

CAUSES OF HATCHING FAILURE IN THE PIED FLYCATCHER¹

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Abstract. Correlates of egg hatchability in Pied Flycatchers were investigated during a four year study. Hatchability decreased in small eggs, the effect of egg size being more marked among fertile eggs, than in infertile eggs. There was a significant decrease in egg hatchability with increasing clutch size. Hatching success was higher for clutches with larger eggs and was associated with larger numbers of breeding recruits. However, hatching success was unrelated to female condition during incubation or to clutch initiation date. Hatching failure as a whole, and egg infertility in particular, followed a concave-up trajectory across the laying sequence, indicating an optimum for egg hatchability in intermediate positions of the clutch. No single cause can explain the relationship of egg hatchability to laying order. Although hatching success did not differ across female or male ages, it was significantly lower in pairs formed by yearling males and older females than in other pair/age combinations. Results are discussed in the light of possible trade-offs between clutch size and egg size and parental investment theory determining differential effort by males and females depending on their residual reproductive value.

Key words: *Clutch size; egg size; egg infertility; egg inviability; Ficedula hypoleuca; laying order; parental age.*

INTRODUCTION

Hatching failure due to infertility or embryo mortality is a potentially important cause of reduced breeding success in birds (Koenig 1982, Ojanen 1983). Aside from failures due to predation on incubating parents, common causes of hatching failure are inbreeding depression (van Noordwijk and Scharloo 1981) and environmentally-induced stress such as bad weather during the incubation stage (Järvinen and Väisänen 1984) or poor condition of incubating parents, usually females, leading to abandonment of nests (Wiggins et al. 1994).

Egg size has been shown to be related to nestling growth, fledgling size and survival in many avian species, (e.g., Potti and Merino 1994) and is an important cause of hatching failure (Murton et al. 1974). However, in many avian species, egg size varies in predictable ways in the course of the laying sequence (Clark and Wilson 1981, Slagsvold et al. 1984) and thus the chances of survival for individual eggs may differ depending on laying order (Rofstad and Sandvik 1985, Spear and Nur 1994). Clutch size may also affect egg hatchability due to physical constraints of incubation. Large clutches may be covered less ef-

ficiently by incubating parents than small clutch-between clutch size and egg size (Blackburn 1991, Clutton-Brock 1991). A larger clutch may entail a reduction in the size of the eggs in the clutch, thus decreasing the survival prospects of some egg(s) in the clutch.

Almost all of these effects may be confounded by parental, mostly maternal, age or quality (Nisbet 1978, Amundsen and Stokland 1990, Bolton 1991, Meathrel et al. 1993, Williams 1994). For example, in many bird species, egg size, clutch size and breeding success increase with parental age (Sæther 1990), making the relative contributions of different factors difficult to unravel without experimental manipulations. These can provide strong evidence on the nature of the cause-effect relationship of egg size to offspring fitness by experimentally separating egg size effects of parental quality (Amundsen and Stokland 1990, Reid and Boersma 1990, Bolton 1991)

To date, most of the available evidence on those interactions derives from studies of precocial and semi-precocial species (Williams 1994). However, there have been few studies controlling for confounding factors. While experimental manipulations are the most promising means to this end, we have tried to address this goal by expanding the range of factors examined while statistically controlling for some of them.

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This paper analyzes hatching failures of Pied Flycatchers (*Ficedula hypoleuca*) during a four year study in central Spain and attempts to discriminate between failures due to infertility and those due to embryo death. We address both causes of failure by focusing on differences in basic breeding and individual parameters such as breeding phenology, clutch size, parental age, size, and condition, and relating failures to egg size and position in the laying sequence.

METHODS

The study was conducted from 1988 to 1991 in a population breeding in nest boxes in central Spain (see Potti 1993). The area was visited almost daily after the birds' spring migration arrival in late April. Nest boxes were checked for signs of nest building and egg laying and any new egg was distinctively marked with pencil. Maximum length and breadth of all eggs in a clutch were measured to the nearest 0.1 mm during incubation time when females were caught, aged as yearling or older (Karlsson et al. 1986), measured and released. Egg volume, which is strongly correlated with fresh egg weight (Potti 1993), was calculated from egg length and breadth using the formula of Hoyt (1979) and a mean egg volume was calculated for each clutch. Males were caught while feeding nestlings by means of a nest-trap and were aged following Karlsson et al. (1986) and Potti and Montalvo (1991a). After the capture of adult birds we recorded tarsus length (Potti and Merino 1994) with dial calipers to the nearest 0.05 mm and body mass to the nearest 0.1 g. To control for size effects, a "body condition" index was calculated as the residual of within-sex yearly regressions of mass on cubed tarsus length (Potti and Merino 1994).

We recorded the number of eggs hatched, hatching success (eggs hatched/eggs laid \times 100) and number of breeding recruits found until 1993 (see Potti and Montalvo 1991b). On day 13 of nestling age (hatching day = day 1), we broke any unhatched egg in the nest and scored it as either infertile or inviable (containing a clearly visible embryo which died before hatching), noting its position in the laying sequence when possible. Eggs scored as infertile contained no more than a yellow yolk, while we scored as inviable addled eggs where the embryo could have died at an early developmental stage. For an overall analysis of egg hatchability, we have lumped together infertility and inviability as hatching fail-

ure. That is, nests with hatching failure were those where at least one egg failed to hatch.

Nest box quality was ranked by an index based on the proportion of years occupied assuming that in the long term, the most frequently used nest boxes are of higher quality (Askenmo 1984, Potti and Montalvo 1991a, 1991b). Original nest box quality scores were transformed to categorize boxes as high or low quality (Potti and Merino 1994).

The distribution of hatching success was highly skewed and transformations did not improve the fit of data to a normal distribution. We therefore analyzed hatching success with nonparametric statistics when appropriate or as a categorical variable (henceforth "transformed hatching success") by dividing nests into "successful" (all eggs hatched) and "unsuccessful" (at least one egg failed to hatch).

To investigate the variation of hatching success across parental ages and the possibility of interactions among different combinations of ages between pair mates, we conducted log-linear analysis (Sokal and Rohlf 1981). This procedure is analogous to an analysis of variance in that total variance of frequency data is partitioned into different factors, making possible the testing of interactions between them. We ran the test hierarchically beginning with the highest order interaction so that dropping a significant ($P < 0.05$) term would result in a significant lack of fit of the model. Statistical tests are two-tailed. Means are given ± 1 SD except otherwise stated. For simplicity, unstandardized values are presented in the figures even though statistical tests were conducted with standardized or transformed values.

RESULTS

HATCHING SUCCESS

Excluding one entire infertile clutch of seven eggs in 1990, overall hatching success was $92.4 \pm 13.7\%$ ($n = 289$, range 33.3–100%). Hatching success varied significantly across years (Kruskal-Wallis ANOVA, $H = 27.28$ $P < 0.0001$). A *posteriori* comparisons showed that the differences were entirely due to the bad season of 1988, when rainy and cold spells during incubation presumably reduced hatching success. We standardized hatching success for yearly variation by using the deviations from the yearly medians in subsequent analyses.

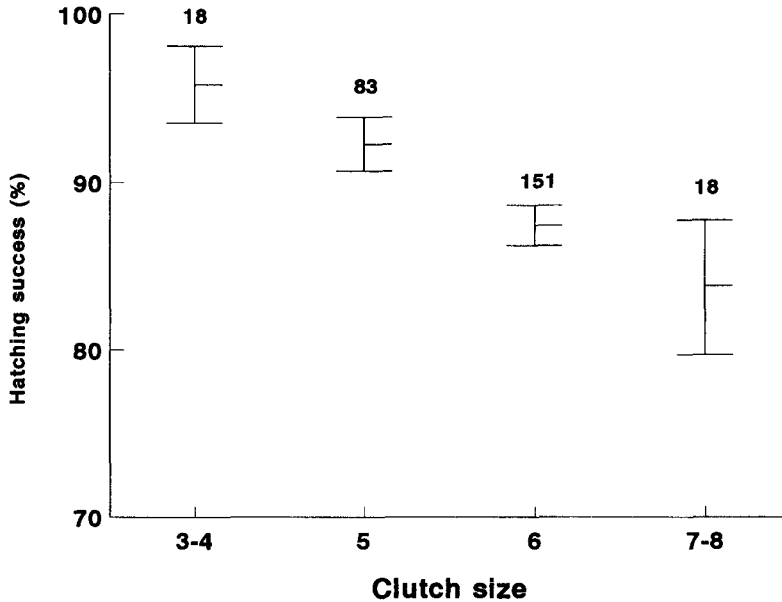


FIGURE 1. Hatching success (\pm SE) in relation to clutch size in the Pied Flycatcher. Numbers are sample sizes.

There was a significant decrease of hatching success with increasing clutch size (Kruskal-Wallis ANOVA, $H = 12.41$, $n = 270$, $P = 0.006$; Fig. 1). Hatching success correlated positively with mean clutch egg volume (Spearman rank correlation, $r_s = 0.17$, $P = 0.007$) and with the number of breeding recruits originating in the clutches ($r_s = 0.18$, $n = 270$, $P = 0.009$), suggesting an association with other fitness factors. Hatching success was unrelated to female condition during incubation ($r_s = 0.04$, $P = 0.55$) or to clutch initiation date ($r_s = 0.00$, $P = 0.96$).

Hatching success did not differ across female or male ages (Mann-Whitney tests, $z = 0.92$, $P = 0.36$ and $z = -1.40$, $P = 0.31$, respectively). However, the interaction term male \times female age was significant in a log-linear analysis of transformed hatching success with male and female age (log-likelihood, $G = 5.67$, $df = 1$, $P = 0.017$), showing that variation of hatching success with female age changed across the age of their mates. Hatching success was significantly lower in adult females paired with yearling males than in the rest of pair age combinations (Fig. 2).

CORRELATES OF HATCHING FAILURE

In 13.3% ($n = 289$) of the clutches, one or more eggs were scored as infertile. In at least 20% (n

$= 280$) of the clutches, one or more embryos failed to hatch. Overall, one or more eggs failed to hatch in 31.1% of the clutches ($n = 289$).

Confirming the previous analyses, clutches with hatching failure were larger than those where all eggs hatched (Table 1). The same is true when the analysis is restricted to clutches with at least one inviable egg (one-way ANOVA, $F_{1,278} = 10.49$, $P = 0.0013$), but not for clutches with infertile eggs ($F_{1,277} = 1.98$, $P = 0.16$). Hatching failure was unrelated to laying dates (Table 1).

Average egg size was significantly smaller in clutches where one or more eggs failed to hatch (Table 1). Clutches with infertile eggs differed significantly from those with all eggs fertile only in egg length, being shorter ($F_{1,277} = 4.23$, $P = 0.041$). Egg volume and breadth were significantly smaller in clutches with one or more unhatched, fertile eggs than in clutches where all eggs hatched ($F_{1,279} = 4.10$, $P = 0.04$ and $F_{1,279} = 6.29$, $P = 0.01$, respectively), while egg length did not differ significantly between both types of clutches ($F_{1,279} = 0.46$, $P = 0.50$). However, when egg dimensions and volume of infertile and unhatched eggs were compared with the mean dimensions of fertile or hatched eggs in the same clutch, no significant differences were found (Wilcoxon's tests for matched pairs, $n = 23$ pairs (infertility) and $n = 33$ pairs (inviability), $P >$

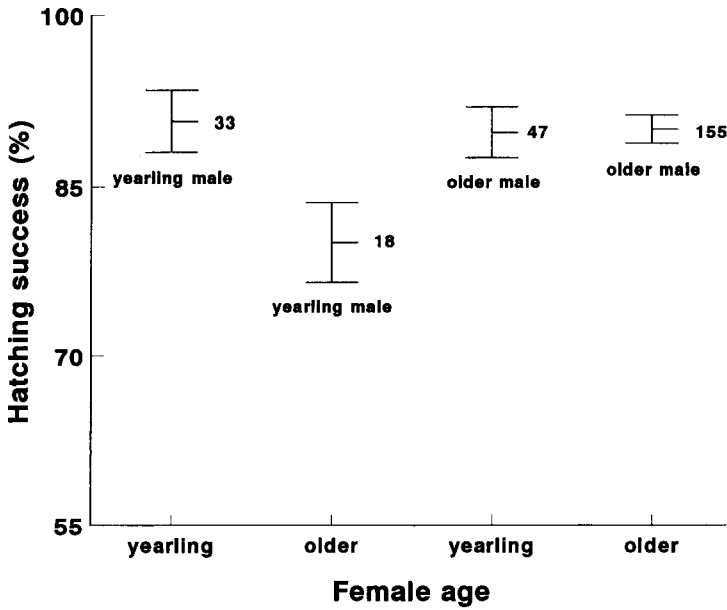


FIGURE 2. Interaction between age of male and female parents on hatching success in the Pied Flycatcher (Kruskal-Wallis ANOVA, $H = 7.89, P = 0.048$). Shown are means \pm SE. Numbers are sample sizes.

0.20 in all comparisons). In other words, clutches with infertile and unhatched eggs tend to have smaller eggs than clutches where all eggs hatch but, within clutches, neither infertile eggs nor eggs that fail to hatch can be distinguished by size from fertile or viable eggs.

Tarsus length, weight, and condition were not significantly related to hatching failure (Table 1), egg infertility or egg inviability, either in females or males ($P > 0.10$ in all ANOVAs). Also, there

were no associations between frequency of hatching failure and female age or nest site quality (chi-square tests, both $P > 0.20$).

LAYING ORDER AND HATCHING FAILURE

Due to small sample sizes of complete laying sequences, the analyses below are restricted to clutches of five and six eggs, the most frequent clutch sizes in our population (Potti et al. 1987,

TABLE 1. Differences in breeding parameters and parental measurements between clutches where all eggs hatched ("Successful") and clutches where at least one egg failed to hatch ("Unsuccessful") in Pied Flycatchers. Shown are means \pm SD. Differences between groups were tested with *t*-tests.

	Unsuccessful		Successful		<i>t</i>	<i>P</i>
	Mean \pm SD	<i>n</i>	Mean \pm SD	<i>n</i>		
Clutch size	5.8 \pm 0.77	90	5.5 \pm 0.74	199	2.95	0.0035
Laying date ¹	0.86 \pm 5.95	90	0.99 \pm 5.47	199	0.20	0.8454
Female tarsus	19.652 \pm 0.572	88	19.571 \pm 0.562	190	1.11	0.2683
Female mass	14.85 \pm 0.90	82	14.91 \pm 0.89	167	0.55	0.5800
Female condition ²	0.02 \pm 0.79	82	-0.03 \pm 0.82	167	0.42	0.6718
Egg volume ³	1.57 \pm 0.12	90	1.61 \pm 0.11	199	2.96	0.0034
Egg length ⁴	17.31 \pm 0.68	90	17.51 \pm 0.66	199	2.36	0.0188
Egg breadth ⁴	13.32 \pm 0.34	90	13.43 \pm 0.33	199	2.53	0.0121
Male mass	12.65 \pm 0.58	72	12.70 \pm 0.80	152	0.48	0.6334
Male condition ²	0.02 \pm 0.58	70	-0.03 \pm 0.49	151	0.67	0.4989

¹ Standardized for yearly variation.
² Residuals from the regression of mass on cubed tarsus length.
³ In cm³.
⁴ In mm.

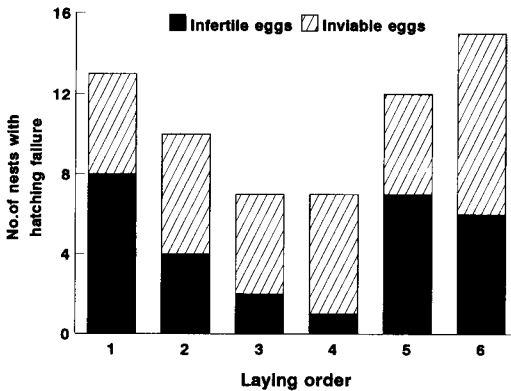


FIGURE 3. Frequencies of hatching failure due to presumed sterility and embryo mortality in relation to laying order and clutch size in the Pied Flycatcher [clutch sizes 5 ($n = 22$) and 6 ($n = 42$) combined].

Potti 1993). We lumped together egg infertility and embryo mortality for an overall analysis of hatching failure in relation to laying order. Grouping together clutches of five and six eggs and lumping positions 5th and 6th in clutches of six eggs, hatching failure significantly changed with laying order, with more frequent failures in first and, especially, last positions in the laying sequence $\chi^2_4 = 21.6$, $P = 0.0002$; Fig. 3).

There was also a similar trend for egg infertility associated with laying order, with infertility being relatively more common for eggs laid early and late in the laying sequence $\chi^2_4 = 17.4$, $P < 0.002$; Fig. 3). An analysis of embryo mortality in relation to laying order did not reach statistical significance $\chi^2_4 = 8.2$, $P = 0.08$). Contrary to the case with infertility, no clear pattern is apparent in the variation of hatchability with laying order, except that the last egg seems to have low viability (Fig. 3).

DISCUSSION

We have shown that hatching failure in the Pied Flycatcher is dependent on at least four different factors: the mother's clutch size, the mean size of the eggs in the clutch, the position of the eggs in the laying sequence, and the interaction between the age of male and female parents. A drawback in the interpretation of our data when trying to gain insight into the causes of hatching failure is that some eggs that we scored as "infertile" could be in fact fertile ones where the embryo died at an early stage of development (Seel 1968; Birkhead, Fletcher and Veiga, un-

publ.). Although this uncertainty does not affect our conclusions on overall hatching failure, it should be considered when examining correlates of egg infertility or embryo mortality.

Unhatched, fertile eggs were more frequent in large clutches. A linear decrease of hatching success with increasing clutch size in the Pied Flycatcher was not observed by Creutz (1955), although reduced hatchability was evident in his study above a threshold clutch size of eight eggs. In our study, reduced hatching success was entirely due to embryo mortality rather than egg infertility and thus may reflect a cost, in terms of hatching success, of laying larger clutches. Reduced hatchability in larger clutches might be due to the fact that these may be more difficult to cover efficiently by the incubating females, although this explanation does not seem plausible for altricial birds (Klomp 1970). Reduced hatchability in large clutches could also reflect the inability of females to produce an entire batch of viable, high-quality eggs. That is, large clutches may contain one or more low-quality eggs and this difference might be reflected in some other, more subtle and as yet unknown, aspect of egg quality (Monaghan et al. 1995).

An alternative hypothesis might be that the viability of eggs may decline in larger clutches due to the longer time the eggs are exposed to environmental factors before incubation begins (Veiga 1992). Furthermore, larger clutches take longer to hatch (Moreno and Carlson 1989, Smith 1989, Järvinen 1990, Veiga and Viñuela 1993) and are energetically more costly to incubate (Moreno and Carlson 1989, Moreno and Sanz 1994). Both these factors could cause energetic bottlenecks affecting embryos.

In a study of the related Collared Flycatcher (Moreno et al. 1991) experimental clutch enlargements led to reduced hatching success. However, this trend should not be confounded by the effect of female condition as measured in our study, as there is a positive relationship between clutch size and both weight and condition in female Pied Flycatchers (Askenmo 1982, Potti and Merino, unpubl.). The absence of any relationship between female condition and egg hatchability in our population does not imply that parental quality is unimportant, only that our index may not reflect relevant aspects of parental quality while even it is positively and significantly related to other traits related to parental performance such as female persistence at

incubation during cold spells (Wiggins et al. 1994) and fledgling condition (Potti and Merino, unpubl.).

Our results show that hatching success may pose a limit to the evolution of clutch size in altricial birds, particularly if there is a trade-off between egg size and clutch size (Blackburn 1991, Clutton-Brock 1991, Hillström 1992, Potti 1993). Such a trade-off is very difficult to demonstrate (van Noordwijk and de Jong 1986, Lessells et al. 1989), although some correlative evidence points to its existence in the Pied Flycatcher (Hillström 1992, Potti 1993).

Small eggs were a second cause of reduced hatchability, especially embryo death. This supports previous studies demonstrating that nestling growth and survival of chicks (e.g., Grant 1991) and fledgling size (Potti and Merino 1994) are positively correlated with egg size. Egg size in the Pied Flycatcher seems an *a priori* good predictor of the energetic content of the yolk and, especially, of the albumen (Ojanen 1983, Hillström 1992). Hence, embryos in small eggs may have died from insufficient reserves to complete normal development. Alternatively, small eggs may cool faster during the periods females are out of the nest, which would impair the embryo development (O'Connor 1979).

In Pied Flycatchers, egg size increases along the laying sequence (Potti 1993) and reduced egg size and subsequent decreased hatchability could therefore account for the high rates of failure of eggs laid early in the sequence. But this cannot be the only cause of reduced hatchability because we should then also expect higher viability of the larger, last-laid eggs. This was not observed, which may mean that within-clutch variation in egg size is a poor predictor of egg contents (see Bryant 1978). Alternatively, the presumed increase in energy contents of eggs is not sufficient to overcome increases in the mortality rate of last-laid eggs.

The hatching advantage of large eggs in the population was not observed within clutches. This could be taken as evidence that egg size itself might not be related to hatchability and a third, unknown variable should be responsible for both small eggs and low hatchability. However, the apparent inconsistency may be due to low statistical power of our tests. This is because a large percentage of variation in egg size, around 60–70%, is explained by differences between females (Potti 1993), making it difficult to detect within-

clutch differences in hatchability related to small differences in egg size.

There was a clear pattern for hatching failure as a whole to follow a concave-up trajectory across the laying sequence, with relatively high rates of failure in both first and last positions in the clutch. This indicates an apparent optimum for hatchability in intermediate positions of the clutch. This result agrees with those of Creutz (1955) and Ylimaunu and Järvinen (1987), who found reduced fledging success from first and final eggs. "Terminal egg neglect" (Evans and Lee 1991) could be invoked to explain the high rate of failure in last eggs, as females could "neglect" incubation of last eggs due to feeding trips for recently hatched nestlings, or the embryo development could be hampered by the already hatched siblings, leading to increased mortality of last eggs. Although this seems a plausible explanation for the Pied Flycatcher, where asynchronous hatching is common (Slagsvold 1985), the increase of mortality of embryos in later positions of the laying sequence was not statistically significant. Also, early onset of incubation and subsequent hatching asynchrony cannot account for the high rate of failure of first eggs in the clutches.

The reduced hatchability of early-laid eggs could be due to their greater temporal exposure to environmental factors (Arnold et al. 1987 for precocial birds; Veiga 1992 and Veiga and Viñuela 1993 for the altricial House Sparrow), or to the fact that the physiological efficiency of egg production may improve along the laying sequence (Leblanc 1987).

In contrast, egg infertility combined with embryo mortality may explain the overall pattern of variation of hatching failure with laying sequence. This relationship is also concave-up and can be explained by several complementary hypotheses. Leblanc's (1987) hypothesis could account for the high rate of failure early in the sequence, but not for failures late in the sequence. Reserve depletion, i.e., decreased quantity/quality of albumen and yolk reserves, may be invoked for explaining failures late in the laying sequence. The increase of egg weight and volume across the laying sequence in the Pied Flycatcher (Potti 1993) apparently contradicts this latter idea: larger eggs are more likely to hatch, as shown by our between-clutch analyses of hatchability (but see above).

Finally, we speculate that reduced fertility of

eggs laid late in the laying sequence may be explained by reduced sperm and ova viability, or by sperm depletion (Birkhead and Møller 1992: 191). Although there are no published data on this relationship for any bird species (Birkhead and Møller 1992), both processes are possible in the Pied Flycatcher, where females may store sperm in their utero-vaginal junction, opening the possibility of reduced viability of sperm stored for longer time, and males engage in extra-pair copulations (Lundberg and Alatalo 1992), which could deplete sperm reserves (Birkhead and Møller 1992). In summary, no single cause can explain the curve of hatchability across the laying sequence, and we believe that several different phenomena in conjunction may explain it.

In an across-species analysis of hatchability in birds revealing the role of various ecological and social factors on egg hatchability, Koenig (1982) was unable to find significant effects of egg size or clutch size, but found evidence suggesting that breeding date and female age could be involved in the hatchability of eggs in at least some bird species. In fact, both breeding date (Bird and Laguë 1982) and parental age or quality have been found to affect hatchability of eggs in some intraspecific studies of birds (Reid and Boersma 1990, Williams et al. 1993).

Among birds in general, breeding success is higher in adult than in yearling birds (Sæther 1990). In this study, there were significant effects of parental age on hatching success but not as expected, as the nests of some older females had significantly lower hatchability than those of younger females. In fact, Sæther (1990) found that, among the reproductive traits he examined in a review of age-specific variation of breeding success in birds, hatchability showed the smallest differences between juveniles and adults, with 37% of species ($n = 19$ species) showing lower hatching success in adult than in yearling females.

Our study is one of the first demonstrating a significant interaction between the age of male and female parents on hatching success, so that older females paired to yearling males had reduced hatchability. This result may be interpreted in light of some models of parental investment predicting decreased reproductive effort by one parent when the other sex increases its effort (reviewed in Clutton-Brock 1991). Consistent with this model are the findings of Pärt et al. (1992) working with the related Collared

Flycatcher *Ficedula albicollis*, who found that yearling males put less effort on brood rearing when they were paired to older females because they were capitalizing on the terminal effort of "senescent" females. Thus, reduced hatchability in these nests in our study may have been due to reduced males' help to their females e.g., during incubation feeding (Lifjeld and Slagsvold 1986), thus forcing their mates to more frequently abandon incubation duties to forage.

This study points out that future work on the relationship of egg size to both parental and offspring fitnesses in altricial birds should expand the range of traits usually considered to affect egg viability. In particular, while it is clear that both egg size and laying order are important for hatching success, more work is necessary to disentangle the complex interplay between these factors. This task will probably be difficult until non-destructive methods for ascertaining egg quality are developed.

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