Integrated signal systems in birds: context and meaning
Grant closing report

Below we discuss the main findings for each of the four points of the detailed research plan.

1) Temporal dynamics of signal integration: information content and use

We continued the previous long-term data collection on great tit plumage reflectance, and finally analysed data from seven "moult years", i.e. winter and spring data after the same summer moult season (autumn 2006 to spring 2013). We found that the correlation structure of reflectance traits was similar between 1) winter and spring (i.e. little abrasion and great abrasion), 2) males and females, 3) yearlings and adults, and 4) different years. Two melanin-coloured plumage areas, the crown and the breast stripe, appeared in common principal components of brightness and UV chroma, so colour of these two plumage areas was developmentally integrated. However, individual reflectance traits showed higher information content in terms of both repeatability and condition-dependence than integrated colour variables. There was robust assortative mating (an indicator of mutual sexual selection) only for an informative (condition-dependent) individual colour measure, crown UV chroma. Therefore, we concluded that

1) colour integration across the plumage was highly stable, but
2) this developmental integration did not translate to functional integration, i.e. preferential use of composite over individual colour traits in sexual selection.

This finding contrasts with previous findings in collared flycatchers (obtained under a previous research grant) where both developmental and functional integration of plumage colour had been suggested. The difference between the two species may have originated from the fact that in great tits the distinct but correlated plumage areas conveyed distinct information to the receiver.

2) The use and the costs of integrated signal traits during courtship

We planned to measure ambient light in the courtship positions of collared flycatcher males in the forest canopy. However, the spectroradiometer depended on a physical connection to a computer on the ground. We found that even with a signal enforcer cable, more than 10m of cable prevented the recognition of the radiometer by the computer. (We could not learn this unfortunate fact before purchasing and applying the device.) Therefore, we could not measure light at canopy heights greater than 12m. Our cooperation attempts with the distributor to develop a wireless version of the device failed because the wireless version depended on a heavy battery that would be impossible to elevate into the canopy together with the radiometer.

Finally, we relied on indirect methods of courtship light quantification, and calibrated these methods with the radiometer. We chose a forest area with a sufficiently low canopy, measured many points across the canopy with the radiometer, including but not restricted to flycatcher singing positions. We found that vertical position in the canopy had little effect on light, and much of the variation in both brightness and UV chroma of light was attributable to a simple distinction between "shade" and "gap" (sun) light. Moreover, we found based on spectroradiometry that we could visually tell "shade" and "sun" positions from each other with a sufficient reliability. Finally, we conducted two different studies using visual categorization of light environment.

First, we classified individual singing positions of collared flycatcher males as shade or sun. Second, we categorized light environments around all nestboxes in our central study plots based on the density of canopy cover

1) above the nestbox,
2) around the tree, and
3) east-southeast of the tree (because flycatchers court in the morning hours).

These categorizations were found to be repeatable between two observers. However, neither of these indirect attempts gave any robust pattern. We found that males did not appear to preferentially use either of the two light environment categories, and courtship light use did not seem to depend robustly on light availability in the territory either. Likewise, we found no overall effects of light availability on occupation by flycatcher males, and no robust relationship emerged between the light conditions of occupied nestboxes and the pairing latency of males. As all of the above listed results were indirect and also non-significant, no reliable conclusion can be drawn at this point. We will be able to make significant progress with this topic as a more convenient wireless light measurement tool becomes available.

Independent of light measurements, we assessed relationships between integrated male plumage reflectance at courtship and the pairing success and pairing latency of males, as indicators of intersexual selection on integrated reflectance. We collected spectral data from 76 courting males over three successive years, of which 30 obtained a mate. Relationship between integrated plumage colour measures and pairing probability or pairing latency was weak and non-significant.

We are currently compiling data on courtship activity and energy expenditure as predictors of pairing patterns. As the last round of plasma lipid metabolite samples (indicators of energy store changes) have just been processed in Switzerland, this work is still in progress.

3) Integrated signals and parental quality

We tested correlative relationships between current year reproductive parameters and the integrated measures of plumage reflectance of males and females. Females with darker melanised plumage parts bred earlier. Similarly, males with brighter structural colour and higher plumage UV chroma bred earlier. Finally, females mated to males with higher UV chroma in dark plumage areas laid more eggs than expected from their laying date.

We further tested relationships between integrated plumage colour and the parental care of both sexes in the incubation phase. Incubation is an extremely poorly known period from the viewpoint of parental quality and sexual signalling. This study was added to the project as the experimental part was delayed by several years due to a predation wave. We found that the incubation-related behaviour of both sexes jointly determined hatching success and hatching latency. Males with brighter white plumage areas visited the nestbox more regularly. The mates of males with more UV chromatic plumage spent less time in the nestbox. Finally, male wing patch size was related to both male and female behaviour.

We ultimately conducted the planned experimental study of the ornament-related nestling care of both sexes (brood size manipulation) in two years. Feeding activity of both parents increased and nestling mass decreased with increased experimental brood size, and there was no difference between years in the effect of the manipulation. There was no relationship between the plumage reflectance traits of males or females and their own feeding rate, irrespective of manipulation category. Male feeding rate was negatively related to the structurally based brightness of the female irrespective of manipulation (Figure 1).

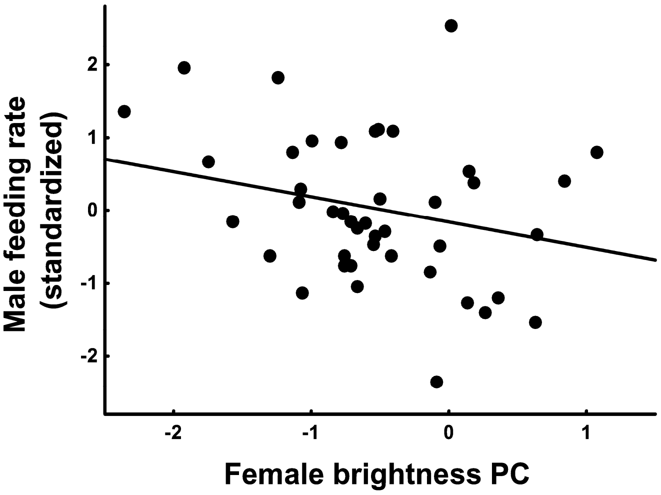

Figure 1. Relationship between female brightness principal component and male feeding rate in the collared flycatcher. Male feeding rate was standardized for brood size manipulation group

Female feeding rate was positively related to male wing patch size across manipulation groups. Relationship between male forehead patch size and the body size of fledglings turned from negative to positive with increasing manipulation, and this was shown to be due to intrinsic nestling quality and not parental care. However, the number of offspring produced was related to female wing patch size and male forehead patch size, but not to female or male reflectance traits.

Our studies therefore detected relatively little relationship between integrated plumage reflectance and parental quality, but somewhat more effects of ornamentation on partner investment, and they suggested poorly explored but fruitful directions for plumage colour research. During this part of the project, we also compiled and meta-analysed literature data, publishing the first review paper on the parental quality indicator value of sexual signals for more than a decade.

4) The condition-dependence of integrated signals

We assessed correlations between the reproductive parameters (laying date, clutch size) and body condition of males and females and their next year ornament expression. We found that females laying larger clutches tended to develop less contrasting brown and white wings by the next year. Females with higher body condition during breeding developed darker melanised plumage areas by the next breeding season. In males, there was no relationship between condition or reproductive parameters and next year integrated reflectance traits. Therefore, if anything, it seems that female melanin-based darkness during breeding may be condition-dependent.

Repeated spectral data from the same individuals for robust analyses of condition-dependence and repeatability were notoriously difficult to obtain for most of the grant period, due to the high predation rate and therefore high disappearance and turnover rate of individuals from 2009 to 2014 (predation was successfully controlled from 2015 onwards). When we recently collated the available data, we first aimed to assess the between-year repeatability of reflectance traits before looking at the determinants of between-year changes. We assessed within-year repeatability of reflectance in males (from courtship to breeding) as a “control trait”, expecting high within-year repeatability and lower between-year repeatability. Repeatability of male reflectance traits between two consecutive breeding seasons was calculated for adults because yearlings replace their plumage to a completely different one by the next year. In adults, repeatability was moderate and significant for brightness (Z transformed meta-analytic mean correlation across five plumage areas: Z = 0,341, 95% CI from 0,195 to 0,488), but non-significant for UV chroma (Z = 0,090, CI from -0,051 to 0,231). When assessing within-year correlations for comparison, we compared adult and yearling relationships. For brightness, adult and yearling within-year correlations did not differ and gave a moderate and significant overall estimate. For UV chroma, however, the yearling estimate was moderate while the adult estimate was significantly lower and overall negative (Figure 2). That is, adult males with the highest UV chroma at courtship tended to be the ones with the lowest UV chroma by nestling rearing.

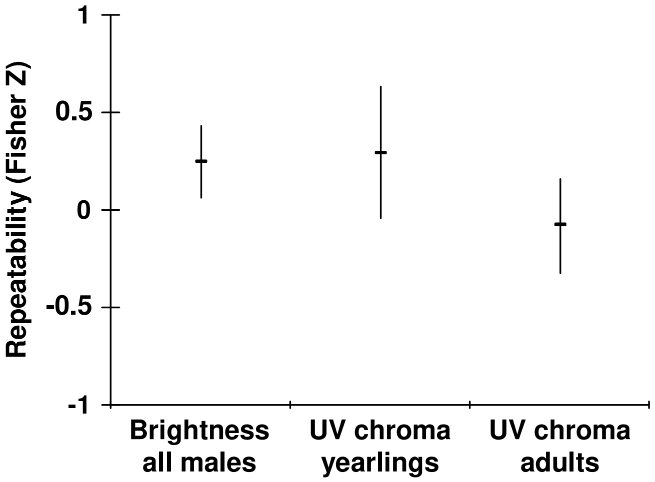

Figure 2. Within-individual correlations (repeatability) of reflectance traits between courtship and nestling rearing, averaged across five plumage areas of collared flycatcher males (means ± 95%CI)

Analogously, within-year changes of reflectance traits from courtship to the nestling stage were non-significant for brightness and for yearling UV chroma, but significantly negative for adult UV chroma (i.e. great decline, Figures 3 and 4).

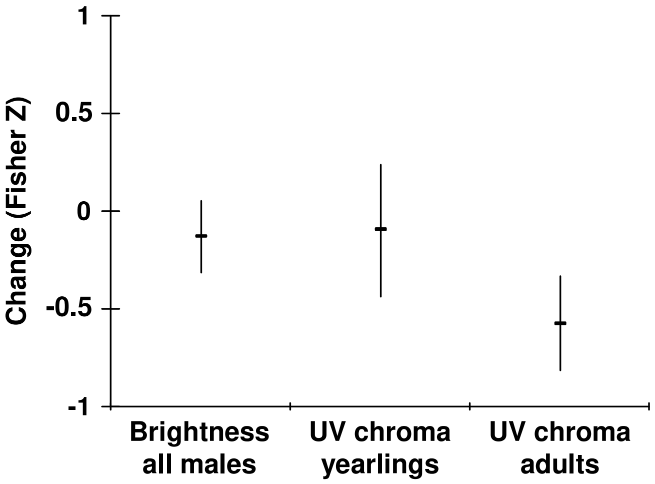

Figure 3. Effect sizes for within-individual change of reflectance traits between courtship and nestling rearing, averaged across five plumage areas of collared flycatcher males (means ± 95%CI)

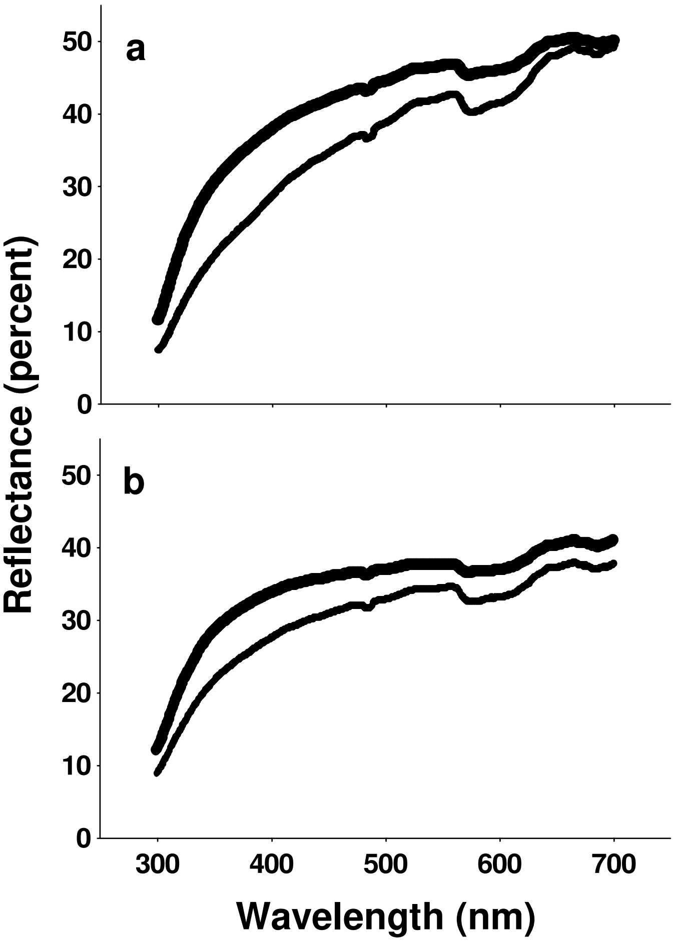

Figure 4. Mean reflectance spectra of the same adult males at courtship (thick lines) and nestling rearing (thin lines) for two plumage areas exhibiting a significant within-individual change (a, forehead patch; b, wing patch)

In other words, we arrived at the completely novel conclusion that that some reflectance traits are not repeatable and change greatly from courtship to the nestling stage although no moult or other visible change occurs in the plumage during this period. We therefore had to realize that between-year changes of plumage reflectance measured in the nestling period may not be reliable indicators of condition-dependence or repeatability of plumage colour development in our population, and the main goal should rather be to clarify the short-term determinants of plumage reflectance traits within the breeding season. Along this line, we now plan to direct our research towards the detailed patterns of within-season reflectance changes in both males and females, the mechanism of such rapid reflectance changes (particularly feather structural decay and seasonal changes in preen wax cover), and their consequences for partner behaviour. In sum, this part of the project yielded some unexpected, novel findings that opened new perspectives for our future work.

Summary

Our research projects yielded the following main novelties.

1) Stable reflectance integration across the plumage and among seasons and years may occur in birds. However, if the information content of the correlated plumage traits is drastically

different, then developmental integration may not translate to functional integration, i.e. the traits may still be used independently by the birds.

2) Incubation-related parental cooperation may depend on the plumage ornamentation of both partners, with an effect on reproductive success. Due to the role division between parents, the incubation stage is an ideal period to examine the information content of mutual ornaments and their consequences for partner investment.

3) We conducted a brood size manipulation experiment where we comprehensively assessed parental care, nestling traits, and reproductive success in relation to multiple ornaments of both males and females. Some plumage ornaments were correlated with parental care, while others were related to nestling development, and a third set of traits determined reproductive success. This suggests that stage- and ornament-specific studies may not be sufficiently informative. Integrated studies of male and female ornamentation with parental care and reproductive success under manipulated environmental conditions are needed to learn the selection forces affecting multiple ornamentation systems in the wild.

4) We highlighted a hitherto very poorly known dimension of plumage reflectance variation. We found that reflectance may not remain stable or even repeatable within the same breeding attempt. Accordingly, if we aim to reliably measure sexually selected plumage colour expression, we may need to do this before breeding. Most published studies did not follow this rule, and their conclusions may need to be reinterpreted. In addition, the rapid change of plumage reflectance may contain information for the partner and may elicit behavioural responses from the partner. The information content and function of rapid change as a signal trait is a promising new direction for plumage colour research.

Our new publications related to the project in the last study year are the following.

Kötél D, Laczi M, Török J, Hegyi G 2016. Mutual ornamentation and the parental behaviour of male and female Collared Flycatchers in the incubation period. Ibis 158: 796-807.

Szöllősi E, Garamszegi LZ, Hegyi G, Laczi M, Rosivall B, Török J 2016. Haemoproteus infection status of collared flycatcher males changes within a breeding season. Parasitology Research 115: 4663-4672 (discussed as a manuscript in the research report of the previous year)

Laczi M, Kötél D, Török J, Hegyi G 2017. Mutual plumage ornamentation, parental care and reproductive success: an experiment. Submitted

Hegyi G, Laczi M, Boross N, Jablonszky M, Kötél D, Krenhardt K, Markó G, Rosivall B, Szász E, Garamszegi LZ, Török J 2017. Is this the same male? Plumage color changes from courtship to nestling rearing. Submitted