

Original Article

Multimodal begging signals reflect independent indices of nestling condition in European starlings

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Parental food allocation decisions are based on information about nestling condition conveyed by begging signals. It is expected that parents should have evolved the ability to obtain detailed information about their nestlings' condition through multiple independent signals, thus allowing them to use optimal food allocation strategies depending on resource availability. In this study, we explore 1) which components of acoustic and visual begging signals produced by European starling nestlings (*Sturnus vulgaris*) vary independently from each other and consequently have evolved as separate signals and 2) whether these multimodal signals convey multiple or redundant information about nestling condition. We measured nestling stature and an estimate of lipid reserves, 2 independent indices of nestling phenotypic quality that have been suggested to be used in parental food allocation decisions. In multivariate analyses, we show that 1) acoustic and visual begging signals consist of several components that vary independently from each other and that 2) begging components correlated with nestling lipid reserves were different from those correlated with stature. Our results show that nestling begging signals include independent components in multimodal sensory channels that can provide parents with information about 2 independent indices of nestling condition that could be used by parents for flexible allocation strategies when facing changing environmental conditions. *Key words*: begging, independent indices, multimodal signals, parent–offspring conflict, signal redundancy. [*Behav Ecol*]

INTRODUCTION

Understanding the evolution of signals has attracted the attention of biologists because signals are implicated in communication among living organisms. A signal has been defined as an act or a structure produced by a signaler that evolved to alter the behavior of the receiver; in turn, the receiver response is also under selection from the signaler (Maynard-Smith and Harper 2003). Signals are expected to improve communication among individuals but are associated with production costs for signalers (Chappell and Bachman 2002; Moreno-Rueda 2010; Noguera et al. 2010) and acquisition costs for receivers (Iwasa and Pomiankowski 1994). Communication between individuals often involves multiple signals, elicited in one or more sensory modalities (Candolin 2003; Partan and Marler 2005). Recent theoretical work has been devoted to explain the evolution of multiple signaling in animal communication (Candolin 2003; Bro-Jørgensen 2010), aiming to understand what are the cost–benefit functions of the different components of the signals for the signalers and the different mechanisms associated with the receivers perception and responses (Partan and Marler 2005; Otovic and Partan 2009). Other studies on multiple signaling have examined whether environmental fluctuations lead to oscillations in selection pressures leading to differential expression of multiple signals (Chaine and Lyon 2008; Bro-Jørgensen 2010).

Several hypotheses have been advanced to explain the evolution of multiple signals (reviews by Candolin 2003; Otovic and Partan 2009; Bro-Jørgensen 2010). As regard to the information they convey, 2 main hypotheses can be considered. First, the “multiple message” hypothesis (MMH) predicts that multiple signals should be correlated with multiple independent messages about the signaler's condition, leading to information about different messages being potentially available for receivers (Johnstone 1996). Second, the “redundant signal” hypothesis (RSH, also referred in the literature as the “backup hypothesis”) assumes that some multiple redundant signals are correlated with the same message, thus reducing potential errors of information coding, transmission, or acquisition (Møller and Pomiankowski 1993; Johnstone 1996). Although these 2 hypotheses are generally considered as alternatives (Johnstone 1996), they are not always biologically exclusive, and a combination of both can be expected, as it has been recently suggested for information content in bird song (MacDougall-Shackleton et al. 2009; Rivera-Gutierrez et al. 2010). When multiple signals are expressed across different sensory pathways, they are defined as multimodal (Otovic and Partan 2009; Bro-Jørgensen 2010).

Nestling begging in altricial birds provides an unexplored framework for the study of multimodal signaling communication because offspring begging typically entails displays in the auditory/visual sensory pathways, such as skin and flange coloration, postures and repetitive calls (Kilner 2002). Trivers's (1974) theoretical work pointed out the evolutionary conflict of interest between parents and their offspring where the offspring optimum of parental investment is greater than parents are selected to provide (Godfray 1995; Parker et al. 2002). Theory predicts that parental food allocation decisions

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should be directed to offspring that maximize their fitness returns (Godfray 1991), thus requiring that parents obtain accurate information about nestling needs and condition (Clutton-Brock 1991). Multiple begging signals may therefore help to solve parent–offspring conflicts by supplying parents with accurate information about their offspring (Godfray 1991, 1995; Kilner and Johnstone 1997). Efficient information transmission will be particularly important in situations when receivers face time and energy constraints. In this case, multimodal signals should be particularly efficient by increasing signal detection thresholds or eliciting shorter reaction times (Otovcic and Partan 2009).

In the context of parent–offspring signaling, it is still unresolved whether multimodal acoustic and visual begging displays produced by nestlings should be considered as one globally redundant signal or have to be addressed as multiple independent signal components. It has recently been found that in barn swallows, *Hirundo rustica*, nestling mouth coloration included several independent components that could function and evolve as separate signals (Ayala et al. 2007). For heuristic reasons, in this study, we refer to “begging signals” as a communication complex, including visual displays such as skin and mouth coloration, acoustic displays such as the begging calls, and behavioral displays such as the nestling postures. We will use the term “components of begging signals” for statistically independent components forming the begging signals.

In passerines, nestling body condition can vary according to their “stature,” a measure of their overall size and weight resulting from their growth over an extended period of time (nestlings with high stature are larger and heavier than nestlings with low stature). Nestlings can also differ in their lipid reserves, which can vary over short time intervals (Ardia 2005). Nestling lipid reserves and stature have been found to vary independently from each other, thus representing 2 separate components of nestling condition (Ardia 2005; Bize et al. 2006). Theoretical models predict and empirical data suggests that parents should use information on independent components of nestling body condition to adopt flexible food allocation decisions in relation to ecological conditions they face (Davies et al. 1999; Bize et al. 2006). In these decision processes, it is expected that multiple signals improve parental information gathering (Otovcic and Partan 2009; Bro-Jørgensen 2010).

Here, we investigated 1) which components of nestling multimodal begging signals vary independently from each other and 2) whether separate components of begging signals convey multiple messages (the MMH) or redundant signals (the RSH) about nestling condition. First, we predicted that multimodal acoustic and visual begging signals should include several independent components, evolving separately from each other, as suggested by the results of Ayala et al. (2007). An alternative hypothesis would be that begging components are all redundant and not independent from each other. Second, we predicted that components of begging signals associated with a message on nestling lipid reserves should differ from those associated with a message of stature (Figure 1a), allowing parents to potentially obtain information about two independent indices of nestling condition. Moreover, we also expected that several components of begging signals, in different sensory modalities, should be associated with each of the 2 indices of nestling condition (Figure 1a), a redundancy expected to improve the reliability of information conveyed (Møller and Pomiankowski 1993; Johnstone 1996). Alternatively, if the components of multiple begging signals correlated with lipid reserves are the same of those correlated with nestling stature, all signal components are redundant, and parents would not have information available to discriminate between the 2 indices of

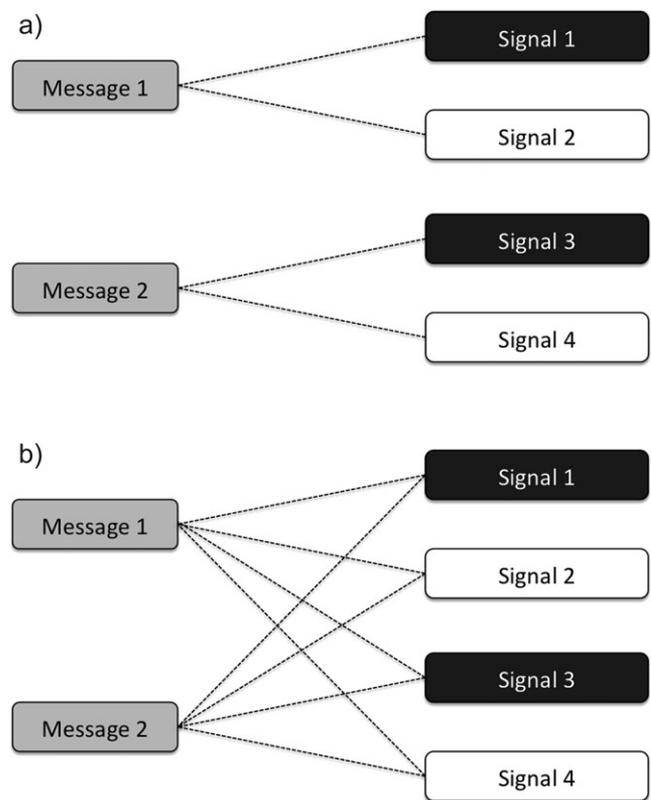


Figure 1

Scenarios associating begging signal components to 2 different messages of nestling condition. (a) An association between separate signal components and independent messages allows parents to discriminate between 2 indices of nestling body condition (as expected for the MMH). Some redundancy can be expected (e.g., 2 signal components correlated to the same message). (b) Alternatively, parents are not able to use different signals to discriminate between the 2 messages if signal components correlated with one index are the same from those correlated with the second (as expected for the RSH). Signals are produced in 2 sensory modalities (black or white).

nestling body condition (Figure 1b). Redundant multimodal signals could improve signal efficacy, for example, by alerting parents or by being more detectable, independently of their information content (Rowe 1999; Heeb et al. 2003; Otovcic and Partan 2009).

MATERIALS AND METHODS

Experimental design

The study was carried out on 58 nestlings 6 or 7 days after hatching from 29 broods in nest-boxes installed in the surroundings of the University of Lausanne, Switzerland. We retained for the analyses 43 nestlings from 29 broods for which all measurements were available. Nest-boxes were made of an internal wooden box with a thick and opaque plastic cover, and European starlings in this population breed twice a year (Loyau et al. 2005; Bize et al. 2006). At 2 days old, each nestling was marked by selectively removing a tuft of down feathers. When 6 or 7 days old, we ranked nestlings according to their mass within the brood (measured in the field with an electronic weigh scale to the nearest 0.1 g). For our study, we recorded begging signals of 2 nestlings from each brood, avoiding to record nestlings in extreme poor body condition (e.g., runts or emaciated nestlings that have low survival probability and reproductive value for their parents, Heeb 1994).

Nestlings were carried directly from the nest to the laboratory in a bag where temperature was kept constant (30 °C) using a hot water bottle. In each nest, we left 2 or 3 nestlings to avoid parental desertion (no desertion occurred in this study). Tarsus length was measured to the nearest 0.1 mm with vernier calipers. Nestlings were placed alone (to prevent the potential influence of nest mates on the begging behaviors of focal individuals) in artificial wood nest-boxes (10 × 10 × 20 cm) filled with cotton wool located in an experimental room. The temperature of the artificial nest-boxes was kept at 32–33 °C (Reid et al. 2002) using a Philips infrared light (PAR38 IR 100R).

Because nestlings beg only when they are hungry, we applied to all nestlings a standardized food deprivation of 3 h, a mean time interval that corresponds to the duration when nestlings are not fed during a spell of heavy rainfall (Heeb P, personal observation). After 3 h, skin and flange reflectance was measured (see procedure below), and each nestling was weighted again and replaced in the artificial nest-box for the parental provisioning simulation test. At 6–7 days old, starling nestlings are still blind and beg in response to any loud sound or physical contact. After placing the nestling in the nest-box, we waited between 2 and 3 min until the nestling ceased to beg in order to start the tests. We conducted tests that consisted in a standardized scratch sound obtained from separating a Velcro band followed by one soft rap on flanges using tweezers. Each nestling experienced 3 successive tests, each test lasted approximately 4 min (mean ± standard error [SE] = 3.93 ± 0.29) or until the young stopped begging completely. We recorded nestling behavior using a video camera placed 80 cm in front from each nestling. After the recordings, nestlings were fed ad libitum with grounded beef meat before being replaced into their nests within 4 h after removal. Our experiment did not negatively impact nestling condition, as their body mass was significantly greater when returned to the nest than before the experimental treatment (paired *t* test, *t* = -2.3, degrees of freedom [df] = 42, *P* = 0.027). Experiments were carried out under Swiss national regulations.

Reflectance measurements

Reflectance spectra of skin and flanges were measured using an USB2000 spectrometer with DH-2000 deuterium-halogen lamp and OOIBase32 software (Ocean Optics, Inc., Dunedin, FL). All measurements were carried out with the probe placed perpendicularly to a tangent to the surface, and reflectance data were expressed comparatively to a white standard disk (type WS; Labsphere, Congleton, United Kingdom). We measured skin reflectance at 6 body regions (near right wing insertion point, near femur insertion point, forehead, throat, breast, and belly). Flange reflectance was measured at the 4 corners of nestling flanges. Skin spectra showed only one reflectance peak located in the ultraviolet (UV) part of the spectrum (300–420 nm), whereas flange spectra showed 2 peaks, one in the UV part, the other in the visible part of the spectrum (420–700 nm). Reflectance data were highly correlated between the 6 skin regions and between the 4 flange corners (correlation coefficients *r* > 0.80 for all comparisons). Spectra were therefore summarized using Avicol-2 software (Gomez 2006) to obtain, for each nestling, mean spectra for flanges and for skin. In order to generate independent color variables containing the whole reflectance information, we summarized reflectance spectra using a principal component analysis (Cuthill et al. 1999; Ayala et al. 2007) with a bin size of 1 nm. Three principal components for the flange and 2 for the skin spectra were retained using scree plotting method to determine which components to retain (see RESULTS). A bootstrap analysis was con-

ducted on each principal component in order to assess the stability of the components (Montgomerie 2006). As all bootstrap scores were greater than 99%, we considered the 5 principal components as robust indicators of nestling skin and flange reflectance.

Video analyses

Video recordings were analyzed using Noldus The Observer XT software (Wageningen, Netherlands). For each parental provisioning simulation test, nestling maximum posture intensity was assessed based on the scale described by Leonard et al. (2003): 0 = head down, no gaping; 1 = head down, gaping, sitting on tarsi; 2 = head up, gaping, sitting on tarsi; 3 = 2, plus neck stretched upward; 4 = 3, but body lifted off tarsi; and 5 = 4, plus wing waving. We conducted our statistical analysis on the mean value of the 3 tests performed.

Acoustic analyses

Acoustic recordings were extracted from the complete video recordings at 44.1 kHz and 32 bits using iMovie software (iMovie 7.1.4, Apple Inc., Silicon Valley, Cupertino) and analyzed using Praat 4.2.05 (free online software, Netherlands, <http://www.praat.org>; Boncoraglio and Saino 2008; Levréro et al. 2009). Our nestlings emitted 2 different call types after stimulation: first, they started by producing complex begging calls and after a while produced simple calls. These simple calls were composed of one constant syllable (spectrographs very similar to those shown in Bulmer et al. 2008). Here, we only focused on the complex calls because it has been suggested that simple calls appear to play a role mostly in communication among nestlings and only indirectly to parent-offspring communication (respectively named “parent-present” and “parent-absent” begging, Bulmer et al. 2008; see also Roulin et al. 2000). We extracted from spectrographs and oscillographs of begging calls 1) the mean call number, 2) the mean total duration between first and last begging call, 3) the mean number of different (i.e., based on the number of syllables) calls, 4) the mean number of syllables per call, 5) the mean duration of each call, 6) the mean frequency at the maximum of intensity of each call (Hertz), and finally 7) the mean intensity of the call using the root-mean square (Gil et al. 2001; Levréro et al. 2009). Our measures of begging calls were made with a Sony Handycam DCR-TRV240E, Digital 8 video camera. These cameras employ automatic gain control that, if related to signal intensity, could have affected our measurements by compressing the bandwidth, thus reducing overall variance. However, an analysis showed that the intensity of background noise during the recordings was not correlated with begging call intensity (Pearson’s correlation, *t* = -0.134; df = 42; *P* = 0.89), suggesting that our measures of call intensity are reliable, enabling us to examine the variation in call intensity between nestlings. However, as reducing overall variance in this begging component could affect our results, we performed additional analyses without including call intensity in the models (see Statistical analyses). Because most of the 7 variables used to describe nestling begging calls are highly correlated (data not shown), we summarized them into the first 2 independent principal components from a principal component analysis, using scree plotting method to determine which components to retain (Table 1; Gil et al. 2001).

Statistical analyses

Nestling body condition was assessed using 2 indices following the methods described by Ardia (2005) and Bize et al. (2006). We computed nestling stature as the first principal

Table 1
Coefficients for the first 2 principal components on the characteristics of European starling nestling begging calls

	Call structure	Call intensity
Begging length	-0.899	0.200
Number of calls	-0.695	0.549
Number of different calls	-0.868	-0.284
Number of syllables per call	-0.886	-0.400
Call length	-0.816	-0.464
Frequency at the maximum intensity	-0.892	0.128
Intensity	-0.418	0.729

Variables included into Call structure or Call intensity are presented in bold.

component scores from a principal component analysis on tarsus length and body mass (after food deprivation). This first principal component explained 97.91% of the total variance of the original variables. Higher scores of the principal component indicated higher stature (loading factors: tarsus length = 0.989, body mass = 0.989). Nestling lipid reserves were assessed as the residuals of a linear regression of body mass (after food deprivation) on tarsus length (body mass = $-52.63 + 3.49 \times \text{tarsus length}$, $r^2 = 0.92$, $F_{1,41} = 458.9$, $P < 0.0001$; Ardia 2005). High scores indicated that nestlings have high lipid reserves. In accordance with Ardia (2005) and Bize et al. (2006), we found that the 2 indices of nestling condition were not significantly correlated (linear mixed model with nest as random factor, stature as dependent variable, and lipid reserves as fixed effect: estimate = -0.024 ± 0.047 , $t = -0.52$, $P = 0.61$).

To investigate the patterns of covariation between indices of nestling condition and behavioral and color begging signals, we performed linear mixed models using R software (version 2.11.1, R Development Core Team 2008). The dependent variables in each model were nestling lipid reserves or stature. Nest was included as random factor in order to take into account the nonindependence of nestlings from the same nest. We used components of begging signals (i.e., Call structure, Postural intensity, Flange Brightness, see below) as fixed

effects in the models. Moreover, age of nestlings, brood size, and breeding attempt (i.e., first or second breeding attempt) as well as the interactions between breeding attempt and all begging signals were included as fixed factors. We performed a backward selection procedure to eliminate variables based on their effects on nestling condition, allowing us to retain only the relevant variables in final models (Stephens et al. 2007). We also performed the same analyses on nestling lipid reserves and stature without including call intensity as fixed effect in the models because overall variance of this component could be reduced due to the recording equipment used (see above).

RESULTS

Principal components of reflectance and begging calls

We extracted 3 principal components from nestling flange reflectance, which together accounted for 97.84% of variance of the original spectra. The coefficients linking the first component (Flange PC1) to the original spectra were positive and greater than 0.69% (mean \pm SE = 0.83 ± 0.004 , Figure 2a) throughout the spectra, indicating that Flange PC1 stand for flange brightness variation ("Flange brightness"). The coefficients linking Flange PC2 to the original spectra were negative between 380 and 520 nm and positive between 520 and 700 nm (Figure 2a), indicating that Flange PC2 represented the amount of long wavelength (i.e., 520–700 nm) relatively to medium wavelength (i.e., 380–520 nm). This part of the spectrum is affected by carotenoid reflectance ("Flange carotenoid"). The coefficients from Flange PC3 were positive between 300 and 400 nm and negative between 400 and 700 nm, corresponding to the proportion of reflectance in the UV compared with medium and long wavelength (higher Flange PC3 scores indicating higher proportions of UV reflectance; "Flange UV").

From the 2 principal components, we extracted from skin spectra and which accounted for 99.11% of the original spectra, Skin PC1 also represented variations of skin brightness ("Skin brightness"). As the coefficients relating Skin PC2 to the original spectra were negative between 300 and 406 nm and positive between 407 and 700 nm, this component stands for the proportion of reflectance in the UV compared with

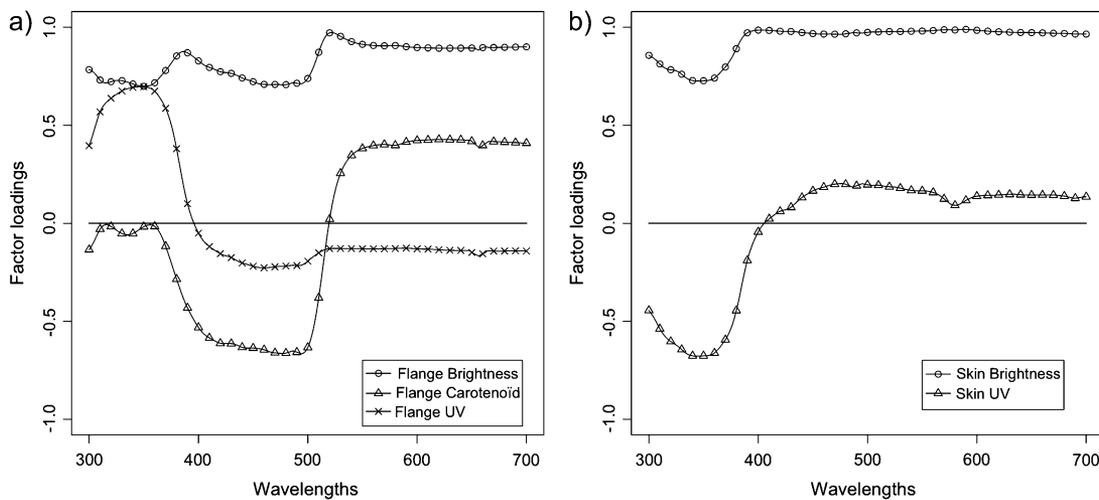


Figure 2

Coefficients of principal component analyses of nestling flange and skin reflectance spectra. (a) First 3 principal components of flange reflectance spectra, accounting for 69.08%, 18.90%, and 9.86% of the original spectra, respectively. (b) First 2 principal components on skin reflectance spectra accounting for 88.12% and 9.48% of the variance, respectively.

medium and long wavelength (lower Skin PC2 values matching higher proportions of UV reflectance; “Skin UV”).

From our principal component analysis on nestling begging calls, we extracted 2 principal components, which together accounted for 83.02% of the variation of the 7 original variables. The first component (Call PC1) accounted for 63.81% of the original variation in variables of begging calls and included the 6 first of 7 original variables of begging calls. Call_PC1 scores stand for changes in the structural part of begging calls (high scores are negatively associated with the 6 variables included, “Call structure”). The second component (Call PC2) accounted for 19.22% of the variation and stands for the intensity of begging calls with higher call_PC2 scores indicating higher intensity of begging calls (“Call intensity,” Table 1).

Nestling condition indices and components of begging signals

We found that higher nestling lipid reserves were predicted by lower values of Call structure, lower Postural intensity, and a greater Flange UV reflectance during begging (Table 2). Our analyses revealed that higher nestling stature was predicted by higher Call intensity, lower values of Postural intensity, and higher values of Flange “carotenoid” and Skin UV reflectance (Table 2).

When we performed the analysis on nestling lipid reserves without including Call intensity as factor, and we found that the same begging components predicted nestling lipid reserves (factors retained: Calls structure, Postural intensity, and Flange UV; Table 2). After removing call intensity from the analysis of nestling stature, the final model retained the flange reflectance associated with carotenoids and proportion of skin UV reflectance (factors retained: Flange carotenoid, estimate = 0.10 ± 0.02 , $t = 5.27$, $P = 0.0001$ and Skin UV, estimate = -0.18 ± 0.05 , $t = -3.67$, $P = 0.0022$), whereas postural intensity was dropped from the final model.

DISCUSSION

In this study, we found that begging signals produced in different sensory modalities by European starling nestlings contain several independent components, which could function as separate signals providing multiple messages to the parents. Our results provide support for both the MMH and the RSH as we found that multiple components of begging signals are associated with 2 independent indices of nestling condition (in accordance with the MMH) and that each index is correlated with several components of begging signals (in accordance with the RSH).

Table 2
Components of begging signals that predict nestling lipid reserves and stature

	df	Estimate	SE	<i>t</i> value	<i>P</i> value
Lipid reserves					
Call structure	1	0.669	0.215	3.112	0.0076**
Postural intensity	1	-1.118	0.306	-3.656	0.0026**
Flange UV	1	0.378	0.146	2.594	0.0212*
Stature					
Call intensity	1	0.400	0.112	3.269	0.0061**
Postural intensity	1	-0.321	0.115	-2.787	0.0154*
Flange “carotenoid”	1	0.114	0.017	6.542	<0.001***
Skin UV	1	-0.118	0.049	-2.407	0.0317*

Final models are shown; factors not retained in the model were nonsignificant. See MATERIAL AND METHODS for a description of the statistical procedures used to define the principal components. Significant effects are annotated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

We found that the proportion of long versus medium wavelength reflected by nestling flanges was independent from the proportion of UV wavelength reflected. As suggested by Ayala et al. (2007), and according to the shape of the reflectance curve (Figure 2a), the proportion of long versus medium wavelength represents variations of flange pigment-based coloration (i.e., carotenoids), whereas the proportion of UV wavelength represents flange structural coloration (Prum and Torres 2003; Ayala et al. 2007). Several studies have shown that nestling flange reflectance is a condition-dependent trait (e.g., Saino et al. 2003; Ayala et al. 2007; Dugas and Rosenthal 2010). Here, we found that nestling flange UV was correlated with lipid reserves, whereas flange carotenoid was correlated with nestling stature (Figure 3), a result that is consistent with the MMH. Ayala et al. (2007) found in Barn swallow nestlings that flange UV reflectance was used in parental allocation decisions, and results of Ewen et al. (2008) with the Hibi (*Notiomystis cincta*) suggested that parents used flange carotenoid to adaptively allocate food between their nestlings. In summary, flange UV and carotenoid reflectance are condition-dependent components of begging signals that vary independently and are used by parents in their allocation decisions in other species. As a result, they have the necessary properties to function as independent signals in parent–offspring communication. We also found that skin UV was correlated with nestling stature (Figure 3), a result in accordance with earlier results obtained in the same population (Bize et al. 2006). In European starling nestlings, skin UV reflectance is used by parents in their allocation decisions (Jourdie et al. 2004; Bize et al. 2006) and might therefore function as another independent signal in parent–offspring communication.

Our study also revealed that the structure and the intensity of nestling’s begging calls could be considered as 2 independent components of vocal begging signals. Nestling call structure was correlated with lipid reserves, whereas call intensity was correlated with stature (Figure 3), thus supporting the MMH. The association between call structure and nestling lipid

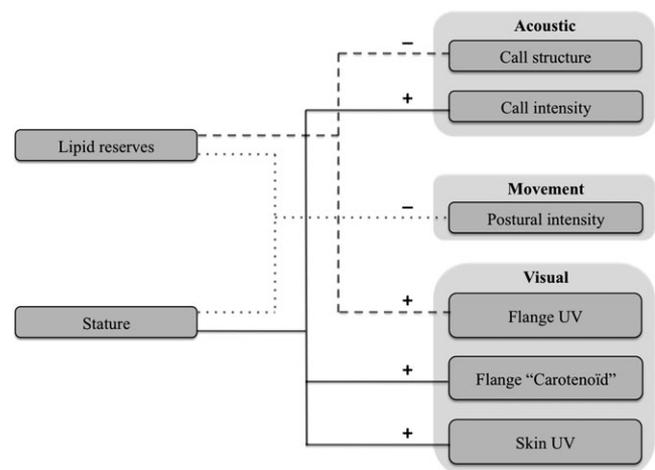


Figure 3
Components of begging signals associated with nestling lipid reserves and stature in European starling nestlings in this study. Dashed line indicates signal components associated with nestling lipid reserves. Solid line indicates signal components associated with nestling stature. Dotted line shows that begging postural intensity was associated with both measures of nestling condition. Signal components positively correlated to nestling condition are annotated by “+,” those negatively correlated are annotated “-” (see Table 2 for more details).

reserves appears to be strong and remains significant after call intensity is removed from the model, thus call structure could provide information on nestling lipid reserves. In contrast, the effect of postural intensity of nestling stature disappears when call intensity is removed from the model indicating that both factors covaried with nestling stature.

We showed that call structure and flange UV, begging components correlated with lipid reserves were different from call intensity, flange carotenoid, and skin UV reflectance correlated with nestling stature (Figure 3). In accordance with the MMH, these results suggest that parents could potentially use these multimodal components of begging signals to assess 2 independent indices of nestling condition. Moreover, our results also provide support for the RSH where the 2 indices of nestling condition are associated with redundant signals potentially increasing their probability to be accurately coded, transferred, and acquired (Møller and Pomiankowski 1993; Johnstone 1996; Partan and Marler 2005). As a consequence, parent starlings should be able to obtain reliable information about both nestling lipid reserves and stature, allowing them to adopt conditional allocation decisions (Bize et al. 2006).

Extrapair paternity and intraspecific parasitism have been described in European Starlings and in the closely related Spotless starlings, *Sturnus unicolor* (Feare 1984; Loyau et al. 2005; Garcia-Vigon et al. 2009). A decrease in genetic parentage within broods is likely to increase parent-offspring conflict, and parent starlings might use begging signals to modify their parental feeding decisions accordingly (Garcia-Vigon et al. 2009). In both Starling species, parents have been shown to use color-based begging signals in their food allocation decisions (Jourdie et al. 2004; Bize et al. 2006; Soler et al. 2007). Parental strategies may be affected by intersibling competition where increased nestling competition leads to an increase in begging intensity (Kacelnik et al. 1995). It remains to be determined whether begging competition among nestlings plays a role in the evolution of multimodal signals.

Here, we also showed that nestling postural intensity varied with stature and lipid reserves, 2 independent measures of offspring condition. An increase in postural intensity with nestling hunger level and stature has been previously reported in other species (Leonard and Horn 2001; Lotem 1998). Our result supports the “alerting signal” hypothesis in which postural intensity serves to improve signal efficacy by attracting parental attention in order to maximize information transfer efficiency (Rowe 1999; Otovic and Partan 2009). However, when call intensity was removed from our analyses, the effect of postural intensity on nestling stature was not significant anymore. Consequently, the separate information contents of calls and postural intensity require further investigation as they appear to covary.

To explain the evolution of multiple components of begging signals, the “manipulative begging” hypothesis has been proposed by Godfray (1995). Under this evolutionary scenario, components of begging signals evolve in order to manipulate parental allocation to obtain additional resources, where parents feed preferentially nestlings eliciting the most extravagant displays. However, this prediction is not always supported by experimental data, as it was recently shown that with deteriorating conditions, parent starlings, and Alpine swifts, *Apus melba*, preferred to feed nestlings with low signal intensities (Bize et al. 2006). The “honest signaling” hypothesis proposes an alternative where components of begging signals should have been selected by parents to honestly reflect nestling condition (Godfray 1991, 1995). A theoretical model by Davies et al. (1999) predicted that parental allocation decisions should vary according to the ecological context faced during reproduction. This prediction was empirically supported by the study on European starlings and Alpine swifts

(Bize et al. 2006). When facing good breeding conditions, parents had enough resources to raise nestlings, all offspring should be of high stature, and parents should allocate food according to the nestlings’ lipid reserves. Conversely, when resources become scarce, parents are unable to raise all their offspring and therefore should maximize the survival of high stature nestlings by preferentially feeding them (Davies et al. 1999; Bize et al. 2006). By conveying information about both these 2 indices of nestling condition, multimodal begging signals should therefore allow parents to make these flexible allocation decisions.

In conclusion, our study shows that nestling begging includes multiple independent components in different sensory systems that could potentially provide parents with information about 2 independent indices of nestling condition. Recent studies have suggested that other nestling characteristics such as sex (Saino et al. 2008), immune responses (Saino et al. 2003), or extrapair paternity (Boncoraglio and Saino 2008) are correlated with components of begging signals.

Here, we addressed the redundancy and independence of multiple and multimodal signaling components that can provide parents with information about separate nestling condition indices. Future studies should examine the mechanisms by which these multiple signals lead to responses by the parents. For example, an interaction between different signal components could be necessary for the emergence of the message (Partan and Marler 1999, 2005). Alternatively, the observed redundancy of multimodal begging signals would be necessary to increase the speed and efficiency of the providing parents (Otovic and Partan 2009). Thus, in order to understand the function of multiple signals given in multimodal functions, we need to address the receivers’ psychology (Guilford and Dawkins 1991) because nonredundant signals can have different effects on the receivers depending on the neural factors shaping multisensory integration (Otovic and Partan 2009). Multimodal signaling is efficient when transmitting across environments, and future research will benefit by examining the role played by different signaling components in changing environmental conditions (Bize et al. 2006; Bro-Jørgensen 2010). Future research will need to identify the nature of the fluctuations in ecological and social factors that favor the coevolution of multimodal signaling by nestlings and the associated parental strategies.

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