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Do spotless starlings place feathers at their nests by ultraviolet color?

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Abstract A considerable number of bird species carry feathers to their nests. Feathers' presence in the nests has traditionally been explained by their insulating properties. Recently, however, it has been suggested that feathers carried to the nests by females of the spotted starling (*Sturnus unicolor* L.) could have an ornamental function based on their ultraviolet (300–400 nm) and human-visible longer wavelength (400–700 nm) coloration. In our population, 95.7% of feathers found inside next-boxes occupied by nesting starlings were rock dove fly feathers. Of these feathers, 82.7% were naturally positioned with their reverse side oriented toward the entrance hole and 42.4% of all found feathers were situated within the nest-cup. Here we experimentally assess the signaling function of ultraviolet coloration of feathers in nests of spotless starlings by providing nests with a number of pigeon flight feathers that were respectively treated on their obverse, reverse, both, or neither side with a UV blocker. Starlings placed 42.5% of the experimental feathers in the nest-cup irrespective of the UV block treatment. Orientation of feathers toward the entrance hole was not related with their ultraviolet radiation. However, feathers placed within the nest-cup were more likely found with their reverse side oriented toward the entrance hole confirming our correla-

tive findings. These results suggest a minor role of ultraviolet coloration on feather location by spotless starlings.

Keywords Nest decoration · Feather function · Sexual selection · Ultraviolet coloration

Introduction

The use of feathers in nest constructions is a widespread phenomenon among birds and its functioning has been traditionally related to the thermal properties of feathers that would improve the environment of growing embryos and nestlings (Møller 1991; Lombardo et al. 1995; Hansell 2000). Feathers, when used for covering the eggs, may also reduce the risk of clutch detection by visual predators (Götmark and Ahlund 1984), avian brood parasites (Clark and Robertson 1981), or mates (Valera et al. 1997). Furthermore, based on their chromatic properties, a signaling function in the context of intra-specific communication has very recently been suggested (Veiga and Polo 2005).

The hypothetical signaling function of feathers was suggested on the base of results showing non-randomly positioned feathers within nest-boxes of spotless starlings (*Sturnus unicolor*; Veiga and Polo 2005). Briefly, Veiga and Polo (2005) found that starlings located a considerable amount of feathers out of the nest-cup piled up below the entrance hole where they would be highly conspicuous to possible nest visitors. Furthermore, with respect to feather side positions (obverse vs. reverse), feathers of different species tended to be located exposing their more reflective side toward the entrance hole (Veiga and Polo 2005). Because these results suggested that feathers are arranged to maximize their conspicuousness within the nest, Veiga and

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Polo (2005) proposed a signaling function of feathers in an intra-specific context.

Feathers are predominantly carried to the nests of spotless starlings by females, and, consequently, the receptors of this potential signals could be males in a context of post-mating sexual selection and differential investment in relation to signal exaggeration (Burley 1988; Soler et al. 1998; Sheldon 2000; Veiga and Polo 2005). In addition, females may display feathers to other females as a status signal. The amount of feathers carried to the nest is related to female's reproductive experience and laying date (Polo and Veiga 2006), thus, the visible amount of feathers at the nest may inform other females about the quality of individual neighbors or territories. Actually, spotless star-ling nests are frequently visited by prospective individuals (Parejo et al. 2008) who might view these feathers and respond to their informative content.

Under the signaling hypothesis (Veiga and Polo 2005) feather coloration is, in general, an important trait. Furthermore, because materials constituting the nest line reflect minimally at shorter wavelengths (e.g., Avilés et al. 2008), those traits or objects carried to the nest reflecting at UV wavelengths (300–400 nm) would be particularly important in enhancing conspicuousness (Hunt et al. 2003; Avilés et al. 2006a, 2008). Moreover, several studies report empirical and experimental evidences showing a role of UV coloration of feathers in process as different as mate choice (e.g., Bennett et al. 1997), parent–offspring com-munication (e.g., Tanner and Richner 2008), and a variety of intrasexual interactions (e.g. Alonso-Alvarez et al. 2004, Pryke and Griffith 2006). Thus, Veiga and Polo (2005) hypothesized a particularly prominent role of UV reflec-tance of feathers enhancing their conspicuousness within the starling nests.

One possibility for testing the conspicuousness role of UV reflectance of feathers is to experimentally block UV reflectance of feathers and analyze feather location by females. This experiment is necessary (Veiga and Polo 2005) to disentangle the relationship between UV reflec-tance of the obverse and reverse sides of the feathers and any other variable that covaries with differences in reflectance, such as feather curvature (e.g. Veiga and Polo 2005). Therefore, to explore the importance of UV reflectance of feathers in the context of sexual (i.e. female) signaling, experimental manipulation of the trait indepen-dently of feather curvature is necessary.

Here, we experimentally assess the signaling function of ultraviolet coloration of feathers found in nests of spotless starlings by providing nests with a number of dove feathers that were respectively treated in their obverse, reverse, both, or neither side with a UV blocker. We adopted this experimental approach since females "decorate" nests with previously collected nest materials that were not immedi-

ately used, but accumulate in the nests (see examples in Hansell 2000). Furthermore, the differential signaling properties (i.e. UV reflectance) of feather sides should be evaluated by females within the nest-hole environment, where the signaling function of feathers is hypothesized. The study of location (within vs. outside the nest-cup) and orientation (reverse vs. obverse side toward the entrance hole) of feathers will allow us to explore the importance of UV reflectance of feathers located at the nests by females as a sexual signal in spotless starlings (Veiga and Polo 2005). According to the predicted role of UV reflectance, feathers should be arranged exhibiting up the side with the highest UV reflectance irrespective of their location within or outside the nest-cup.

Methods

The field study was carried out in Guadix (37°18' N, 3°11' W), south-eastern Spain, during the breeding seasons of 2007 and 2009, in nest-boxes installed within one colony of spotless starlings already established in old buildings. In our population clutch size is typically four to five eggs and, except for a few exceptions, incubation is a female task (Soler et al. 2008). Male assist with caring for chicks and are polygynous (Veiga et al. 2001), therefore, females would benefit by signaling to males after mating (e.g. Soler et al. 2008).

We recorded the number and kind (i.e. contour or flight) of feathers present in each of 19 starling clutches at day 13 from clutch initiation. We also recorded the avian species to which the feathers belonged, as well as if they were placed with their obverse or their reverse side oriented toward the entrance of the nest. In addition, we annotated the position of these feathers as found inside (i.e. placed lining the nest-cup) or outside the nest-cup.

Experimental design

Starlings carry a variable number of feathers to their nest (range 0–42 feathers) from a few days before laying their first egg until hatching (Polo and Veiga 2006). We performed our experiment during the laying period (mean ±SD, 3.1±1.2 eggs, range 1–5 eggs) in 28 nest-boxes. The experiment consisted on the addition of eight individually ink-marked flight feathers of pigeons to the nest material. Feathers were situated on the nest-cup, randomly positioned regarding their side, assuring that females detected the new experimental material that we expected were relocated within the nest-box depending of experimental treatment. Feather marks were numbers in black, lower than 3 mm in size and written at the quill of every feather rachis. None of

our experimental nests were abandoned due to our experimental manipulation (i.e., 2 days after the experiment females were incubating the eggs or new eggs were detected in the nest), and in all of them some of experimental feathers were used as nest material (see "Results"), whereas others disappeared suggesting selective selection of feathers by female starlings. Consequently, feathers were visualized and used by incubating females which is a prerequisite of our experimental approach.

Experimental feathers were flight feathers (secondary remiges and retrices; average length (range)=13.24 (10.30–16.55) cm) collected from naturally predated Rock doves (*Columba livia*) in a dovecote within the study area. We decided to use rock dove fly feathers because these were by far the most frequent ones occurring naturally in our starling nest-boxes (see "Results"). The "-UV" treatment consisted of coating pigeon feathers with an ultraviolet-light blocker (50/50 *w/w* blend of Parsol 1789 and MCX, Roche) that minimally affect reflectance at the human-visual part of the spectrum (400–700 nm; Avilés et al. 2006a, 2006b). Dyads of feathers in every nest were randomly assigned to four treatments: (1) UV blocked in the reverse; (2) UV blocked in the obverse; (3) UV blocked in the obverse and reverse; and (4) non-treated feathers. Forty-eight hours after placing the feathers, we scrutinized the nest searching for experimental feathers. Detected feathers were individually classified depending on location (i.e. within or outside the nest-cup, and orientation (with their reverse or obverse side toward the entrance hole)).

We estimated changes in spectral shape of 14 experimental feathers before and after coating them with the UV blocker (Fig. 1). Reflectance spectra in the range 300–700 nm were obtained using a spectrometer with a deuterium and a halogen light source (DH 2000, Ocean Optics Europe) connected with a bi-furcated micron fiber optic probe that reached the feather surface at a 45° angle and illuminated an area of 1 mm^2. Using OOIBase, a spectra acquisition software package, we sequentially recorded 10 spectra relative to a standard white reference (WS-2) and averaged the spectra to reduce electrical noise from the collection array within the spectrometer. After white calibration, three spectra were collected from randomly selected points within the proximal, distal, and middle parts of the feather, respectively. These measurements were used to estimated average ultraviolet (300–400 nm) and human-visible (400–700 nm) chroma, a measure of spectral purity, by dividing the summed reflectance in these two bands by the summed reflectance of the entire spectrum (300–700 nm; e.g. Montgomerie 2006). Chroma of obverse and reverse sides of pigeon feathers did not differ either in the ultraviolet (Paired *t* test: UV wavelength, $t_{14}=1.58$, $P=0.14$) or in the human-visible part of the spectrum (Paired *t* test: visible wavelength, $t_{14}=$

1.26, $P=0.23$; Fig. 1a). Furthermore, the UV block treatment minimally affected chroma of feathers in the human-visible spectrum (effect size, 19.0%; paired *t* test: visible wavelength, $t_6=2.03$, $P=0.09$), while markedly reduced UV chroma (effect size, 94.3 %; paired *t* test: UV wavelength: $t_6=5.11$, $P=0.002$; Fig. 1a). We did not find any sign that the treatment leaked from the side on which it was applied to the other side of the feather (Fig. 1b).

We used GLMMs for binary dependent variables (link function: logit, SAS Macro program GLIMMIX, SAS Institute 1999) to test the effect of the UV block treatment on: (1) probability of finding a feather within versus outside the nest-cup (i.e. location) and (2) probability of finding a feather with their reverse versus obverse side oriented toward the entrance hole (i.e. orientation). Laying date, clutch size, and time of experiment (i.e. number of eggs in the nest at the time of the experiment) were included as covariables in our models to control for possible confounding factors that might affect both nest building activity and phenotypic quality of experimental females (i.e., nest). Furthermore, orientation of feathers could depend on their
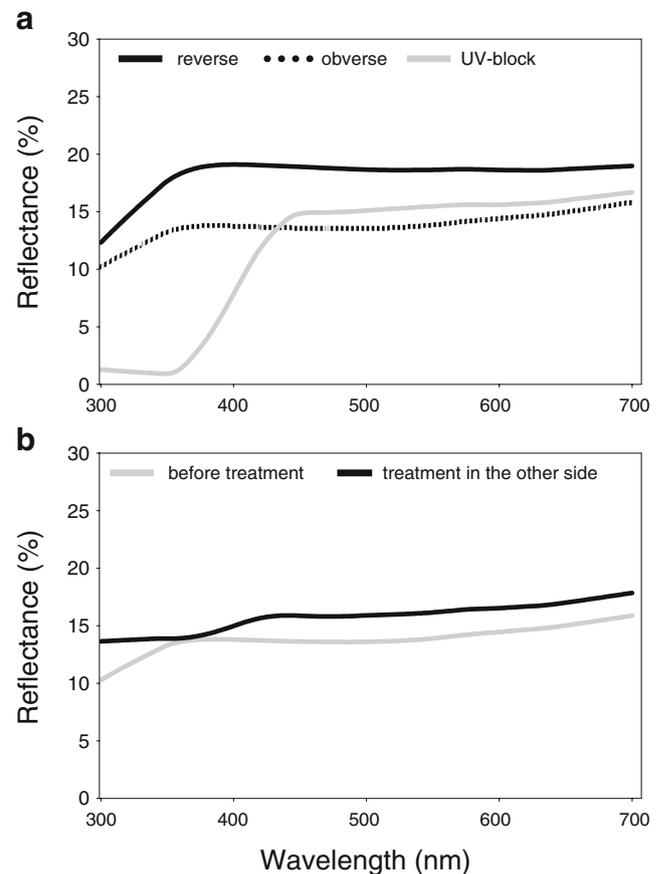

Fig. 1 Average reflectance spectra of dove rock feathers in their reverse and obverse side before and after treatment with an UV-blocker (**a**) and before and after treatment with an UV-blocker in the other side of the feather to test for leak effects (**b**; *n*=14)

coloration, but the role of coloration may vary with location since feathers found lining the nest would hardly be perceived by signal receivers. Therefore, we also tested in our model the interaction between the UV block treatment and location (i.e., inside versus outside the nest-cup) on feather orientation. Nest identity and the interaction between nest identity and experimental treatment were entered as random factors in the models to control for non-independence of the resulting orientation of experimental feathers within the same nest. Model selection was carried out by removing, one by one, the effects that were furthest from statistical significance, except for the two random terms, starting with the highest-order interactions down to the main effects.

Results

Baseline data

The average number of feathers per nest found in our population was 16.2 feathers (SD=8.2; range=5–32; N=19 nests). Out of 307 feathers identified in the nest-boxes, 95.7% were rock dove fly feathers. The remaining 13 feathers belonged to hens (N=10), hoopoe *Upupa epops* (N=1), and house sparrow *Passer domesticus* (N=2). Out of 307 found feathers, 82.7% were naturally positioned with their reverse side oriented toward the entrance hole, whereas 42.4% of them were situated within the nest-cup.

Experimental manipulation of UV reflectance of feathers

Forty-eight hours after the experiment we recovered 71.4% (160 out of 224) of pigeon feathers experimentally introduced within the nests. We found no effect of the application of the UV blocker on the probability of recovering a feather in the nest ($F_{1,53}$=1.03, P=0.31), suggesting no bias by handling in our experiment. Of experimental feathers, 42.5% were placed lining the nest-cup while the remaining were positioned vertically against the back wall of the nest-boxes (14.9%) or laid down out of the nest-cup (42.6%). Different females showed similar proneness to locate the pigeon feathers within versus outside the nest-cup (random effect of nest: Z=0.99, P=0.16), and the effect of UV blocker treatments was similar in different nests (random effect of nest×treatment: Z=0.09, P=0.46). Furthermore, the probability that a pigeon feather was placed within the nest-cup was not affected by the UV blocker treatment ($F_{3,92}$=0.25, P=0.86), laying date ($F_{1,62}$=1.61, P=0.21), clutch size ($F_{1,63}$=1.15, P=0.28), or the number of eggs in the nest at the time of experiment ($F_{1,63}$=0.00, P=0.98).

With respect to the orientation of all recovered pigeon feathers a higher proportion was found exposing their reverse (61.9%) versus their obverse side (38.1%) toward the entrance hole (Yates corrected χ^2=4.11, d.f.=1, P=0.043). Orientation of pigeon feathers was not related to the UV block treatment as a main effect, or by interacting with feather location (Table 1). Orientation of feathers inside and outside the nest-cup was different (Table 1): feathers located within the nest-cup were more frequently oriented with their reverse side toward the entrance (Yates corrected χ^2=6.72, d.f.=1, P=0.009), while feather located outside the nest-cup showed similar trend to be oriented with their obverse versus reverse side toward the entrance (Yates corrected χ^2=0.18, d.f.=1, P=0.67; Fig. 2).

Discussion

We did not find support for a role of ultraviolet radiation in starling's location and orientation of feathers within their nests. Starlings oriented the feathers more frequently with their reverse side toward the entrance when located within the nest-cup, while feathers located outside the nest-cup, and thus visible to possible nest visitors, were randomly oriented with respect to feather curvature and UV blocking treatment.

Veiga and Polo (2005) noted that flight feathers carried to starling nests were mainly located outside the nest-cup, without contacting the eggs or the incubating females, where they would be highly conspicuous to possible nest visitors. Here by individually ink-marking feathers we proved that in our study population starlings placed nearly half of the experimental feathers within the nest-cup. Many of these feathers were used to line the wall nest, and therefore were partly covered by dry-grass and not evident to possible nest visitors as would be expected from the

Table 1 General linear mixed model analyzing determinants of feather orientation toward the entrance hole in spotless starling nests

Independent effect	d.f.	F/Wald-Z	P value
Excluded terms			
UV-block × treatment location	3.59	0.30	0.82
Number of eggs	1.62	0.08	0.78
Laying date	1.61	0.08	0.78
UV-block treatment	3.93	0.56	0.64
Clutch size	1.62	0.23	0.63
Included terms			
Location	**1.62**	**6.17**	**0.01**
Nest		0.04	0.48
Nest × UV-block treatment		1.04	0.15

Independent effects are ordered as they were removed. Significant effects are reported in bold
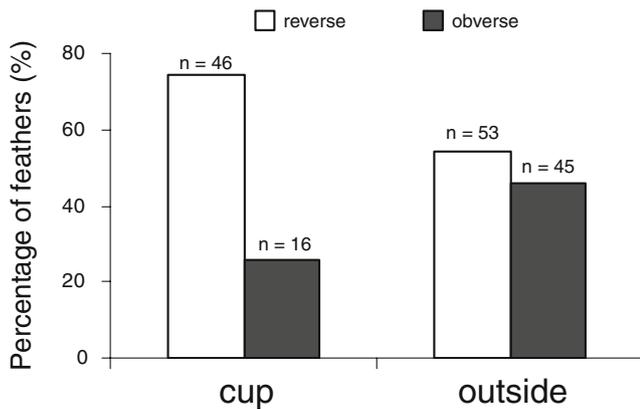
Fig. 2 Orientation of pigeon feathers (obverse versus reverse side toward the entrance) found within versus outside the nest-cup in spotless starling nests. Numbers of feathers per orientation and location are above percentage bars

hypothesis of feather coloration being visual signals for con-specific receivers.

It has been suggested that ultraviolet colors may enhance the conspicuousness of feathers carried to the nests with an ornamental function (Veiga and Polo 2005), because materials constituting the nest backgrounds are generally poor in ultraviolet wavelengths (Avilés et al. 2008). Experimental evidence has shown that spotless starlings have the visual potential to detect subtle differences in ultraviolet coloration within their nests (Avilés et al. 2006a). Here, we have failed, however, to find support for a role of ultraviolet radiation on feather location inside or outside the nest-cup and orientation. It could be argued that starlings may have cued on visible (400–700 nm) rather than ultraviolet radiation when locating the feathers since rock dove's feathers were more reflective in their reverse side irrespective of the UV block treatment (Fig. 1). Contrary to this possibility, only the feathers that were found hidden within the nest line were placed with their more reflective reverse side oriented toward the entrance hole, while those found outside the nest-cup were randomly oriented toward the entrance hole. Alternatively, it could be argued that pigeon feathers used for this experiment provided a low intensity ultraviolet stimulus for spotless starlings because their flat spectrum in the ultraviolet waveband (Fig. 1). However, the intensity of the ultraviolet signal should be assessed considering the background in which the signaling elements are perceived (Endler 1990). In a previous study, we showed that materials used to line spotless starling nests, as well as the cork that constitutes our next-boxes, have low ultraviolet reflection while they are highly reflective at longer wavelengths (Avilés et al. 2008). Thus, pigeon feathers used in our experiment provide a high contrast with the background in the ultraviolet part of the spectrum, which given changes in reflection at the ultraviolet waveband of pigeon feathers

produced by our experiment (Fig. 1), made our test of the effect of changes in the intensity of an ultraviolet signal reliable. Also, we used pigeon feathers for our experiment rather than to use more ultraviolet reflective feathers of other bird species because we found that most of feathers naturally placed in the nest-boxes were pigeon feathers (this study), which, against Veiga and Polo (2005)' conclusion, suggests a minor role of ultraviolet chroma in feather placement within the nest-boxes for spotless starlings.

Veiga and Polo (2005) found in their study population that only contour feathers were predominantly placed within the nest-cup; result that was interpreted as consistent with the insulation hypothesis. In our population, wing feathers located within the nest-cup were predominantly oriented matching the curvature of the nest, which following Veiga and Polo (2005) suggests a thermoregulatory function. This possibility does not exclude, however, that orientation of feathers in the nest-cup responded to easiness of handling wing feathers to be part of the nest line. Finally, feathers available to adorn the nest are abundant in our population as compared to Veiga and Polo' population which may affect the costs of carrying feathers to the nests.

A potential weakness of our experimental design is the placement of experimental feathers within rather than outside the nest-box. First, experimental feathers may have fallen into the nest-cup and become oriented reverse-side-up simply due to an incubating bird sitting on them. Second, females may not be able to accurately assess coloration of feathers with the luminance conditions of nest-boxes. Finally, Veiga and Polo (2005) found mainly contour feathers in the nest-cup, but we use flight rather than contour feathers in our experiment, which might not be preferentially used by spotless starlings. However, four different lines of evidence argue against these potential pitfalls and justify our experimental approach. (1) With the light condition of nest-boxes, spotless starlings can distinguish between colored eggs that differ in UV reflectance (Avilés et al. 2006a), thus supporting the assumption that they would be able to do so with feathers. (2) Some of the experimental feathers that we provided were removed from the nest-box (i.e., found outside the nest), suggesting that females were actively selecting feathers for orienting them. (3) Some feathers were sewed within the nest line material, or in the background of the nest, while others were found outside the nest-cup suggesting that females were actively manipulating them. (4) Finally, wing feathers as the used in our experiment are frequently found in the nest-cup at our study site. Contour feathers were only detected in seven out of the 19 sampled nests of the pilot study, whereas all sampled nests have a minimum of two wing feathers in the nest-cup (average=6.78, range=2–16, n=19 nest). Consequently, although supplying feathers outside the next-box

could have provided us with additional insights on feather's selection by spotless starlings, Veiga and Polo's hypothesis (2005) deals with decoration within the nests rather than with selection outside the next-box and consequently our approach is correct.

In summary, we have not found support for an ornamental role of UV coloration of feathers in spotless starlings. Although only feathers located in the nest-cup were predominantly located with their more visible-reflective reverse side oriented toward the entrance we cannot discard a role of visible coloration on feather location without an experimental manipulation. Furthermore, we cannot discard that intra-specific signaling may occur while the birds are carrying the feathers to their nests, rather than when the feathers are in the nest. In such a case, feather quantity itself may signal female or male phenotypic quality or willingness to invest in reproduction (e.g. Moreno et al. 1994; Soler et al. 2001). Future research should focus on testing other features than UV coloration as the cause that feathers were used as sexually selected signals in spotless starlings.

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