OXFORD

Low heritability of social phenotypes in a nonpasserine waterbird

Piotr Minias*, ⓘ, **Joanna Drzewińska-Chańko, and Radosław Włodarczyk**

Department of Biodiversity Studies and Bioeducation, Faculty of Biology and Environmental Protection, University of Łódź, Banacha 1/3, 90-237 Łódź, Poland

*Address correspondence to Piotr Minias. E-mail: pminias@op.pl.
Handling editor: David Swanson

Abstract

Most behavioral traits are known to be weakly heritable, possibly due to their extreme complexity and flexibility. Despite this general pattern, within-species variation in avian colony size choice has been reported to have a strong additive genetic component, but we are aware of no attempts to assess the heritability of avian sociality at the finer spatial scale. Here, we used an animal model and parent–offspring regression to quantify additive genetic variance in social phenotype (local nesting density) in a nonpasserine waterbird, the common tern *Sterna hirundo*. For this purpose, we used a novel experimental framework, where variation in the social environment was generated by providing birds with artificial patches of attractive nesting substrate that markedly varied in size. During 2011–2019, we collected data on social preferences for either low or high nesting density in over 250 individuals, either kin (mostly parent–offspring relationships) or non-kin recorded breeding multiple times across years. All heritability estimates of local nesting density were low (<0.10), irrespectively of fixed effects (sex and year) included in the models, data used in the modeling (all individuals vs. early recruits), or methodological approach (animal model vs. parent–offspring regression). We conclude that avian sociality, as measured at the local scale, may be much less heritable than colony size choice, as measured at the landscape level. Our study adds to the understanding of additive genetic variance in avian behavior, and it underlines a scale dependency in the heritability of behavioral traits.

Key words: animal model, birds, common tern, heritability, parent–offspring regression, sociality.

Behavioral traits are known to be highly complex and show large levels of phenotypic variation and flexibility, which is thought to be highly adaptive (Boake et al. 2002). However, phenotypic selection may only have evolutionary implications when phenotypic variation has a heritable basis (Kingsolver and Pfennig 2007) and thus, information on how it corresponds to underlying genetic variation is crucial to draw reliable evolutionary inferences and avoid the pitfalls of the phenotypic gambit (Dochtermann et al. 2015). Despite its evolutionary importance, we still seem to have limited knowledge of the additive genetic variance in complex behavioral traits, such as sociality. In general, social predisposition may have profound fitness consequences for individuals (e.g., Bilde et al. 2007; Silk 2007; Brown et al. 2016). In birds, the highest degree of sociality is observed in colonial species, which breed in densely distributed nesting territories that contain no resources other than nesting sites (Perrins and Birkhead 1983). Although coloniality is relatively common in birds, with 13% of avian species being classified as colonial (Rolland et al. 1998), avian colonies show extreme variation in size within species (up to several orders of magnitude) (Brown et al. 1990; Jovani et al. 2008). Since colonies are often extensively scattered in space, variation in colony size is only detectable at relatively large spatial (landscape) scales (Griffinn and Thomas 2000; Jovani and Tella 2007).

There may be, however, a strong variation in sociality prevailing at the local scale, as even within a single colony, individuals may prefer to settle and nest in either lower or higher nesting densities, which can determine the intensity of intraspecific interactions (Pius and Leberg 1997) and affect fitness (Stokes and Boersma 2000; Tella et al. 2001). In general, the structure of large avian colonies is often highly complex and heterogeneous, often being composed of relatively well-separated reproductive social breeding aggregations (often referred to as subcolonies). The size of these local reproductive groups was reported to be crucial for bird reproductive performance, as hatching and fledging success tends to be higher in larger subcolonies (e.g., Barbosa et al. 1997; Liljesthröm et al. 2008). These patterns are primarily attributed to a larger ratio of peripheral to central nests in smaller subcolonies. Peripheral nests are usually occupied by individuals of lower quality (younger, less dominant, in weaker condition) and are more vulnerable (accessible) to predation (Götmark and Andersson 1984; Vergara and Aguirre 2006). Also, nests from smaller subcolonies may be primarily targeted by predators, as the effectiveness of communal defense is lower in smaller breeding aggregations (fewer individuals are actively involved in defense behaviors). At the same time, per capita investment in defense behaviors is likely to be higher in smaller subcolonies, resulting in trade-offs with

investments in reproduction, self-maintenance, and survival (Brown and Hoogland 1986; Arroyo et al. 2001). Birds from larger subcolonies were also reported to initiate laying earlier in the season (Doxa et al. 2012), lay larger eggs (MartÍn and Soler 2006), and show greater patch reoccupation probability (Parejo et al. 2006; Zador et al. 2009), supporting conclusions that variation in local group size within avian colonies is driven by adaptive processes.

To date, the heritability of avian sociality has only been investigated at the level of colony size choice, that is, at relatively large spatial scales. Although phylogenetic coverage of these analyses was limited to swallows and kestrels, the results provided consistent evidence for a relatively strong genetic component in the choice of colony size (Brown and Brown 2000; Møller 2002; Serrano and Tella 2007). While these results were largely unexpected, as complex behavioral traits are unlikely to be highly heritable (Dochtermann et al. 2019), they were primarily attributed to strong individual variation in social predisposition and also to a possibly strong heritability of competitive abilities, which determine an ability to settle in an optimal social environment (Serrano and Tella 2007). To the best of our knowledge, it has never been assessed whether this strong genetic component in avian sociality also prevails at the scale of the local social environment.

Here, we took advantage of 2 traditional approaches (animal model and parent–offspring regression) to estimate the heritability of preferences for a local social environment in a nonpasserine waterbird, the common tern *Sterna hirundo*. Common terns nest in a variety of inland and coastal habitats, including inshore islands, sandy beaches, or saltmarshes, and they naturally show a huge variation in colony size, ranging from just a few to a few thousand breeding pairs (del Hoyo et al. 1996). Large tern colonies may, however, show complex spatial structure, and in this study, we used a novel experimental framework, where variation in the social environment was generated by providing birds with artificial patches of the attractive nesting substrate (floating rafts) that markedly varied in size. As all habitat patches were provided at a single site with a shared environment, we expected that settlement patterns in our population should be primarily governed by a social predisposition toward nesting in either larger or smaller groups (henceforth referred as higher or lower local nesting densities) rather than by ecological factors (e.g., resource availability or predation) and it should not be confounded by large-scale spatial variation in the availability of nesting habitat or differences in individual dispersal capacity. So far, we have recorded marked variation in reproductive performance, physiology, behavior, and immune function in common terns nesting on the rafts of different sizes (Minias et al. 2015, 2019, 2020; Drzewińska-Chańko et al. 2021). While this provides a strong support for an adaptive choice of local social environment in the common tern, it remains to be tested whether these processes reflect environmentally induced phenotypic plasticity or whether they have a heritable genetic basis.

Materials and Methods

Experimental framework and local social environment

To study social phenotypes in common terns, we adopted a novel experimental approach, where attractive artificial nesting substrates (floating rafts) were provided for terns at a site with no availability of natural nesting habitat. For this purpose, we chose a large dam reservoir (Jeziorsko; 51°40′N, 18°40′E) in central Poland, which was optimal for our study species in terms of food resources and was expected to sustain a large tern population. To promote variation in a local social environment, we installed rafts that varied 4-fold in the nesting area (10–40 m²). As a consequence, the sizes of breeding aggregations varied from 10 to ca. 100 breeding pairs (max. 112 in 2019) at different rafts (consistent with over 10-fold variation). The first raft was installed during the pilot study in 2010 (data not included in analyses) and it was immediately occupied by terns in the first available breeding season. By 2011, 4 rafts (3 small and a large one) were available for terns and by 2017, there were 7 rafts installed (2 large ones and 5 small ones). No rafts of intermediate size were provided for terns during the entire study. The distance between neighboring rafts ranged from 200 to 500 m, and although direct interactions between birds from different nesting aggregations were limited (see Minias et al. 2015 for details), all rafts were easily accessible for any bird which decided to recruit in the local population, and the choice of either large or small rafts incurred no dispersal costs. Bird arrival in spring was always highly synchronized (early May), and the processes of settlement proceeded simultaneously at different rafts, so most individuals could choose either small or large rafts for breeding (except the latest breeders, as nest site availability tended to decrease at some rafts toward the end of the season). Also, the differences in a number of breeding pairs per raft (i.e., local nesting density) usually became apparent from the very beginning of the breeding season, so in most cases, individuals were expected to effectively perceive this variation at the moment of nest-site choice and settlement decisions. Finally, many birds may have had a prior knowledge on the social environment at each raft from previous breeding seasons due to the high repeatability of nesting densities at different rafts and high return rates in our population (R. Włodarczyk, unpublished data).

Field data

During 2011–2019, we ringed 2,453 nestlings and 154 adult birds, but our final database included 349 measurements of social phenotypes (local nesting densities) in 258 individuals, either kin (mostly parent–offspring relationships) or non-kin, but recorded breeding for multiple times across years. Specifically, we recorded social phenotypes in 67 recruits (individuals that were marked as nestlings), including 13 birds that were measured in more than 1 year (up to 3 measurements per individual), resulting in a total of 84 measurements. These birds were of known age (2–8 years old). Social phenotypes of their parents were also known (during the season when the nestlings were originally marked) and incorporated in the database (*n* = 134 measurements). Finally, social phenotypes of 57 individuals originally marked as adults were measured multiple times across years (on average 2.39 ± 0.09 [SE] measurements per individual, maximum 5 measurements), allowing to quantify intraindividual variation in social predisposition. The data mostly consisted of isolated families (mean relatedness coefficient 0.029 ± 0.002 across the entire dataset) with virtually no links between them (no half-sib relationships recorded). We performed no molecular analyses of kinship, and all parent–offspring relationships were assumed based on the observations of social bounds, but extra-pair

copulations and extrapair paternity are known to be very infrequent in the common tern (González-Solís et al. 2001; Griggio et al. 2004), and thus alternative mating strategies (genetic polygamy) should introduce no major bias in our analyses.

Blood was sampled from all captured adults (ca. 50 μL from the ulnar vein into 96% ethanol), and we used molecular methods (Fridolfsson and Ellegren 1999) to determine their sex. The subsample of birds with known sex also included 40 recruits that were recaptured and sampled for blood as adults. To minimize observer bias, blinded methods were used during recording and analyzing behavioral data (e.g., observers had no access to data on natal nesting density while resighting birds). Social phenotypes were quantified as local nesting density, that is, the maximum number of pairs simultaneously nesting on a raft in a given season.

Heritability estimates

We used 2 approaches to estimate heritability in social phenotypes of common terns. First, to decompose phenotypic variance into genetic and environmental sources, we used the special form of a general linear mixed model known as the animal model, which can handle all types of genealogical information within complex pedigrees that can be found in natural populations (Lynch and Walsh 1998; Kruuk et al. 2000). All animal models were run using the *MCMCglmm* v.2.24 package (Hadfield 2010) developed for R v.3.3.2 statistical environment (R Core Team 2016), following guidance by Wilson et al. (2010). A univariate repeated measures model was used to estimate additive genetic (V_A), permanent environment (V_{PE}), and residual (V_R) components of phenotypic variance (V_P). We used full (all recruit) data to run 4 models with either no fixed effects, or with fixed effects of sex and year (and their combination) incorporated in the model structure (models 1.1–1.4 in Table 1). As social predisposition may be age-dependent and the highest heritability in avian sociality may be apparent during the first breeding (recruitment) season (Brown and Brown 2000; Roche et al. 2011), we also reran the analysis for the first breeding records ($n = 37$) of individuals aged 2–4 years (henceforth referred to as early-recruit models). This model was run with and without the fixed effect of the year (models 2.1 and 2.2 in Table 1), as it had not enough power to test the

effect of sex. The effect of age could not be entered as an explanatory variable in the general model, as the exact age during breeding was known for only a fraction of individuals. The animal term and individual identity were entered in all *MCMCglmm* models as random factors to associate and disassociate individual records with/from their records in a pedigree, respectively. Setting traditional uninformative inverse Wishart prior ($V = 1$, $nu = 0.002$) or parameter expansion in G structure (*alpha.mu* = 0, *alpha.V* = 1000) did not produce appropriate chain mixing (as assessed with trace plots). Thus, following recommendations by Wilson et al. (2010), priors for both G and R structures were set by dividing the observed phenotypic variation in a trait (i.e., social phenotype) by the number of variance components ($n = 3$) and by setting the degree of belief parameters (*nu*) to one, so that it had little effect on model fitting. To assess prior sensitivity, we reran the models using random starting points and *nu* varying between 1 and 10, but there was little effect on the posterior distribution of parameter estimates. Each *MCMCglmm* model was run for the Gaussian distribution of the response variable with 2 chains, one million iterations per chain, the thinning value of 100, and a burn-in period of 250,000, resulting in 7,500 samples per chain. The effective sample size for posterior mean estimates of variance components averaged 6,496 ± 269 (SE) across the models (min. 4,575). Chain convergence was confirmed with a visual inspection of trace plots (Supplementary Figure S1) and multivariate potential scale reduction factor values <1.05 (Gelman and Rubin 1992), as computed for 2 chains per model. Repeatability (R) of social phenotypes was estimated as the proportion of phenotypic variance explained by among-individual effects (i.e., additive and permanent environment variance, $V_A + V_{PE}/V_P$), while heritability (h^2) was estimated as the proportion of phenotypic variance explained by additive genetic effects (V_A/V_P).

Because pedigree in our dataset was primarily based on parent–offspring relationships, which was likely to limit the power of the animal model, we also used a traditional parent–offspring regression to estimate heritability. In general, parent–offspring regression computes covariance between the mean trait values of offspring (midoffspring) and either the mean trait values of both parents (midparent) or the trait value of one parent. The slope of the linear regression is an estimate of heritability (both parents) or half of heritability (one parent) (Falconer and Mackay 2009). So

Table 1 Heritability (h^2) and repeatability (R) of social phenotypes (local nesting density) in the common tern, as assessed for all and early (aged 2–4 years) recruits

Dataset	Model no.	Model	h^2	h^2 95% HPDI	R	R 95% HPDI	DIC
All recruits	1.1	Social phenotype ~ 1 + sex + year	0.06	0.03–0.18	0.21	0.11–0.34	3,135.4
	1.2	Social phenotype ~ 1 + sex	0.10	0.03–0.19	0.24	0.11–0.35	3,149.0
	1.3	Social phenotype ~ 1 + year	0.07	0.03–0.16	0.19	0.10–0.33	3,471.1
	1.4	Social phenotype ~ 1	0.07	0.03–0.17	0.21	0.10–0.34	3,483.3
Early recruits	2.1	Social phenotype ~ 1 + year	0.07	0.03–0.19	0.17	0.09–0.32	2,437.9
	2.2	Social phenotype ~ 1	0.08	0.02–0.18	0.21	0.09–0.33	2,440.2

Fixed effects of sex and year were included. Modes and 95% HPDI of the Bayesian posterior distributions are reported for each estimate. Model fit was assessed with DIC.
HPDI, highest posterior density intervals.

far, a direct comparison of both approaches showed that the animal model tends to yield slightly lower heritability compared with parent–offspring regression, mostly reflecting the inclusion of replicated measurements of individual phenotypes in the animal model rather than the inclusion of more extended pedigree information (Åkesson et al. 2008). Because animal models fitted to our data provided support for the effect of year and sex (see Results for details), we also corrected for variation in these effects in the parent–offspring regression. Following Åkesson et al. (2008), we regressed the average offspring social phenotypes on average parent social phenotypes (i.e., local nesting density). For this purpose, we used the full-sib average values to avoid pseudo-replication in the regression analysis. The estimated heritability corresponded to the slope of the midparent–midoffspring regression.

Results

All heritability estimates of social phenotypes (local nesting density) in the common tern were low and ranged from 0.06 to 0.10 (Figure 1), irrespective of the fixed effects and the dataset used in the modeling (Table 1). The 95% highest posterior density intervals of the Bayesian posterior distributions were relatively narrow, with upper limits ≤0.19. The best-fitting model (as assessed with the lowest deviance information criterion value) for all recruit data conditioned heritability on the effect of sex and year (Table 1), although the effect of the year had little effect on model fit. Heritability estimates were similar for the early recruit data, indicating no apparent effect of age. The repeatability of social phenotypes was over 2-fold higher than heritability estimates (Figure 1). Repeatability estimates were similar across all the models, ranging from 0.17 to 0.24 (Table 1), and their upper limits of 95% highest posterior density intervals were ≤0.35 (Table 1). Variance components for each model are shown in Supplementary Table S1. Heritability estimates from parent–offspring regressions were also low and nonsignificant, yielding $h^2 = 0.01$ for all recruits ($P = 0.93$) and $h^2 = 0.09$ for early recruits ($P = 0.65$). Finally, observations of tern settlement patterns at the rafts of different sizes supported low consistency in social phenotypes between parents and offspring. We found that during the first recorded breeding attempt,

57.4% of recruits selected rafts different in size from their natal rafts (i.e., the rafts selected by their parents). Similarly, we found low individual consistency in the raft size choice within individuals, as 45.6% of birds with multiple breeding events recorded across years ($n = 68$) changed raft size during their lifetime.

Discussion

Our study provided evidence for a weak heritable basis of local nesting density in the common tern, which was supported by both animal model and parent–offspring regression. These results are roughly consistent with relatively low heritability of animal behavioral traits, but they clearly contrasted with earlier studies on swallows and kestrels, which found relatively high additive genetic component in colony size choice, as measured at the landscape level (Brown and Brown 2000; Møller 2002; Serrano and Tella 2007). This suggests that avian sociality may show strong scale dependency in heritability, although this conclusion needs further empirical support under much broader phylogenetic coverage.

The most recent meta-analysis of heritability in animal behavior revealed a moderate contribution of additive genetic variance to most behavioral traits (average $h^2 = 0.24$) (Dochtermann et al. 2019). At the same time, there was considerable variation among behaviors as to how heritable they were, with migratory and dispersal behaviors being the most heritable ($h^2 = 0.46$) and foraging behaviors being the least heritable ($h^2 = 0.20$) (Dochtermann et al. 2019). Ca. 25% of heritability estimates were ≤0.1 (Dochtermann et al. 2019), indicating that our heritability estimates of social phenotypes were within the lower quartile of the h^2 distribution. Consequently, social predispositions in our study population of common terns had relatively weak additive genetic component when compared with other types of behavior in birds ($h^2 = 0.25$) (Dochtermann et al. 2019), which clearly contrasted with previous estimates of heritability in colony size choice in other avian species, including swallows and kestrels. The pioneering study on cliff swallows *Petrochelidon pyrrhonota* estimated the colony size choice heritability of 0.33–0.38 from the midparent–offspring regression across the entire dataset (Brown and Brown 2000), and long-term monitoring
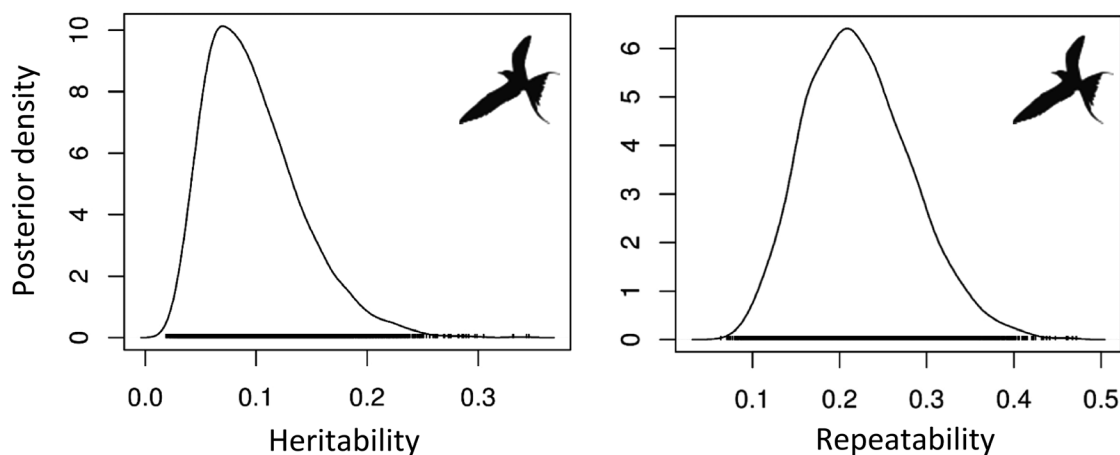

Figure 1 Bayesian posterior densities for heritability and repeatability in social phenotypes (local nesting density) by common terns, as quantified with the best-fitting model (details of model structure and posterior modes are given in Table 1).

of the population revealed 0.41 repeatability of colony size choice over the individual lifetime (Brown and Hannebaum 2022). Even higher heritability estimates were obtained in the barn swallow *Hirundo rustica* (h^2 = 0.47) (Møller 2002) and the lesser kestrel *Falco naummanni* (h^2 = 0.53) (Serrano and Tella 2007). In none of these study systems, heritability in colony size choice could be attributed to shared environment effects, maternal effects, or philopatry. Instead, it has been argued that a heritable basis of colony size choice could be established through genetic correlations between cognitive decision processes and other phenotypic traits (e.g., morphological, behavioral, or physiological), which vary with the social environment (Brown and Brown 2000).

Contrasting patterns of strong genetic basis in colony size choice by swallows and kestrels and relatively low heritability of local nesting density by common terns from our study population suggest a scale dependency in the mechanisms which determine social phenotypes. It seems likely that genetic component in social preferences could be manifested only under strong variation in social environment, that is, reflecting the full spectrum of natural variation in social phenotypes. In the common tern, natural colony size shows immense variation, ranging from small aggregations of several breeding pairs to huge colonies reaching several thousand individuals (del Hoyo et al. 1996). Obviously, the size of our experimental social groups showed much less variation (ca. 10–100 breeding pairs) and consequently, preferences for any particular social environment were expected to have much lower fitness consequences when compared with landscape-scale settlement decisions. At the same time, the variation in the social environment should be easily perceivable for birds from our experimental population, and it was previously shown to affect not only reproductive success but also offspring condition and immune function, possibly having carry-over effects on post-fledging survival and recruitment rate (Minias et al. 2015, 2019). The biological significance of this variation was non-negligible, as differences in reproductive success between large and small rafts in our population were estimated at 30% (more chicks fledged at larger rafts; Minias et al. 2015). This suggests that our experimental design should be appropriate and sufficient to examine the behavioral mechanisms and additive genetic variance of social predisposition at the local scale. On the other hand, the biological effects of natural colony size variation are still expected to be much larger. For example, a comparison of tern colonies that ranged from less than 10 to over half a thousand breeding pairs showed 3-fold differences in the mean reproductive success between the largest and smallest colonies (Szostek et al. 2014).

Apart from scale dependency, some alternative explanations for the contrasting patterns in heritability estimates of social preferences are also worth considering. First, our data were restricted to individuals recruited into their natal population and including birds that showed natal dispersal could possibly alter our heritability estimates. Nevertheless, the natal dispersal rate was apparently low in our population (no resighting evidence for recruitment of offspring from our study site in non-natal colonies during the entire study period) and thus, it should not introduce any major bias. Second, the common tern is ecologically and phylogenetically distant from the avian species, which were previously studied for heritability of social behavior. Thus, we cannot exclude that heritability in social phenotypes may show considerable between-species variation, although much more empirical

research across different avian lineages is required to explicitly test this hypothesis. While, in general, heritability of behavioral traits did not vary systematically among taxa and negligible percent of heterogeneity in h^2 estimates was attributable to phylogeny, these effects could have been difficult to detect under poor and unbalanced phylogenetic coverage (Dochtermann et al. 2019). Taking all this into account, our results seem to support the notion that narrow taxonomic focus in behavioral research may have major implications for our understanding (or misunderstanding) of animal behavior and its sources of variation (Rosenthal et al. 2017).

Despite early evidence for a strong heritable basis in colony size choice by cliff swallows, further research on the same population indicated that genetic effects on colony choice prevailed only in the year of recruitment but not in the successive breeding seasons (Roche et al. 2011). It was concluded that genetically based colony size preferences during recruitment could be a way to ensure the matching of their phenotype to an appropriate social environment as yearlings, but familiarity with particular colony sites and available information on site quality (experience) may override innate colony size preferences in older birds (Roche et al. 2011). Although in our study species we found no evidence for higher heritability of local nesting density by early recruits, we acknowledge that expression of genetic component in social behaviors may not only vary across life cycle, but it can also be context-dependent. Our previous research on common terns showed that social predisposition was primarily driven by the current immunological status rather than by fixed immunogenetic traits, allowing birds to make flexible settlement decisions across years (Drzewińska-Chańko et al. 2021). These flexible decisions were manifested by low within-individual repeatability of local nesting density across years and weak effects of natal nesting density on the future choices of the social environment during reproduction by recruits. Low fidelity to the subcolony of birth and annually changing subcolony choices were previously reported for a common tern population in Germany; however, variation in the size of different subcolonies was much less apparent when compared with our study site (Becker 2015).

Although our modeling provided consistent evidence for the relatively low heritability of social phenotypes within our study system, we acknowledge some methodological limitations of our study. In fact, the simple structure of pedigree in our dataset primarily relying on parent-offspring relationships (scarcity of full- and half-sib relationships) should be considered a major limitation. Taking this into account, we only aimed to fit animal models of relatively simple structure that well matched our data and estimated basic variance components, such as additive genetic and permanent environment variance. In fact, the power of the animal model was insufficient to yield precise estimates of variance components, which require complex pedigrees over several generations, for example, the common environment effects (Wilson et al. 2010). Although heritability estimates can be upwardly biased when common environment effects among kin are not considered, this should not pose a problem for datasets mostly consisting of single offspring families. While we could not deal effectively with a common environment, our repeated sampling of individuals across years allowed us to estimate permanent environment effect variance, which may be due to constant differences in conditions experienced by individuals throughout their

lives (e.g., permanent variation in physiological condition or variation in personality) or to long-term effects of conditions experienced at a critical stage of life (Kruuk and Hadfield 2007). The latter may refer to early developmental conditions, which could lead to natal habitat (or social environment) preference induction (Davis and Stamps 2004), where recruits select their social environment based on their natal experiences. Our analyses showed that the permanent environment explained slightly more variance in local nesting density than genetic additive effects (heritability explained less than half of the repeatability), but its general effect on the settlement decisions of terns was relatively minor within our study population.

In conclusion, we showed that the heritability of local (within-population) social preferences by common terns was relatively low when compared with across-landscape colony size choice estimates reported in other avian species. This suggests a scale dependency in the mechanisms which determine social phenotypes, yielding stronger genetic component under a coarse-scale variation in social environment. At the same time, we cannot exclude that genetic component in avian sociality may show considerable variation between species or phylogenetic lineages. We postulate that our results should ideally be replicated using longitudinal data collected under natural variation in colony size in the common tern and that factors driving within- and between-species variation in heritability of behavioral traits, including sociality, require further consideration under much broader phylogenetic coverage.

Author Contributions

P.M. conceived the experiment, R.W. and J.D.CH. conducted field work, and P.M. and J.D.CH. analyzed the data. All authors contributed critically to the manuscript and gave final approval for publication.

Conflict of Interest

The authors declare no conflict of interests.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

References

Åkesson M, Bensch S, Hasselquist D, Tarka M, Hansson B, 2008. Estimating heritabilities and genetic correlations: Comparing the "animal model" with parent-offspring regression using data from a natural population. *PLoS ONE* **3**:e1739.

Arroyo B, Mougeot F, Bretagnolle V, 2001. Colonial breeding and nest defence in Montagu's harrier *Circus pygargus*. *Behav Ecol Sociobiol* **50**:109–115.

Barbosa A, Moreno J, Potti J, Merino S, 1997. Breeding group size, nest position and breeding success in the chinstrap penguin. *Polar Biol* **18**:410–414.

Becker PH, 2015. In search of the gap: temporal and spatial dynamics of settling in natal common tern recruits. *Behav Ecol Sociobiol* **69**:1415–1427.

Bilde T, Coates KS, Birkhofer K, Bird T, Maklakov AA et al., 2007. Survival benefits select for group living in a social spider despite reproductive costs. *J Evol Biol* **20**: 2412–2426.

Boake CR, Arnold SJ, Breden F, Meffert LM, Ritchie MG et al., 2002. Genetic tools for studying adaptation and the evolution of behavior. *Am Nat* **160**:S143–S159.

Brown CR, Brown MB, 2000. Heritable basis for choice of group size in a colonial bird. *Proc Natl Acad Sci USA* **97**:14825–14830.

Brown CR, Brown MB, Roche EA, O'Brien VA, Page CE, 2016. Fluctuating survival selection explains variation in avian group size. *Proc Natl Acad Sci USA* **113**:5113–5118.

Brown CR, Hannebaum SL, 2022. Birds of a feather flock together: Extent of long-term consistency of colony-size choice in cliff swallows. *Front Ecol Evol* **10**:860407.

Brown CR, Hoogland JL, 1986. Risk in mobbing for solitary and colonial swallows. *Anim Behav* **34**:1319–1323.

Brown CR, Stutchbury BJ, Walsh PD, 1990. Choice of colony size in birds. *Trends Ecol Evol* **5**:398–403.

Davis JM, Stamps JA, 2004. The effect of natal experience on habitat preferences. *Trends Ecol Evol* **19**:411–416.

Dochtermann NA, Schwab T, Anderson Berdal M, Dalos J, Royauté R, 2019. The heritability of behavior: a meta-analysis. *J Hered* **110**:403–410.

Dochtermann NA, Schwab T, Sih A, 2015. The contribution of additive genetic variation to personality variation: Heritability of personality. *Proc R Soc B* **282**:20142201.

Doxa A, Robert A, Crivelli A, Catsadorakis G, Naziridis T et al., 2012. Shifts in breeding phenology as a response to population size and climatic change: A comparison between short-and long-distance migrant species. *Auk* **129**:753–762.

Drzewińska-Chańko J, Włodarczyk R, Gajewski A, Rudnicka K, Dunn PO et al., 2021. Immunocompetent birds choose larger breeding colonies. *J Anim Ecol* **90**: 2325–2335.

Falconer DS, Mackay TFC, 2009. *Introduction to Quantitative Genetics*. ?Impact-delete?>London (UK): Pearson..

Fridolfsson AK, Ellegren H, 1999. A simple and universal method for molecular sexing of non-ratite birds. *J Avian Biol* **30**:116–121.

Gelman A, Rubin DB, 1992. Inference from iterative simulation using multiple sequences. *Stat Sci* **7**:457–511.

González-Solís J, Sokolov E, Becker PH, 2001. Courtship feedings, copulations and paternity in common terns *Sterna hirundo*. *Anim Behav* **61**:1125–1132.

Götmark F, Andersson M, 1984. Colonial breeding reduces nest predation in the common gull *Larus canus*. *Anim Behav* **32**:485–492.

Griffinn LR, Thomas CJ, 2000. The spatial distribution and size of rook *Corvus frugilegus* breeding colonies is affected by both the distribution of foraging habitat and by intercolony competition. *Proc R Soc B* **267**:1463–1467.

Griggio M, Matessi G, Marin G, 2004. No evidence of extra-pair paternity in a colonial seabird, the common tern *Sterna hirundo*. *Ital J Zool* **71**:219–222.

Hadfield JD, 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R Package. *J Stat Softw* **33**:1–22.

del Hoyo J, Elliott A, Sargatal J, 1996. *Handbook of the Birds of the World*. Vol. **3**. Barcelona (Spain): Lynx Edicions.

Jovani R, Mavor R, Oro D, 2008. Hidden patterns of colony size variation in seabirds: a logarithmic point of view. *Oikos* **117**:1774–1781.

Jovani R, Tella JL, 2007. Fractal bird nest distribution produces scale-free colony sizes. *Proc R Soc B* **274**:2465–2469.

Kingsolver JG, Pfennig DW, 2007. Patterns and power of phenotypic selection in nature. *Bioscience* **57**:561–572.

Kruuk LEB, Clutton-Brock TH, Slate J, Pemberton JM, Brotherstone S et al., 2000. Heritability of fitness in a wild mammal population. *Proc Natl Acad Sci USA* **97**:698–703.

Kruuk LEB, Hadfield JD, 2007. How to separate genetic and environmental causes of similarity between relatives. *J Evol Biol* **20**:1890–1903.

Liljesthröm M, Emslie SD, Frierson D, Schiavini A, 2008. Avian predation at a Southern rockhopper penguin colony on Staten Island, Argentina. *Polar Biol* **31**:465–474.

Lynch M, Walsh B, 1998. *Genetics and Analysis of Quantitative Traits*. Sunderland (MA): Sinauer.

MartÍn J, Soler M, 2006. Subcolony characteristics and breeding performance in the chinstrap penguin *Pygoscelis antarctica*. *Ardeola* **53**:19–29.

Minias P, Gach K, Włodarczyk R, Bartos M, Drzewińska-Chańko J et al., 2020. Colony size as a predictor of breeding behaviour in a common waterbird. *PLoS One* **15**: e0241602.

Minias P, Gach K, Włodarczyk R, Janiszewski T, 2019. Colony size affects nestling immune function: A cross-fostering experiment in a colonial waterbird. *Oecologia* **190**:333–341.

Minias P, Włodarczyk R, Janiszewski T, 2015. Opposing selective pressures may act on the colony size in a waterbird species. *Evol Ecol* **29**:283–297.

Møller A, 2002. Parent-offspring resemblance in degree of sociality in a passerine bird. *Behav Ecol Sociobiol* **51**:276–281.

Parejo D, Oro D, Danchin E, 2006. Testing habitat copying in breeding habitat selection in a species adapted to variable environments. *Ibis* **148**:146–154.

Perrins CM, Birkhead TR, 1983. *Avian Ecology*. Glasgow (UK): Blackie.

Pius SM, Leberg PL, 1997. Aggression and nest spacing in single and mixed species groups of seabirds. *Oecologia* **111**:144–150.

R Core Team. 2016. *R: A Language and Environment for Statistical Computing*. Vienna (Austria): R Foundation for Statistical Computing. Available from: https://www.R-project.org/.

Roche EA, Brown CR, Brown MB, 2011. Heritable choice of colony size in cliff swallows: Does experience trump genetics in older birds? *Anim Behav* **82**:1275–1285.

Rolland C, Danchin E, Fraipont MD, 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: A comparative analysis. *Am Nat* **151**:514–529.

Rosenthal MF, Gertler M, Hamilton AD, Prasad S, Andrade MC, 2017. Taxonomic bias in animal behaviour publications. *Anim Behav* **127**:83–89.

Serrano D, Tella JL, 2007. The role of despotism and heritability in determining settlement patterns in the colonial lesser kestrel. *Am Nat* **169**:E53–E67.

Silk JB, 2007. The adaptive value of sociality in mammalian groups. *Philos Trans R Soc B* **362**:539–559.

Stokes DL, Boersma PD, 2000. Nesting density and reproductive success in a colonial seabird, the Magellanic penguin. *Ecology* **81**:2878–2891.

Szostek KL, Becker PH, Meyer BC, Sudmann SR, Zintl H, 2014. Colony size and not nest density drives reproductive output in the common tern *Sterna hirundo*. *Ibis* **156**:48–59.

Tella JL, Forero MG, Bertellotti M, Donázar JA, Blanco G et al., 2001. Offspring body condition and immune competence are negatively affected by high breeding densities in a colonial seabird: a multi-scale approach. *Proc R Soc B* **268**:1455–1461.

Vergara P, Aguirre JI, 2006. Age and breeding success related to nest position in a white stork *Ciconia ciconia* colony. *Acta Oecol* **30**:414–418.

Wilson AJ, Reale D, Clements MN, Morrissey MM, Postma E et al., 2010. An ecologist's guide to the animal model. *J Anim Ecol* **79**:13–26.

Zador SG, Parrish JK, Punt AE, 2009. Factors influencing subcolony colonization and persistence in a colonial seabird, the common murre *Uria aalge*. *Mar Ecol Progr Ser* **376**:283–293.