Tongue spots of dunnock nestlings vary in number and position over time but exert no clear influence on parental allocation

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Abstract – The nestlings of many bird species have ornaments in their mouths (e.g., tongue spots), yet the within-species variation of these ornaments remains poorly explored. Here, we described a subtle and intriguing pattern of variation in the tongue spots of dunnock (*Prunella modularis*) nestlings and further evaluated their potential influence on parental feeding allocation. We observed that tongue spots in nestling dunnocks decrease along with nestlings aging and that tongue spots correlate with body condition, but the effects of nestling's tongue spots on parental allocation were statistically unclear. This nature note invites further investigations into within-species variation of mouth marks in nestling birds, paving the way to a better understanding of these intriguing ornaments.

Keywords: bird ornaments, signalling theory, individual condition, behaviour

The nestlings of many bird species display a variety of ornaments in their mouths (Butler 1898, Ingram 1907, Ingram 1920). Naturally, one would predict that the ornamented nestlings' mouths would convey information to breeding parents. Indeed, parental feeding allocation, within a species, seems to be associated to variation in the colour of the nestlings' mouth, which has in turn been proposed as a signal of nestling's condition and need (Kilner 1997, de Ayala *et al.* 2007). However, the function of other mouth ornaments, such as mouth spots, still remains unclear.

Between species, nestlings' mouth spots can vary in size, colour, and shape, and can be found in the palate, tongue, and flanges. An explanation for the presence of mouth spots comes from studies on the diverse mouth patterns displayed by the nestlings of African Estrildid finches (Hauber & Kilner 2007). As some of these

Estrildid finches are subject to brood parasitism, their mouth spots are proposed to be a host response to discriminate among nestlings. Yet, other Estrildid finches are not subject to brood parasitism and still display mouth spots, and consequently, their presence is proposed to be a ‘ghost’ of evolutionary history. Within a species, variation in mouth spots has been less explored, but Schuetz (2005) removed mouth spots of nestlings in a population of common waxbills (*Estrilda astrild*) and found that individuals with spots removed were fed less than those with their spots intact. Thus, Schuetz’s study indicates that, in addition to mouth colour, mouth spots could also correlate with parental feeding allocation. However, if mouth spots predict parental feeding allocation within a species, they would have to signal the condition of chicks to breeding parents.

Signalling theory posits that parents rely on offspring signals to allocate food among their nestlings (Godfray 1991). Yet, two main types of signals occur in nestling birds. Signals of need usually typified by begging behaviour and signals of condition such as mouth colour. Particularly mouth color correlates with body mass (Kilner 1997, de Ayala *et al.* 2007), and in general, body mass has used as a proxy of condition (Tinbergen & Boerlijst 1990, Magrath 1991), whereby high body mass signals good condition. Nonetheless, it is important to stress that signals are the clues used by breeding parents, but underlying causes of parental decisions (e.g., parental biased favouritism, see Lessells 2002) encompass a mixture of the direct consequence of sexual–conflict (Dickens & Hartley 2007), parent–offspring conflict (Trivers 1974, Godfray 1995), and environmental quality (Davis *et al.* 1999, Caro *et al.* 2016). Therefore, to fully check the functionality of mouth spots as signals, it is important to account for the influence of these underlying causes.

While conducting a long-term study of sexual–conflict in a population of introduced dunnocks (*Prunella modularis*) to New Zealand (Santos *et al.* 2015), we observed that within a nest, nestlings can have different number of tongue spots (hereafter TS) (Fig. 1). TS are dark pigmented marks located on the tongue that contrast with the colour of the tongue and the palate. TS in dunnocks were first reported by Pycraft (1907) who observed 2-TS, and then by Ticehurst (1908) who observed that the third spot (at the top of the tongue) disappears after 4-5 days of hatching. To date, in dunnocks, the TS variation and their potential association to parental food allocation has not been assessed. Accordingly, in this study, our first aim is to describe the variation in the TS of dunnock nestlings and to examine if TS reflect the condition of the nestlings. Our secondary aim is to test whether TS predict parental provisioning while taking into account the social statuses that arise as a consequence of the dunnocks' sexual conflict.

Methods

Study population

For seven breeding seasons (September–January, 2009–2016), we monitored a population of dunnocks at the Dunedin Botanic Garden, New Zealand (45.856°S, 170.518°E, area 7.2 ha, ~80 resident breeders, also see Santos & Nakagawa 2013, Holtmann *et al.* 2017). We captured and colour-banded all the adults present within the study site. We then monitored the social breeding groups through both direct behavioural observations and nest surveillance. Following Davies (1992), we classified the breeding groups as monogamous pairs and polyandrous trios. Thus, the five social categories are referred throughout: monogamous males, monogamous females, polyandrous alpha males, polyandrous beta males, and polyandrous females.

Tongue spots and nestling body mass

During two breeding seasons (2014–2015 and 2015–2016), we collected a total of 734 observations of tong spots from 203 nestlings from 80 nests (2.43 nestlings per nest on average, SD = 0.87). We checked the nests nine times starting from the day that the first nestling hatched (day 0) and continuing the days 1, 3, 5, 6, 7, 8, 9, and 10 post-hatching. During each visit, we gently opened the beak of each nestling to check the number of TS and weighed the nestlings with a digital scale (to the nearest 0.01 g).

Parental feeding allocation

Of those 80 nests, we video recorded 55 with GoPro 3+ cameras to monitor adult feeding behaviour. We attempted to video record each nest for two hours daily from days 5 to 9 (see above). However, the actual number of hours filmed per day was lower than two hours, because of uncontrollable conditions (e.g., adverse weather). In total, we analysed 284.1 hours of effective footage (5.17 hours/nest, SD = 1.26), totalling 2,224 parental visits. Note that we defined the effective time per video as the time after the first visit occurred until the video ended (Nakagawa *et al.* 2007). For each visit, we recorded the breeder identity, the nestling being fed, and the number of feeds per nestling. To distinguish the nestlings within a nest, we marked their cheeks with markers (either 100-Black or R29-Red, Imagination Intl. We analysed the videos using the VLC media player version 2.1.1 (Free Software Foundation).

Statistical analyses

Tongue spots and body condition

We conducted all the statistical analyses in R version 3.6.1 (R Core Team 2019). To assess whether TS reflected nestling condition, we used a Bayesian Generalized Linear Mixed-Effects Model (BGLMM) with the binomial error distribution and with the *probit-link* function implemented in the *MCMCglmm* package (Hadfield, 2010). The number of TS was the binary response variable (2-TS and 3-TS). We included nestling weight (g) and nestling age (days) as fixed effects. These two covariates were z-transformed so that the regression coefficients were comparable (Schielzeth 2010). Nestling age included five time points (1, 3, 5, 6, and 7 days old) because after the seventh day post-hatching, all the nestlings had 2-TS. We included nestling identity and nest identity as random effects (the details of Bayesian priors and MCMC parameters are found in Supporting information). We reported the estimates of the regression coefficients as the mean of the posterior distribution along with 95% credible intervals (CI's) and considered the effects statistically significant if the CI did not overlap with zero. We used this statistical criterion in all instances.

Parental allocation and tongue spots

To evaluate whether nestling condition predicted paternal food allocation, we fitted two BGLMMs with the *Poisson* error distribution and with the *log-link* function, using *MCMCglmm*. The total number of feeds per visit per nestling was the response variable in all models. We separately analysed data from monogamous pairs and from polyandrous trios to avoid a triple interaction that is very complex to interpret (breeding group type×TS×individual status). Thus, we fitted two models including nestling TS as a fixed effect (one model for monogamous pairs, and one model for polyandrous trios). We included four additional fixed effects in all models: individual social status, brood size, effective time per video, and nestling age (day 5, 6, and 7), and three random effects, which were video identity, nestling identity, and feeder identity. We also included the interaction between TS and social categories to obtain the regression coefficients and credible intervals for each TS social category and a random slope for the TS of each nest.

Results

Tongue spots variation and body size

Dunnock nestlings' TS are blackish dots located in the tongue. Two TS are located at the base of the tongue and one is located on the tip (distal part) of the tongue (Fig. 1, Fig. 2). Nestlings mainly hatched with 3-TS (87.2% on day 1), but a small proportion of nestlings hatched with only 2-TS (12.8% on day 1). Nestlings that hatched with three TS lost their TS located on the tip of the tongue 3 to 6 days after hatching, and the two remaining TS (at the base of the tongue) did not disappear during the rest of the nesting period. The nestlings that hatched with two TS did not exhibit any change in spot numbers during the nestling phase as they retained both TS during the entire nesting period. Five days after hatching, the proportions of nestlings with 3-TS and 2-TS were similar (44.3% and 55.7%, respectively), and 6 days after hatching, most of the nestlings had only 2-TS (83.6%). After 7 days post-hatching, all the nestlings had only 2-TS (Fig. 2). The TS completely disappeared within a month after fledging; a time when the young start to care for themselves. We found that nestling weight was a positive and clear predictor of the TS change ($\beta_{[weight]}$ = 1.410, 95% CI = 0.883 to 1.950; Table S1) after controlling for the effect of age ($\beta_{[age]}$ = 1.116, 95% CI = 0.653 to 1.662; Table S1). In other words, lighter nestlings were more likely to have 3-TS compared to heavier nestlings that were most likely to have 2-TS (Fig. 3, Table S1).

Tongue spots and parental allocation

We found that males, from monogamous pairs, fed nestlings with 3-TS more often than nestlings with 2-TS. This effect was small but statistically clear ($\beta_{[monogamous\text{-}males]}$ = −0.312, 95% CIs = −0.616 to −0.020; Fig. 4, Table S2). Individuals from polyandrous trios, on the other hand, fed nestlings with 2-TS slightly more often than nestlings with 3-TS (Fig. 4, Table S3), but the differences among the three social categories were statistically unclear ($\beta_{[TS\ alpha\text{-}polyandrous\text{-}males]}$ = 0.078, 95% CI = −0.101 to 0.262; $\beta_{[TS\ beta\text{-}polyandrous\text{-}males]}$ = 0.011, 95% CI = −0.356 to 0.359; $\beta_{[TS\ polyandrous\text{-}females]}$ = 0.196, 95% CI = −0.012 to 0.245; Fig. 4, Table S3).

Discussion

We have described the variation of TS in a wild population of dunnocks and investigated their potential function for the first time by exploring whether parental allocation varied according to different numbers of TS. During the first part of the nestling period (ca. 64% of the nestlings' period), TS may reflect nestling condition as body mass predicted the number of tongue spots. Our results, however, indicated that dunnocks do not preferentially fed nestlings according to the TS.

TS are very conspicuous marks to breeding parents and could, therefore, provide parents with an easy guide for evaluating nestling condition, but parents do not seem to be doing so. The existence of TS, therefore, could be explained under alternative scenarios, but the most common ones may not apply to dunnocks. First, TS in dunnocks can be an old evolutionary trait no longer in use (a ‘ghost’ of the past, Hauber & Kilner 2007), but its functionality in the past is equally intriguing. We argue that TS may not be an old co-evolutionary response to brood parasitism, because nowadays dunnocks lack the initial mechanisms of defence against brood parasites such as foreign egg recognition (Davies 1992, Davies 2000). Second, it may also be that TS serve as a guide for feeding to breeding parents, but dunnocks are open cup nesters and experience good light conditions, thus TS do not appear to be an important trait to select for.

It could also be possible that TS are true signals of condition, but monogamous females and polyandrous individuals disregard the signal and fed their nestlings evenly. Such even feeding pattern can arise as a consequence of an environment in which food resources are not limited (Caro *et al.* 2016). In other words, parental preferences may not occur in environments of high abundance of food resources, and consequently, in our studied population all the individuals might have fed their nestlings under the same rules (i.e. evenly). Alternatively, the similar feeding patterns observed across polyandrous males (feeding even but less than monogamous males) might be a consequence of their uncertainty of paternity. (Burke *et al.* 1989, Santos *et al.* 2015). For instance, co-breeding males in polyandry may adjust (reducing) their feeding rates without prioritizing nestlings, as they do not want to prioritize a nestling that may not be biologically theirs

Finally, in dunnocks, as in other passerine birds, nestling begging has been shown as the main driver of parental feeding decisions (Muller & Smith 1978, Kilner

& Johnstone 1997, Godfray & Johnstone 2000). Indeed, video recordings of our dunnock population, collected over 7 years (data not shown here), suggested that nestlings that beg more receive also more food to those that does not beg. Thus, it is possible that such strong offspring-parent communication system via begging may have made the potential signalling function of TS redundant.

In conclusion, we have shown that, although subtle, the number of TS reflect the condition of nestling dunnocks, and that, overall, parental allocation does not seem to be influenced by TS. We also call for more within-species studies on nestling mouth spots to fully evaluate if they represent ornaments, which will ultimately help us to unveil the evolutionary reasons for the mouth marks existence and maintenance through time. Mouth marks are intriguing ornaments first noted over 120 years ago (Butler 1898), and since then they have and will continue to fascinate us.

Supporting Information

Table S1. Outputs from the Bayesian Generalized Linear Mixed Model that assesses whether nestling weight and age predicted tongue spots. Standardized regression coefficients (β) and variance components (σ_2) are reported with the 95% credible intervals. Values corrected and presented in *probit* (standard normal) scale. Statistically significant regression coefficients are in bold

Table S2. Outputs from the Bayesian Generalized Linear Mixed Model that assesses whether nestling tongue spots (TS) predicts parental allocation (number of feeds per nestling per visit) in monogamous pairs. Standardized regression coefficients (β) and variance components (σ_2) are reported with the 95% credible intervals. Values presented in *log-link* scale. Statistically significant regression coefficients are in bold

Table S3. Outputs from the Bayesian Generalized Linear Mixed Model that assesses whether nestling tongue spots (TS) predicts parental allocation (number of feeds per nestling per visit) in polyandrous trios. Standardized regression coefficients (β) and variance components (σ_2) are reported with the 95% credible intervals. Values presented in *log-link* scale. Statistically significant regression coefficients are in bold.

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Figure 1. Tongue spots in nestling dunnocks (*Prunella modularis*). (a) The tongue of a 2-day old nestling depicting 3-TS, two at the base of the tongue and one on the tip of the tongue. (b) The tongue of an 8-day old nestling depicting 2-TS at the base of the tongue. (c) An upper view of a nest with four nestlings showing one of them displaying tongue spots.

Figure 2. Illustration of tongue spot ontology in the nestling dunnock (*Prunella modularis*). Although subject to variation, the illustration represents the most common pattern of variation in the dunnock nestling tongue spots: nestlings can have up to three tongue spots from day 0 to day 5 and, invariably, two tongue spots from day 7. Note that most of the variation is concentrated in days 5 and 6, where either two or three dots can be present (see arrows in plate; original painting by G. Villada).

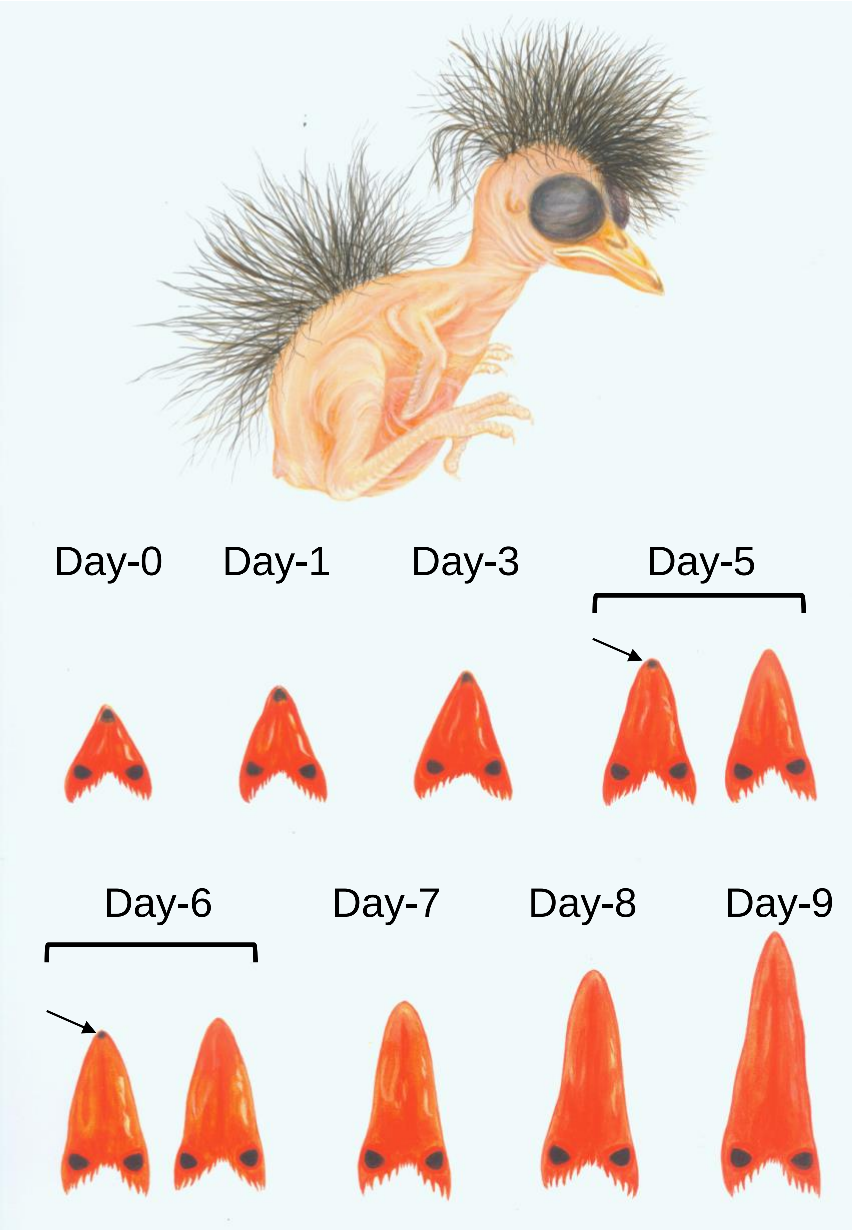


Figure 3. The dunnock nestling tongue, spots divided by nestling's age in days, plotted against the nestlings' weight (grams). Green boxplots are associated to 3-TS and blue boxplots are associated to 2-TS. Raw data points are horizontally jittered on the background.

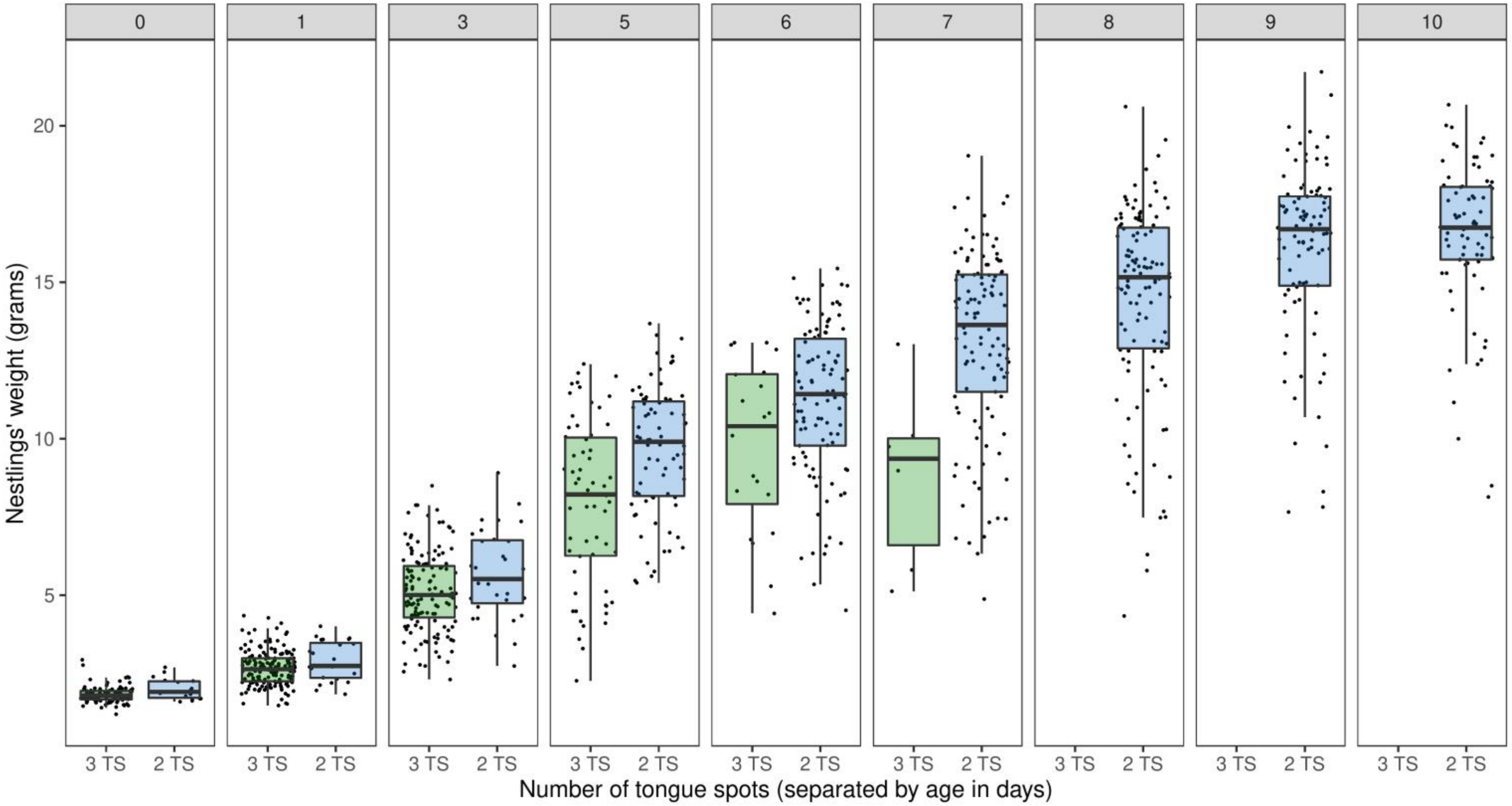
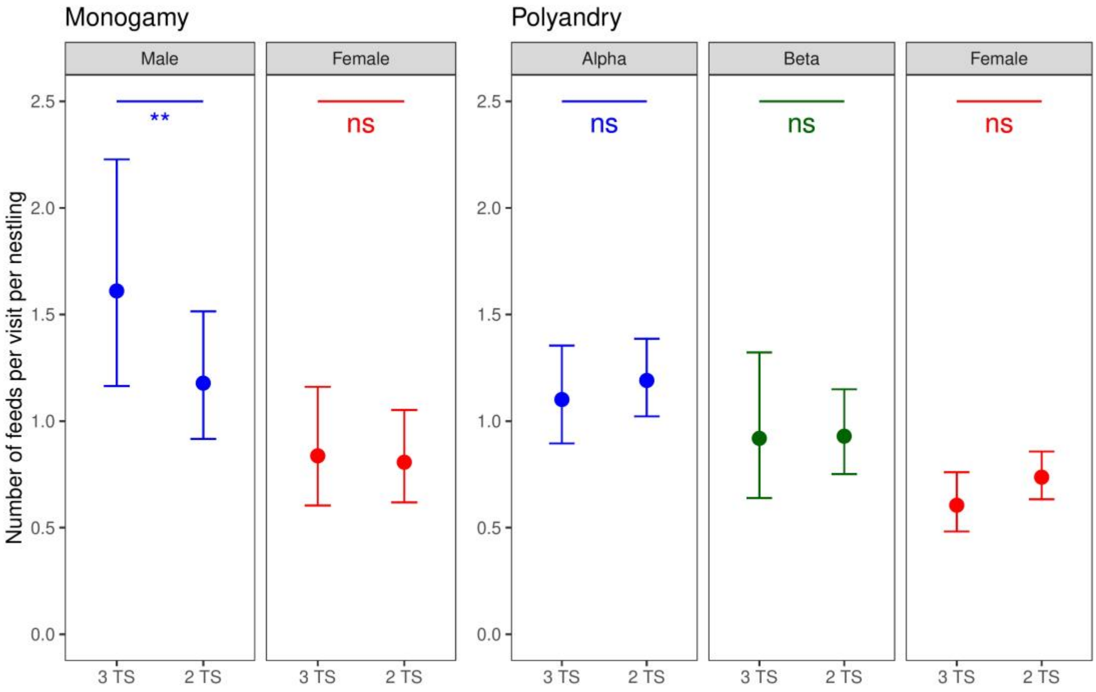


Figure 4. The number of feeds per visit per nestling in the social statuses evaluated over the two nestling stages (3-TS, 2-TS). The left panel depicts monogamous males (blue) and monogamous females (red), and the right panel contains polyandrous alpha males (blue), polyandrous beta males (green), and polyandrous females (green). ns = no significant. ** = α 0.01. The bars represent 95% credible intervals.



Supporting information

Settings for the Bayesian priors and MCMC parameters

For all the Bayesian Generalized Linear Mixed-Models (BGLMM), we used default priors for the fixed effects in MCMCglmm (Hadfield 2010). Also, to obtain at least 1,000 posterior samples, we ran each model for 6,500,000 MCMC iterations, with a burn-in period of 1,500,000 iterations, and a thinning interval of 5,000. Specifically for the BLMM that evaluated tongue spots and body condition, we fixed the unit variance or more precisely the over-dispersion parameter (*V = 1, fix = 1*) because *MCMCglmm* required a non-zero variance for the additive over-dispersion parameter for binomial BLMM (Nakagawa & Schielzeth, 2010); this fixed variance and the other parameter estimates were adjusted afterwards. For this model, we also used a parameter-expanded prior for each of the two random effects (*V = 1, nu = 1, alpha.mu = 0, alpha.V = 1,000*).

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Table S1. Outputs from the Bayesian Generalized Linear Mixed-Model (BGLMM) that assesses whether nestling weight and age predicted tongue spots. Standardized regression coefficients (β) and variance components (σ2) are reported with the 95% credible intervals. Values corrected and presented in *probit* (standard normal) scale. Statistically significant regression coefficients are in bold.

	Number of spots	
Fixed effects	β	95% Credible intervals
Intercept	**−0.229**	**−0.683 to −0.174**
Nestling weight (grams)	**1.410**	**0.883 to 1.950**
Nestling age (days)	**1.116**	**0.653 to 1.662**
Random effects	σ2	
Nestling identity	4.247	1.951 to 8.097
Nest identity	1.219	0.056 to 3.126

Table S2 Outputs from the Bayesian Generalized Linear Mixed-Model (BGLMM) that assesses whether nestling tongue spots (TS) predicts parental allocation (number of feeds per nestling per visit) in monogamous pairs. Standardized regression coefficients (β) and variance components (σ_2) are reported with the 95% credible intervals. Values presented in *log-link* scale. Statistically significant regression coefficients are in bold.

Monogamous pairs – Tongue spots	Number of feeds per nestling per visit	
Fixed effects	**β**	**95% Credible intervals**
Intercept (females, 3-TS)	−0.178	−0.479 to 0.152
TS (female’s difference, 2-TS vs. 3-TS)	−0.036	−0.332 to 0.265
TS (male’s difference, 2-TS vs. 3-TS)	**−0.312**	**−0.616 to −0.020**
Sex 3-TS (difference males vs. females at 3-TS)	**0.654**	**0.301 to 0.993**
Sex 2-TS (difference males vs. females at 2-TS)	**0.378**	**0.144 to 0.647**
Nestling age	0.052	−0.139 to 0.133
Brood size	**−0.226**	**−0.364 to −0.076**
Effective time per video	0.063	−0.026 to 0.140
TS × sex (males *vs*. females)	−0.276	−0.573 to 0.040
Random effects	**σ_2**	
Video identity	0.018	<0.001 to 0.048
Nestling identity	0.066	<0.001 to 0.145
Feeder identity	0.088	<0.001 to 0.199
Nest identity	0.054	<0.001 to 0.180
TS (slopes at the nest identity level)	0.051	<0.001 to 0.171
Additive over-dispersion	0.238	0.168 to 0.309

Table S3. Outputs from the Bayesian Generalized Linear Mixed-Model (BLMM) that assesses whether nestling tongue spots (TS) predicts parental allocation (number of feeds per nestling per visit) in polyandrous trios. Standardized regression coefficients (β) and variance components (σ_2) are reported with the 95% credible intervals. Values presented in *log-link* scale. Statistically significant regression coefficients are in bold.

Polyandrous trios – Tongue spots	Number of feeds per nestling per visit	
Fixed effects	**β**	**95% Credible intervals**
Intercept (females, 3TS)	0.096	−0.109 to 0.300
TS (alpha male’s difference, 2-TS vs.3-TS)	0.078	−0.101 to 0.262
TS (beta male’s difference, 2-TS vs. 3-TS)	0.011	−0.356 to 0.359
TS (female’s difference, 2-TS vs. 3-TS)	0.196	−0.012 to 0.245
Sex 3-TS AB (difference alpha males vs. beta males at 3-TS)	0.180	−0.198 to 0.535
Sex 2-TS AB (difference alpha males vs. beta males at 2-TS)	**0.248**	**0.049 to 0.459**
Sex 3-TS AF (difference alpha males vs. females at 3-TS)	0.598	−0.356 to 0.847
Sex 2-TS AF (difference alpha males vs. females at 2-TS)	**0.478**	**0.317 to 0.621**
Sex 3-TS BF (difference beta males vs. females at 3-TS)	**0.417**	**0.049 to 0.786**
Sex 2-TS BF (difference beta males vs. beta males at 2-TS)	**0.232**	**0.005 to 0.435**
Nestling age	−0.010	−0.068 to 0.042
Brood size	**−0.220**	**−0.329 to −0.111**
Effective time per video	0.059	−0.003 to 0.127
TS × social status (alpha males vs. females)	−0.067	−0.442 to 0.318
TS × social status (alpha males vs. beta males)	0.118	−0.108 to 0.373
TS × social status (beta males vs. females)	0.182	−0.167 to 0.583
Random effects	**σ_2**	
Video identity	0.004	<0.001 to 0.015
Nestling identity	0.053	<0.001 to 0.103
Feeder identity	0.024	<0.001 to 0.054
Nest identity	0.004	<0.001 to 0.124
TS (slopes at the nest identity level)	0.008	<0.001 to 0.035
Additive over-dispersion	0.249	0.186 to 0.315