Age-related sexual plumage dimorphism and badge framing in the European Robin *Erithacus rubecula*

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Male and female European Robins *Erithacus rubecula* display their red breasts in year-round territorial contests. Despite the clear signalling role of the red breast, little is known about its sexual dimorphism or trends in size when Robins age. We studied these patterns in resident and migrant Robins in a Mediterranean population. Both male and female first-year Robins had smaller red breasts than second-year individuals. Females, but not males, showed a reduction in badge area after the second year of life, leading to sexual dimorphism in red breast area in the oldest Robins. The grey fringe around the red breast showed a steady increase in width in males when ageing, but not in females, also leading to sexual dimorphism in this trait among oldest Robins. The contrast between the red breast and its surrounding grey fringe was higher than that between the breast and the back at both high and low environmental light intensities. This suggests that the grey fringe could function as a frame to highlight the perimeter of the red breast, and that the Robin's plumage is equally suited to display in open areas and forest understoreys. Our study suggests that the extent of the red breast and its grey frame could confer information about the age and sex of the birds, and thus be used as a signal in territorial contests and mating decisions.

Keywords: age, colour patterns, feathers, plumage, sex, territoriality.

His observation of a European Robin *Erithacus rubecula* unexpectedly attacking a headless decoy led David Lack to perform his famous experiments to understand 'just how much of a stuffed Robin was needed for a wild Robin to treat it as an intruder and attack it' (Lack 1943, p. 144). Lack found that the red breast alone triggered the attack of territory owners, but that although male and female Robins defended territories vigorously, encounters between intruders and territory owners rarely ended in real fights. Rather, encounters often only involved singing and facing the red breast towards the intruder to display it to its full extent (Lack 1943), suggesting that Robins may communicate important information with the red breast to resolve conflicts. Surprisingly, although some studies have been carried out on the relevance of

the red breast in Robins' territorial behaviour (Chantrey & Workman 1984), little is known about basic features of this badge, such as how its size differs according to age and sex. Furthermore, the Robin's red breast is surrounded by a grey fringe that frames the badge, except along its lowest margin where it meets the white belly (Fig. 1), but the functional role of this grey fringe has so far been largely overlooked. Previous evidence based on only a few individuals suggested that males may have wider grey fringes than females, and adults wider fringes than juveniles (Diego 1983, Cramp 1988). Here we explore the patterns of variation of both the red breast and the grey fringe according to Robin age and sex.

As both male and female Robins actively defend a territory throughout the year (Lack 1943), we expected that both sexes would have similarly sized red breasts and grey fringes. Regarding age variation, it is well known that in many bird

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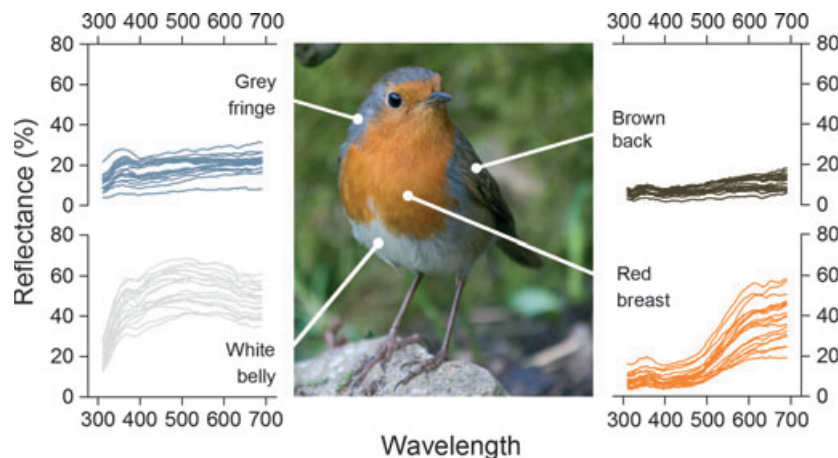
Figure 1. Reflectance (nm) patterns of 19 adult male European Robin plumage tracts. (Photo: Graham Racher).

species the area or colour intensity of status- or condition-dependent signals increases with age, particularly between juveniles and adults (Török *et al.* 2003, Morales *et al.* 2007, Vergara *et al.* 2009). Thus, we expected this may also hold true for Robins. We also expected that the plumage of the Robin would be especially suited for low-light environments such as occur at dusk or inside forests, because Robins are especially active at this time and in this habitat (Cramp 1988). Furthermore, we predicted that the grey fringe may have evolved as a contrast element to highlight better the conspicuousness of the red breast. Therefore, we measured the chromatic contrast of the breast against the grey frame, the brown back and the whitish belly to assess whether the grey fringe enhances the conspicuousness of the badge.

METHODS

Fieldwork

This study was conducted from December 1995 to February 2000 at La Muntada (41°97′N, 2°13′E, Barcelona, NE Spain) in the wet valley floor of a pine forest dominated by Scots Pine *Pinus sylvestris* with dense understorey and a small pond with permanent water. Robins were captured with mist-nets and clap-nets throughout the year a median of 2 days (range 0–8 days) each month. The red badge was drawn on tracing-paper after placing the Robin gently on its back on a table. Badge outlines were scanned and their area was measured to the nearest 0.1 mm^2 with the software SIGMASCAN PRO® 5.0 (SYSTAT Software, Inc., San Jose, CA,

USA). The extent of the grey fringe on the forehead was scored in three categories: 0 (absent), 1 (grey feathers covering from the forehead's red strip to up to half the distance between the red strip and an imaginary line between the midpoint of both eyes), and 2 (covering the upper parts of the head from the red strip to an imaginary line going between the midpoint of both eyes). This was done because the width of the grey fringe is difficult to measure on the flanks but easy to categorize (and highly variable) on the head. All field measurements (including ageing, see below) were undertaken by R.J., and all breast area measurements by F.R.-S.

Plumage age

Robins replace their feathers each summer. Juveniles leave the nest in spring–summer with a brownish plumage without the characteristic red breast. In their first summer of life, they undertake a partial moult, including some tail feathers, some wing coverts and all body feathers, thus attaining their first red breast with a grey fringe and whitish belly. Birds that have undergone this partial moult can be identified by the contrast between old feathers (particularly great coverts; Jenni & Winkler 1994) grown while nestlings and newer feathers grown during this partial moult. In the second summer of life, in most cases after breeding for the first time, they replace their entire plumage, attaining their second red breast and grey fringe, and they do so each subsequent summer (Svensson 1992). As a result, after the first complete moult, it is impossible to determine the age of an adult bird.

Accordingly, plumage age was scored in five categories: category 1, for birds with their first red breast and grey fringe; categories 2 and 3, for birds captured in category 1 that were subsequently recaptured 1 or 2 years later, respectively; categories 4 and 5 for birds captured for the first time after finishing a complete moult (i.e. adult birds of unknown age). The age of these birds must have been from 1½ up to 19 years (the maximum age recorded for this species; Fransson *et al.* 2010). Age category 4 was assigned to all birds captured as adults for the first time. If recaptured in subsequent years, they were then assigned an age category 5. Thus, categories 4 and 5 clumped the oldest birds in the population. When we started this study, we were capturing birds of all ages in the population. Those in their first year of life were assigned an age category 1, the others (of any age > 1) were assigned to category 4.

Resident and wintering birds

The Mediterranean basin forms the wintering area for Robins breeding in northern European latitudes. With the capture of brownish, early-fledged chicks during spring–summer and the sudden arrival of un-ringed birds in autumn (some of them later recaptured during winter and disappearing thereafter), it is clear that resident and migrant wintering birds coexisted in our study area during autumn and winter. As the body size of Robins varies with latitude and sex (Cramp 1988, Cuadrado 1991, Pérez-Tris *et al.* 2000) and different subspecies may differ in the size of the grey fringe and red breast patch (Cramp 1988), combining both resident and wintering individuals into a single analysis might bias the results. Hence we defined as resident those Robins captured in the study area at least once between April and August, as well as some individuals captured in September with juvenile plumage; the remaining birds (i.e. those never captured between April and August) were classified as 'wintering'. The latter category may actually include non-migrant birds coming from local populations but we chose this criterion against a distinction based on morphology/size alone because the latter could bias our results (e.g. as only the largest males and smallest females could have been clearly classified, we would find that males have larger badges than females). Most resident birds were sexed according to the incubation patch and their cloacal protuberance (Svensson

1992). Unsexed Robins were used in analyses when accounting for sex was not necessary (e.g. for analysing overall ageing patterns).

Statistical analyses of breast and grey fringe extent

Some Robins (mainly residents, but also some wintering birds) were recaptured repeatedly and re-measured. Repeatability (*R* intra-class correlation coefficient) was analysed using a mixed model with individual fitted as a random factor, using the PROC MIXED procedure in SAS 9.2 (SAS Institute 2008) following the methods of Nakagawa and Schielzeth (2010). Repeatability of the red breast area measured on different captures of 45 individuals was 78.9% (null model likelihood ratio test from PARMS statement: $\chi_1^2 = 43.56$, $P < 0.0001$), suggesting a good degree of repeatability in the measurements. Measurements from the same bird and plumage age were averaged to increase precision (and thus slightly increase *R*; Falconer & Mackay 1996).

In contrast, repeated measurements of the same individuals with successive plumages can reveal morphological changes within the life of a bird. These repeated measurements are not statistically independent (e.g. due to temporal autocorrelation). Therefore, we used SAS PROC MIXED with REML to model the change in red breast area over time, taking into account within-individual covariance. We used a type = ar (1) covariance structure that assumes that there is some autocorrelation of red breast area between consecutive years. We specified Robin identity as the random effect and the age of the plumage as the repeated measure. As recaptured individuals contributed more than one measurement to the analysis, we corrected the effect of this pseudoreplication (Hurlbert 1984) on the degrees of freedom of the model by using an *F*-distribution with degrees of freedom calculated with the Kenward–Rogers method (Schaalje *et al.* 2001). Moreover, for birds with multiple measurements we used paired *t*-tests to assess changes in red breast area between consecutive years. Sample sizes differed somewhat between tests, as not all measurements (e.g. sex) could be taken each time a bird was trapped. Sample sizes are reported in Figure 2. For the red breast of unsexed birds, sample sizes from ages 1 to 5 were 40, 7, 1, 6 and 2, respectively, whereas for the grey fringe the sizes were 29, 6, 0, 4 and 1. Tests are two-tailed throughout.
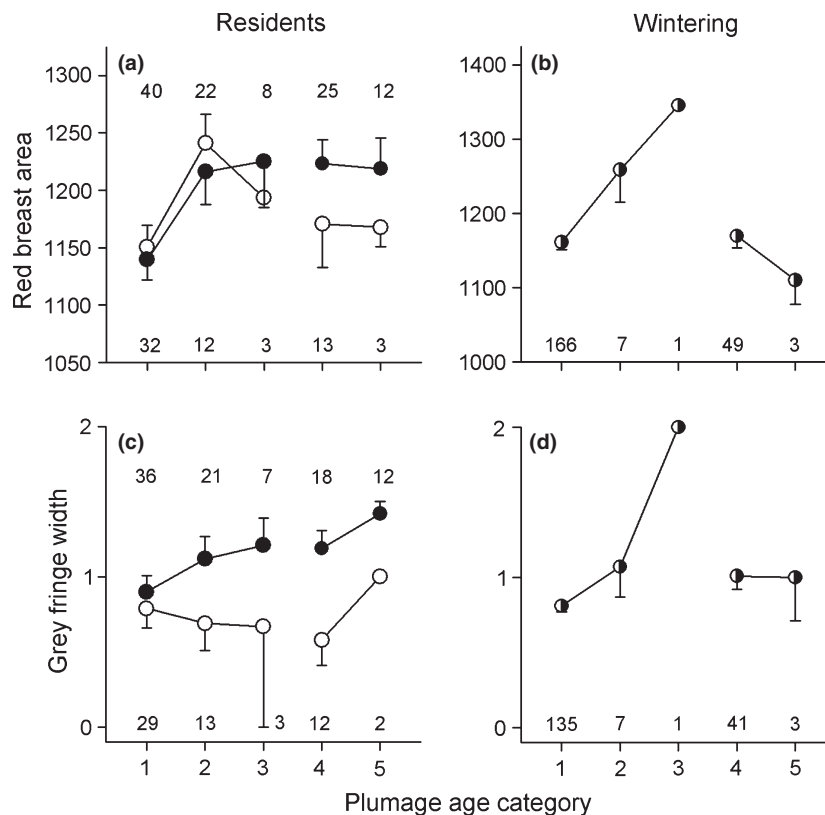
Figure 2. Plumage characteristics according to age and residency. Mean (± se) red breast area (mm²) and grey fringe width (categories, see Methods) for resident and migrant birds are given. Inset numbers show sample sizes; in (a) and (c) the top line represents the sample size for males and the bottom line for females. Black dots represent males and white dots represent females; semi-filled dots (in b and d) represent the mixture of males and females among migrant Robins. Plumage age categories 1–3 represent the first to third plumages (red breast and grey frame). However, categories 4 and 5 group the oldest birds in the population that were initially captured when already adults (see Methods for age category details).

We assessed whether the area of the red breast changed with age by analysing whether the oldest birds (i.e. classes 4 and 5) differed from younger ones (classes 2 and 3). This is a conservative test because whereas in age classes 4 and 5 all adults are grouped together (potentially up to 19 years; see above), in age classes 2 and 3 only birds with their second and third plumage are included, respectively. This was done with a GLM using SAS PROC GENMOD (note that a mixed model does not apply here because a bird in age classes 2 and 3 cannot, by definition, be in age classes 4 and 5 and vice versa, see above), using Wald Chi-squared tests (adjusted for overdispersion with the DSCALE option). For this analysis, when an individual was measured at two different age classes, their breast area at age 2 was selected if it was measured at age 2 and 3, and the breast area at age 5 was used if the bird was measured at age 4 and 5. The reason for this was that we aimed to compare ages as far apart as possible to test for senescence. To assess sexual dimorphism at the oldest ages, when one individual was measured at ages 4 and 5, the measurement at age 5 was used. This was done because our aim was to compare the oldest birds in the population.

We used a chi-squared test to assess differences in grey fringe width between sexes on their first plumage and among oldest birds. Because of the ordinal categories for age and grey fringe width, we tested for the existence of a linear trend on grey fringe width with respect to age using the Mantel–Haenszel chi-squared statistic (Mantel & Haenszel 1959).

Colour measurement and visual modelling

To assess whether the grey fringe increases the conspicuousness of the red breast, we quantified

plumage coloration in 19 specimens of European Robin stored at the museum of the Estación Biológica de Doñana (Sevilla, Spain). We only measured adult male specimens showing no obvious signs of moult that were collected within the previous 50 years to ensure that their coloration would closely resemble that of live birds (Armenta *et al.* 2008). Specimens were collected between September and April in southern Spain (14 birds) and North Africa (five individuals). A list with the museum codes is available in the Supporting Information Data S1.

We quantified the reflectance of the plumage of Robins with a spectrometer on four body regions: the red breast, the grey fringe, the white belly and the brown back. We used S2000 Ocean Optics equipment connected to a deuterium-halogen light (D2-W, mini) by a coaxial reflectance probe (QR-400-7-UV–vis) and OOIBASE32™ operating software (Ocean Optics, Inc., Dunedin, FL, USA). Reflectance was measured with a 45° angle probe completely touching the Robin to prevent stray light from entering. Measurements were relative and referred to a white standard (WS-2) and to complete darkness (i.e. blocking the entering light by placing an opaque cap on the end of the reflectance probe and switching off the light in the room), which we calibrated before the measurement of every individual Robin. All measurements were taken in an unlit room. Measurements were repeated three times for every plumage tract and mean values per individual used in the analyses. All measurements were done by J.M.A.

We ran physiological models (Vorobyev *et al.* 1998) with AVICOL software v3 (Gómez 2006), which account for environmental luminosity and bird sensitivity, to assess the conspicuousness of Robin plumage tracts. Using this approach, we assessed whether the chromatic signal emitted by the red breast patch was amplified by the grey fringe. We obtained chromatic contrasts expressed as just noticeable differences between different plumage patches of Robins for all sampled individuals.

The perception of Robin red breasts is probably affected by the interaction between ambient light coloration and the reflectance spectra of the breast and the surrounding body parts. Robins are particularly active at dusk and often occur in dark habitats such as forests (Cramp 1988). Thus, we used published irradiance spectra for low and high luminosity in the nests of altricial birds (Avilés *et al.*

2008) to assess the conspicuousness of Robin plumage in a light environment common to Robins (i.e. low light), compared with highly illuminated environments. This contrast allowed us to investigate the role of environmental light variation on Robin plumage perception.

As sensitivity data for Robins were unavailable, we used single-cone photoreceptor spectral sensitivities, photoreceptor noise and the transmission properties of avian ocular media for the Blue Tit *Cyanistes caeruleus* as representative of a UVS system (Hart *et al.* 2000) to parameterize our visual model. This was justified given that most Passeridae, with the exception of members of the groups Corvidae and Tyrannidae, have UVS vision type (Ödeen & Håstad 2003). Furthermore, no splits in the type of vision have been reported within a bird family, suggesting that vision type has a strong phylogenetic inertia in birds (Cuthill *et al.* 2000). Finally, recent evidence suggests that there are negligible differences between model calculations obtained using spectral sensitivity data for different passerine species (Spottiswoode & Stevens 2010).

We used SAS PROC MIXED to assess differences in chromatic matching between different body parts of Robins as a fixed factor. We specified Robin identity as a random effect to control for non-independence of different body contrasts attained for a bird. Similarly, we modelled chromatic contrasts in relation to plumage tracts and luminosity as fixed factors and Robin identity as a random effect, aiming to test for the effect of luminosity on Robin conspicuousness. *Post-hoc* differences were assessed using the Scheffe test.

RESULTS

Red breast area

Red breast area differed among age classes in resident ($F_{4,154} = 4.47$, $P = 0.002$; Fig. 2a) and migrant Robins ($F_{4,18.6} = 4.21$, $P = 0.013$; Fig. 2b). In resident Robins, the second red breast was on average 5% larger than the first one ($F_{1,68.1} = 10.72$, $P = 0.002$); the same occurred in migrant Robins (10% increase; $F_{1,15.7} = 6.37$, $P = 0.023$). In residents, this increase was similar in males (6% increase) and females (7%; age*sex: $F_{1,55.4} = 0.07$, $P = 0.795$). Paired *t*-tests for recaptured residents (sexes combined) also suggested the tendency for Robins to increase badge size from first to second badge, although the trend did

not achieve statistical significance (3% increase, mean increase ± se = 39.5 ± 21.5 mm², $t_{34} = 1.84$, $P = 0.075$). The sample size was not sufficient to test this for migrant birds.

Resident males showed no appreciable change in badge size when comparing plumage categories 2 and 3 with 4 and 5 (Wald $\chi^2_1 = 0.04$, $P = 0.846$; Fig. 2a). However, an average 8% reduction was found in females (Wald $\chi^2_1 = 5.34$, $P = 0.021$; Fig. 2a). Migrant Robins showed a similar reduction (7%; Wald $\chi^2_1 = 3.79$, $P = 0.052$; Fig 2b). In residents, this uneven reduction in badge size with age led to old males displaying roughly 6% larger badges than old females (Wald $\chi^2_1 = 3.61$, $P = 0.057$).

Grey fringe extent

The first grey fringe did not differ between young male and female residents ($\chi^2_2 = 0.66$, $P = 0.720$; Fig. 2c). The grey fringe of males became wider with plumage age ($\chi^2_1 = 12.56$, $P < 0.001$) but this did not happen in females ($\chi^2_1 = 0.230$, $P = 0.632$). As a result, the oldest males (those in age categories 4 and 5) had wider grey fringes than females ($\chi^2_2 = 12.78$, $P = 0.002$). Interestingly, all old males had at least some grey on their head, and 58% displayed the largest width category, whereas more than a third (36%) of old females had no appreciable grey fringe on their head, and only 14% achieved the widest category. Migrant Robins showed a very slight increase in grey fringe width with age ($\chi^2_1 = 7.49$, $P = 0.006$; Fig. 2d).

Colour and perception of plumage patterns

The reflectance patterns of adult male Robin breast, belly, fringe and back are shown in Figure 1. The breast showed a peak in the yellow-red region (550–700 nm, peak around 650 nm) and the spectral shape of a typical orange-red object to the human eye. The belly region homogeneously reflected the most in all the wavelengths included in the visible part of the spectrum (400–700 nm), appearing typically white to the human eye. Finally, reflectance spectra of the fringe and back increased continuously from the blue region (from 400 nm) onwards, although the back was darker than the fringe.

Visual model calculations revealed significant differences in chromatic contrast between plumage
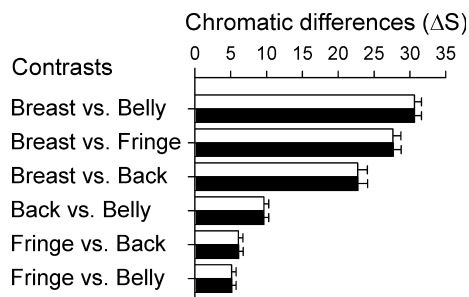
Figure 3. Chromatic contrasts between plumage tracts. Chromatic contrasts (± se) between different body parts of adult male Robins. White and black bars correspond to model calculations under low and high luminosity levels, respectively.

sections (e.g. red breast vs. white belly, grey fringe vs. brown back; $F_{5,90} = 172.93$, $P < 0.001$; Fig. 3). Interestingly, despite the brown back contrasting only slightly with the grey frame, the contrast between the red breast and the grey frame was greater than that between the breast and the back (Scheffe test, $P = 0.009$; Fig. 3). The chromatic contrasts between the different body parts of Robins were unaffected by light conditions (high vs. low illumination; light conditions: $F_{1,198} = 0.002$, $P = 0.960$; light conditions*body section: $F_{5,198} = 0.0001$, $P = 0.99$; Fig. 3).

DISCUSSION

Our results have identified some previously unknown patterns of variation in the red breast and grey fringe of European Robins. The size of the red breast increased from the first to the second year in both males and females, and in residents and migrant Robins. Furthermore, old males showed consistently larger badges (and grey fringes) than old females, due to a decreasing trend in badge extension for females after their second year. The oldest females of the population (in age categories 4 and 5) showed evidence of senescence by displaying average red breast areas similar to first-year birds. This pattern was also consistent among migrant birds. This remarkable variation across sexes and over time suggests that the red breast may convey information in the context of territorial fights or mate choice. Interestingly, Lack (1943) interpreted his results as suggesting that the red breast was only a signal used in species recognition, which may also serve to differentiate fledglings from adults. However, our results suggest that the red breast could also reveal important

information regarding individual differences in terms of sex, age or related condition-dependent traits (e.g. Nakagawa *et al.* 2007). Thus, the extent of the red breast, together with the grey fringe, which was also wider in older males, might be involved in sex recognition, mate choice and territorial contests in this species.

Besides their size variation, we also assessed whether the grey fringe could enhance the perception of the red breast by using a physiological model of visual perception. Our results show that the grey fringe could function as a frame to highlight the red breast, because the red breast showed greater chromatic contrast against the grey fringe than against the brownish back of Robins. Interestingly, the grey fringe is missing at the transition between the red breast and the whitish belly of Robins, where the colour contrast is already very high. Thus, the existence of the grey fringe in Robins might be explained by its role in enhancing the conspicuousness of an important signal (the red breast). The additional variation found in the extent of the grey fringe between sexes and ages points out the need for additional studies to disentangle whether the grey fringe functions as a signal on its own or as an amplifier of the red breast.

Finally, our approach to assess plumage patterns at contrasting light environments, previously applied to studies of eggs (Avilés 2008) and bird plumage perception (Gómez & Thery 2007), revealed that the plumage colour pattern of Robins is equally suited for open areas (high light conditions) and dense understoreys (low light conditions). Previous work has shown that birds perform their sexual displays only in a portion of the available light environments within their natural habitats, aiming to maximize visual contrasts during their displays by exhibiting more particular colours and behaviour (Endler & Théry 1996). This may suggest that the Robin's signalling pattern is particularly suited to a wide range of light conditions. More generally, this 'all-purpose' plumage may be particularly adaptive in year-round territorial species such as Robins that exploit a mosaic of different spectral environments throughout the year. However, we cannot rule out the possibility that Robins suit their plumage pattern to the prevailing light environments by modifying their behaviour. Also, as we relied on irradiance measures collected at the nests of open and hole-nesting birds (Avilés *et al.* 2008), it is possible that low differences in Robin signal intensity in high and low light conditions were due

to the fact that irradiance measurements used to parameterize the visual models did not cover all the possible light irradiance spectra of Robins.

Our study is a first step in understanding the role of the red breast and the grey frame in the life of Robins. The age- and sex-related patterns we have found, and the important between-individual variation in the reflectance of these colour patterns (Fig. 1), suggest that Robins may communicate important information with their plumage, and thus we encourage future studies to address the link between these individual plumage patterns and their physiology. Also, further experiments similar to those of Lack (1943) with stuffed Robins with different combinations of red breast sizes and grey fringe widths are encouraged to understand the function of the red breast and how it shapes the Robin's life.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article:

Data S1. Museum codes for the 19 sampled European Robins *Erithacus rubecula* in the collection of the Estación Biológica de Doñana (Seville, Spain).

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