in breeding performance in the shag, rather than differential environmental conditions that young and older breeders experience. Improvements in competence are probably important in explaining this pattern, and there is some evidence for selective effects. What seems clear is that several mechanisms are likely to be operating simultaneously. There is now a need for further detailed observations and carefully designed experiments to test hypotheses across a range of species, to improve our understanding of the mechanisms explaining the patterns of age-specific reproductive performance among the many that have been proposed.

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APPENDIX 1: The cost of incubation in the shag

Until recently, the cost of incubation in birds has been underestimated (Thomson *et al.* 1998). However, research has shown that artificially increasing incubation demands can have a detrimental effect on reproductive success (Heaney and Monaghan 1996; Bryan & Bryant 1999; Reid *et al.* 2000). I carried out an experiment on the shag *Phalacrocorax aristotelis* on the Isle of May NNR in the summer of 1997 where I manipulated the demands of incubation and monitored its effect on chick growth rates and survival.

The experiment was restricted to nests containing three-egg clutches, the modal clutch size in the shag (Stokland & Amundsen 1988). The experimental protocol was identical to that employed by Heaney & Monaghan (1996). In brief, the breeding performance of pairs laying a clutch of three but incubating clutches of two, three and four were compared. The three groups were established in the following way. Nests from all three groups were matched for initial laying date. The majority of birds involved in the experiment were adults of unknown age, but I have no reason to believe that there was any bias towards young breeders in any of the groups, and there were no two-year-olds, the age at which lower breeding performance has been recorded in this species (Potts *et al.* 1980; Aebischer 1993; chapter 2). One egg was removed from a nest from Group R (reduced cost, $n = 13$) within three days of clutch completion and placed in another nest with a complete clutch, this latter nest thereby forming part of Group I (increased cost, $n = 13$). The extra egg remained in the Group I nest throughout incubation. Group C ($n = 13$) was the experimental control, subject to no egg manipulations but the same level of disturbance. Therefore, Group R nests contained 2 eggs, Group I nests contained 4 eggs, and Group C nests contained 3 eggs throughout incubation. The increase and decrease in clutch size still resulted in clutches within the natural range (Stockland & Amundsen 1988). Just prior to hatching the extra egg in the Group I nests was returned to its original Group R nest.

Fledging success was compared in a Generalized Linear Model (GLM) with a binomial distribution and logit link function, corrected for overdispersion (ANODEV – see Crawley 1993). Surviving chicks were weighed approximately every 4 days, and the gradient of the linear phase of growth (chick age 8-30 days) was taken as the measure of growth. A mean was taken for each brood.

A number of nests in all groups lost all or part of their clutch, and were removed from analyses because they had not been subjected to the correct incubation demand (see table A.1).

	Reduced	Control	Increased
Original sample size	13	13	13
Failed during incubation	4	2	2
Partial loss of clutch leading to incorrect cost	0	4	3
Effective sample sizes	9	7	8

Table A.1: Outcome of nests in three groups during incubation.

There was no difference in fledging success between the three groups (GLM: $F_{2,21} = 0.28$, ns; figure A.1). There was also no difference in chick growth rate (ANOVA: $F_{2,16} = 0.41$, ns; figure A.2).

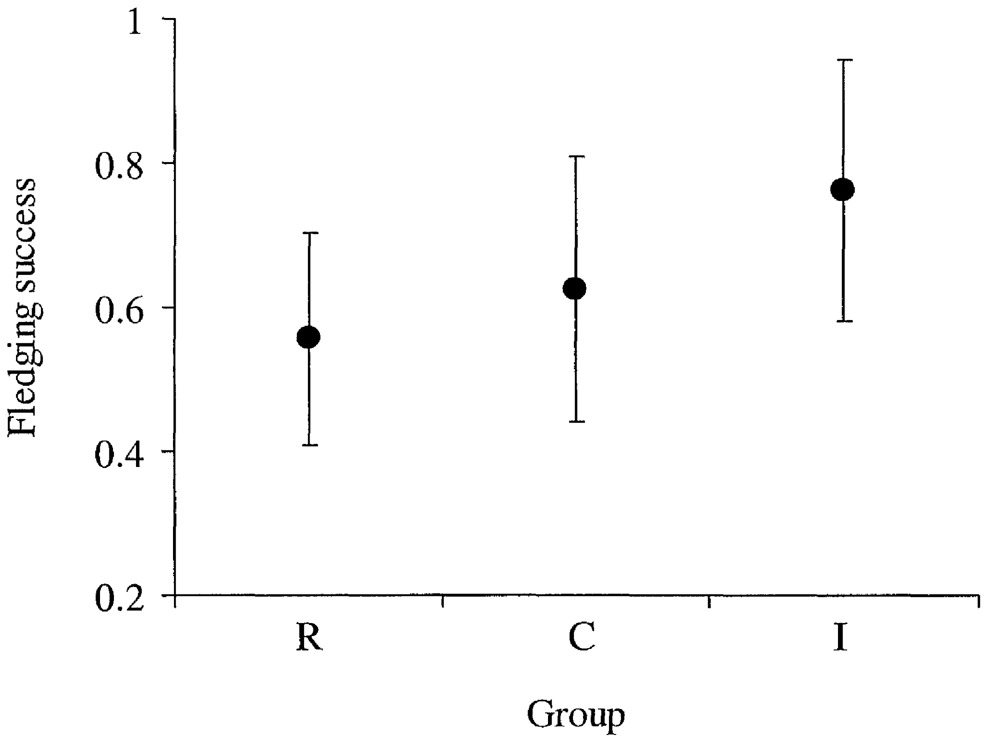

Figure A.1: Fledging success of three experimental groups (R = reduced incubation cost; C = control; I = increased incubation cost).

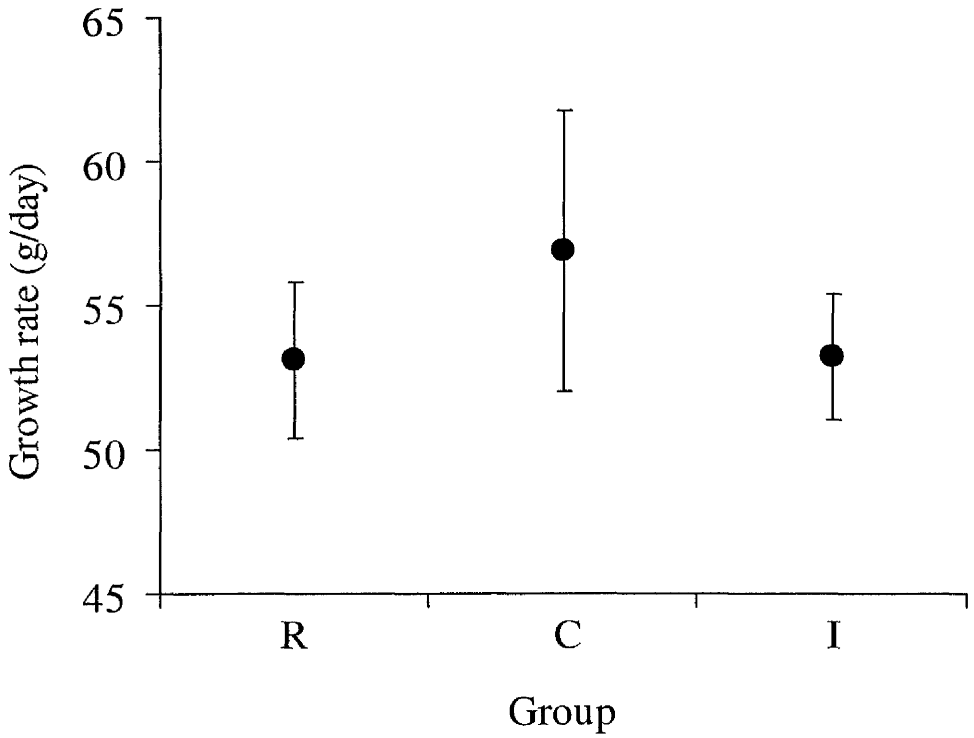

Figure A.2: Chick growth rates of three experimental groups groups (R = reduced incubation cost; C = control; I = increased incubation cost).

Male shags are 20% heavier than female shags (Wanless & Harris 1997). Therefore, the analysis on growth rate was repeated with chick sex incorporated (a blood sample of each chick was taken (under licence), from which the DNA was extracted and the chicks sexed using two *CHD 1* genes, Griffiths *et al.* 1996). Separate ANOVAs were carried out on the first-hatched and second-hatched chicks (sample sizes prevented analysis of third-hatched chicks) to avoid pseudoreplication within nests. However, there was no effect of chick sex or group (ANOVA on first-hatched chicks: sex: $F_{1,17}$ = 1.53, ns; group: $F_{2,15}$ = 0.12, ns; interaction term: $F_{2,13}$ = 0.02, ns; ANOVA on second-hatched chicks: sex: $F_{1,13}$ = 1.58, ns; group: $F_{2,11}$ = 0.18, ns; interaction term: $F_{2,10}$ = 0.02, ns).

Although the samples sizes are small, it appears that the addition or removal of one egg from a three-egg clutch during incubation has no effect on the subsequent growth or survival of the chicks, in contrast to the findings of Heaney & Monaghan (1996) on the common tern. This may relate to differences in relative egg size, and thereby in the unit energetic cost of incubation between the two species. A clutch of three eggs represents 9% of body mass in shags (Lack 1968), whereas a clutch size of two represents 33% in common terns (Thomson *et al.* 1998). In addition, the magnitude of the manipulation was lower in this experiment (33% increase in clutch size compared with 50% in the common tern study). Finally, Heaney and Monaghan (1996) manipulated pairs with an original clutch size of two because they were likely to represent low quality individuals on average (many common tern pairs lay three eggs). Low quality birds are probably least able to cope with increasing incubation demands. In our study, however, we carried out the manipulation on pairs that laid the modal clutch size of three.

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