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Social behaviour at the beginning of life: the role of quality signals and family size

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Social interactions facilitate information exchange for, among others, decision making and conflict resolution in animal societies. A central component of social interactions is the expression of signals of quality, and the role of signals can be expected to become more relevant in densely populated environments, in which social interactions are more frequent and the degree of conflict is probably stronger. We tested this hypothesis using the family context to explore whether a signal of quality expressed by the offspring modulates intrafamily interactions and whether it plays a more prominent role when the social density is increased. To this aim, we experimentally blocked a signalling trait, the ultraviolet (UV)/yellow reflectance of breast feathers and used brood size as a proxy of social density in a small passerine, the blue tit, *Cyanistes caeruleus*. We found that UV-blocked offspring were involved in fewer social interactions than control nestlings, suggesting that the expression of quality signals might affect the position within the family social network. Interestingly, this effect was independent of brood size. Moreover, we detected an overall preference to be in physical contact with nestmates of a different UV colour phenotype, which was stronger in small broods. Our results suggest that quality signals expressed by the offspring can influence the intrafamily social structure and that this effect is modulated by social density and, presumably, by the degree of conflict.

Social interactions are an essential feature of life in all animals. From birth to death, interactions with other individuals provide vital information that allows the modulation of decision making and determines, among others, the resolution of conflicts (Conradt & List, 2009; Arganda et al., 2012) and the occurrence of cooperation (Santos et al., 2008; Akçay, 2018). Interacting individuals constitute structured social networks (Whitehead, 2008), and the position and influence within such social networks are tightly linked to the access to resources and, ultimately, to fitness (Hamede et al., 2009; Silk et al., 2010; Royle et al., 2012; McFarland & Majolo, 2013; Nuñez et al., 2015; Lehmann et al., 2016; Turner et al., 2021; see Luo et al., 2017; Snyder-Mackler et al., 2020; Levy et al., 2021 in humans).

However, despite the benefits of being social, there is significant variation in the level of sociality within species (e.g. Mills & Faure, 2000; Cote & Clobert, 2007; Réale et al., 2007; Harcourt et al., 2009; Cote et al., 2012). This may be explained by ecological and social conditions shaping the cost–benefit balance of sociability and hence the structure of social networks. For instance, a high social density allows access to a greater amount of information (Oro, 2020) or a better defence against predators (Gilby et al., 2013; Goodwin & Podos, 2014; Grabowska-Zhang, et al., 2012). Yet, it may also increase the level of conflict in the form of aggression (Carere et al., 2001; Akçay et al., 2009; Geffroy et al., 2014), competition over resources (Stamps & Krishnan, 2001), social stress (Rowell, 1974; Verbeek et al., 1996), and it may lead to a higher susceptibility to contagious diseases (Barthélemy et al., 2005; Hamede et al., 2009; Drewe, 2010; Stroeymeyt et al., 2018).

Among-individual variation in sociability may thus reflect differences in individual quality. High-quality individuals might be better able to bear the costs of holding central positions and to enjoy the benefits of being connected with more individuals (e.g. Brent et al., 2013, 2017; Holekamp et al., 2012; Luo et al., 2017; McCowan et al., 2011; Sade et al., 1988). One way in which individuals can inform others about their quality is by expressing

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signals (Laidre & Johnstone, 2013, reviewed by Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005). The expression of signals of quality is hence likely to play a crucial role in the establishment of positions within a social network. In humans, there is evidence that physical attractiveness is used as a signal of quality when deciding who to mate with (see review by Gangestad and Scheyd, 2005), which also has implications outside the sexual selection context, as more attractive individuals have been found to be more influential and to occupy more central positions in social networks (e.g. Lott, 2008; O'Connor & Gladstone, 2018). In birds, two nonexperimental studies also reported a positive correlation between the expression of signals of quality and centrality (Toth & Griggio, 2011, in rock sparrows, *Petronia petronia*; Lantz, 2017, in red-backed fairywrens, *Malurus melanocephalus*). Yet, the potential relationship between signal expression and the position in a social network has been little explored experimentally.

It is, however, well known that signals of quality impact on social interactions, as is clearly exemplified in the context of assortative mating based on ornamentation (e.g. Mountjoy & Robertson, 1988; Hill, 1993; Amundsen et al., 1997; Andersson et al., 1998; Roulin, 1999; Jawor et al., 2003). Outside the sexual context, too, individuals tend to interact preferentially with conspecifics that are similar to themselves, which is usually referred as 'homophily' (Fu et al., 2012; Farine & Whitehead, 2015). Homophily has been suggested to facilitate the transmission of information (Centola, 2011) and the evolution of cooperation, as it may reduce quality differences within groups (Antal et al., 2009). Heterophily (i.e. a preference for the dissimilar) may also benefit high-quality individuals by improving their relative signal expression with respect to low-quality signallers that are next to them (Bateson & Healy, 2005). Still, the interplay of signals of quality with patterns of homophily or heterophily and with social network positions has rarely been addressed. Exploring this relationship would help us to understand how informative signals are used for the establishment of social groups.

Family life in species with parental care represents a suitable test case for studying the influence of signals on the structure of social networks. Family members are continuously interacting and expressing informative signals to adjust how the resources provided by parents are allocated (see Morales & Velando, 2013 for a review). Concretely, the offspring may constitute a social network (Royle et al., 2012), in which individuals exhibit begging behaviours and morphological features that signal quality. These signals have been found to play a role in parent–offspring interactions by affecting parental provisioning rates (e.g. Barrios-Miller & Siefferman, 2013; Griggio et al., 2009; Ligon & Hill, 2010; Lyon et al., 1994; Parejo et al., 2010; Romano et al., 2016), but also in competitive interactions among nestmates (e.g. Roulin et al., 2000; Bulmer et al., 2008; Dreiss et al., 2010; Ruppli et al., 2013; Jimeno & Gil, 2015). On the other hand, it has been suggested that the expression of signals by the offspring becomes more relevant with increasing brood or litter size, when the degree of conflict for parental resources is likely to be increased (see Morales et al., 2019, at the interspecific level). Nevertheless, within species, little is known about whether the expression of signals of quality determines the family network structure and whether this is influenced by family size.

This study aimed at testing the hypothesis that the expression of signals of quality by the offspring affects their position within the family social network (that is, the number and strength of interactions with other nestlings) and the tendency to associate with or separate from nestmates of a similar phenotype (i.e. homophily or heterophily) based on signal expression. For this purpose, we experimentally manipulated (1) the expression of a signal of quality in the offspring (i.e. ultraviolet (UV) reflectance of yellow breast feathers) and (2) family size, using the blue tit, *Cyanistes caeruleus*, as a model species. We predicted that nestlings signalling lower quality (i.e. with experimentally blocked plumage UV colour) would be less socially interactive and more likely to occupy peripheral positions within the nest. This difference should become more evident in enlarged families, where more social individuals have more opportunities to interact given the greater number of nestlings. Second, as our experimental manipulation created two distinct phenotypes (UV-blocked and, as a control, non-UV-blocked), we expected that chicks that received the same treatment would cluster together in the social network (homophily) if they compete for specific positions within the nest. Alternatively, we expected a pattern of heterophily if this, for example, increased the 'attractiveness' of high-quality chicks through comparative evaluation (Bateson & Healy, 2005). These patterns should be emphasized in experimentally enlarged broods where the degree of conflict for resources is expected to be higher.

METHODS

Study Population and General Procedures

The study was conducted during the spring of 2019, in the locality of Miraflores de la Sierra, Madrid, Spain (40° 48′N, 03° 47′W) in a wild blue tit population. This is a socially monogamous species with intense biparental care. Brood size is relatively large and variable (in our study population, on average ± SD 9.6 ± 1.8 eggs, $N = 464$ clutches, range 4–15; data from 2011, 2017–2019 and 2021). In this study, we considered the UV reflectance of yellow breast feathers as a signal of the nestling's quality. UV coloration of feathers and skin has been proven to function as a signal in other species (Jourdie et al., 2004; Bize et al., 2006) and in blue tit adults, at least in crown feathers (Sheldon et al., 1999). Blue tit nestlings develop UV-reflecting yellow breast feathers close to fledging (Jacot & Kempenaers, 2007; Morales & Velando, 2018). That UV coloration can function as a condition-dependent signal in blue tits has been shown experimentally by Jacot and Kempenaers (2007): nestlings reared in enlarged broods (with presumably suboptimal growth conditions and developmental stress) showed lower UV chroma than those reared in reduced broods. Also, previous results in the study population have shown that nestlings with experimentally blocked UV colour were treated as being of lower condition by their parents (Morales & Velando, 2018; García-Campa et al., 2021; see also Galván et al., 2008, in the closely related great tit, *Parus major*), and begged more to receive food from their parents, thus affecting parent–offspring interactions, as well as competitive interactions among nestmates in the absence of their parents (Morales & Velando, 2018).

In the study area, there are 180 nestboxes placed in a deciduous forest of Pyrenean oak, *Quercus pyrenaica*, at an elevation of 1250 m. Nestboxes were checked regularly to determine laying date, hatching date and clutch size. Hatching date (day 0) was established as the day when at least half of the clutch had hatched. From day 6, a trap was placed inside the nestbox at its entrance, and the first parent to arrive was ringed and marked with a white Edding 751 (code 049) marker pen (Edding, Ahrensburg, Germany) on the scapular region. On day 11, all nestlings were ringed, weighed and their tarsus length was measured. The colour of the yellow breast feathers was measured with a portable Jazz spectrophotometer (Ocean Optics, Orlando, FL, U.S.A.). After colour measurements, plumage UV colour was blocked in half of the nestlings of each brood while the other half remained unmanipulated (see Manipulation of nestling plumage colour below). Then, the first brood size manipulation was carried out, by exchanging nestlings between two broods with similar hatching date (± 1 day)

and brood size (± two nestlings). Thus, one nest was left with two more nestlings than it originally had and the other one was left with two fewer (see Manipulation of family size and Fig. 1). Within each dyad, it was randomly decided which nest was enlarged and which brood was reduced first. After brood size manipulation, the original nestbox was changed for a recording box with an open roof and a false camera on top, to familiarize parents with the set-up 1 day before the video recording started.

On day 12, we placed a night-vision video camera (wide-angle 8-LED IR DVR camcorder, DX, London, U.K.) on the nestbox and recorded the behaviour of all family members for 1.5 h, and always between 0930 and 1300 hours. The camera was placed approximately 10 cm from the nest. Just after the first video was recorded, a second reversing brood size manipulation was performed, in which, within a dyad of nests, the brood with the enlarged manipulation became reduced and vice versa (see Fig. 1). On day 13, a second video was recorded for 1.5 h. After the second video recording, all nestlings were returned to their original nests.

Manipulation of Nestling Plumage Colour

Prior to UV treatment, there were no differences in UV chroma between treatment groups (linear mixed model (LMM): 0.001 ± 0.001, $F_{1,332.96} = 0.36$, $P = 0.55$). UV chroma was calculated as the sum of reflectance in the UV range of wavelength divided by the sum of reflectance in the avian vision range of wavelength ($R_{320–400}/R_{320–700}$), adapted from Johnsen et al. (2003).

On day 11, coinciding with the peak of plumage development in nestling blue tits (Peters et al., 2007), one half of the nestlings of each brood were UV-blocked, where the UV reflectance of yellow breast feathers was reduced by applying an Edding 4500 (code 005) marker pen. This marker has been shown to reduce reflectance in the UV part of the spectra of blue tit and great tit feathers (Delhey et al., 2006; Galván et al., 2008; Johnsen et al., 2005; Morales & Velando, 2018). To avoid possible undesirable side-effects of the marker, in the other half of the brood that received the control treatment, the marker was applied on the interior surface of the flight feathers, where it was not visible while occupying an area similar to that of the yellow breast feathers. We aimed at mainly reducing UV reflectance (UV chroma) while maintaining yellow reflectance almost unmodified (see also Morales & Velando, 2018; see also García-Campa et al., 2022, where the same experimental manipulation was performed in adults). However, note that colour manipulations in general may create artificial phenotypes (see Delhey et al., 2014).

The first nestling that was handled was randomly assigned (using a random number generator) to one of the two treatments, and its nestmates were sequentially assigned to the other one. UV-blocked nestlings were marked with a white line on the left side of the head using an Edding 751 (code 049) marker pen, while control nestlings were marked with a white line on the right side. Observation of behaviour, however, was blind to treatment (see below).

Manipulation of Family Size

Each nest was subjected to two manipulations of its original family size: (1) enlarged brood size, with two nestlings added, and (2) reduced brood size, with two nestlings removed. The order of these manipulations on day 11 was assigned within nest dyads using a random number generator. On the following day, for each nest within a dyad the treatment was reversed (e.g. enlarged if the brood had been reduced on the previous day). Nestlings were exchanged between pairs of nests with similar natural brood size (± two nestlings) and hatching date (± 1 day). On day 11, the first family size manipulation started as follows (Fig. 1): in each dyad (for example, nests X and Y) the original nestlings from nest X were marked with white paint (the same used for the head) on the right scapular region and the ones from nest Y on the left one. Thus, it

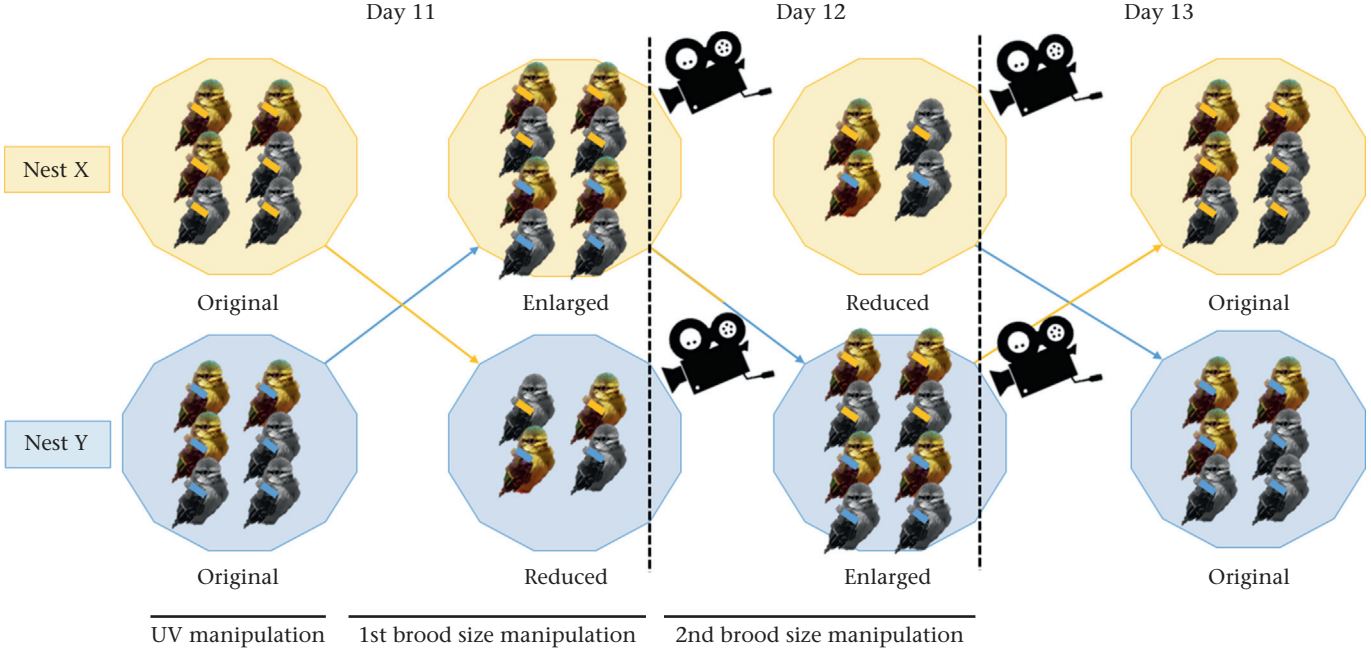

Figure 1. Scheme of the experimental procedure for a focal dyad of nests. Nestlings with grey breast colours depict chicks with blocked UV colour (on day 11) and those with yellow breast colour represent control chicks that did not receive a UV reduction treatment on the breast feathers. After UV colour manipulation, we performed the first brood size manipulation by exchanging chicks within nests. The colour of the wing stripe (yellow or blue) illustrates the nest of origin. On day 12, we performed the second reversal brood size manipulation. Nests were filmed on days 12 and 13 after each brood size manipulation. After the second video recording, we returned chicks to their original nests. In this example, both nests have an original brood size of six chicks.

was possible to ascertain the original nest of each nestling after the exchange. To increase the family size in nest X, four nestlings from nest Y were transferred to X and, simultaneously, two nestlings from X were transferred to Y. This exchange ensured that both nests received at least two chicks from a foreign nest. In each exchange, the same number of UV-blocked and control nestlings were transferred. On day 12, four nestlings were transferred from nest X to nest Y, two of them originally from nest Y and two from nest X, and ensuring a similar number of UV-blocked and control chicks. Thus, both nests again had at least two chicks from the foreign nest. After this second exchange, brood X was reduced by two nestlings and brood Y was enlarged by two ones. To maintain the offspring size hierarchy between nestlings, we exchanged nestlings from intermediate positions in the body mass hierarchy.

Behavioural Observations

Videos were analysed by an observer who had no prior knowledge about how white head marks of nestlings had been assigned according to UV treatment. For each video, the first 30 min and the last 10 min of recording were discarded to avoid possible side-effects of the presence of researchers when placing and removing the camera.

Then, behaviour was scored in 10 events between parental visits, that is, when no parent was present and the nestmates were, therefore, the only potential receivers of UV signals (hereafter, parent-absent events). We considered that a parent-absent event started as soon as all nestlings stayed quiet in their positions after the parents had left the nest (which on average occurred very fast: mean ± SE 2.80 ± 1.5 s), and as long as the parents were not back in less than 5 s. Events were closer in time in some nests than in others because of the variation in parental feeding rate, the mean interval between sample events (± SD) being 112 ± 150 s. Feeding events were avoided due to the usually intense vocal and postural begging behaviour of the nestlings in the presence of parents, which hampers the registration of individual positions. Nestlings change positions mainly during or right after feeding events (A. García-Antón, personal observation); thus, we did not sample more than one time point between parental visits. In some recordings (three of the 64 included in the analysis), it was not possible to observe 10 parent-absent events (range 5–10 observations per recording; average 9.9), because one or more nestlings were not visible in certain events. The video was paused at the beginning of each parent-absent event, after the parents had left the nest, and each nestling was assigned an individual number. We considered a social interaction as the direct physical contact between two nestlings. Although blue tit nestlings share a small nest cup and they are very close to each other, in most cases it is possible to establish which nestlings are in direct contact and which ones not (A. García-Antón, personal observation; see also Royle et al. (2012) in the closely related great tit). With this information, we created an $N \times N$ matrix where N is the number of individuals, and each cell indicates the existence of an interaction between two individuals (1) or the absence of interaction (0).

Social Network Analysis

We used UCINET (Borgatti et al., 2002) and R (R Core Team, 2020) to calculate the metrics of interest at the level of nodes (individual offspring level) and of the whole network (brood level; for more details of the calculation of these metrics, their correlation and their distribution, see the Glossary of network metrics, Table A1 and Figs. A1–A3 in the Appendix).

Node level metrics

We calculated node degree centrality and node average strength. Node degree centrality is defined as the number of edges connected to a specific node (Whitehead, 2008), that is, the number of interactions of a specific individual. This metric can be a good indicator of access to information (Newman, 2010). Node degree centrality was obtained for each individual and in each of the 10 observations.

Node average strength describes the importance or strength of contacts. For example, if an individual frequently changes its position and with whom it is interacting, the strength of interactions should be low. This is a weighted metric (i.e. it considers the strength of the edges, not only the number). Therefore, a weighted matrix was calculated as the average of all the interaction matrices (on average 10) obtained in each parent-absent event per nest and recording date. To do so, the values of all the specific cells within the matrices (corresponding to the interaction of a specific nestling with another nestmate in the network) were summed and divided by the total number of observations (generally 10). In the weighted matrix, values range from 0 to 1, with 0 meaning that two nestlings were never in contact and 1 that they always were. Node average strength was obtained by summing the values of all the edges connected to a specific node and dividing this value by the total number of edges. This variable was log-transformed to fulfil the assumption of normality in model residuals.

Network level metrics

At the network level, we calculated the network degree centrality, the network average strength and the UV assortment coefficient. Network degree centrality is the average of the degrees for all the nodes (the average number of interactions of all the individuals in the network). The average strength of the interactions was calculated by adding the values of all the edges in the network divided by the total number of edges. Since UV colour was manipulated within nests, we cannot explore the effect of UV treatment on network degree centrality and network average strength. However, these network level metrics were calculated to confirm that brood size manipulation by two chicks had an effect on the network structure.

Finally, the UV assortment coefficient was obtained to characterize the tendency of nestlings to associate (or not) with individuals similar to them (Whitehead, 2008), in our case, with similar UV treatment. It was obtained by using the ASSORTNET package (Farine, 2016) in R (R Core Team, 2020), which allowed us to use an algorithm that considers the strength of the interactions (i.e. it is derived from weighted matrices, such as strength).

Statistical Analyses and Sample Size

The statistical analyses were carried out in R (v 4.1.1, R Core Team, 2020). The lme4 package (Bates et al., 2015) was used to run generalized linear mixed models (GLMM) with Poisson distribution (log link function) for node degree centrality and linear mixed models (LMM) with normal distribution for the other variables (network degree centrality, node and network average strength and UV assortment coefficient). In the Poisson model, we checked for overdispersion of residuals following Bolker et al. (2017), which was not the case. Nest ID was included as a random factor in all the models. Nestling ID was included as an additional random factor in the analysis of node degree centrality, for which there were on average 10 values per individual, but not for node average strength (a weighted metric), for which there was one average value per nestling. For node level analyses, brood size manipulation (enlarged versus reduced brood size), UV treatment, the interaction between treatments, original brood size and

recording date were included as fixed factors. For the network level metrics, brood size manipulation, original brood size and recording date were included as fixed factors. Nonsignificant interactions were dropped from full models. The ANOVA table was obtained using the car package (Fox & Weisberg, 2019), applying a chi-square test for the GLMM model and *F* tests for the LMM models.

In total, 32 nests with two observations each (one during the reduced brood size manipulation and one during the enlarged one, that is, 64 networks in total) were included in the analyses. We could observe 559 individual nestlings (282 on the first day of recording: 183 in enlarged and 99 in reduced broods; 277 on the second day: 160 nestlings in enlarged and 117 in reduced).

Ethical Note

The study was conducted in compliance with the ASAB/ABS guidelines for the treatment of animals for research and with special consideration of the three Rs principles (Russell & Burch, 1959). All the methods were performed in compliance with the Spanish laws on animal research. The study and the experimental protocols were approved by the Spanish Research Council (CSIC, ref. 639/2017) and the Consejería de Medio Ambiente, Administración Local y Ordenación del Territorio, Comunidad de Madrid (ref. 10/056536.9/18; PROEX 237/17). We tried to complete each nestling manipulation in about 3 min to minimize the stress due to handling. It is likely that this causes some discomfort, but such short-term handling has no lasting effect, for example on survival to fledging (Sheldon et al., 2008). As we only needed our colour manipulation of the feathers to last 1 day, no additional products were added (see also Johnsen et al., 2005; Morales & Velando, 2018). Nestlings were swapped among nests with similar laying dates and clutch sizes to avoid size asymmetries that could affect their likelihood of obtaining food. Video-recordings inside the nest have no apparent effect on the behaviour or reproductive performance; blue tit parents in fact resume offspring feeding normally in less than 10 min (A. García-Antón, J. García-Campa & J. Morales, personal observation). It is unlikely that our treatment affected the mortality of the nestlings, as there were only two dead chicks during the experiment.

RESULTS

Node Level Metrics

The interaction between brood size manipulation and UV treatment had no significant effect on node degree centrality (Table A2) and was dropped from the final model. However, both treatments alone did have a significant effect. Node degree centrality was smaller in reduced broods (Table 1, Fig. 2), as expected in less complex networks with fewer possible nodes. Moreover, UV-blocked nestlings had lower node degree centrality, that is, they held more peripheral positions, than control nestlings (Table 1, Fig. 2), independently of brood size manipulation. Node degree centrality was not significantly affected by recording date (Table 1). However, the larger the original brood size, the higher the node degree centrality (Table 1).

Node average strength was not affected by the interaction between treatments (Table A2, Fig. 3). However, it was affected by brood size manipulation (Table 1, Fig. 3) and by the original brood size (Table 1). Node average strength was higher in reduced broods and when the original family size was smaller (Table 1), which implies that nestlings interacted more often with the same nestmates in smaller broods.

Network Level Metrics

Brood size manipulation had a significant effect on all the network level metrics (Table 2). In reduced broods, network degree centrality was lower (Table 2), while network average strength was higher (Table 2). This implies that, in reduced broods, the number of interactions in the network is lower but that they are stronger than in enlarged broods, that is, the same interactions happened more often among the same individuals. The original brood size was positively related with network degree centrality and negatively with network average strength (Table 2).

Most of the nests showed a negative value for the UV assortment coefficient (mean ± SE = −0.12 ± 0.02; 53 of 64 nests). Also, brood size had a significant effect on this variable: the coefficient was less negative in enlarged broods than in reduced ones (Table 2, Fig. 4). This means that, in reduced broods, chicks had stronger interactions with nestlings of the opposite UV treatment.

DISCUSSION

In this experimental field study, we tested whether the manipulation of UV/yellow breast feathers of blue tit nestlings affected their social network position, and how this was modulated by social density. We found that control chicks (which we expected to be perceived by nestmates to be in better condition) had more contacts with other nestlings and held slightly more central positions in the brood network. Moreover, the UV assortment coefficient was influenced by the brood size manipulation. In reduced broods, chicks interacted more strongly with nestmates of a different UV treatment.

Effect of UV Colour Manipulation on Nestling Sociability

As we predicted, we found a significant effect of UV colour treatment on nestlings' sociability (i.e. degree centrality). This result suggests that the expression of signals of quality by offspring influences the position within the social network. However, note that the overall variation in this metric was relatively high, also when compared to the magnitude of the effect of UV treatment. Nevertheless, we can speculate about some possible explanations

Table 1
Effects of brood size manipulation and UV colour treatment on node degree centrality (GLMM) and node average strength (LMM).

	Node degree centrality			Node average strength		
	Estimate (SE)	χ^2	*P*	Estimate (SE)	$F_{(df)}$	*P*
Intercept	1.01 (0.14)	–	–	0.13 (0.28)	–	–
Brood size manipulation	0.19 (0.021)	80.38	**<0.001**	−0.05 (0.02)	$9.40_{(1,\ 525.40)}$	**0.002**
UV treatment	−0.04 (0.02)	4.45	**0.035**	−0.02 (0.02)	$1.29_{(1,\ 526.26)}$	0.26
Date	−0.001 (0.002)	0.34	0.56	−0.009 (0.005)	$3.93_{(1,\ 34.36)}$	0.055
Original brood size	0.029 (0.007)	17.74	**<0.001**	−0.03 (0.01)	$5.97_{(1,\ 28.74)}$	**0.021**

The effects of date and original brood size were controlled for. The nonsignificant interaction between treatments was dropped from the model. Significant *P* values are shown in bold. See Table A1 for the initial mixed full model.

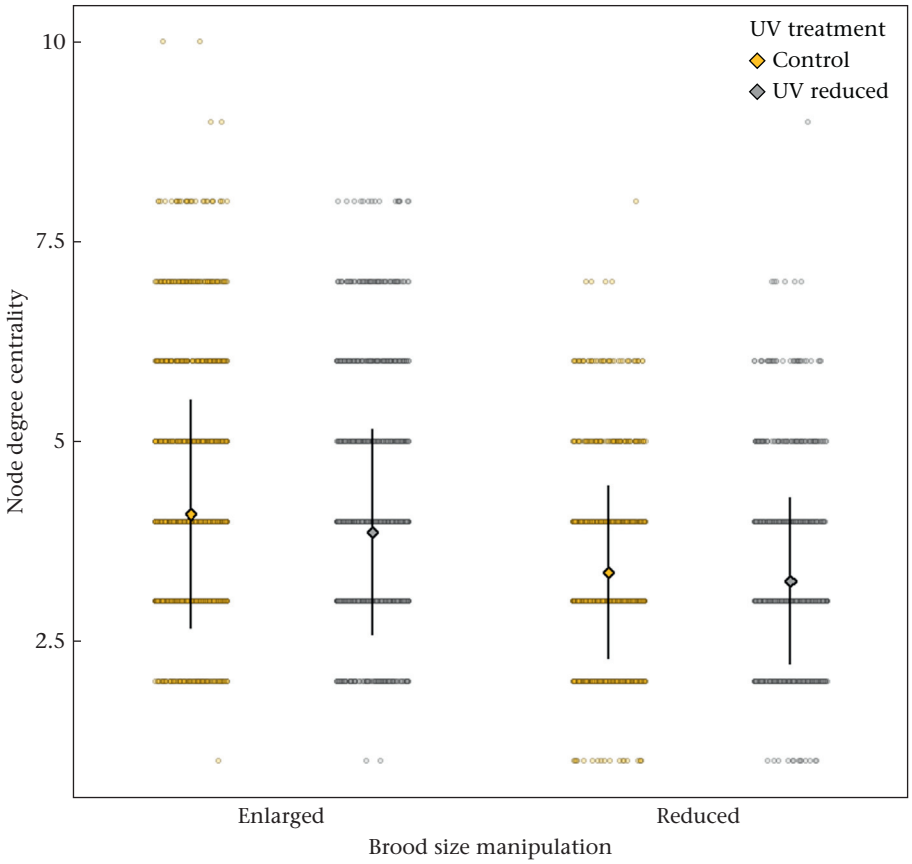

Figure 2. Node degree centrality in relation to UV colour and brood size treatments. The diamonds indicate the mean and the black lines the standard deviation. Data points are also plotted.

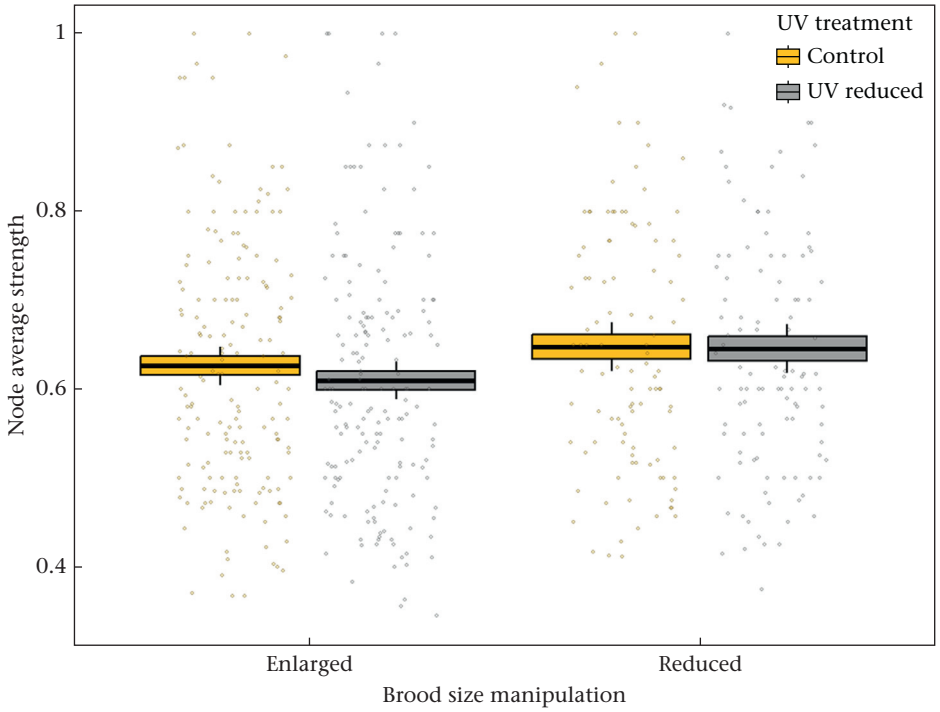

Figure 3. Node average strength in relation to UV colour and brood size treatments. The black line indicates the mean value, the limits of the box the standard error and the whiskers the 95% confidence interval. Data points are also plotted.

Table 2
Effect of brood size manipulation on network metrics.

	Network degree centrality			Network average strength			UV assortment coefficient		
	Estimate (SE)	$F_{(df)}$	*P*	Estimate (SE)	$F_{(df)}$	*P*	Estimate (SE)	$F_{(df)}$	*P*
Intercept	2.32 (0.46)	–	–	1.08 (0.17)	–	–	−0.44 (0.23)	–	–
Brood size manipulation	0.75 (0.05)	$204.10_{(1, 30.963)}$	**<0.001**	−0.05 (0.02)	$4.38_{(1, 30.976)}$	**0.045**	0.10 (0.03)	$8.36_{(1, 30.976)}$	**0.007**
Date	−0.006 (0.008)	$0.52_{(1, 30.261)}$	0.48	−0.004 (0.003)	$1.87_{(1, 29.805)}$	0.18	0.002 (0.004)	$0.27_{(1, 29.805)}$	0.61
Original brood size	0.13 (0.02)	$34.01_{(1, 29.005)}$	**<0.001**	−0.03 (0.01)	$9.17_{(1, 29.003)}$	**0.005**	0.02 (0.01)	$2.77_{(1, 29.003)}$	0.11

The effects of date and original brood size were controlled for. Coefficients are shown for enlarged broods. Significant *P* values are shown in bold.

for this pattern. A more central network position is likely to be correlated with a central position in the nest cup (as would be expected from being in contact with more nestmates), which could be at the core of the parents' attention (McRae et al., 1993). In blue tits, each parent usually feeds the nestlings from the same location on the nest rim, and usually this location does not overlap with that of the other parent (Dickens & Hartley, 2007). From the offspring's perspective, it is thus possible that holding a more central position in the nest cup means either being more reachable from both parents' locations or being more able to compete for the parent's attention (Ostreiher, 2001). Still, central positions are expected to be costlier to keep, both in the context of the number of interactions (Webber & Vander Wal, 2018) and in the physical position within the nest (i.e. the centre of the nest cup; Ostreiher, 2001). Our manipulation has been proven to cause UV-blocked chicks to gain less body mass (Morales & Velando, 2018); thus, this could explain why chicks that signal high quality are better at holding these positions than their nestmates. On the other hand, our network metrics are based on proximity and do not measure information exchange, so we cannot discount the possibility that reduced UV colour itself leads to lower parental provisioning and thus to within-brood variation in hunger level, which may subsequently affect the nestlings' position in the nest cup. In this case, UV colour would affect social position, although indirectly through parental feeding rates. In addition, it could be that having more interactions within the brood network allows nestlings to obtain greater access to information, as suggested for other types of social networks (Aplin et al., 2012). In a nest, the main impediments to the reception of informative signals are transmission noise and interference from nestmates (Horn & Leonard, 2002). Therefore, one might speculate that being closer to more nestmates may improve signal efficacy of the vocal and postural displays that nestlings use to contest the next prey item to be delivered (Roulin et al., 2000). However, social centrality likely implies a more central position within the nest cup, and with the current data we cannot differentiate between spatial and social network effects. Future studies should take that into account by measuring both the spatial and social positions of the nestlings, and how they relate to the above-mentioned benefits.

Finally, there was no difference in the node average strength of interactions between UV-blocked and control nestlings. This implies that UV does not influence how often individuals change their position within the nest cup.

Our hypotheses are supported under the assumption that yellow/UV colour functions as a signal of quality, but it has also been proposed that carotenoid-based coloration plays a role in crypsis, with highly coloured individuals being more cryptic (Delhey et al., 2010). This does not, however, rule out a role for coloration in intrafamily interactions, as suggested by previous experimental studies (Morales & Velando, 2018; García-Campa et al., 2021). Besides, although UV manipulation mainly reduced UV reflectance within the natural range of variation, we cannot discount the possibility that we created an artificial phenotype that is perceived differently from natural colour (Delhey et al., 2014). However, we do not expect a major effect of these deviations on the behaviour of the blue tits, given that cavity-nesting passerines are better at detecting changes in UV-reflectance than in visible reflectance (Avilés et al., 2006; Hunt et al., 2003; Wiebe & Slagsvold, 2009). Further studies are needed to analyse with visual models how such manipulations are perceived within the darkness of a nestbox.

Preference for Nestmates with Dissimilar UV Coloration

Nestlings showed a general preference to be in contact with nestmates with a different UV treatment (i.e. heterophily), as indicated by the negative values in the UV assortment coefficient, which contrast with the pattern of homophily observed in certain animal networks outside the family context (e.g. Krause et al., 1996; Croft et al., 2009; Aplin et al., 2013; Massen & Koski, 2014). On the one hand, control chicks signalling (on average) higher quality may try to remain close to UV-blocked nestlings so that they are more easily spotted by parents inside the nest (i.e. 'comparative evaluation'; see Bateson & Healy, 2005). On the other hand, one may speculate that UV-blocked chicks may try to be close to high-quality (i.e. control) nestmates, if the latter are better at attracting parental attention. Taken together, our results suggest that a signal of offspring quality may affect the number and type of social interactions among nestlings. We cannot rule out, however, an effect of UV colour on the bearer's own preference to interact with others. This would imply a mechanism of self-perception, possibly by observing the behaviour of other family members in response to the manipulated signal, as suggested in previous studies (e.g. Burley, 1986; Cline et al., 2016).

The Social Context

Given that control chicks held more central positions in general, we might have expected a pattern of homophily, in which similar chicks cluster and interact more strongly. On the contrary, nestlings' interactions were less heterophilic in enlarged broods, in which social density was higher and thus competition was likely to be stronger (e.g. Robinson & Rotenberry, 1991; Saino et al., 1997; Sanz, 1997). This, in turn, would lead to a more intense competition for the best positions, which may result in high-quality chicks being more able to keep them (Ostreiher, 2001; Webber & Vander Wal, 2018). Additionally, UV-blocked nestlings could be more often challenged when holding a central position, given that they are signalling poorer quality, so they might have to retreat to peripheral positions, thus leading to a reduction in heterophily in enlarged broods. Whatever the exact explanation for the observed patterns, our results suggest that offspring signals might have evolved to establish social interactions at the beginning of life in blue tits.

Independently of UV colour, our brood size manipulation had a significant effect on both node and network level metrics. While these effects are likely to be a function of the greater probabilities of

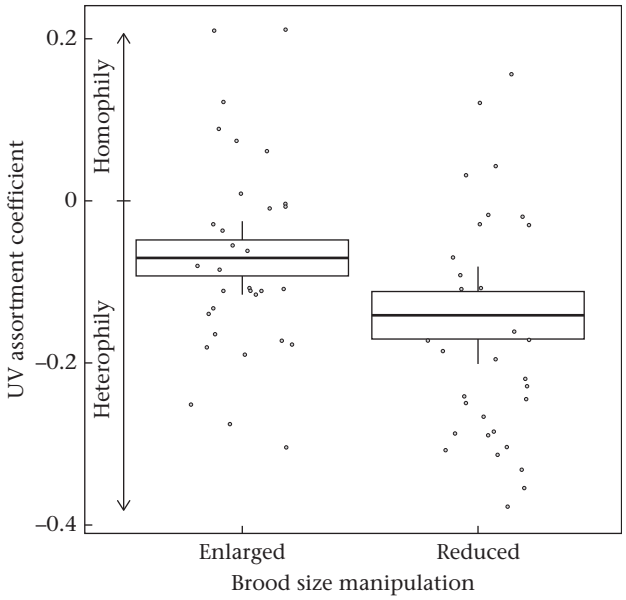

Figure 4. UV assortment coefficient in relation to brood size manipulation. The black line indicates the mean value, the limits of the box the standard error and the whiskers the 95% confidence interval. Data points are also plotted.

interacting when brood size increases, it allowed us to test the role of UV-based signalling in different family structures. As expected, network degree centrality was higher in enlarged broods, because there were many more nestmates to interact with in a more complex network. In contrast, the node and network strength (i.e. the proportion of times that two specific individuals interacted) were higher in reduced broods, probably because it was easier to interact with all possible individuals in a reduced brood. These results just emphasize that the social density manipulation by two nestlings was enough to trigger changes in the nestmates' network structure. To better grasp the fitness consequences of these observed patterns, it would be interesting to explore how individual social network metrics affect growth and feeding patterns and ultimately social status postfledging.

Conclusions

The results of the present work suggest that nestling UV colour (either directly or indirectly through parental feeding preferences) determines the position in the social network early in life, and the preference of other nestlings to interact with the signaller. This might have significant fitness consequences as reported for a closely related species (Royle et al., 2012). Intriguingly, nestlings preferentially interacted with individuals with opposite signal expression, and this heterophily was stronger in small families. This implies that changes in social density alter the individuals' preference for associating with others based on signals of quality.

Author Contributions

A.G-A. and J.G-C. contributed equally to this work. J.G-C., W.M. and J.M. conceived and designed the study. J.G-C. and J.M. collected field data. A.G-A. analysed the video data and performed the statistical analyses with help from J.M. A.G-A. wrote the manuscript with input from all authors. All authors read, reviewed and approved the final manuscript.

Data Availability

Data used for the analyses described here can be accessed at Mendeley Data: https://doi.org/10.17632/ct66fr6hkf.1.

Declaration of Interest

None.

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Appendix

Node level metrics:

Node degree centrality is defined as the number of links (edges) connected to a particular node. Defining the degree of a node i as D_i, then, for node 1 of the network:

$$D_i = 5$$

Node average strength is defined as the average of the values of all the edges connected to a particular node. Defining the average strength of a node i as S_i, then:

$$S_i = \frac{\sum_{1}^{D_i} v_j}{D_i}$$

where v_j is the value of link j from node i and D_i is the degree (i.e. the number of links) of node i. For example, for node 1 of the network:

$$S_1 = \frac{\sum_{1}^{D_1} v_j}{D_1} = \frac{\sum_{1}^{5} v_j}{5} = \frac{0.4 + 0.1 + 1 + 0.3 + 0.6}{5} = 0.48$$

Network level metrics

Network degree centrality is defined as the average of the degrees of all the nodes in the network. Defining the network degree as $\overline{D}$, then:

$$\overline{D} = \frac{\sum_{i}^{n} D_i}{n}$$

where n is the number of nodes present in the network. For example, in the network above

$$D_1 = 5;\ D_2 = 3;\ D_3 = 4;\ D_4 = 5;\ D_5 = 4;\ D_6 = 3$$

$$\overline{D} = \frac{\sum_{1}^{6} G_i}{6} = \frac{5+3+4+5+4+3}{6} = 4$$

Network average strength is defined as the sum of the values of all the links in the network divided by the total number of links present in the network. Defining the network average strength as $\overline{S}$ then:

$$\overline{S} = \frac{V}{L}$$

where V is the sum of all values in the network and L is the total number of links present in the network. For example, in the network above:

$$V = 0.4 + 0.1 + 1 + 0.3 + 0.6 + 0.9 + 1 + 1 + 1 + 1 + 0.7 + 1 = 9$$

$$\overline{S} = \frac{9}{12} = 0.75$$

Assortment coefficient is a measure of the degree of homophily/heterophily of the network, that is, the tendency to establish links with nodes of the, respectively, same/different phenotype (here: UV phenotype). This coefficient ranges between −1 and 1. Values close to 1 indicate homophily and those close to −1 heterophily, with values close to 0 indicating random links. It is calculated as follows:

$$r_d^w = \frac{\sum_i e_{ii}^w - \sum_i a_i^w b_i^w}{1 - \sum_i a_i^w b_i^w}$$

with $e_{ii}^w = \frac{\sum_i w_{ii}}{W}$, the proportion of the total values of links between nodes of type i ($\sum_i w_{ii}$ is the sum of the values of all links between nodes of type i); $a_i^w = \sum e_{ij}^w$, the proportion of the total values of links starting at nodes of type i (and ending at any other node type); $b_j^w = \sum e_{ij}^w$, the proportion of the total values of links ending at nodes of type j (and starting at any other node type). For an undirected network (where the interaction of node A with node B implies interaction of node B with node A, as is the case in our networks), the proportion of links starting at a given node and ending at that same node is the same ($\sum_i e_{ij}^w = \sum_j e_{ij}^w$). For example, in the network above, each class being the colour of the nodes (1 = white/control, 2 = black/UV-blocked):

$$W = 9$$

$$\sum_i e_{ii}^w = e_{11}^w + e_{22}^w = \frac{w_{11} + w_{22}}{W} = \frac{(1) + (1 + 1 + 0.1)}{9} = 0.3444$$

$$a_1^w = \sum_j e_{1j}^w = \sum_i e_{i1}^w = b_1^w = \frac{\sum_i w_{1i}}{W} = \frac{w_{11} + (w_{12})/2}{W} = \frac{1 + (0.4 + 0.9 + 1 + 0.6 + 0.7 + 0.3 + 1 + 1)/2}{9} = 0.4389$$

$$a_2^w = \sum_j e_{2j}^w = \sum_i e_{i2}^w = b_2^w = \frac{\sum_i w_{2i}}{W} = \frac{w_{22} + (w_{21})/2}{W} = \frac{(1 + 1 + 0.1) + (0.4 + 0.9 + 1 + 0.6 + 0.7 + 0.3 + 1 + 1)/2}{9} = 0.5611$$

$$\sum_i a_i^w b_i^w = a_1^w b_1^w + a_2^w b_2^w = \left(a_1^w\right)^2 + \left(a_2^w\right)^2$$

$$= 0.4389^2 + 0.5611^2 = 0.5075$$

$$r_d^w = \frac{\sum_i e_{ii}^w - \sum_i a_i^w b_i^w}{1 - \sum_i a_i^w b_i^w} = \frac{0.3444 - 0.5075}{1 - 0.5075} = -0.3312$$

The values between the heterophilic links (V_{12}, V_{21}) are divided by 2 to distribute them among each type of node.

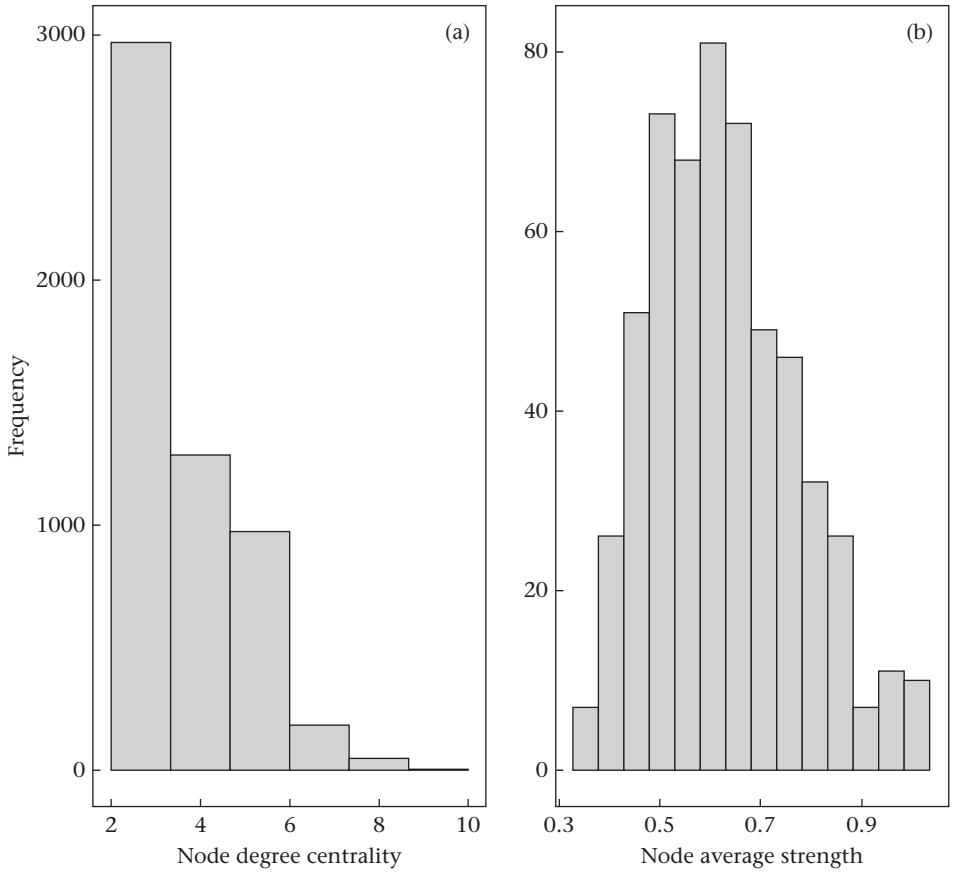

Figure A1. Distribution of (a) node degree centrality and (b) node average strength.

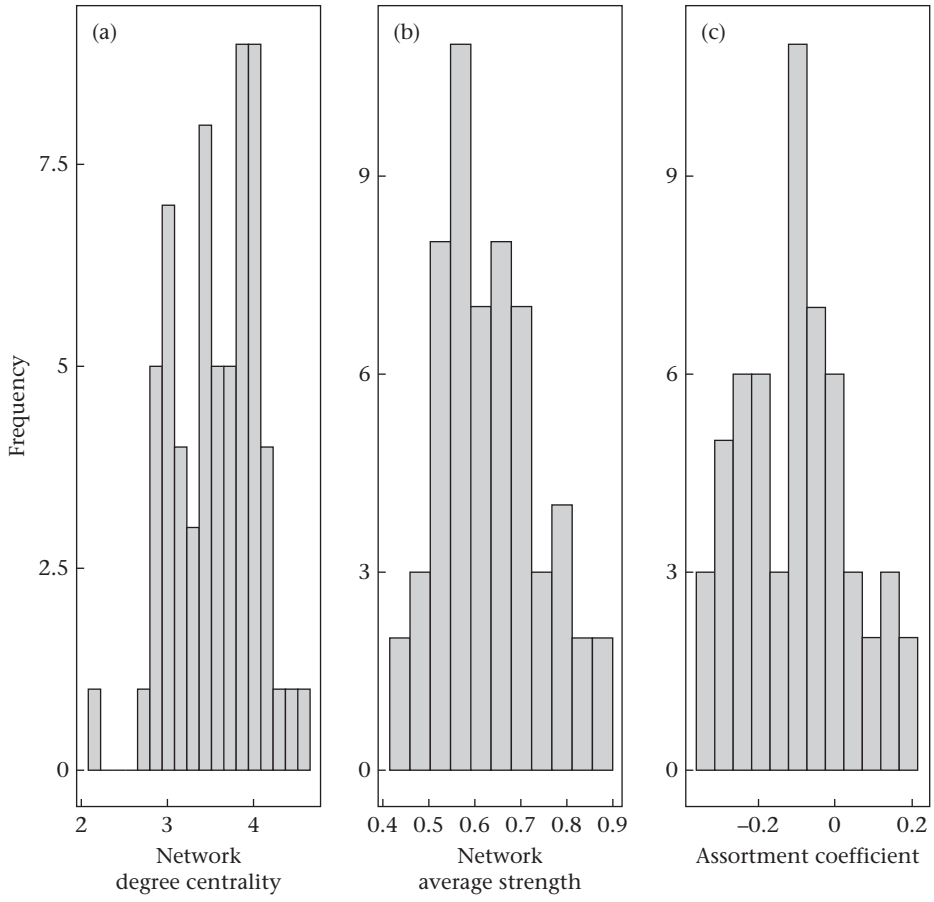

Figure A2. Distribution of (a) network degree centrality, (b) network average strength and (c) assortment coefficient.

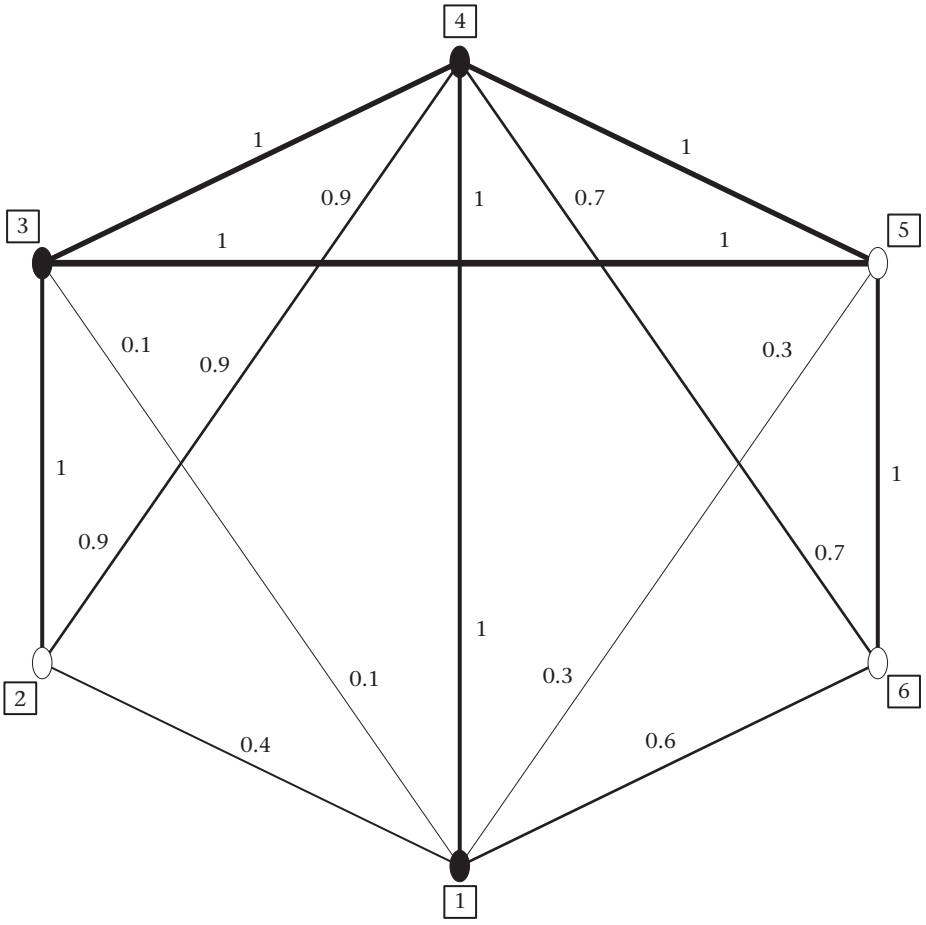

Figure A3. An example of a weighted network. Each node represents an individual and the lines represent interactions. The filling of the nodes indicates the UV phenotype of the individual (black = UV-blocked, white = control). The thickness of the lines indicates their strength and the exact value is indicated above the respective line.

Table A1
Pairwise correlations of the network metrics calculated

	Network degree centrality	Network average strength	Assortment coefficient
Network degree centrality	1	−0.71	0.33
Network average strength	−0.71	1	−0.42
Assortment coefficient	0.33	−0.42	1

Table A2
Initial mixed full model (including all the factors) for node level analyses

	Node degree centrality			Node average strength		
	Estimate (SE)	χ^2	*P*	Estimate (SE)	$F_{(df)}$	*P*
Intercept	0.10 (0.14)	–	–	0.34 (0.28)	–	–
Brood size manipulation	0.20 (0.03)	44.73	**<0.001**	−0.04 (0.02)	$2.67_{(1,\ 524.42)}$	0.10
UV treatment	−0.03 (0.03)	0.71	0.40	−0.004 (0.027)	$0.02_{(1,\ 524.87)}$	0.88
Date	−0.001 (0.002)	0.33	0.57	−0.009 (0.005)	$3.90_{(1,\ 34.45)}$	0.056
Original brood size	0.03 (0.01)	17.96	**<0.001**	−0.03 (0.01)	$5.96_{(1,\ 28.74)}$	**0.021**
Brood size manipulation∗UV treatment	−0.02 (0.04)	0.30	0.60	−0.02 (0.03)	$0.50_{(1,\ 524.05)}$	0.48

Nest identity was included as a random factor for all the variables and nestling identity only for node degree centrality. Node average strength was log transformed to normalize residuals. Coefficients are shown for enlarged broods and for UV-blocked chicks. Significant *P* values are shown in bold.