ORIGINAL ARTICLE

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Parent-offspring resemblance in degree of sociality in a passerine bird

Abstract The tendency to aggregate with conspecifics is a common type of social behavior, and interspecific differences in degree of sociality may indicate that evolutionary changes in sociality have been shaped by past selection pressures. A pre-requisite for such evolutionary change is that the behavior in question has an additive genetic basis. I investigated parent-offspring resemblance in two characteristics of sociality (colony size and nearest neighbor distance) in the semi-colonial barn swallow *Hirundo rustica*. Heritability estimates of these phenotypic characters were statistically significant. Offspring that were transferred to foster nests as part of brood size manipulation or cross-fostering experiments resembled their original parents more than their foster parents with respect to sociality. There was little evidence of phenotypic characteristics of mothers being significantly related to colony size or nearest neighbor distance of their offspring. Maintenance of genetic variation in sociality in this species may be related to the facts that the relationship between reproductive success and colony size differs among years, and that individuals differing in phenotypic quality have different optimal colony sizes.

Keywords Coloniality · *Hirundo rustica* · Maternal effects · Nearest neighbor distance · Optimal colony size

Introduction

Social behavior is usually defined as the evolved social interactions between conspecifics (Wilson 1975). There is enormous variation in degree of sociality ranging from

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eusociality in certain insects, crustaceans and mole rats to less pronounced sociality in many other organisms. The factors contributing to the evolution of social behavior (e.g. Hamilton 1964), and the maintenance of high degrees of sociality despite considerable costs (Alexander 1974), are a central theme in evolutionary ecology. Coloniality in birds is widespread and has evolved independently a large number of times (Rolland et al. 1998). Such coloniality is not simply a reflection of the mere number of individuals that breed within a limited range, since a whole suite of behavioral characters change with degree of sociality. These range from increased synchrony of behavior and reproduction, reduced inter-neighbor distance, increased frequency of social foraging and social anti-predator behavior and a number of other phenotypic changes in social behavior (Turner and Rose 1989; Brown and Brown 1996). While extensive studies of the functional significance of coloniality exist (reviews in Brown et al. 1990; Danchin and Wagner 1997), there is much less information on the factors that contribute to variation in group size.

Natural populations of animals typically show a wide range of colony sizes varying by several orders of magnitude even within a single population. Although colony size may be determined by food availability and the amount of other resources, individuals may choose to nest in a given site and thereby influence colony size. What maintains variation in colony size and the predisposition of individuals to nest in a colony of a given size is an open question of considerable interest for students of social evolution. Although optimal colony sizes may exist in theory, there is little evidence that such an optimum ever can be achieved (Sibly 1983). The main reason is that while certain individuals may benefit from joining an already existing colony, recruitment may actually be at a fitness detriment to individuals already present. Costs and benefits of a given degree of sociality may thus differ among individuals, and few if any individuals may enjoy the benefits of an optimal colony size. If such variation in preference for social context exists, environmental and/or genetic factors may contribute to this pref-

erence. For example, the social environment of mothers may affect the quality of their eggs in terms of testosterone (Schwabl 1997), and such allocation of testosterone to eggs depending on social environment may affect the future choice of social context by the resulting offspring. Alternatively, the social predisposition of individuals may reflect the ability to cope with a given level of social life without compromising fitness. Thus, certain individuals may be able to live close to conspecifics without excessive expenditure on social interactions, and the physiological basis for such abilities may partly be under genetic control.

A recent study of heritability of choice of breeding group size in the North American cliff swallow *Petrochelidon pyrrhonota* revealed evidence of parent-offspring resemblance using extensive cross-fostering of offspring. Brown and Brown (2000) reared more than 1,900 offspring that resulted in more than 700 recruits from foster nests and determined the relative contribution of nest of origin and nest of rearing on subsequent choice of colony size in this highly social species that breeds in colonies ranging from a few to 3,700 nests. Common environment effects, maternal effects and philopatry did not account for this resemblance. In particular, recruits tended to avoid colony sizes similar to those at which they were reared, providing little evidence of late maternal effects (Brown and Brown 2000). While this single study does provide compelling evidence of parent-offspring resemblance in choice of breeding group size, more studies of other species are clearly needed to investigate the generality of apparent genetic components of sociality.

The aims of the present study were to investigate parent-offspring resemblance in sociality in a semi-colonial passerine bird, the barn swallow *Hirundo rustica*, using colony size and nearest neighbor distance as characteristics of the degree of sociality. Colony size can be viewed as a measure of the number of potential competitors present in the area where a pair is breeding, while nearest neighbor distance can be regarded as a measure of the intensity of local competition in the neighborhood. Thus, these two measures of sociality will reflect slightly different aspects. The degree of resemblance was also investigated in relation to maternal effects such as conditions during reproduction (laying date, clutch size, and offspring quality) and morphological characteristics of the mother. The barn swallow is an excellent study organism for this purpose because considerable variation exists in coloniality ranging from solitary pairs to colonies of more than 200 pairs creating natural variation in social context. Furthermore, the aggressive behavior of individual males varies considerably from 'solitary' males being able to defend barns of more than 100 m² from access by other males to 'social' males may that nest less than 20 cm from the nearest neighbor without much aggressive interaction (Møller 1974).

The barn swallow is a small, semi-colonial, insectivorous, socially monogamous passerine. Females lay one or two clutches of 2–7 eggs per breeding season and per-

form all incubation. Young hatch approximately 2 weeks after the start of incubation and fledge when 18–20 days old. Both parents feed the young until a few days after fledging, although females contribute slightly more feeding than their mates. Adult survival is relatively low, as only 35% of the breeding individuals survive from one breeding season to the next (Møller 1994a). Offspring usually disperse considerable distances from the natal site, with only ca. 5% being philopatric, while adults almost always return to their once chosen breeding colony (Møller 1994a). Colony size may reach more than 200 pairs (Møller 1994a). A number of fitness costs and benefits of coloniality have been identified, and these vary among sex and age classes (Møller 1987). For example, mate guarding, within-pair and extra-pair copulations, infanticide, intraspecific brood parasitism and song features all increase with increasing colony size (Møller 1985, 1987, 1988b, 1989; Galeotti et al. 1997). Nearest neighbor distances range from 10 cm to more than 100 m, and close neighbors run a high risk of extra-pair paternity and intraspecific brood parasitism (Møller 1989; Saino et al. 1999).

Methods

The present study was conducted at Kraghede (57°12′N, 10°00′E), Denmark, May–September 1984–2000, as part of a long-term population study. The study site consists of open farmland with scattered plantations, ponds, and hedgerows. The main crops on dairy farms are grass, beets and wheat, while other farms that have abandoned dairy farming mainly have barley, wheat, potatoes, rape and other crops. The total study area covered was originally 30 km², but was increased in 1987 to 45 km² and in 1998 to 55 km² to increase the population size as the population has been declining. All potential breeding sites were checked every year, resulting in more than 25 breeding sites being found annually. A detailed description of the study site and its breeding population of barn swallows is given in Møller (1994a).

Adults were captured using mist nets at windows and doors from the start of the breeding season. Upon capture each adult was provided with a numbered aluminum ring and usually a colored ring on the other leg. A total of 11 morphological characters were measured and the abundance of four different ectoparasites was recorded in a highly repeatable and standardized way (see Møller 1994a). A blood smear and a blood sample for genetic analyses were also taken at first capture each year. The ownership of nests was determined by regular watches of adults with binoculars, and adults that incubated (females) and fed offspring (males and females) were considered to be nest owners. When nestlings were 12 days old, they were fitted with an aluminum ring, measured, weighed and blood sampled.

Colony size was simply the number of breeding pairs recorded in a single farm, which were separated from neighboring colonies by distances that exceeded the nearest neighbor distance within a colony by more than an order of magnitude. Nearest neighbor distance was the distance to the nearest neighboring nest active during the first clutch of a given year. This was measured on a map drawn to scale to the nearest 0.5 m.

Extensive brood manipulation experiments with cross-fostering in 1992 and 1996–1998 and cross-fostering experiments in 1988 resulted in a total of 24 recruits that had been reared in a nest different from the nest of origin. Since all these recruits were reared in a colony different from that of their origin, these offspring allowed partitioning of the effects of origin from the effects of rearing on parent-offspring resemblance.

Resemblance between offspring and their parents with respect to sociality was assessed by means of linear regression analysis of values for offspring and parents when they were the same age (Falconer and Mackay 1996). An estimate of heritability is provided by the slope of the linear regression between the offspring value and the mid-parent value (Falconer and Mackay 1996). Each nest only contributed a single offspring, and each parent only contributed a single offspring, which makes the observations used in the present study statistically independent. Total sample size was 146 recruits. A total of 8 offspring recruited in their natal colony (5.5% of 146 recruits), and to avoid any problem of dependence of data these observations were excluded from a second series of analyses, where sample size therefore was 138.

The two measures of sociality are highly negatively correlated (see Results), and I controlled for any effect of the other variable on the focal variable by using residuals from a linear regression of the focal variable on the other variable. Since nearest neighbor distance had a logarithmic distribution, this variable was $\log_{10}$-transformed before statistical analyses.

The importance of maternal effects for parent-offspring resemblance in sociality was investigated in two different ways. First, in a series of regression analyses with the social variable of offspring as the dependent variable and the social variable of the parent as the independent variable, maternal reproductive variables (breeding date, clutch size, offspring size and body mass, first or second clutch) and maternal morphological variables were entered as additional independent variables. Significant variables in a backwards stepwise regression were considered to be potentially important maternal effects on parent-offspring resemblance. Second, for cross-fostered offspring parent-offspring resemblance was estimated using both the social variable for the colony of origin and the colony of rearing as independent variables in a multiple regression. A significant origin effect would indicate early maternal and/or additive genetic effects, while a significant rearing effect would indicate late maternal effects.

Fig. 1 Nearest neighbor distance (*m*) in relation to colony size in barn swallow *Hirundo rustica* offspring. *n*=146

a

b

Fig. 2 Parent-offspring resemblance for **a** colony size and **b** nearest neighbor distance in the barn swallow. The *lines* are the linear regression lines with the slope 0.458 (SE=0.066) for colony size and 0.348 (0.069) for nearest neighbor distance. *n*=146

Results

Barn swallows breeding in larger colonies generally bred more aggregated as shown by their smaller nearest neighbor distances [Fig. 1; linear regressions for offspring: F=186.88, df=1,144, r^2=0.565, P<0.0001; slope (SE)= –0.035(0.003); parents: F=75.04, df=1,144, r^2=0.343, P<0.0001; slope (SE)=–0.028(0.003)].

Offspring resembled their parents with respect to their choice of colony size since there was a positive linear regression [Fig. 2a; F=53.78, df=1,144, r^2=0.272, P<0.0001; slope (SE)=0.458(0.066)]. That was also the case when excluding the few offspring that bred in the same colony as their parents [F=42.93, df=1,136, r^2=0.237, P<0.0001; slope (SE)=0.469(0.072)]. This equals a heritability of 0.469. Similarly, offspring resembled their parents with respect to their choice of distance from the nearest neighbor [Fig. 2b; F=25.03, df=1,144, r^2=0.148, P<0.0001; slope (SE)=0.348(0.069)]. Again, this positive relationship was unaffected by the exclusion of offspring that bred in the same colony as their parents [F=23.97, df=1,138, r^2=0.148, P<0.0001; slope (SE)=0.345(0.071)]. This equals a heritability of 0.345.

Since colony size and nearest neighbor distance were negatively correlated, I used multiple linear regressions to obtain independent estimates for colony size and nearest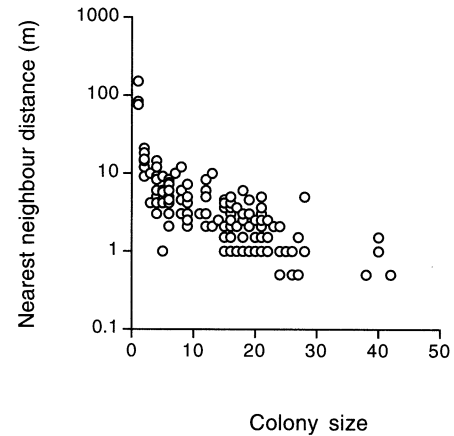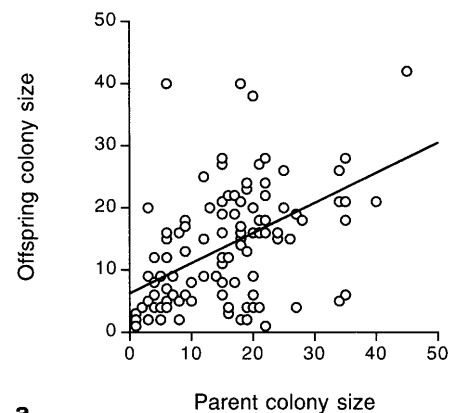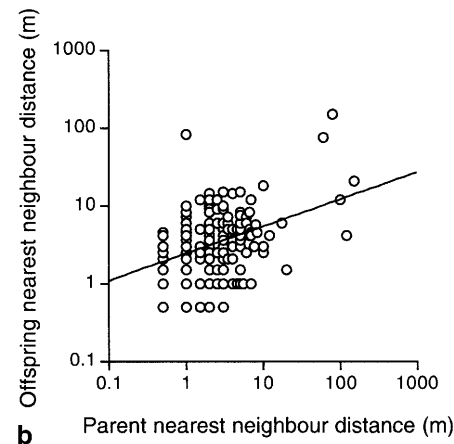 neighbor distance. Offspring resembled their parents with respect to residual colony size [multiple regression: F=28.03, df=1,144, r^2=0.282, P<0.0001; slope (SE) for parental colony size=0.419(0.081), t=5.15, P<0.0001; slope (SE) for parental nearest neighbor distance= –2.330(1.675), t=1.39, P<0.167]. That was also the case

Table 1 Multiple linear regressions between social environment of offspring when adults and their social environment of origin and rearing

Independent variable	Slope (SE)	t	P
Colony size			
$F=8.93$, $df=2,21$, $r^2=0.460$, $P=0.0016$			
Colony of origin	0.805(0.192)	4.20	0.0004
Colony of rearing	0.403(0.235)	1.72	0.101
Nearest neighbor distance			
$F=3.41$, $df=2,21$, $r^2=0.245$, $P=0.052$			
Colony of origin	0.520(0.217)	2.41	0.025
Colony of rearing	0.353(0.235)	1.50	0.148

when offspring that bred in the same colony as their parents were excluded from the calculations [multiple regression: $F=22.42$, $df=2,135$, $r^2=0.247$, $P<0.0001$; slope (SE) for parental colony size=0.397(0.091), $t=4.38$, $P<0.0001$; slope (SE) for parental nearest neighbor distance=−2.291(1.765), $t=1.30$, $P<0.196$]. This equals a heritability of 0.397. Similarly, offspring resembled their parents with respect to residual nearest neighbor distance [multiple regression: $F=15.98$, $df=1,144$, $r^2=0.183$, $P<0.0001$; slope (SE) for parental colony size= −0.010(0.004), $t=2.46$, $P=0.015$; slope (SE) for parental nearest neighbor distance=0.226(0.084), $t=2.69$, $P=0.004$]. That was also the case when offspring breeding in the same colony as their parents were excluded [multiple regression: $F=13.67$, $df=2,135$, $r^2=0.166$, $P<0.0001$; slope (SE) for parental colony size=−0.008(0.005), $t=1.74$, $P=0.084$; slope (SE) for parental nearest neighbor distance=0.250(0.089), $t=2.81$, $P=0.006$]. This equals a heritability of 0.250.

Multiple regression analyses with offspring colony size or nearest neighbor distance as dependent variables and parent colony size or nearest neighbor distance and maternal reproductive variables and maternal morphological variables as independent variables did not reveal any statistically significant effects of maternal phenotype (all $P>0.10$). Thus, there was little evidence of maternal influences on parent-offspring resemblance in sociality.

A separate analysis of a small sample of offspring that were cross-fostered in a colony different from that of their origin revealed a significant resemblance for colony of origin, but not for colony of rearing for colony size (Table 1). The multiple regression model for nearest neighbor distance was not statistically significant (Table 1). However, the partial regression coefficient for colony of origin was significant while that was not the case for colony of rearing (Table 1).

The barn swallow population has decreased considerably during the last 30 years (Engen et al., in press), and this could potentially pose a problem if there were a temporal trend in the measures of sociality. However there were no significant temporal trends in natal colony size ($r=0.159$, $n=146$, $P=0.056$) or nearest neighbor distance ($r=−0.128$, $n=146$, $P=0.124$). Similarly, the proportion of barn swallows breeding in large colonies with more than 15 pairs did not change during 1970–2001 ($r=0.040$, $n=32$, $P=0.950$). Thus, there was little potential for bias in estimates caused by temporal changes in measures of sociality.

Discussion

The main findings of the present study were that offspring of the semi-colonial barn swallow resemble their parents with respect to two variables indicating social environment during reproduction: the size of the breeding colony and the distance to the nearest neighboring nest. For the North American cliff swallow Brown and Brown (2000) reported heritabilities of 0.18–0.54 for cross-fostered offspring in different samples, while the value for offspring not cross-fostered was 0.480. This compares with a value of 0.458 in the present study. Studies of heritability of behavioral traits have generally found estimates of this magnitude for a wide range of different characters (review in Mousseau and Roff 1987). This similarity between offspring and parents in terms of social breeding environment may be due to environmental or genetic factors or a combination.

Heritability is defined as the proportion of phenotypic variance that is due to additive genetic effects (Falconer and Mackay 1996). Heritability can be estimated from parent-offspring regression or similar genetic analyses or from selection experiments. Other components of phenotypic variance may bias heritability estimates (Falconer and Mackay 1996). In particular, common environment and maternal effects may influence the estimate of heritability. Could parents be influenced by their social environment and transfer this effect to their offspring? The most likely mechanism is the effect of coloniality on maternal testosterone deposited into eggs (Schwabl 1997). Studies of the house sparrow *Passer domesticus* have shown that females deposit more testosterone in eggs in colonies as compared to females breeding in solitary conditions (Schwabl 1997). This differential allocation of testosterone has an effect on the subsequent behavior of nestlings (Schwabl 1997). Testosterone has traditionally be implicated in the production of aggressive behavior (review in Balthazart 1983), and that is also the case for features of the song of the barn swallow (Galeotti et al. 1997). If testosterone in eggs also influenced the subsequent adult phenotype, such maternal effects may affect territorial interactions and hence the social environment for reproduction. However, if such an hypothetical mechanism was at work, this should result in birds from large colonies having been exposed to more testosterone during early development and hence being more aggressive. In fact, barn swallows from large colonies produced offspring that bred in large colonies at short distances from their neighbors, while solitarily breeding barn swallows were the most aggressive ones. This is exactly opposite to what would be expected if testosterone in eggs as mediated

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by the social environment affected subsequent aggressive behavior.

Maternal effects can have profound effects on offspring phenotype, but also on trans-generational similarity among relatives (Mousseau and Fox 1998). There was little evidence of maternal effects in the present study. For example, phenotypic correlations between maternal phenotype (including maternal morphology and reproductive variables) and offspring social environment were all non-significant. Obviously, such correlational evidence is not very convincing. However, results from extensive cross-fostering and brood manipulation experiments revealed that the social environment of offspring resembled that of the adults at the nest of origin, but much less so that of the foster adults (Table 1). This suggests that late maternal effects are relatively weak, although early maternal effects cannot be excluded by this method of analysis. Early maternal effects may also have influenced the heritability estimates reported by Brown and Brown (2000) as well as all other estimates from cross-fostering experiments in general.

How can the variation in parent-offspring resemblance with respect to social environment be maintained? If the origin of the resemblance is entirely environmental or maternal, there is no problem of maintenance. However, if the basis for the resemblance is additive genetic variation, we have to explain the maintenance of variability. Tail length of male barn swallows is a phenotypic marker of individual condition, with long-tailed males enjoying an advantage in terms of mating success, extra-pair paternity, parasite resistance, survival and recruitment of viable offspring (Møller 1988a, 1994a, b; Møller and Tegelström 1998; Møller et al. 1998; Saino et al. 1998). Male tail length was not significantly related to colony size across the entire study, although significantly positive relationships were found in 2 out of 17 years and significantly negative relationships were found in 2 out of 17 years (A.P. Møller, unpublished data). Since male tail length is positively associated with mating success including paternity in own and neighboring nests (Møller 1988a, 1994a; Møller and Tegelström 1998; Saino et al. 1997; Møller et al. 1998), this result may suggest that males of superior phenotypic quality in some years are predominantly found in large colonies and in some years in small colonies. Annual reproductive success measured in terms of number of fledglings per year was significantly negatively correlated with colony size across the entire study, but in individual years there was only a significant relationship in 1 out of 17 years with barn swallows breeding in large colonies having lower reproductive success (A.P. Møller, unpublished data). These preliminary analyses indicate that there is no single optimal colony size, and that optimal colony size may differ among years. The exact basis for such apparent temporally varying selection remains to be determined, although it seems likely that either the relationship between colony size and environmental conditions may vary among years, and/or the distribution of phenotypes across colony sizes may vary among years.

In conclusion, offspring of the barn swallow resembled their parents with respect to their chosen social breeding environment. Since there was little evidence of late maternal or common environment effects affecting the resemblance, it is likely that it reflects early maternal and/or additive genetic effects.

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