

Neophobia and social tolerance are related to breeding group size in a semi-colonial bird

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Abstract In semi-colonial species, some individuals choose to breed in isolation while others aggregate in breeding colonies. The origin and the maintenance of this pattern have been questioned, and inherited phenotype dependency of group breeding benefits has been invoked as one of the possible mechanisms for the evolution of semi-coloniality. Using field observations and behavioural tests in the semi-colonial barn swallow (*Hirundo rustica*), we tested the hypothesis that breeding group size is related to personality. We measured neophobia (the fear and avoidance of new things) and social tolerance of adults and showed that these two independent traits of personality are strongly related to breeding group size. The biggest colonies

hosted birds with higher neophobia, and larger groups also hosted females with higher social tolerance. This parallel between group size and group composition in terms of individual personality offers a better understanding of the observed diversity in breeding group size in this species. Further studies are, however, needed to better understand the origin of the link between individual personality and group breeding strategies.

Keywords Group breeding · *Hirundo rustica* · Bird colony · Temperament · Boldness · Frequency-dependent selection

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Introduction

Close proximity during reproduction results from multiple interacting factors, including habitat selection and, particularly, the choice of breeding sites, and it has major consequences for individual fitness. Breeding site selection is dependent on environmental characteristics (particularly the distribution of resources), species characteristics (for example, cognitive capacities or life history traits such as philopatry) and individual characteristics, such as past experience, personality or morphology (Brown and Brown 2000; Danchin et al. 2008; Bergmüller and Taborsky 2010). As the environment is seldom homogeneous and individuals are never identical, breeding site choice should be addressed at the individual level (Safran et al. 2007) by considering the interaction between environmental characteristics and the individual's state.

Group breeding may improve individual reproductive success by improving vigilance and defence against predators, improving foraging efficiency, facilitating mate acquisition or promoting extra-pair copulations (Hoogland and Sherman 1976; Hoi and Hoi-Leitner 1997; Danchin et al. 2008). Group breeding may also improve inclusive fitness by promoting cooperation among kin (Komdeur

1994). But it may also bear some costs, such as increased detection by predators, increased cuckoldry or increased level of parasitism (Rolland et al. 1998; Krause and Ruxton 2002; Brown and Brown 2004).

The benefits of group breeding not only vary among species but also with the heterogeneity in physical, biological and social environments (Brown and Brown 2000; Brown et al. 2000; Danchin et al. 2008) and with individual characteristics (Clobert et al. 2009). Phenotype dependence of group breeding benefits could lead to individual differences in the decision to breed in a group or not and was proposed as one possible mechanism by which semi-colonial strategies may have evolved (Møller 1987, 2002). In line with this, Møller (2002) reported that barn swallows appear to be generally less aggressive when breeding in large colonies than when breeding in isolation, but his observation was not quantified.

Among the inherited individual characteristics, differences in behavioural traits are good candidates to modify the cost/benefit balance of group breeding (Réale et al. 2010; Pruitt and Riechert 2011). Indeed, these consistent behavioural differences among conspecifics, called animal personality traits, behavioural types, coping strategies or temperaments (Réale et al. 2007), are widespread (Dingemanse and Wolf 2010; Sih et al. 2012) and were shown to covary with life history and more generally with lifestyle. Some personality traits were already shown to correlate with dispersal propensity (Cote and Clobert 2007; Cote et al. 2010), with reproductive success (Boon et al. 2007; Cote et al. 2008, Betini and Norris 2012), with polymorphism in habitat and resource use (McLaughlin 2001), as well as with the response to environmental perturbations (Dingemanse et al. 2004) or to social stimuli (Webster and Ward 2011). As such, personality can summarise much of the individual response to social and non-social environments (Réale et al. 2010). Altogether, this suggests that personality may play a prominent role in the establishment and in the persistence of alternative strategies of social environment selection within populations (Clobert et al. 2009; Schoepf and Schradin 2012). It is, therefore, reasonable to hypothesise that individuals with contrasting personality would make contrasting decisions regarding group living. Alternatively, social context can also drive the expression of personality or the selection of different personality types. For example, individuals in a group are bolder or more exploratory than solitary individuals in several species (Magnhagen and Bunnefeld 2009; Ward 2012).

Here, we aimed at testing the relationship between personality traits and breeding site preference in the barn swallow (*Hirundo rustica*). Barn swallows are facultative group breeders: only some individuals choose to breed in groups. Safran (2007) showed no significant advantage for barn swallow group breeding at the group level. Moreover,

group size is loosely related to population density in this species and some breeding habitat remains unoccupied, even in years of high density (Møller 1987; Safran 2007). Therefore, at least some birds actively choose to breed in groups and coloniality seems thus not exclusively habitat-mediated (Danchin and Wagner 1997). We believe that these alternative strategies might be related to individual differences in phenotypic traits. The aim of our study is to investigate if this is the case.

During the reproductive period, we quantified behavioural differences among breeding individuals to investigate the relationship between the size of breeding groups and barn swallow personality. We focussed on two personality traits that may interact with the breeding group size: *neophobia*, the avoidance of a new, unknown object or other aspects of the environment (Greenberg and Mettke-Hofmann 2001), and *social tolerance*, the reaction to the presence of conspecifics (Gosling and John 1999; Réale et al. 2007). Neophobia is a component of the exploration tendency of individuals, a syndrome encompassing boldness or activity traits (Réale et al. 2007), and as such, neophobia can be linked to breeding habitat choice. Highly neophobic individuals might gain from breeding in groups, for instance, by increasing foraging efficiency via copying other group members rather than directly exploring their environment. If personality drives habitat choice, we thus predict groups to be made of more neophobic birds. However, we cannot exclude the possibility that personality is somehow plastic and that grouping can change the expression of personality, leading to less neophobic behaviours in groups (as was shown in tits and in zebra finches: Coleman and Mellgren 1994; van Oers et al. 2005; Schuett and Dall 2009).

The benefits of group living may also differ between individuals that are more or less socially tolerant. Access to extra-pair copulations (Møller and Birkhead 1993) and cooperation among individuals, both regularly invoked as benefits of group living, cannot be obtained without a certain tolerance for conspecifics. We, therefore, expect to observe a positive relationship between social tolerance and group size.

Materials and methods

Study site and data collection

We observed a population of barn swallows over 30 km² in southern Belgium (50°06'32" N, 4°57'22.30" E) during the breeding seasons of 2010 and 2011. This population was a part of an ongoing long-term survey started in 2006. The study area is rural, predominantly cattle farming, with some scattered grain fields, isolated farms and six villages and

hamlets combining farms and single-family houses. Barn swallow nests are distributed across a variety of locations, including working farms, old barns, empty stables or stables occupied by livestock and a variety of other man-made structures around family homes. For the purpose of this study, we called a breeding *room* any building or structure used for nest sites by barn swallows, limited by the structures standing walls. Each nest within the area was georeferenced (GPSMAP® 60Cx). All breeding rooms and nests were visited at least twice weekly throughout the breeding seasons. Laying and hatching dates and clutch size were recorded for the first, second and rare third clutches.

Adults were captured using mist nets and were tagged with numbered rings. To identify adults during observations, a small amount of paint was placed on the tail (Safran 2004). Sex, wing size, body mass, tail length, breast colouration (three levels: bright, pinkish and fawn) and age were also recorded. Age was determined from capture histories, assuming that, during the second year of the long-term survey (i.e. 2007), the unmarked adult birds were yearlings born outside the study area. This assumption is reasonable given the high level of natal dispersal and the very low level of breeding dispersal in this species (Møller 1987).

Social implications of sharing breeding room are probably high. We thus defined the social environment at the room scale: *room occupancy* corresponds to the total number of breeding pairs occupying a room in a given year. Unshared rooms were those in which a single pair bred for the season considered. Shared rooms were those in which at least two pairs bred. We tested if personality was correlated with room occupancy, following the hypothesis that the personality of a bird may affect its decision to breed in different social environments.

The ringing survey initiated in the study zone in 2006 showed that 65 % of the males and 86 % of the females used in this study were nesting for the first time in the study zone and that 86 % of the males and 87 % of the females were in fact using their nesting room for the first time when we observed them for this study. There is thus, overall, little familiarity with the nesting rooms for the birds used in this study, and nesting room choice mostly occurred during the years of the study.

Behavioural measurements

The personality of 78 pairs was measured: we obtained neophobia measurements for 77 pairs and social tolerance for 76 pairs (Table 1). We conducted two types of behavioural tests, each preceded by a period of 20 min during which the birds were allowed to habituate to the presence of the observer hidden in a camouflage tent placed in the room. Our previous experience (during capture sessions) revealed that birds generally resume their usual activity within 10 min after a

Table 1 Number of pairs tested within each room occupancy level

Room occupancy	Test	
	Neophobia	Tolerance
1 pair (i.e. unshared room)	51	51
2 pairs	20	19
3 to 5 pairs	10	10
Total	77 ^a	76 ^a

^a The room occupancy changed for four tested pairs between the first and the second clutches. Thus, the total number of different pairs tested did not correspond to the sum of pairs in the three levels of room occupancy. Seventy-five of the 77 pairs tested for neophobia were also tested for tolerance, and 1 pair was only tested for social tolerance

human enters their breeding room. We, therefore, believe that a 20-min habitation period was sufficient to assume the return to normal behaviour in the presence of a hidden observer. For each test, the environment was modified after the period of habituation (while the birds were foraging outside the room) by placing either a novel object to measure *neophobia* or a pair of fake swallows to measure *social tolerance* in the nesting room. The observer (always hidden) then observed the behaviours of the focal adult birds (see the succeeding paragraphs). All tests were undertaken 7–15 days after hatching of the chicks in the focal nest (thus during chick rearing), with a sequence that regularly alternated the testing order (Fig. S1). We performed a total of 338 tests (171 for neophobia and 167 for tolerance). Each pair was tested twice for each trait during the breeding period. Those pairs that engaged in a second clutch (approximately 50 % of the pairs) were tested a third time. To avoid unwanted behavioural changes due to mate removal, we tested and observed both pair members together.

For each observation, the observer first verified the identity of the social parents during the habituation period. When an individual was seen feeding or incubating a brood on at least five occasions, it was considered its social parent (Møller and Tegelstrom 1997). Then, after the treatment was applied, the observer recorded and timed the full sequence of behaviours around the focal nest for 20 min after one of the focal individuals entered the room. The observer noted all behaviours of adults, either alone in the room (when its mate was foraging outside) or in interaction with other adults (its mate or other adults) or with its nestlings. To measure neophobia, we exposed birds to a novel object placed close to the nest (~10 cm; Fig. S2). We measured neophobia by the *latency* in the approach to the nest closer than 30 cm after entering the room, following the hypothesis that neophobic birds will approach the nest less rapidly (Carere and van Oers 2004). Most birds (68 %) returned to their nest within 20 min; otherwise, the observation was prolonged for an additional 10 min. A

latency of 1,800 s was attributed to the few individuals that failed to come back to the nest after 30 min. We tested neophobia up to three times to measure the consistency in the bird's responses (Réale et al. 2007). To avoid habituation to novel objects, we used six conspicuous objects that differed in shape, colour and relief (Fig. S2).

The fake barn swallows used in the social tolerance tests were stuffed individuals. We confirmed by preliminary observations of males, before pair formation, that these lures were recognised as conspecifics: we observed mating attempts on female lures and eviction attempts on isolated fake males. These harassments decreased when the lures were presented in pairs. In order to measure social tolerance, we thus perched a fake pair (one male perched close to one female) at a distance of approximately 3 m from the focal nest to limit territorial reactions that are expressed only close (<2 m) to the nests. The lures were placed between the main entry of the room and the focal nest to ensure that the focal birds saw the fake pair upon entering the room.

Our prediction was that the behaviour of tolerant birds would either be unchanged by the presence of the lures or they may even evoke positive interest (close roost, twitters, contact calls), while intolerant birds would exhibit aggressive behaviours towards the lures (snap of beak, direct contact). The sequences of behaviours were somewhat stereotyped and could easily be attributed to 1 of 12 categories quantifying the tolerance of birds (Table S1). Scoring was done at the end of each observation and, subsequently by another person, based on the recorded behavioural sequence, in order to check the reliability of our scoring (both scores converged).

Data analysis

All statistical tests were performed with R 2.12.2 (R Development Core Team 2011). Basically, two families of models were built to analyse the variance in behaviours. In the first, the response variable was one of the observed behaviours. With this type of model, we investigated (1) whether the behaviours were repeatable in time and across situations, i.e. we searched for the signature of personality. This family of models was also used to assess (2) if there was a relationship between the behaviours and other phenotypic traits and (3) if there was a relationship between the behaviours observed during both types of tests (behavioural syndrome): in these models, the behaviour observed during the tolerance test (averaged at the individual level) was the response and the behaviour observed during neophobia tests (also averaged) was an explanatory variable. The second family of models used the behaviours as explanatory variables (average values) to investigate (4) their association with the timing of

reproduction or (5) their relationship with the social context in which the birds breed. In all these analyses, we used raw, untransformed response variables, except for the mean neophobia which was square root transformed to fit to the normal distribution in the analysis of the relationship between behaviours and other phenotypic traits.

The score of social tolerance is an ordinal, 12-level variable that should ideally be modelled using cumulative link (mixed) models (CLM or CLMM, *ordinal* R package: Christensen 2011). However, measuring behavioural repeatability, the signature of personality, requires the estimation of the residual variance (see the succeeding paragraphs), which to our knowledge is unavailable for ordinal data. As the distribution of individual scores did not differ significantly from a normal distribution, we considered this variable as a continuous, Gaussian variable (the same bypass was applied in Duckworth 2006). We thus modelled tolerance using linear models (LM) and linear mixed-effects models (LMM) (R package *lme4*: Bates et al. 2011). For this response variable, we performed the model selection as follows: all simpler models derived from a saturated model were compared through their Akaike information criterion (AIC). Then, the top-ranked models (those with $\Delta AICc < 2$ from the model with the lowest AIC) were averaged according to Grueber et al. (2011), as implemented in the *MuMIn* R package (Barton 2011). This averaging estimates the effect of all the variables present in at least one of the top-ranked models: some variables that do not appear in any top-ranked model were thus discarded before the averaging process. Note that a similar selection made on CLM and CLMM arrived at models of the same form as did the selection on LM/LMM, we thus only present LM here.

The latency measured in the neophobia tests has a quasi-Poisson distribution and was modelled using generalised linear mixed models (GLMM) fitted via penalised quasiliikelihood (*glmmPQL* function in *MASS* package: Venables and Ripley 2002). In the analysis of the latency measured in the neophobia tests, as AIC is not available with the *glmmPQL* method, model selection was done by the backward elimination of the term with the least significant effect.

Bird personality

The repeatability of a behavioural response across time and situation is the usual signature of a personality trait (Réale et al. 2007). To identify if individual scores were repeatable for each type of test, we assessed the significance of the addition of the random effect of bird identity in models for each trait with a likelihood ratio test. For tolerance, we contrasted CLM and CLMM. For neophobia, as likelihood is not available with *glmmPQL* (the method used to model the neophobia that has a quasi-Poisson distribution), we

contrasted a GLM to a GLMM (with individual set as the factor with random effect), modelling neophobia as a variable with a Poisson distribution. Then, in a second step, to quantify the repeatability, we used the method of Nakagawa and Schielzeth (2010), with repeatability calculated as $r = s_A^2 / (s^2 + s_A^2)$, where s_A^2 is the variance of the individual random effect and s^2 is the residual variance (Lynch and Walsh 1998). In these two steps of the analysis of behavioural repeatability, the decomposition of the variance was obtained from models that accounted for the effect of several covariates (see Dingemanse and Dochtermann 2013). For this reason, we modelled each trait separately for each sex. In these models, the identity of the bird was included as a random effect. Before model selection, we included all potentially confounding elements that can modify the behaviour of the birds and would obscure their repeatability. These covariates were the trial rank order (to account for possible habituation), the year, the weather (sunny or clouded), the period of the day (morning or afternoon), the brood size, the brood age, the clutch number (first or second) and the interaction between brood size and brood age, all modelled with fixed effects. As we suspected that some copying between partners may occur, the full models (for both neophobia and tolerance) also included the behaviour (neophobia or tolerance) of the partner. For social tolerance, the full model included the same covariates as for neophobia, plus the room surface area and the distance between the nest and the lures, both modelled with fixed effects. In both cases, before calculating the repeatability of the behaviour, we performed a selection of the covariates (as explained previously) with the full model as the starting point, and the repeatability was calculated from the partition of the variance in the model with the lowest AIC (which, in all cases, accepted covariates included in the averaged model).

Repeatable individual profiles along different axes are, in some cases, correlated, constituting what is called a behavioural syndrome (Sih et al. 2004). To assess whether individual's neophobia was correlated with individual's social tolerance indicating such a syndrome, we used LM, where the mean tolerance over the three tests was the response variable and the mean neophobia to approach novel objects was the explanatory variable. To account for possible sex-specific correlations, we added the interaction with sex. The mean tolerance of individuals followed a normal distribution.

Personality and other individual traits in adults

To investigate for each sex the relationship between personality traits and age or morphology of the tested individuals, we built LM with the mean personality traits (either the mean neophobia or the mean tolerance) as the

response variable and with independent variables being age, breast colour and three morphological parameters: wing length and body mass, which indicate body size, and tail length, which is under sexual selection in males and uncorrelated with body mass or wing length in males. Mean tolerance was not transformed, but mean neophobia was square root transformed before analysis to fit a normal distribution. Covariates were scaled in the procedure of model averaging, but were not modified otherwise.

Timing of reproduction

The selection of preferred breeding habitat is constrained by the date at which a bird initiates its reproduction since room occupancy is lower, on average, early in the season and more nests are then available for reuse. To verify whether there was a relationship between the time at initiation of reproduction and phenotypic traits (age, morphology and mean personality scores), we used LM where the response variable was the date of breeding initiation and the independent variables were personality traits (mean neophobia or mean tolerance), age and morphology (separately for each sex). We expressed the initiation of reproduction relative to a single reference date (d0): the date at which most birds started laying their first clutch. This variable followed a normal distribution.

Size of breeding groups

To test the hypothesis that bird personality is related to final room occupancy, we modelled room occupancy with a GLM (using a Poisson family with a log link) and personality traits (mean neophobia and mean tolerance), bird morphology, bird age and year as explanatory variables. As the arrival order obviously limits the influence a bird could have on subsequent settlements in its room, this variable (and the interactions with it) was added to the GLM.

Results

Neophobia and social tolerance were both significantly repeatable (all $P < 0.05$ in likelihood ratio tests contrasting models with or without the random effect of bird identity). The latency to return to the nest with the novel object (our estimate of bird's neophobia) had estimated a repeatability of 31 % (95 % CI = 14–47 %) for males and of 38 % (95 % CI = 21–56 %) for females. For social tolerance, repeatability reached 58 % (40–71 %) for males and 46 % (27–62 %) for females. In both cases and for both sexes, the averaged model used to calculate repeatability retained the behaviour of the mate: mates tended to have similar neophobia and similar tolerance (see details in Table 2). The effect of rank

Table 2 Summary of the mixed models used to detect and quantify the repeatability of behaviours in experimental tests: estimated effects of the variables retained after model selection and model averaging on the response variables (neophobia and tolerance for each sex)

Personality trait	Sex	Variables retained in the averaged model	Estimate	Estimated 95 % CI	RW ^a
Neophobia ^b	♂	Intercept	5.68	5.39, 5.97	
		<i>♀ Latency</i>	<i>0.0009</i>	0.0008, 0.001	NA ^c
	♀	Intercept	4.77	3.81, 5.73	
		Weather	0.49	-0.05, 0.85	NA
Social tolerance ^d	♂	<i>♂ Latency</i>	<i>0.001</i>	0.0009, 0.0011	NA
		Intercept	6.69	6.26, 7.11	
		Year	-0.35	-1.19, 0.54	0.25
		Period of day	-0.27	-1.41, 0.87	1.00
	♀	Brood size	0.07	-0.68, 0.82	1.00
		Room surface	0.27	-0.56, 1.10	0.23
		<i>♀ Tolerance score</i>	<i>3.36</i>	2.74, 3.97	1.00
		Intercept	6.83	6.51, 7.15	
		Year	-0.42	-1.08, 0.23	0.28
		Weather	0.37	-0.18, 0.91	0.25
		Period of day	0.83	-0.19, 1.85	1.00
		Brood size	0.02	-0.59, 0.63	1.00
		<i>♂ Tolerance score</i>	<i>3.15</i>	2.57, 3.74	1.00

A random intercept for each individual was allowed in each model. Fixed effects not shown were not retained by model selection before averaging (for the full model before selection, see the “Materials and methods” section). Non-null effects are italicized (i.e. the 95 % CI of their estimate does not cross zero)

CI confidence interval, RW relative weight of the variable in the averaging procedure

^a Relative weight of the models considered in the averaging procedure in which the variable was included (models within 2 points of AICc from the model with lowest AIC were retained for averaging)

^b Neophobia measured by the latency (time) to return to the nest after confrontation with a novel object placed close to the nest

^c As the latency had a quasi-Poisson distribution, it was modelled using GLMM fitted via penalised quaslikelihood (glmmPQL); RW is not available with this method

^d Social tolerance: score attributed from behavioural observations after the introduction of fake barn swallows in the nesting room (Table S1)

order did not appear in any of the top-ranked models (which explains why it does not appear in the averaged models), indicating that there was no temporal trend in social tolerance or in neophobia and, hence, probably no habituation to the tests.

We did not find support for a behavioural syndrome associating neophobia to tolerance: the mean tolerance score of birds was not related to their mean neophobia, their sex or the interaction sex × neophobia (all $P > 0.7$; Table S3).

There was no general relationship between neophobia or social tolerance and age or morphology of the tested birds, with the exception of a positive relationship between neophobia and body mass in females (estimate and 95 % CI, 7.35 [0.39, 14.30]) and a relationship between tail length and neophobia that cannot be differentiated from nullity given very large confidence intervals in both sexes (males: estimate, -5.91 [-13.50, 1.66]; females: estimate, -5.51 [-12.40, 1.40]; Table S2).

The timing of reproduction, on the contrary, was related to personality. Early reproducing birds were, on average,

more neophobic, more tolerant and older than birds that initiated their reproduction later (Table 3).

Finally, the final room occupancy, which in this study ranged between one and five pairs, was also correlated to personality (Table 4): birds of both sexes with high neophobia and tolerant females occupied rooms hosting more breeding pairs. Morphology, timing of reproduction and age of the birds, on the contrary, had no substantial effect on the room occupancy and were removed from the analyses to improve their statistical power (as these variables were unknown for some birds).

Discussion

In this study, we explored whether a relationship exists between breeding group size and individual traits (personality) using field tests. We showed that barn swallows displayed consistent individual differences in neophobia and in social tolerance across successive reproductions (i.e. the first and the

Table 3 Relationships between individual phenotype and timing of reproduction

Sex	Variables retained in the averaged model	Estimate	95 % CI	RW ^a
♀	Intercept	4.44	4.41, 4.47	
	<i>Mean neophobia^b</i>	-0.13	-0.20, -0.06	1.00
	<i>Mean tolerance^c</i>	-0.11	-0.17, -0.05	1.00
	<i>Age</i>	-0.08	-0.15, -0.02	1.00
	Tail length	-0.01	-0.07, 0.05	1.00
	Year	-0.04	-0.11, 0.03	0.29
	Wing length	-0.02	-0.08, 0.04	0.19
♂	Intercept	4.47	4.39, 4.55	
	<i>Mean neophobia</i>	-0.11	-0.17, -0.04	1.00
	<i>Mean tolerance</i>	-0.09	-0.15, -0.02	1.00
	Tail length	0.06	-0.01, 0.12	1.00
	<i>Age</i>	-0.07	-0.14, -0.00	0.8
	Wing length	0.05	-0.01, 0.12	0.52
	<i>Breast colour (pinkish vs. bright)</i>	-0.10	-0.2, -0.00	0.29
	<i>Breast colour (fawn vs. bright)</i>	-0.08	-0.17, 0.01	0.29
	Year	-0.04	-0.11, 0.03	0.10

Summary of averaged LM showing the relationships between the timing of reproduction and the age, personality and morphology of adult birds. The response variable is the time at initiation of reproduction (relatively to d0, the date at which the largest number of birds initiated their first clutch). Fixed effects not shown were not retained in model selection before averaging. Non-null effects are italicized (the 95 % CI of their estimate does not cross zero)

CI confidence interval, RW relative weight of the variable in the averaging procedure

^a Relative weight of the models considered in the averaging procedure in which the variable was included (models within 2 points of AICc from the model with lowest AIC were retained for averaging)

^b Mean neophobia measured by the mean latency (time) to return to the nest after confrontation with a novel object placed close to the nest

^c Mean tolerance: mean score attributed to an individual from behavioural observations after the introduction of fake barn swallows in its nesting room (Table S1)

second clutches), but with no association between both traits or between these traits and age or morphology. We also showed that the timing of reproduction was correlated with these personality traits. Finally, we found that, independent of the timing of reproduction, the use of contrasted social breeding environments was correlated with neophobia and social tolerance of birds.

Evidence of personality traits in barn swallows

We assessed neophobia and social tolerance during the rearing period of two successive clutches. This energetically demanding period corresponds to the challenging conditions under which personality traits are usually strongly expressed (Wilson et al. 1994; Réale et al. 2007). This is

also the only period during which we were certain that our experimental manipulation would not lead to nest abandonment by some birds, an ethical requirement of this study in a natural population of a protected bird species. Our study showed consistency and substantial repeatability for both traits, over a significant time period and across conditions. Our design permitted individual testing in similar physiological conditions (i.e. during brood rearing), while having different moments in this period (i.e. testing at different stages in the same reproductive season), which is required for claims that repeated behaviours are the signal of personalities (Wilson et al. 1994; Réale et al. 2007). Although the general activity of the birds was similar during these two periods, the feeding demand obviously changed between successive tests as the age of chicks changed by 2 to 8 days (Fig. S1). The situation was even more contrasted between the first and the second clutches: not all breeding adults initiate a second clutch (about 50 % in our study area), which causes a sharp alteration in the social context between the first and second clutches. Thus, the risks and social constraints are very different between the successive tests as they were undertaken in situations representing

Table 4 Relationships between individual phenotype and room occupancy

Sex	Variables retained in averaged model	Estimate	Estimated 95 % CI	RW ^a
♂	Intercept	-0.63	-0.98, -0.28	
	<i>Mean neophobia^b</i>	0.91	0.35, 1.47	1.00
	<i>Mean tolerance^c</i>	0.66	-0.08, 1.41	0.74
	Arrival order	0.26	-0.54, 1.07	0.59
	Tolerance×arrival order	-0.79	-2.10, 0.51	0.13
	Neophobia×arrival order	0.97	-0.16, 2.11	0.43
♀	Intercept	-0.69	-1.04, -0.33	
	<i>Mean tolerance</i>	0.89	0.17, 1.61	1.00
	<i>Mean neophobia</i>	0.92	0.42, 1.43	1.00
	Arrival order	0.45	-0.25, 1.16	0.61
	Neophobia×arrival order	0.50	-0.46, 1.46	0.22

Averaged LM investigating the relationship between the personality, age and morphology of barn swallows and the final room occupancy. The response variable is the room occupancy. Fixed effects not shown were not retained by model selection. Non-null effects are italicized (the 95 % CI of their estimate does not cross zero)

CI confidence interval, RW relative weight of the variable in the averaging procedure

^a Relative weight of the models considered in the averaging procedure in which the variable was included (models within 2 points of AICc from the model with lowest AIC were retained for averaging)

^b Mean neophobia measured by the mean latency (time) to return to the nest after confrontation with a novel object placed close to the nest

^c Mean tolerance: mean score attributed to an individual from behavioural observations after the introduction of fake barn swallows in its nesting room (Table S1)

different challenges and with different reward expectations and, hence, can be considered different conditions. Although inter-annual variation in behavioural responses of individuals is also of interest, for instance, to investigate how personality acts on mate selection, we believe the time interval used here was adequate to show bird personalities. Bell et al. (2009) indeed showed that individuals were more consistent in their behaviours over short intervals compared to longer intervals. Only seven birds were tested both in 2010 and in 2011. Of these, two used different breeding rooms over the two seasons and selected a similar social environment (in terms of room occupancy) after this change. This sample size is of course too small for a formal analysis of the consistency in behavioural response to the tests, but we showed that the behavioural scores generally converged in 2010 and 2011, particularly for tolerance (Fig. S3).

Despite this high consistency of both behaviours, we found no support for a behavioural syndrome (*sensu* Sih et al. 2004) linking them: social tolerance and neophobia consequently appear as rather independent facets of bird personality. As we found significant repeatability for both traits, it is unlikely that the absence of correlation between traits was due to low statistical power, but we cannot rule out the possibility that it resulted from the particular experimental conditions, such as field tests with dyads tested together (Webster et al. 2007). Behavioural syndromes are widespread (Sih et al. 2004; van Oers et al. 2004), and some studies showed relationships between social tendency and other personality traits (activity and boldness), but to date, no clear pattern in these correlations have emerged, and these correlations were generally weaker than those observed between other personality traits (Cote et al. 2010, 2011). Our results confirm that, in swallows, social tolerance is partly independent from the well-studied boldness–neophobia–exploration syndrome, but further studies are needed to determine in which contexts social tolerance is correlated with other personality traits.

The personalities of males and females were strongly correlated within pairs (see Table 2). This resemblance between mates may be due to an active or a passive assortative mating (Taborsky et al. 2009; Schuett et al. 2010), as well as to copying between partners. Webster and Ward (2011) indeed suggested that social environment may influence individual behaviours, resulting in the alignment of behaviours in neighbourhoods. Additionally, it might be that individuals sharing a given environment behave similarly as a response to the particular conditions of this environment. We tested personality in pairs, in order to avoid stress due to mate removal: our experimental design thus creates a lack of independency between partners. Further studies are thus needed to tease apart the assortative mating, copying and common environment hypotheses. Whatever the mechanism,

this resemblance could, however, increase the reproductive success of birds, via, for instance, a better dispersion of chick feeding events (Spoon et al. 2006) or a better coordination in incubation (Schuett et al. 2010).

Personality and group breeding

Our study clearly showed that individuals are not distributed across the varied social breeding environments independently of their personality: males and females have higher neophobia in rooms with big colonies and females in these rooms have also higher social tolerance. The association between room occupancy and personality can either be the result of birds with different personalities choosing different habitats or, alternatively, it can be that the personality was tuned by the social environment, as suggested by Webster and Ward (2011). Several studies where birds were tested alone or accompanied showed that birds may plastically change their behaviour when challenged in contrasting social environments (Coleman and Mellgren 1994; van Oers et al. 2005; Schuett and Dall 2009; Mainwaring et al. 2011). The fact that swallow personality was here correlated with breeding strategy, and particularly with the breeding group size, might result from a similar plastic response to the social environment, but it may also be that personality is involved in the maintenance of differences in breeding strategies. To our knowledge, no study to date had investigated the distribution of personalities in contrasting social environments. Those that have investigated the plastic expression of personality when individuals are placed in contrasting environments generally showed a decrease in neophobia when neophobic birds were tested in groups (*i.e.* the opposite of our result, *e.g.* Coleman and Mellgren 1994; van Oers et al. 2005; Schuett and Dall 2009; but see Mainwaring et al. 2011). We thus still have no indication that one hypothesis is more likely than the other. Despite this incertitude, we believe that the implications of a relationship between group size and group composition remain interesting. Indeed, it may have significant implications for ecological and evolutionary processes acting within populations that merit further investigation. In the succeeding paragraphs, we discuss several hypotheses about the origin of this association between personality and breeding strategy. As we still lack the arguments to tease apart these hypotheses, we insist that the following discussion only aims at feeding the debate.

As was expected, breeding group size was positively correlated with social tolerance and neophobia. For example, recent studies showed that more aggressive and less social mice are leaving groups to be alone (Schöpf and Schradin 2012) and that asocial mosquitofish were less tight to shoals (Cote et al. 2012) and were dispersing from their social groups to colonise empty habitat (Cote et al. 2010). Our results concur

with these, and it is possible that intolerant females (and neophobic individuals of both sexes) seek isolation while the more tolerant females (and the less neophobic) decide to breed in groups. However, as mentioned earlier, a relative plasticity of personality exists, and individuals may change their behaviour according to, for example, their social environments. For instance, the sharing of vigilance in larger groups, freeing up time for other activities, and/or an individual in colonies might become more explorative or more aggressive than when alone, a pattern that was observed in tits and zebra finches (Coleman and Mellgren 1994; van Oers et al. 2005; Schuett and Dall 2009). Here, we observed the opposite, with large colonies hosting neophobic males and females, which is coherent with the theory of group forming. A similar pattern, however, can also result from plasticity in behaviour, for instance, Mainwaring et al. (2011) showed that zebra finches (a highly gregarious species) were less exploratory in the presence of companions than when the same individuals are isolated. Mainwaring et al. (2011) suggested that this pattern might either come from birds in groups devoting more time to social interactions at the expense of exploration or from fear caused by novelty propagating among birds. Similar explanations might explain the pattern we observed in barn swallows. Our result could also occur if individual neophobia drove preferences of habitat selection, with more neophobic birds choosing to breed in groups rather than alone. Neither of these explanations can, for the moment, be favoured over the others.

The association observed between personality and breeding group size might also be direct and causal if the cost/benefit balance associated with group breeding differs for contrasted behavioural types. Provided that there is a relationship between neophobia and aggressiveness, as shown in great tits (Verbeek et al. 1994, 1996), our results would confirm the hypothesis of Møller (2002) who suggested that birds breeding in colony are less aggressive than those breeding in isolation. The reduced aggressiveness of neophobic (or socially tolerant) birds can be a mechanism reducing the costs of group living for those birds. The frequency-dependent selection of group breeding was regularly invoked to explain the evolution of semi-coloniality (Danchin et al. 2008), and it might be that, in barn swallows, groups vary in size because individuals with different behavioural profiles perform better in differently sized groups, causing this frequency-dependent selection.

Then, the association between personality and social environments might be indirect. If, for instance, birds with different behavioural profiles arrive at the breeding grounds at different moments (which is the case in our study), this may lead them to select contrasted breeding habitats, simply because the “offer” is not the same for all birds. In our study, neophobic and tolerant birds indeed arrived earlier, but there was no direct association between the timing of arrivals and the habitat selected: early and late birds had the

same chance to occupy shared or unshared rooms, and each year, some suitable rooms remained empty. Thus, even if bird personality is related to both arrival date and group size, there is no evidence for a relationship between arrival date and habitat selection. If it is indirect, the link between personality and habitat choice thus probably passes through another causal mechanism, for example, contrasted resistance to parasites, contrasted strategies of resource use or contrasted success in alternative reproductive strategies (extra-pair fertilisations and brood parasitism), conditions that all are known to vary with group size (Krause and Ruxton 2002). Behavioural profiles were shown to covary with many traits, including the reproductive success (Boon et al. 2007; Cote et al. 2008), the resistance to parasites (Barber and Dingemanse 2010; Dunn et al. 2011) or the polymorphism in habitat and resource use (McLaughlin 2001), and it is thus theoretically possible that individuals with contrasted personality also have contrasted phenotypes for these traits and, consequently, have different costs and benefits associated with group living. The data needed to test this hypothesis of a causal but indirect association between personality and the social environment are, however, currently lacking: we encourage future studies to address this topic.

Finally, the association we observed between high neophobia or high tolerance and the use of habitats with larger groups may be due to random drift. If the choice of breeding habitats, and particularly the colony size, is partly heritable (Møller 2002; Serrano and Tella, 2007; Roche et al. 2011), this could lead to reduced gene flow between individuals with contrasting preferences. This genetic isolation might in turn cause a random drift on other traits, including personality traits. Although preliminary results of population genetics in the study area show no significant departure from Hardy–Weinberg equilibrium (SD and VMS, unpublished data), an argument against this hypothesis of random drift, only a Q_{ST} – F_{ST} comparison would clarify this point properly (Merilä and Crnokrak 2001; Leinonen et al. 2008).

Conclusion

Showing no significant group-level advantage for group breeding in the barn swallow, Safran (2007) proposed that group breeding in this species is the by-product of several birds selecting the same habitat, a hypothesis coined as ‘commodity selection’ (Danchin and Wagner 1997). However, group size is only loosely related to barn swallow population density and some rooms suitable for breeding remain unoccupied, even in years of high density (Safran 2007), indicating that at least some birds actively choose to breed in groups. The question of why some birds seek to

breed in groups thus remains open: our study sheds some new light on this question, showing that personality traits might play a role in the maintenance of contrasting breeding strategies, as evidenced by a significant correlation between group size and group composition in terms of individual personality traits. Further studies are, however, needed to verify whether, and to what extent, personality drives habitat selection or, alternatively, if birds develop different personalities in contrasting breeding environments.

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Conflict of interest The authors declare no conflict of interest.

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