



Colour composition of nest lining feathers affects hatching success of barn swallows, *Hirundo rustica* (Passeriformes: Hirundinidae)

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Many bird species use feathers as lining material, and its functionality has traditionally been linked to nest insulation. However, nest lining feathers may also influence nest detection by predators, differentially affect reproductive investment of mates in a post-mating sexual selection process, and affect the bacterial community of the nest environment. Most of these functions of nest lining feathers could affect hatching success, but the effect might vary depending on feather coloration (i.e. pigmented versus white feathers). This would be the case if coloration is related to: (1) thermoregulatory properties; (2) attractiveness of feathers in the nest for mates; (3) eggshell bacterial density. All of these hypothetical scenarios predict that feathers of different colours would differentially affect the hatching success of birds, and that birds should preferentially choose the most beneficial feather colour for lining their nests. Results from two different experiments performed with a population of Danish barn swallow, *Hirundo rustica*, were in accordance with these predictions. First, *H. rustica* preferentially selected white experimentally offered feathers for lining their nests. Second, the experimental manipulation of the feather colour composition of nests of *H. rustica* had a significant effect on hatching success. Experimental nests with more white feathers added at the beginning of incubation had a lower probability of hatching failures, suggesting differential beneficial effects of lining nests with feathers of this colour. We discuss the relative importance of hypothetical functional scenarios that predicted the detected associations, including those related to sexual selection or to the community of microorganisms associated with feathers of different colours. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, 102, 67–74.

ADDITIONAL KEYWORDS: bacteria – feather colour – hatching success – lining material – nest building – sexual selection.

INTRODUCTION

Many birds use feathers as nest lining material (Harrison, 1975; Hansell, 2000), and their function has commonly been assumed to arise from nest insulation. Among the nest lining materials tested for insulating properties, down were the best at reducing egg

cooling rates in artificial nests (Hilton *et al.*, 2004). Comparative evidence consistent with the insulation function of feathers as nest lining material indicates that early breeding species of European passerines are more likely to use feathers than later breeders, and that smaller species use feathers in their nests more frequently than large species (Møller, 1984). There also exists strong experimental support for this function, as feather removal from the nests of barn swallows (*Hirundo rustica* L.) and tree swallows

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(*Tachycineta bicolor*) caused an increased rate of heat loss from eggs, and increased incubation effort, and resulted in longer nestling periods (Møller, 1991; Winkler, 1993; Lombardo *et al.*, 1995). The colour of feathers could also be related to their thermal properties, and, as for other biological structures, influence the thermoregulation of the animals (e.g. Endler, 1978; Stuart-Fox & Moussalli, 2009). When used as nest lining material, feathers of different colour could therefore affect thermoregulation of the nest environment, and consequently incubation behaviour and hatchability of eggs. Feathers in the nest cup might also act as a barrier between nest parasites and nestlings (Lombardo *et al.*, 1995), but the detected association between the experimental removal of feathers and parasite load of nestlings could more readily be related to changes in temperature of the nest environment (Winkler, 1993; Lombardo *et al.*, 1995).

The colour composition of nest lining feathers may also affect the reproductive success of birds (i.e. hatching success). Nest building behaviour is known to be an energetically costly activity (Hansell, 2000), which in some species is sexually selected because of the relationship between nest building effort and the differential reproductive investment of the individual pair (Palomino *et al.*, 1998; Soler *et al.*, 1998). In particular, the use of feathers as nest lining material has recently been suggested as a potential female signal in the spotless starling (*Sturnus unicolor*) (Veiga & Polo, 2005), in which females make adjustments to the male sexual display (Polo & Veiga, 2006). This hypothetical function of feathers as sexual display for females highlights the importance of feather coloration, suggesting that feathers are arranged to maximize their conspicuousness within the nest (Veiga & Polo, 2005). Thus, feathers of different colour would affect the reproductive investment of males and females, i.e. clutch size, incubation effort, and hence hatching success, in a scenario of sexual selection.

Nest size in general (Slagsvold, 1989), and nest lining feathers in particular (Møller, 1987a), affect the conspicuousness of the nest for predators. Feathers of different coloration could differentially affect nest crypsis, and consequently the rate of nest detection by predators. Because nest conspicuousness is likely to affect the time spent in the nest by incubating individuals (Kreisinger & Albrecht, 2008), it is possible that in this scenario feathers of different colour influence incubation behaviour, and therefore egg hatchability.

The use of feathers as lining material of nests might also affect the abundance of microorganisms (Peralta-Sanchez *et al.*, 2010). Most of these would be feather-degrading bacteria or fungi (Pugh & Evans, 1970, e.g. Shawkey, Pillai & Hill, 2003; Cristol *et al.*,

2005) that could infect incubating adults or growing nestlings. The microorganisms associated with feather material could also affect the probability of *trans*-eggshell pathogenic infection of embryos if pathogens occur on feathers. Likewise, non-pathogenic microorganisms associated with feathers could have beneficial effects if, for instance, they occupy space and prevent the establishment of pathogens on the eggshell, and/or produce antimicrobial substances against egg pathogens (Soler *et al.*, 2010). Interestingly, feather colour affects bacterial growth and the bacterial community on feathers (Goldstein *et al.*, 2004; Grande, Negro & Torres, 2004; Gunderson *et al.*, 2008). Therefore, the colour of feathers used to line nests could influence the bacterial community of the nest environment (i.e. eggshells) (Peralta-Sanchez *et al.*, 2010), which simultaneously could affect hatching success (Soler *et al.*, 2010).

The above scenarios predict that colour composition of feathers in *H. rustica* would affect hatching success. Here, we tested this prediction in a Danish population of *H. rustica*. In a first experimental approach we determined the colour preferences of nest lining feathers in *H. rustica*. In a second experiment, by manipulating the colour composition of nest lining feathers we explored the effect on hatching success.

MATERIAL AND METHODS

FIELDWORK

The fieldwork was carried out in May–June 1982 and 2008, during the breeding season of *H. rustica* at Kraghede, Denmark (57°12'N, 10°00'E). For a detailed description of the study area, see Møller (1987a). In 1982, our experiment was performed at one farm, whereas the observational data were collected in non-experimental farms in the study area. In 2008, we used four farms for the experiment, including that used in 1982.

In 1982 most of the nest lining feathers in natural nests of *H. rustica* were from chickens (>70%), and thus we selected feathers from this species to perform the colour preference experiment. In 2008, only one of nine farms in the Kraghede area had chickens (Plymouth Rock), and consequently chicken feathers were unavailable for most *H. rustica* (i.e. we did not find any chicken feathers in the *H. rustica* nests checked in 2008). Furthermore, because of the absence of chickens on the farms, the availability of white feathers of appropriate size greatly decreased in 2008. In contrast to 1982, more than 90% of all feathers in *H. rustica* nests in 2008 were the body feathers of gulls (*Larus* spp.), with additional pigmented feathers from partridge *Perdix perdix*, pheasant *Phasianus colchicus*, blackbird *Turdus merula*, and several other

species (A.P. Møller, unpubl. data). Feathers from gulls were either pigmented feathers from juvenile birds or white feathers from adults. Feather colour composition between years highlight the importance of performing experiments that allow the study of both feather colour preference and the differential effects of feather colour on hatching success.

1982 FEATHER SUPPLEMENTATION STUDY

The experiment consisted of offering white and pigmented feathers at a similar relative frequency (50%) to determine feather colour preference. Feathers for the experiment were collected from a single chicken farm rearing a mixture of White Leghorn and Plymouth Rock, and were sorted into two categories of white and pigmented (i.e. mainly brownish) feathers, respectively, with all feathers longer than 4 cm being excluded because *H. rustica* prefer smaller feathers for nest lining. Subsequently, 250 feathers of each of the two categories were dyed black at the base of the shaft with water-resistant ink to distinguish experimental feathers from other feathers in the environment. On 22 May 1982, A.P.M. put out all 500 feathers in the farmyard in the morning at 07:30 h, at a time when *H. rustica* are typically engaged in nest building. On 1 June 1982 A.P.M. removed all feathers from the 26 occupied *H. rustica* nests on the farm, counting the number of white and pigmented feathers with a black shaft. A.P.M. also recorded nest lining feathers in 56 non-experimental nests in non-experimental farms during the incubation period in 1982 by removing all feathers from the nest lining and simply recording the number of white feathers and the number of feathers of other colours. All feathers were subsequently returned to the nests.

We tested the null hypothesis of no colour preference by testing the actual proportion of non-pigmented feathers observed in the nests against the null hypothesis of 50% non-pigmented feathers.

2008 FEATHER REPLACEMENT EXPERIMENT

During May–June 2008 we visited nests twice weekly to determine the laying date and clutch size. Once the clutch was complete, we counted feathers of the two colours in each nest. The experiment consists of removing all pigmented feathers from a set of nests chosen to be white, thereby leaving the nests with only white feathers. The removed pigmented feathers were subsequently added to the sampled pigmented experimental nests from which white feathers had been removed for use in subsequent experimental white nests. Thus, we alternated experimental treatment among sampled nests. After excluding nests that hatched before the second sampling (six), and

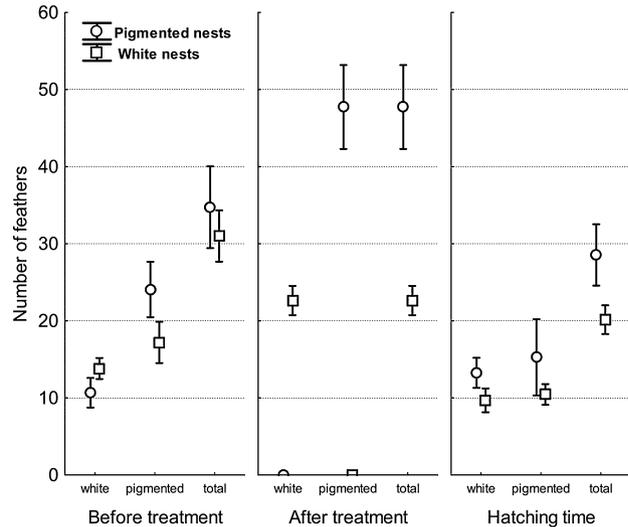


Figure 1. Average number (\pm SE) of white, pigmented, and total number of feathers before and after treatment, and at the end of incubation, in *Hirundo rustica* nests.

those that failed to hatch because of predation (one), desertion (one), or because the nest fell down (one), we collected data from 22 experimental 'white nests' and 14 experimental 'pigmented nests'.

To prevent bacterial contamination between nests, we wore new latex gloves, sterilized with 70% ethanol, for each nest. Because pigmented feathers are more numerous than white feathers in the nests of swallows (see Results), this experimental approach implies that not only feather colour, but also the number of feathers, differed between treatments (Fig. 1). Thus, in addition to experimental treatment, we took into account the experimental change in number of feathers in the nests of *H. rustica* [i.e. the number of feathers of different colour that were experimentally added (positive values) or removed (negative values) from experimental nests]. *Hirundo rustica* were randomly chosen for each treatment, and our experiment was blind with respect to parental quality, clutch size and nest size. A few days before hatching, we again visited the nests and counted the number of white and pigmented feathers present in the nest lining material. Subsequently we visited nests on the day of hatching to determine hatching success, defined as the percentage of successfully hatched eggs relative to clutch size.

STATISTICAL METHODS

Hatching success did not approach a normal distribution, and we used the information as a dichotomous variable (i.e. nests with or without hatching failure). The numbers of white, pigmented, and total feathers were approximately normally distributed

Table 1. Comparisons of the number of white and pigmented feathers in *Hirundo rustica* nests that did and did not experience hatching failures

	With hatching failures ($N = 13$)	Without hatching failures ($N = 23$)	Wald statistics	P
	Mean (SE)	Mean (SE)		
Model I				
No. feathers at laying	36.46 (5.08)	28.39 (3.02)	0.21	0.646
No. exp. added feathers	-1.00 (5.68)	1.30 (2.51)	1.65	0.199
No. added feathers	13.77 (1.66)	9.78 (1.38)	3.46	0.063
No. feathers at hatching	25.85 (3.20)	22.04 (2.75)	0.01	0.921
Treatment			1.65	0.198
Model II				
No pigmented feathers at laying	21.92 (3.65)	17.52 (2.53)	1.56	0.211
No. exp. added pigmented feathers	1.00 (7.83)	-2.39 (4.44)	0.18	0.671
No. added feathers	13.77 (1.66)	9.78 (1.38)	2.19	0.139
No. pigmented feathers at hatching	10.38 (3.20)	13.96 (2.95)	1.49	0.222
Treatment			0.07	0.790
Model III				
No. white feathers at laying	14.54 (2.23)	10.87 (1.16)	0.04	0.840
No. exp. added white feathers	-2.00 (2.75)	3.70 (2.44)	4.46	0.035
No. added feathers	13.77 (1.66)	9.78 (1.38)	2.13	0.145
No. white feathers at hatching	15.46 (2.00)	8.09 (1.22)	5.60	0.018
Treatment			3.96	0.047
Model IV (best model)				
No. exp. added white feathers	-2.00 (2.75)	3.70 (2.44)	6.53	0.011
No. white feathers at hatching	15.46 (2.00)	8.09 (1.22)	5.05	0.025
Treatment			4.11	0.043

All models included experimental treatment as a factor. The term 'No. experimentally added feathers' refers to the number of feathers after treatment minus that before treatment. The term 'No. added feathers' refers to the number of feathers of the experimentally removed colour that were found in nests of *H. rustica* at hatching. Results are from generalized linear models with binomial errors and logistic link functions.

(Kolmogorov–Smirnov tests for continuous variables, $P > 0.15$). Proportions were square-root arcsine-transformed before tests, reaching normality. Therefore, we used parametric statistical tests in our analyses of these variables.

For exploring the effect of experimental treatment on within-nest variation we used repeated-measures ANOVAs with experimental treatment as a between-factor, and with effect of feather number or feather colour as within-factors. To explore the effect of number of feathers and experimental treatment on the probability of hatching failure we used generalized linear models with a binomial error and logistic link function. Akaike's information criterion (AIC) was used for selecting models that best explained hatching success. This best model was selected with the smallest AICc (AIC with a second-order correction for small sample sizes) and highest Akaike weight ω_i (Table 1). Statistics associated with each term in the best model were estimated in a generalized linear model.

Reported values were means (SE) and statistical tests were two-tailed. STATISTICA 7.1 was used for all analyses performed.

RESULTS

FEATHER COLOUR PREFERENCE

In 1982, the mean (SE) number of feathers found in experimental nests at the beginning of incubation was 28.0 (2.0) ($N = 26$). In natural non-experimental *H. rustica* nests white feathers were more common than pigmented feathers [white feathers 73.0% (2.0), $N = 56$]. In 2008, on average *H. rustica* nests harboured 31.3 (2.7) ($N = 36$) feathers, with a larger proportion of pigmented feathers [white feathers 42.3% (3.3), $N = 36$].

All experimental nests in 1982 had more than the expected 50% white experimental feathers, ranging from 56 to 90%. The percentage of white feathers in nests derived from the experiment was 79.0% (2.0),

differing significantly from the random expectation of 50% (one-sample Student's *t*-test, $t_{25} = 59.43$, $P < 0.0001$). Therefore, swallows preferred white feathers for lining their nests.

HATCHING SUCCESS, NUMBER AND COLOUR OF NEST LINING FEATHERS, AND EXPERIMENTAL TREATMENT

Before the experiment, nests with different experimental treatments did not differ significantly in the total number of feathers or number of pigmented and white feathers ($t_{35} < 1.6$, $P > 0.12$). However, before the experiment and for completely random reasons, experimental pigmented nests harboured a larger proportion of feathers of pigmented colour than experimental white nests, as revealed from within-nest comparisons [Fig. 1; repeated-measures ANOVA, experimental treatment (between factor), $F_{1,35} = 0.40$, $P = 0.53$; feather colour (within factor), $F_{1,35} = 20.06$, $P < 0.0001$; interaction colour \times treatment, $F_{1,35} = 7.19$, $P = 0.011$].

Our experimental change in colour composition of feathers in *H. rustica* nests did not significantly affect the probability of hatching failure (i.e. nests with or without a hatching failure) after controlling for the non-significant effects of number of feathers before treatment, number of experimentally added feathers, and number of feathers at hatching time (Table 1). Subsequently we separately analysed the effect of the numbers of white (model III in Table 1) and pigmented feathers (model II in Table 2) on the probability of hatching failures. The effect of experimental treatment, as well as number of white feathers that were experimentally added, and those found in nests at hatching, were significantly related to the probability of hatching failure (Table 1). Experimental white nests where at least one egg failed to hatch had lower hatching failures than nests receiving the pigmented feathers (42.9%, $N = 14$, of pigmented nests; 31.8%, $N = 22$, of white nests). Nests with a larger number of experimentally added white feathers experienced a lower probability of hatching failure. We found the same trend for nests with a smaller number of white feathers at hatching (Table 1). These results were independent of the inclusion of information on both white and pigmented feathers, or the exclusion of non-significant terms in the model (results not shown).

When including information on the number of feathers of different colour in these analyses, the best model explaining probability of hatching failure (Table 2) included treatment and the number of white feathers at hatching, plus information on the number of white feathers experimentally added (Table 2). All these results in combination suggest a direct effect of feather colour on the hatching success of *H. rustica*.

Table 2. Best model explaining hatching success in *Hirundo rustica*

Hatching success	AICc	Weight	Evidence ratio
No. exp. added white feathers	38.32	21.1	1
No. exp. added white feathers	38.46	19.6	1.07
No. exp. added white feathers	39.6	11.1	1.89
No. exp. added white feathers	40.01	9	2.33
No. exp. added white feathers	40.1	8.7	2.43
No. exp. added white feathers	40.29	7.9	2.68
No. white feathers at laying	40.82	6	3.49
No. exp. added white feathers	40.84	6	3.52
No. exp. added white feathers	41.05	5.4	3.92
No. pigmented feathers at laying	41.08	5.3	3.98
Treatment			
No. added feathers			
No. white feathers at hatching			
No. white feathers at hatching			
No. exp. added pigmented feathers			
No. exp. added pigmented feathers			
No. exp. added pigmented feathers			
No. exp. added pigmented feathers			
No. exp. added pigmented feathers			
No. exp. added white feathers			
No. exp. added white feathers			
No. white feathers at hatching			
No. white feathers at hatching			
No. pigmented feathers at hatching			
No. pigmented feathers at hatching			
No. white feathers at hatching			
No. white feathers at hatching			

Results are based on the Akaike information criterion where hatching success was used as a dependent factor and treatment as explanatory categorical factor. 'No. experimentally added feathers' refers to the number of feathers after treatment minus that before treatment. 'No. added feathers' refers to the number of feathers of the experimentally removed colour that were found in nests of *H. rustica* at hatching. 'No. feathers at laying' and 'No. feathers at hatching' refer to the number of feathers of each colour at those moments in the incubation period. Models were run without interactions terms. AIC weights (w) were calculated from the ten best models.

Our experimental approach resulted in experimental pigmented nests harbouring almost twice as many feathers as experimental white nests, and therefore the detected effect of feather colour treatment on hatching failures could be confounded by the effect of experimental feather number. However, several pieces of information suggest that this is not the case. First, experimentally added feathers did not explain the probability of hatching failures (model 1 in Table 2). The effect of treatment reached statistical significance only in the case that information on the number of white feathers was included in the models (models III and IV in Table 1), and appeared even after controlling for the effect of total number of feathers added to experimental nests (model IV in Table 1). Finally, we tested the robustness of results related to experimental treatment by sequentially excluding from the analyses pairs of cases with the most extreme (i.e. positive and negative) values of number of feathers in the nest after treatment, and calculating effect sizes associated with treatment effect in the best model explaining probability of hatching failure (model IV; Table 1). As effect sizes do not depend on sample size, we expect to find a negative relationship between effect size and degrees of freedom if differences in the number of feathers between experimental pigmented and white nests were important in explaining the detected effect size of experimental treatment. However, estimates of effect size of the first nine models (reducing degrees of freedom from 32 to 16) were not significantly related with degrees of freedom ($R = 0.001$, $N = 20$, $P = 0.997$). Therefore, all these analyses suggest that the relationship between hatching success and treatment was independent of the larger number of feathers that pigmented nests received compared with white ones.

VARIATION IN THE NUMBER OF FEATHERS AND THEIR COLOUR COMPOSITION IN *H. RUSTICA* NESTS THROUGHOUT THE INCUBATION PERIOD

At the time of hatching the experimental effect on feather colour composition (Fig. 1: percentage of white feathers, $t_{35} = 0.88$, $P = 0.38$; number of pigmented feathers, $t_{35} = 1.10$, $P = 0.28$; number of white feathers, $t_{35} = 1.45$, $P = 0.16$), but not that of total number of feathers (Fig. 1; $t_{35} = 2.11$, $P = 0.042$), disappeared, suggesting that nest maintenance activity partially counteracted the experiment. The number of feathers of the removed colour in experimental nests at hatching did not differ significantly between white and pigmented experimental nests [pigmented nests, mean (SE) = 13.3 (1.9); white nests, mean (SE) = 10.4 (1.3); $t_{35} = 1.23$, $P = 0.23$], suggesting that neither feather colour composition nor the number of feathers

significantly affected the rate of addition of feathers to nests.

The total number of feathers in experimental nests decreased from laying to hatching when considering either the number of natural (repeated-measures ANOVA, effect of time: $F_{1,35} = 13.4$, $P = 0.0008$; Fig. 1) or experimental feathers at the beginning of incubation (repeated-measures ANOVA, effect of time: $F_{1,35} = 29.3$, $P < 0.0001$). However, the experimentally manipulated number of feathers decreased at a larger rate in pigmented than in white experimental nests (repeated-measures ANOVA, interaction treatment \times time: $F_{1,35} = 13.44$, $P = 0.0008$; Fig. 1).

DISCUSSION

Hirundo rustica females, like many other birds, spend considerable periods of time searching for feathers to line their nests during a period of several weeks before and during laying and incubation (Møller, 1987b). Females transporting feathers are chased by other nest owners, and by males seeking extra-pair copulations, suggesting that this behaviour may entail costs.

Experimental change in feather composition may have implications for thermal insulation, nest detectability by predators, attractiveness of nests for mates, or may change the nest bacterial community, including pathogenic or beneficial microorganisms. Because these potential effects could affect egg hatchability (see Introduction), we predicted that our experiment on nest lining feathers could affect hatching success. In accordance with this prediction we found that experimental white nests with a larger number of experimentally added white feathers experienced a lower probability of hatching failure than experimental pigmented nests. Furthermore, our experiment in 1982 indicated that *H. rustica* preferred white feathers for nest lining. These results suggest beneficial effects of white feathers at the beginning of incubation and an adaptive preference of *H. rustica* for white feathers.

An experimental manipulation of the number of feathers in nests of birds has previously been performed (Peralta-Sanchez *et al.*, 2010). Feather removal experiments caused an increase in the rate of heat loss from eggs and an increase in incubation effort, but a direct effect on hatching success had never previously been detected (Møller, 1991; Lombardo *et al.*, 1995). Here, we manipulated the number of feathers in *H. rustica* nests and, similarly to previous works, failed to show an effect of the number of feathers on egg hatchability. However, when separately considering white and pigmented feathers, we recorded a statistically significant effect, and found

that experimental white, but not pigmented, nest lining feathers affected the hatching success of *H. rustica*.

Following the hypothetical scenarios that allowed us to predict that feathers of different colour may differentially affect hatching success, the detected beneficial effect of white feathers suggest that feathers of this colour have superior thermoregulatory ability that could enhance incubation and/or could be more attractive for mates than pigmented feathers. Furthermore, white feathers in *H. rustica* nests might be less conspicuous for predators, and thus females would be able to incubate more efficiently as a result of the lower risk of predation. Finally, white feathers could affect the probability of embryo infection by pathogenic microorganisms (Peralta-Sanchez *et al.*, 2010). Our experiment does not allow us to distinguish between these different scenarios, although we can exclude the possibility that attraction of nest predators plays a role, because nest predation is virtually absent in *H. rustica* (Møller, 1994). These hypothetical scenarios are in any case not mutually exclusive, and it is possible that differential effects of feathers of different colour associated with each of the proposed scenarios have additive effects, explaining the associations detected here. Further research is therefore necessary for exploring the function of white nest lining feathers in preventing hatching failure.

The positive relationship between white nest lining feathers and hatching success predicts that individuals should preferentially select white feathers for their nests. In accordance with this hypothesis, we found that most *H. rustica* preferred experimentally offered white feathers over those of other colours. Experiments of feather-colour selection by *H. rustica* for lining their nests were performed 26 years before the experiment of colour composition of nest lining feathers. During this period, the availability of feathers of different colour changed, and thus the natural colour composition of nest lining feathers of *H. rustica* nests also changed. Results from 1982 were, however, experimental, and we have no reason to believe that *H. rustica* preference for white feathers has changed during this period.

Adults counteracted our experimental manipulation in 2008, and at hatching the percentage of white feathers did not differ from that found before the experiment. This counteracting behaviour by nest owners did not impair our experimental approach because the effect of the experimental number of feathers was still present at the end of incubation. In any case, and apparently in contradiction to the detected experimental beneficial effects, we found that the number of white feathers at the end of the incubation was positively related to the probability of hatching failure. The composition of nest lining feath-

ers at the end of the incubation is not a result of the experiment, and paired statistical tests suggested that colour composition at this stage did not differ from that before the experiment. Thus, any factor that covaries with a particular colour composition of nest lining feathers, and that also affects the probability of hatching failure, would explain the association. For instance, it is possible that birds adjusted the number of beneficial white feathers to the environmental conditions of the nest that predicted hatching success. In this case, and taking into account the experimentally demonstrated beneficial effect of white feathers, *H. rustica* should increase the number of white and scarce feathers in nests in risky environments (i.e. relatively high probability of hatching failures). In 2008 white feathers were rarer than pigmented feathers, suggesting a significant effort on the part of *H. rustica* to restore feather composition, especially important when they have to differentially increase the number of white feathers. In any case, this result is not experimental and is consequently more difficult to interpret. Feather proportion during the incubation period is an interesting question in need of further studies.

In conclusion, we have shown that experimental manipulation of the number and colour composition of nest lining feathers at the beginning of incubation influenced the hatching success of *H. rustica*, suggesting that nest design may have important consequences for the reproductive success of birds. The experimental addition of white nest lining feathers at the beginning of the incubation enhanced hatching success, and *H. rustica* preferred feathers of this colour for nest lining. The experimentally detected effects of feather colour on hatching success and preferences for white feathers can be explained by different ecological scenarios that should be further investigated before conclusions about the different functions of white feathers can be reached.

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