

Ultraviolet reflectance of plumage for parent–offspring communication in the great tit (*Parus major*)

Marion Tanner and Heinz Richner

Zoological Institute, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland

Ultraviolet (UV) reflectance has been implicated in mate selection. Yet, in some bird species the plumage of young varies in UV reflectance already in the nest and long before mate choice and sexual selection come into play. Most birds molt the juvenile body plumage before reaching sexual maturity, and thus, some conspicuous traits of the juvenile body plumage may rather have evolved by natural selection, possibly via predation or parental preference. This second hypothesis is largely untested and predicts a differential allocation of food between fledging and total independence, which is a time period of 2–3 weeks where offspring mortality is also highest. Here, we test the prediction that parents use the individual variation in UV reflectance among fledglings for differential food allocation. We manipulated UV reflectance of the plumage of fledgling great tits *Parus major* by treating chest and cheek feathers with a lotion that either did or did not contain UV blockers and then recorded food allocation by parents in an outdoor design simulating postfledging conditions. The visible spectrum was minimally affected by this treatment. Females were found to feed UV-reflecting offspring preferentially, whereas males had no preference. It is the first evidence showing that the UV reflectance of the feathers of young birds has a signaling function in parent–offspring communication and suggests that the UV traits evolved via parental preference. *Key words*: great tit, parental care, parent–offspring communication, signal, ultraviolet reflectance. [*Behav Ecol* 19:369–373 (2008)]

Conspicuous body plumage traits of young birds do not evolve by sexual selection because body feathers are molted before reaching sexual maturity (Jenni and Winkler 1994). Young of most bird species show a cryptic plumage (Jenni and Winkler 1994; Kilner 2006), but in a few species the juvenile plumage is already similar to the one of adults. This poses the question of how such conspicuous plumage traits can evolve in the absence of sexual selection. In large-brooded passerines, as, for example, in the Paridae, the highest offspring mortality occurs in the first weeks after fledging where parents still tend their young (Perrins 1965; Naef-Daenzer et al. 2001). Thus, to optimize postfledging investment, parents should be sensitive to signals that may aid investment decisions.

Most passerines are visually sensitive to both ultraviolet (UV) wavelengths and the spectral range also visible to humans (Hart 2001; Ödeen and Håstad 2003; Cuthill 2006). Feather patches reflecting in the UV range are found in several bird species across various families (Eaton and Lanyon 2003; Hausmann et al. 2003). In various species, those UV-reflecting feathers were found to have a function in sexual selection (Bennett et al. 1996; Andersson and Amundsen 1997; Bennett et al. 1997; Andersson et al. 1998; Hunt et al. 1998; Johnsen et al. 1998; Doucet et al. 2005). Hence, it is possible that the intensity of the UV reflectance is a signal of individual quality to conspecifics. The honesty of such a signal might be ensured either by a cost of the precision in the building of nanostructures required to reflect UV wavelengths (Shawkey et al. 2003; Doucet et al. 2006) or through a trade-off between plumage coloration and other feather functions, such as flight or thermoregulation (Andersson 1999). This of course does not

exclude other hypotheses for the evolution of UV reflectance of bird plumage, as for example sensory bias, male–female discrimination, or evolution as a by-product.

In altricial species with numerous offspring, where sibling competition is high and parents may thus have to make decisions on which offspring to feed, it is adaptive for parents to feed high-quality nestlings preferentially (Mock and Parker 1997). Consequently, nestlings may have evolved various traits to advertise their relative value. Nestlings could signal their quality by showing their vigor through begging behaviors, such as visual or auditive displays (Leonard and Horn 2001b). Skin or plumage coloration could also be used by parents as cues to assess offspring quality (Lyon et al. 1994; but see Tschirren et al. 2005) or need (Kilner 1997). Mouth flanges of begging nestlings in various passerine species reflect in the UV wavelengths and are likely to have an effect on the conspicuousness of the nestlings' gape to feeding parents (Hunt et al. 2003). UV reflectance of body skin (Bize et al. 2006) or feathers (Johnsen et al. 2003) may be related to nestling body condition. In many species, body condition is itself correlated with offspring survival (Nur 1984; Smith et al. 1989; Tinbergen and Boerlijst 1990). Furthermore, UV reflectance of skin can influence food allocation by parents (Jourdie et al. 2004; Bize et al. 2006). Hence, there is a possibility for UV reflectance to be an honest signal of quality also in young birds.

Feathers containing carotenoid pigments responsible for the yellow, orange, and red plumage colors were in a number of species found to present bimodal reflectance spectra with a secondary peak in the UV (MacDougall and Montgomerie 2003; Bleiweiss 2005; Shawkey and Hill 2005). In great tits, the UV peak is already present in the fledglings' yellow chest and cheek feathers (Richner H, personal observation). In the closely related blue tit, UV reflectance of yellow chest feathers is condition dependent in fledglings (Jacot and Kempenaers 2007). It could therefore be used for signaling individual quality to feeding parents. In both species, parental care extends

Address correspondence to M. Tanner. E-mail: marion.tanner@esh.unibe.ch.

Received 27 April 2007; revised 21 November 2007; accepted 21 November 2007.

for about 2 weeks beyond fledging (Gosler 1993), a period where mortality is high (Perrins 1965; Naef-Daenzer et al. 2001). Due to the difficulty of tracking birds during this highly mobile period (but see Sasvári 1990), little is known about parental food distribution and investment decisions during this period. The aim of the present experiment was to investigate the effect of UV reflectance on parental food allocation to great tit offspring at the fledging stage where the plumage is fully developed and visible to parents. For this purpose, we treated half of the young within a brood with UV-blocking chemicals, whereas the other half was used as a control, and then measured food provisioning rates by parents in an outdoor design where all offspring were simultaneously visible and directly facing the arriving parent. If UV reflectance carries information to feeding parents, we expected that the UV-blocking treatment would influence feeding frequencies and potentially also mass gain of young.

METHODS

The study was conducted in spring 2005 on a wild population of great tits breeding in nest-boxes in a forest near Bern, Switzerland, the "Könizbergwald." Nest-boxes were checked regularly from the beginning of April to determine precise laying and hatching dates. When nestlings were 6 days old, 2–5 μL of blood was taken from the metatarsal vein and kept in ethylenediaminetetraacetic acid for subsequent molecular sex determination. Nestlings were ringed with numbered aluminium rings (Station Ornithologique Suisse, Sempach, Switzerland) 9 days after hatching. Fledging in great tits takes place between the 19th and the 21st day after hatching (Gosler 1993). Therefore, our experiment was conducted on the 18th day after hatching. In 2 nests where nestlings were less developed, it was done on the 19th day after hatching. Between 7:40 AM and 8:50 AM in the morning of the experimental day, ready-to-fledge young ($n = 155$) in 25 different nests were weighed. Then in each nest, half of the fledglings ($n = 2$ –4, average: 3.1) were randomly assigned to either a treatment of UV blocking or a control treatment. In the UV-blocking treatment, chemical UV filters (Eusolex 2292 and 9020, Merck, Darmstadt, Germany) mixed with duck preen gland fat were carefully applied to the breast and cheek feathers of fledglings whereas in the control group the fledglings were treated with duck fat only. These chemical UV filters were chosen because they do not seem to induce harmful effect on human skin. It seems equally unlikely that the application of duck fat on feathers would have negative consequence on the birds. We tested the effect of our UV-blocking and control treatments on yellow breast feathers collected on twenty 15-day-old nestlings. For each nestling, we used 2 groups of 9 feathers pinned on top of each other to a small piece of black felt. One feather pile per nestling was treated with UV blockers, whereas the other one was control treated. As on live birds, we applied the substances with soft cotton buds. Light reflectance was measured using a newly calibrated USB4000 fiber-optic spectrometer with a DH-2000-BAL UV-NIR deuterium tungsten halogen light source (Ocean Optics, Inc., Dunedin, FL) and an FCR-7UV200-2-ME reflectance probe (Avantes, Inc., Eerbeek, The Netherlands). Using the program Avicol version 1 (Gomez 2006), we calculated the reflectance at the wavelength of maximum sensitivity (± 30 nm) of each of the 4 types of cone photoreceptors, as determined in a closely related species, the blue tit (Hart et al. 2000). In the UV range, the reflectance of UV-blocked feathers was significantly lower compared with control fledglings (Figure 1; $F_{1,19} = 43.5$, $P < 0.001$). In the visible range, the reflectance between treated and control feathers was not significantly different in the range of the peak sensitivities

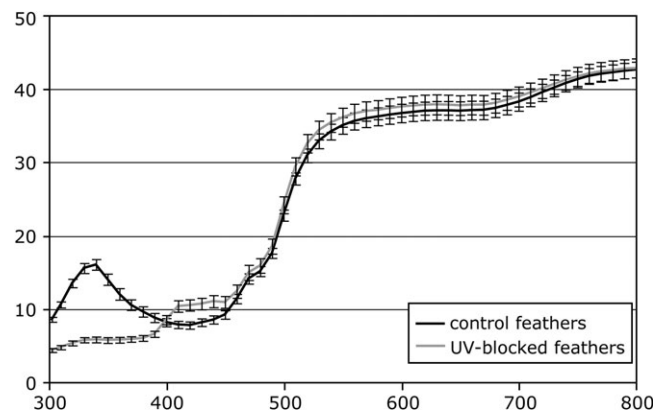


Figure 1

Reflectance spectra of yellow breast feathers of great tit nestlings ($n = 20$) when treated with UV blockers and control treated.

(± 30 nm) corresponding to the blue ($F_{1,19} = 2.6$, $P = 0.12$), green ($F_{1,19} = 0.74$, $P = 0.40$), and red ($F_{1,19} = 0.35$, $P = 0.56$) retinal receptors. We did not include untreated young in this experiment because they cannot be considered as a proper control for the UV-blocking treatment. After application, fledglings were kept separately in contiguous numbered small grid cages facing the arriving parents, hung on a tree nearby their nest-box. This set-up simulated a postfledging situation where parents feed young outside of the nest-box. The broods were left for about 4 h for parents to get accustomed to the set-up and then filmed for 2 h and 15 min. The fledglings were weighed again between 19:00 PM and 20:30 PM in the evening of the experimental day and brought back to their nest-box at dawn to reduce the risk of premature fledging. Video recordings were used to determine food distribution by the male and female parent among individual offspring, with the observer being blind with respect to the treatment applied to fledglings. Because great tits are single-prey loaders, and parents usually feed 1 single nestling at each feeding bout, the number of feeding visits to each nestling was used as a measure of food allocation. Parental sex was unambiguously determined using the sexually highly dimorphic size of the black breast stripe. Mass loss of individual fledglings was calculated as the difference in mass between the beginning and the end of the experiment. From about the age of 15 days until fledging, great tit nestlings in our population generally lose weight (Tanner M, personal observation), probably due to a decreased food provisioning by parents to induce fledging or an increased physical activity for strengthening wing muscles before flying (Gosler 1993).

Data were analyzed with general linear mixed-models using R version 2.0.1 (R Development Core Team 2004). Nest was included as a random factor in all models. In the analysis of food allocation, where average feeding rates for both the male and female parents were available for each fledgling, the identity of the fledgling was also included as a random factor, nested in the nest factor. Data were log or square root transformed where necessary to meet the assumptions of normality and homoscedasticity. Hatching date, brood size, and sex of nestling were included in the models as covariates. Nonsignificant covariates and interactions were backward eliminated. Body mass at the start of the experiment was not different between UV-blocked and control young ($F_{1,121} = 0.21$, $P = 0.64$). Male and female fledglings were not differently allocated to both treatments ($\chi^2 = 2.44$, degrees of freedom = 1, $P = 0.12$).

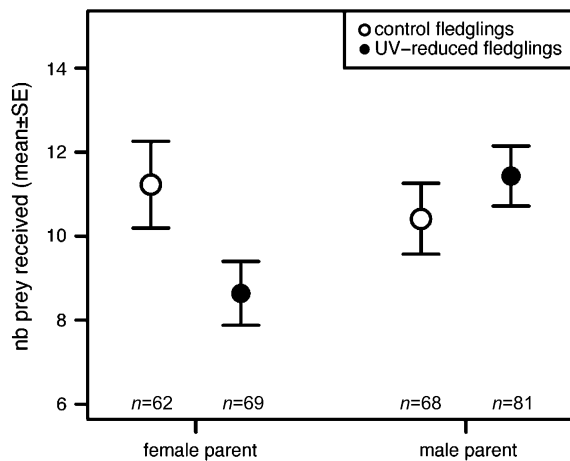


Figure 2
Number of feedings received from the male and female parents by UV-blocked and control fledglings in a period of 2 h and 15 min.

RESULTS

Food allocation by parents

The response of male and female parents to UV manipulation was different, as shown by the significant interaction effect between the sex of the feeding parent and the UV manipulation on the number of feeding visits received by a fledgling (Figure 2; interaction: $F_{1,126} = 5.4$, $P = 0.021$). Females fed control fledglings preferentially over UV-blocked fledglings ($F_{1,110} = 6.6$, $P = 0.012$), whereas males fed both types of fledglings at similar rates ($F_{1,125} = 1.29$, $P = 0.26$). Male and female fledglings were fed equally often ($F_{1,126} = 0.09$, $P = 0.75$) by both male and female parents (interaction sex of parent \times sex of young: $F_{1,125} = 1.55$, $P = 0.22$) and independently of their UV treatment (interaction sex of young \times UV treatment: $F_{1,125} = 0.41$, $P = 0.52$). The total number of visits to a fledgling did not depend on the treatment it received ($F_{1,121} = 1.13$, $P = 0.29$).

Mass loss of young

We found no difference in weight loss between UV-blocked and control fledglings ($F_{1,121} = 0.70$, $P = 0.41$). Mass loss was not different between male and female offspring ($F_{1,121} = 1.08$, $P = 0.30$) independently of their UV treatment (interaction sex of young \times UV treatment: $F_{1,120} = 0.33$, $P = 0.56$).

DISCUSSION

The postfledging period is critical in the life of birds, and little is known in general on postfledging parental care. In most passerines, young are still dependent on parental care for survival and it is also the period of high offspring mortality (Perins 1965). Parental allocation strategies that will match investment to the individual quality of nestlings will be favored by natural selection. This in turn will select for the evolution of nestling cues that can honestly reveal nestling quality. In most bird species, juvenile and adult plumage differ (Kilner 2006) and juvenile plumage is often void of conspicuous colors in the visible range (Jenni and Winkler 1994). Many tit species are an exception where young show similar carotenoid-based feather pigmentation as adult birds. This may indicate a signaling function that may even extend into the UV range. In our study, females responded to our UV-blocking treatment by decreasing the number of prey items delivered to these fledglings compared with control nestlings. In contrast, males did not seem to use experimental UV treatment for feeding decisions.

UV reflectance in nestlings is naturally variable, and our treatment may have led to nestlings at the extreme end of this variation. We thus need, like all other studies using UV blockers, to assume that the experimental phenotypes lay within the natural range of phenotypes. Under this assumption, our results suggest that the UV reflectance of nestling great tits' feathers has evolved due to a maternal preference for brighter offspring and support the hypothesis that UV reflectance of offspring plumage is a signal, although the precise content of the signal may be open to discussion.

Is UV reflectance of fledglings a signal of low quality ...

Differences in food allocation between mothers and fathers have been found in various bird species with biparental care. In a majority of studies, males seem to favor stronger and larger offspring (Bengtsson and Rydén 1983; Slagsvold et al. 1994) whereas females care for all offspring equally (Krebs et al. 1999) or feed lighter or weaker nestlings preferentially (Bengtsson and Rydén 1983; Gottlander 1987; Sasvári 1990; Slagsvold 1997; Kölliker et al. 1998; Krebs and Magrath 2000; Whittingham et al. 2003). Food allocation by males is mainly based on begging behavior influenced by short-term changes in hunger (Stamps et al. 1985; Sasvári 1990; Krebs and Magrath 2000; Whittingham et al. 2003). Even though offspring begging is related to need (Smith and Montgomerie 1991; Kilner and Johnstone 1997; Kölliker et al. 1998; Leonard and Horn 2001a; Sacchi et al. 2002), it could at the same time depend on competitive ability (Parker et al. 2002) and body size (Sasvári 1990; Sacchi et al. 2002), leading fathers to feed primarily the bigger nestlings. Females in contrast were hypothesized to adjust food provisioning based on more subtle cues when deciding which offspring to feed (Stamps et al. 1985). Such differences in food allocation could be explained through sex-linked trade-offs with other activities (Stamps et al. 1985) or through relatedness asymmetries due to extrapair copulations (Westneat and Sargent 1996), in which case parents would be in conflict over food distribution and possibly over brood reduction (Krebs and Magrath 2000). This would lead females to invest generally more in offspring than males and consequently also more in weaker nestlings (Slagsvold et al. 1995). The difference would be even more pronounced if extrapair young are more frequent among later hatched and thus often lighter nestlings (Gottlander 1987; Slagsvold 1997).

There is growing evidence that UV reflectance may interact with pigmentary coloration. UV reflectance is to a large extent due to the structure of the feather (Andersson 1999; Shawkey et al. 2003), and carotenoid pigments will partly cover this structure (Shawkey and Hill 2005) and thus potentially diminish overall UV reflectance (Andersson and Prager 2006). Lower pigmentation, which is usually taken as a signal of lower individual quality (Hill 1990, 1991; Hill and Montgomerie 1994; Hōrak et al. 2001), would then produce higher UV reflectance and rather lead to a negative correlation between UV reflectance and individual quality (but see Jacot and Kempenaers 2007). The female's preference for fledglings with higher UV reflectance might then lead to increased investment in nestlings with higher need for food.

... or a signal of high quality ...

On the other hand, UV reflectance is considered to be a signal of high quality in adult birds because it is used by females in mate choice in several bird species (Bennett et al. 1996; Andersson and Amundsen 1997; Bennett et al. 1997; Johnsen et al. 1998) and may also determine the level of maternal care to offspring (Limbourg et al. 2004) and influence the sex ratio (Sheldon et al. 1999) in blue tits. It is therefore assumed that

UV-reflecting structures are costly to produce (Shawkey et al. 2003), which could also be the case in young birds. Accordingly, the UV reflectance of yellow breast plumage of blue tit fledglings was reduced in increased broods (Jacot and Kempenaers 2007). Under this hypothesis, females biasing food allocation toward control fledglings would be interpreted as favoring high-quality offspring. Although there is no strong support for a preference for stronger offspring by females in the literature, sex-linked parental response to various signals used as cues in feeding decisions depends on species and may also vary with environmental conditions such as food availability (Boland et al. 1997; Krebs and Magrath 2000; Whittingham et al. 2003) or time in the season (Bize et al. 2006). A differential response to brood hunger, for example, was found in crimson rosella, *Platycercus elegans*, where females switched from favoring last-hatched chicks to feeding first-hatched chicks when the brood was food deprived, whereas males did not alter their feeding behavior (Krebs and Magrath 2000). In canaries, *Serinus canaria*, females attending food-deprived broods changed their perching location compared with control broods, thus favoring more competitive nestlings (Kilner 2002). It is therefore possible that the response of females to offspring characteristics would vary with environmental conditions and that under limited resources they might favor high-quality nestlings more than males.

... or of something else?

UV reflectance of young birds could alternatively signal their gender. For example, in blue tit nestlings there is a sexual dimorphism in UV coloration of tail feathers (Johnsen et al. 2003). Under the hypothesis that young of one sex are brighter, a female preference for UV-reflecting offspring would result in a higher provisioning of this gender. This hypothesis would require different trade-offs or constraints in male and female nestlings in order for the sex-specific difference in UV reflectance to evolve or be stable. Another alternative explanation for a preference of UV-reflecting offspring by females but not males is that offspring UV reflectance has evolved due to sensory exploitation based on a preexisting preference for UV-reflecting partners in their mother (Lyon et al. 1994). Due to a smaller variance in reproductive success and to a generally greater investment in reproduction, females of most species are predicted to be the more choosy sex (Johnstone et al. 1996). Thus, a preference for brighter plumage would be stronger (if not uniquely present) in females. Females might thus favor brighter offspring, even if UV reflectance does not reflect nestling state.

UV-blocked and control fledglings showed comparable mass loss. This is likely to be a consequence of the different behavioral responses of males and females to the manipulation of UV reflectance of their fledglings. Indeed, the total number of prey items received by both types of fledglings was not different, suggesting at least partial compensation by males for female preference. This compensation might be mediated through an increased begging of hungry UV-blocked fledglings (Smith and Montgomerie 1991; Kilner and Johnstone 1997; Kölliker et al. 1998; Leonard and Horn 2001a; Sacchi et al. 2002).

Our study suggests that the UV reflectance of chest and cheek feathers of fledgling great tits has a signaling function in parent-offspring communication, similar to the proposed function of skin UV reflectance (Jourdie et al. 2004; Bize et al. 2006). However, the precise message carried by the UV reflectance of plumage requires further investigation. Studies are needed to understand how the UV signal is produced, the costs associated with the emission of the signal, the trade-off between UV reflection and other signals, in particular with pigment-based plumage color, and the possible presence of

multiple signals within the same feather (Mays et al. 2004). Finally, it may be investigated whether females use the information of the UV signal to respond differentially depending whether the aim is to either reduce brood size under low food abundance or maintain brood size under conditions of higher food availability.

FUNDING

Swiss National Science Foundation (3100A0-102017 to H.R.).

We thank Karine Guichard, Thibault Grava, and Eric Champod for their help during fieldwork; Anne Berthouly and Katharina Gallizzi for interesting discussion; and Fabrice Helfenstein and Blandine Dorigez for precious comments on the manuscript. Elodie Gagliardi helped with video analyses. We are also grateful to Verena Saladin for molecular sexing of nestlings. Experiments were conducted under a license delivered by the Ethical Committee of the Office of Agriculture and Nature of the Canton of Bern, Switzerland.

REFERENCES

- Andersson S. 1999. Morphology of UV reflectance in a whistling-thrush: implications for the study of structural colour signalling in birds. *J Avian Biol.* 30:193–204.
- Andersson S, Amundsen T. 1997. Ultraviolet colour vision and ornamentation in bluethroats. *Proc R Soc Lond B Biol Sci.* 264:1587–1591.
- Andersson S, Örnborg J, Andersson M. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proc R Soc Lond B Biol Sci.* 265:445–450.
- Andersson S, Prager M. 2006. Quantifying colors. In: Hill GE, McGraw KJ, editors. *Bird coloration*. Vol. 1. Cambridge (MA): Harvard University Press. p. 41–89.
- Bengtsson H, Rydén O. 1983. Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit *Parus major*. *Behav Ecol Sociobiol.* 12:243–251.
- Bennett ATD, Cuthill IC, Partridge JC, Lunau K. 1997. Ultraviolet plumage colors predict mate preferences in starlings. *Proc Natl Acad Sci USA.* 94:8618–8621.
- Bennett ATD, Cuthill IC, Partridge JC, Maier EJ. 1996. Ultraviolet vision and mate choice in zebra finches. *Nature.* 380:433–435.
- Bize P, Piau R, Moureau B, Heeb P. 2006. A UV signal of offspring condition mediates context-dependent parental favouritism. *Proc R Soc Lond B Biol Sci.* 273:2063–2068.
- Bleiweiss R. 2005. Variation in ultraviolet reflectance by carotenoid-bearing feathers of tanagers (Thraupini: Emberizinae: Passeriformes). *Biol J Linn Soc.* 84:243–257.
- Boland CRJ, Heinsohn R, Cockburn A. 1997. Experimental manipulation of brood reduction and parental care in cooperatively breeding white-winged choughs. *J Anim Ecol.* 66:683–691.
- Cuthill IC. 2006. Color perception. In: Hill GE, McGraw KJ, editors. *Bird coloration*. Vol. 1. Cambridge (MA): Harvard University Press. p. 3–40.
- Doucet SM, Mennill DJ, Montgomerie R, Boag PT, Ratcliffe LM. 2005. Achromatic plumage reflectance predicts reproductive success in male black-capped chickadees. *Behav Ecol.* 16:218–222.
- Doucet SM, Shawkey MD, Hill GE, Montgomerie R. 2006. Iridescent plumage in satin bowerbirds: structure, mechanisms and nanostructural predictors of individual variation in colour. *J Exp Biol.* 209:380–390.
- Eaton MD, Lanyon SM. 2003. The ubiquity of avian ultraviolet plumage reflectance. *Proc R Soc Lond B Biol Sci.* 270:1721–1726.
- Gomez D. 2006. AVICOL. A program to analyse spectrometric data. Vol. 1.
- Gosler A. 1993. *The great tit*. London: Hamlyn Limited.
- Gottlander K. 1987. Parental feeding behaviour and sibling competition in the pied flycatcher *Ficedula hypoleuca*. *Ornis Scand.* 18: 269–276.
- Hart NS. 2001. The visual ecology of avian photoreceptors. *Prog Retin Eye Res.* 20:675–703.
- Hart NS, Partridge JC, Cuthill IC, Bennett ATD. 2000. Visual pigments, oil droplets, ocular media and cone photoreceptor

- distribution in two species of passerine bird: the blue tit (*Parus caeruleus* L.) and the blackbird (*Turdus merula* L.). *J Comp Physiol*. 186:375–387.
- Hausmann F, Arnold KE, Marshall NJ, Owens IPF. 2003. Ultraviolet signals in birds are special. *Proc R Soc Lond B Biol Sci*. 270:61–67.
- Hill GE. 1990. Female house finches prefer colorful males—sexual selection for a condition-dependent trait. *Anim Behav*. 40:563–572.
- Hill GE. 1991. Plumage coloration is a sexually selected indicator of male quality. *Nature*. 350:337–339.
- Hill GE, Montgomerie R. 1994. Plumage colour signals nutritional condition in the house finch. *Proc R Soc Lond B Biol Sci*. 258:47–52.
- Hörak P, Ots I, Vellau H, Spottiswoode C, Möller AP. 2001. Carotenoid-based plumage coloration reflects hemoparasite infection and local survival in breeding great tits. *Oecologia*. 126:166–173.
- Hunt S, Bennett ATD, Cuthill IC, Griffiths R. 1998. Blue tits are ultraviolet tits. *Proc R Soc Lond B Biol Sci*. 265:451–455.
- Hunt S, Kilner RM, Langmore NE, Bennett ATD. 2003. Conspicuous, ultraviolet-rich mouth colours in begging chicks. *Biol Lett*. 270:25–28.
- Jacot A, Kempnaers B. 2007. Effects of nestling condition on UV plumage traits in blue tits: an experimental approach. *Behav Ecol*. 18:34–40.
- Jenni L, Winkler R. 1994. Molt and ageing of European passerines. London: Academic Press.
- Johnsen A, Andersson S, Örnborg J, Lifjeld JT. 1998. Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (*Aves: Luscinia s. svecica*): a field experiment. *Proc R Soc Lond B Biol Sci*. 265:1313–1318.
- Johnsen A, Delhey K, Andersson S, Kempnaers B. 2003. Plumage colour in nestling blue tits: sexual dichromatism, condition dependence and genetic effects. *Proc R Soc Lond B Biol Sci*. 270:1263–1270.
- Johnstone RA, Reynolds JD, Deutsch JC. 1996. Mutual mate choice and sex differences in choosiness. *Evolution*. 50:1382–1391.
- Jourdie V, Moureau B, Bennett ATD, Heeb P. 2004. Ultraviolet reflectance by the skin of nestlings. *Nature*. 431:262.
- Kilner R. 1997. Mouth colour is a reliable signal of need in begging canary nestlings. *Proc Biol Sci*. 264:963–968.
- Kilner RM. 2002. Sex differences in canary (*Serinus canaria*) provisioning rules. *Behav Ecol Sociobiol*. 52:400–407.
- Kilner RM. 2006. Function and evolution of color in young birds. In: Hill GE, McGraw KJ, editors. *Bird coloration*. Vol. 2. Cambridge (MA): Harvard University Press. p. 201–232.
- Kilner RM, Johnstone RA. 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol Evol*. 12:11–15.
- Kölliker M, Richner H, Werner I, Heeb P. 1998. Begging signals and biparental care: nestling choice between parental feeding locations. *Anim Behav*. 55:215–222.
- Krebs EA, Cunningham RB, Donnelly CF. 1999. Complex patterns of food allocation in asynchronously hatching broods of crimson rosellas. *Anim Behav*. 57:753–763.
- Krebs EA, Magrath RD. 2000. Food allocation in crimson rosella broods: parents differ in their responses to chick hunger. *Anim Behav*. 59:739–751.
- Leonard ML, Horn AG. 2001a. Acoustic signalling of hunger and thermal state by nestling tree swallows. *Anim Behav*. 61:87–93.
- Leonard ML, Horn AG. 2001b. Begging calls and parental feeding decisions in tree swallows (*Tachycineta bicolor*). *Behav Ecol Sociobiol*. 49:170–175.
- Limbouurg T, Mateman AC, Andersson S, Lessells CM. 2004. Female blue tits adjust parental effort to manipulated male UV attractiveness. *Proc R Soc Lond B Biol Sci*. 271:1903–1908.
- Lyon B, Eadie J, Hamilton L. 1994. Parental choice selects for ornamental plumage in American coot chicks. *Nature*. 371:240–243.
- MacDougall AK, Montgomerie R. 2003. Assortative mating by carotenoid-based plumage colour: a quality indicator in American goldfinches, *Carduelis tristis*. *Naturwissenschaften*. 90:464–467.
- Mays HL, McGraw KJ, Ritchison G, Cooper S, Rush V, Parker RS. 2004. Sexual dichromatism in the yellow-breasted chat *Icteria virens*: spectrophotometric analysis and biochemical basis. *J Avian Biol*. 35:125–134.
- Mock DW, Parker GA. 1997. The evolution of sibling rivalry. Oxford: Oxford University Press.
- Naef-Daenzer B, Widmer F, Nuber M. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *J Anim Ecol*. 70:730–738.
- Nur N. 1984. The consequences of brood size for breeding blue tits. 2. Nestling weight, offspring survival and optimal brood size. *J Anim Ecol*. 53:497–517.
- Ödeen A, Håstad O. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Mol Biol Evol*. 20:855–861.
- Parker GA, Royle NJ, Hartley IR. 2002. Begging scrambles with unequal chicks: interactions between need and competitive ability. *Ecol Lett*. 5:206–215.
- Perrins CM. 1965. Population fluctuations and clutch-size in the great tit, *Parus major* L. *J Anim Ecol*. 34:601–647.
- R Development Core Team. 2004. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
- Sacchi R, Saino N, Galeotti P. 2002. Features of begging calls reveal general condition and need of food of barn swallow (*Hirundo rustica*) nestlings. *Behav Ecol*. 13:268–273.
- Sasvári L. 1990. Feeding response of mated and widowed bird parents to fledglings: an experimental study. *Ornis Scand*. 21:287–292.
- Shawkey MD, Estes AM, Siefferman LM, Hill GE. 2003. Nanostructure predicts intraspecific variation in ultraviolet-blue plumage colour. *Proc R Soc Lond B Biol Sci*. 270:1455–1460.
- Shawkey MD, Hill GE. 2005. Carotenoids need structural colours to shine. *Biol Lett*. 1:121–124.
- Sheldon BC, Andersson S, Griffith SC, Örnborg J, Sendecka J. 1999. Ultraviolet colour variation influences blue tit sex ratios. *Nature*. 402:874–877.
- Slagsvold T. 1997. Brood division in birds in relation to offspring size: sibling rivalry and parental control. *Anim Behav*. 54:1357–1368.
- Slagsvold T, Amundsen T, Dale S. 1994. Selection by sexual conflict for evenly spaced offspring in blue tits. *Nature*. 370:136–138.
- Slagsvold T, Amundsen T, Dale S. 1995. Costs and benefits of hatching asynchrony in blue tits *Parus caeruleus*. *J Anim Ecol*. 64:563–578.
- Smith HG, Kallander H, Nilsson JA. 1989. The trade-off between offspring number and quality in the great tit *Parus major*. *J Anim Ecol*. 58:383–401.
- Smith HG, Montgomerie R. 1991. Nestling American robins compete with siblings by begging. *Behav Ecol Sociobiol*. 29:307–312.
- Stamps J, Clark A, Arrowood P, Kus B. 1985. Parent-offspring conflict in budgerigars. *Behaviour*. 94:1–40.
- Tinbergen JM, Boerlijst MC. 1990. Nestling weight and survival in individual great tits (*Parus major*). *J Anim Ecol*. 59:1113–1127.
- Tschirren B, Fitze PS, Richner H. 2005. Carotenoid-based nestling colouration and parental favouritism in the great tit. *Oecologia*. 143:477–482.
- Westneat DF, Sargent RC. 1996. Sex and parenting: the effects of sexual conflict and parentage on parental strategies. *Trends Ecol Evol*. 11:87–91.
- Whittingham LA, Dunn PO, Clotfelter ED. 2003. Parental allocation of food to nestling tree swallows: the influence of nestling behaviour, sex and paternity. *Anim Behav*. 65:1203–1210.