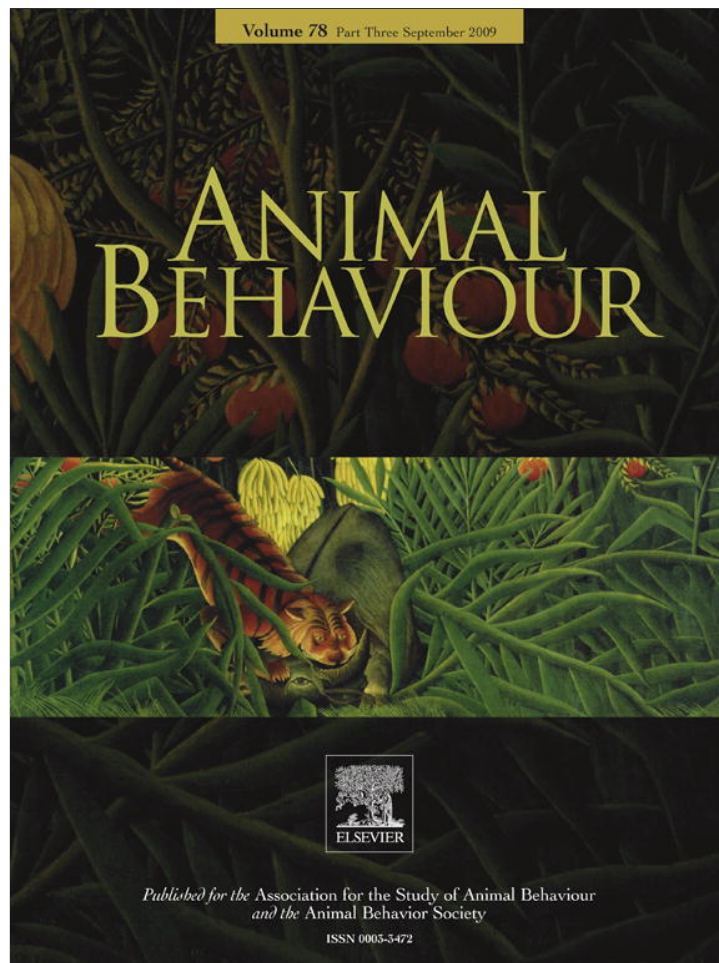


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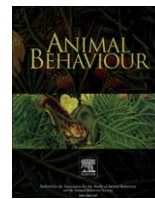
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Breeding synchrony through social stimulation in a spatially segregated population of European starlings

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Breeding synchrony occurs when individuals simultaneously perform portions of the reproductive cycle more often than expected by chance. We tested for the role of social stimulation in driving breeding synchrony of European starlings, *Sturnus vulgaris*, in a spatially-structured population in New Zealand over 11 years. Natural spreads in laying in groups were consistently tighter relative to aggregations of individuals chosen at random. Rather than a decrease in synchrony with increasing density, as would be expected if competition reduces breeding condition, we found that birds in dense breeding areas showed tighter synchrony. As the number of active nests within 500 m of a breeding location (i.e. human-constructed concrete bunkers) increased, the spread in clutch initiation date decreased. There was a correlation between synchrony and fledging success; less synchronous locations had lower fledging success. These results indicate that local and larger-scale levels of social stimulation may help coordinate reproductive timing in group-living birds. While the link between fitness and fledging success may not be causal, our results suggest that factors driving synchrony may also be related to individual quality and reproductive success.

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Birds that nest in social groups or in close proximity can vary in the degree of reproductive synchrony they show (Smith 2004; Weatherhead 2005). Breeding synchrony occurs when individuals simultaneously carry out portions of the reproductive cycle more often than expected by chance (Findlay & Cooke 1982a). In birds, egg laying is synchronous both among and between populations within a species (Findlay & Cooke 1982a; Murphy & Schauer 1996; Wilhelm & Storey 2002; Smith 2004). Synchrony may be adaptive as individuals breeding asynchronously can experience a selective advantage relative to asynchronous individuals (Findlay & Cooke 1982b; Ims 1990; Smith 2004), as possible benefits of synchrony are outweighed by potential costs, such as food depletion and predator attraction. The best supported adaptive hypothesis for reproductive synchrony suggests that synchrony can reduce predation through collective defence by adults, the inability of a predator to choose a specific target, and a dilution effect such that the fraction of vulnerable birds captured by a predator is reduced (Ims 1990;

Westneat 1992; Hernandez-Matias et al. 2003; Smith 2004). Other research suggests synchrony is favoured because synchronous fledglings maximize feeding efficiency through social foraging (Emlen & Demong 1975). Additionally, in species with high levels of extrapair copulations, breeding synchrony may maximize availability of extrapair partners (Yezerinac & Weatherhead 1997; Spottiswoode & Møller 2004). Synchrony may also be favoured when negative consequences, such as increased stress levels or agonistic interactions, occur when individuals are in different breeding stages (Jovani & Grimm 2008). A further possibility is that patterns of synchrony arise as a consequence of other factors, rather than because individuals gain a direct advantage by being synchronous, due to the sum effect of individual breeding decisions (Safran et al. 2007).

The exact mechanism for how multiple females are able to achieve a tight level of synchronous timing in egg production and laying remains unclear. Environmental conditions probably play the largest role in determining broad differences both within and among populations in timing of breeding (Cattadori et al. 2000; Paradis et al. 2000; Engen et al. 2005). For example, the proximate cues of temperature and photoperiod may stimulate females similarly, leading to increasing levels of food resources for all individuals. However, studies investigating breeding synchrony report that environmental conditions alone cannot explain

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synchrony (Findlay & Cooke 1982a; Ims 1990; Reed et al. 2006). Further cues may be necessary to integrate the responses of individuals, which may differ in their ability to reach reproductive readiness. An additional cue may be social stimulation, as courtship displays, singing and nest-building behaviour may all serve to enhance follicular development and facilitate the overlap in reproductive timing within colonial species (Darling 1938; Hailman 1964; Yomtov 1975; Wilhelm & Storey 2002; Waas et al. 2005; Helm et al. 2006).

The aim of this study was to examine the role of social stimulation in determining the extent and fitness benefits of synchronous breeding in the semi-colonial European starling, *Sturnus vulgaris*. Starlings show a high degree of sociality reflected in tight breeding synchrony (Pinxten et al. 1990; Smith & Sandell 1998; Smith 2004), as well as searching for food and migrating as a flock (Cabe 1993). We take advantage of a unique spatially segregated population to test the role of social stimulation on determining breeding synchrony. Our population of starlings breeds in human-constructed concrete bunkers distributed across an open rangeland that represent the only nesting opportunities in the area. The bunkers, which contained 1–16 nest sites, are spread across the landscape in such a way as to create distinct spatially structured social units, which allowed us to test how social interactions may drive breeding synchrony.

We first tested the prediction that starlings are more synchronous within social groups (i.e. bunkers) than expected by chance. We used a resampling approach to sample groups of randomly selected nests from our data set to compare to the average laying spread within a bunker of a given size, while controlling for environmental variation among bunkers. If social stimulation plays a role, natural spreads in laying will be tighter than female laying dates chosen at random. As each bunker represents a small spatial scale, we also tested for the role of social stimulation on a larger scale by examining the role of nest density within 500 m of bunkers. After testing for the role of social stimulation on driving synchrony, we then tested whether the degree of synchrony within a bunker was correlated with fledgling success. Synchronized chick departures within a subpopulation may be favourable because starling juveniles form large foraging flocks that may incur less predation risk because of collaborative defences.

METHODS

We studied a segregated population of European starlings in New Zealand over 10 continuous years (1970–1979) and one additional year (1984). The European starling is native to Europe and Asia, but was first introduced into New Zealand in 1862, leading to high local densities (Flux & Flux 1981). The study site, Waitangirua Farm, runs 1300 cattle and 15 000 sheep on 2400 ha of the Belmont Hills located west of Lower Hutt (41°10'S, 174°54'E). The area contains 51 concrete bunkers that are scattered across the site, approximately 100 m apart. In 1970, 100 nestboxes were constructed and placed in ventilation ports 4 m above the ground and 2–3 m apart (Flux & Flux 1981). Each successive year, 100 boxes were added until there were eventually 500 boxes by 1974. The boxes were 40 cm wide, 20 cm high and 15 cm deep; each box was constrained by a piece of wood that was placed across the interior opening and by an asbestos-cement sheet across the exterior opening. The entrance hole of each box was approximately 6 cm wide. Boxes did not deteriorate during the study period and were renovated (but not cleaned out) each winter (Flux & Flux 1981). The mean \pm SD number of nestboxes per bunker was 13.48 ± 3.12 .

We determined clutch initiation dates and clutch sizes via nest visits, which were conducted every other day. Nest success was

determined by following the fate of nestlings. Nestlings were banded or collected when they were 12 days old, half-way through the nestling period and near final fledging weight. After day 12, nestling mortality is very low (J.E.C. Flux, personal observation), and for the present analysis, chicks collected on day 12 were assumed to have fledged successfully.

Ethical Note

European starling nestlings were collected for government research to determine whether starlings consume agricultural pests in New Zealand sheep pastures (A. Moeed & J. E. C. Flux, unpublished data) and for a concurrent study on clutch size evolution (Flux & Flux 1982). Here, we made use of past data collected for these unrelated studies, and thus, nestling condition values used in the present analyses did not depend on collection of nestlings per se, and no animals were collected explicitly to test the questions in this manuscript. Nestling collection was done under protocols approved by the Animal Ethics Committee of the New Zealand Department of Scientific and Industrial Research.

Data Analysis

We tested whether patterns of observed breeding synchrony within bunkers differed from random using the program Resampling Stats (www.resample.com). To obtain the average level of synchrony for a given bunker size (3–15 breeding pairs/bunker) within each year, we generated 500 resamples of the complete data set for each year and bunker size separately, and then repeated the resampling iteratively for each larger bunker size, from 3 to 15. The averages for each year were then combined to generate an average for each group size across all years. We then tested whether this average level of synchrony between randomly chosen nests differed from the average level of actual synchrony within a bunker of a given size using ANOVA. We included bunker elevation as a covariate to control for environmental variation. We characterized synchrony in two ways: (1) the average number of days taken by females to initiate their clutches relative to the first egg laid in a bunker and (2) the percentage of birds breeding in the first week within each bunker (hereafter 'synchronous period'). Analyses examining the average number of days to clutch initiation used a general linear model (SAS PROC GLM), whereas analyses of the percentage of birds breeding were conducted incorporating binomial errors (SAS PROC GLIMMIX). We tested whether females in more synchronous bunkers had earlier clutch initiation dates using a GLM. Variables were analysed using bunker nested within year as a random effect to correct for pseudoreplication that would arise if bunker was considered independent in each year. All models included the following covariates: year, clutch size, number of nests within 500 m of each bunker, number of nestboxes within the given bunker, elevation and first clutch initiation date. We also included average daily air temperature in the 3-week period prior to the first egg date in each bunker (NZ National Climate Database; <http://www.niwa.co.nz/services/clidb/>). As the number of available nests in the study site increased over the study period as a result of new nestbox construction, the number of available nests each year varied. The influence of synchrony on nest success was analysed by examining factors predicting the number of fledgling produced by each nest using PROC GLM. Bunker nested in year was included as a random factor, whereas the average number of days that females took to initiate their clutches relative to the first egg laid in a bunker, clutch size, standardized clutch initiation date, number of active nests and year were included as covariates. Means are reported with standard deviation unless indicated otherwise.

RESULTS

Differences in Natural Levels of Synchrony from Random Association

Natural spreads in initiation of laying in bunkers were consistently tighter relative to average spreads in laying expected when random groups of equal size were considered (3 nests: $F_{1,15} = 2.85$, $P = 0.01$; 4 nests: $F_{1,35} = 2.76$, $P = 0.008$; 5 nests: $F_{1,36} = 4.06$, $P < 0.001$; 6 nests: $F_{1,42} = 3.59$, $P = 0.001$; 7 nests: $F_{1,65} = 4.14$, $P < 0.001$; 8 nests: $F_{1,72} = 8.13$, $P < 0.001$; 9 nests: $F_{1,65} = 8.22$, $P < 0.001$; 10 nests: $F_{1,41} = 8.65$, $P < 0.001$; 11 nests: $F_{1,12} = 2.51$, $P < 0.025$; 12 nests: $F_{1,10} = 8.23$, $P < 0.001$; 13 nests: $F_{1,8} = 8.38$, $P < 0.001$; 14 nests: $F_{1,9} = 8.88$, $P < 0.001$; 15 nests: $F_{1,8} = 2.49$, $P = 0.3$; Fig. 1). Elevation was nonsignificant in all models ($F_s < 2.03$, $P_s > 0.18$).

Breeding Synchrony

The study area contained 53 bunkers, but nests were not built in all bunkers every year. The average number of bunkers used each year by at least one female was 40 ± 9.9 (range 19–49), and the average number of nestboxes used per bunker per year was 7.0 ± 2.9 . The average clutch size at the site was 4.5 ± 0.7 eggs. Starlings showed high breeding synchrony, with an average of 72.0% of females initiating their first clutch within 7 days of the first egg laid within their bunker (the synchronous period). However, reproductive synchrony varied greatly from year to year; in 1978, only 50.3% of females laid within the synchronous period, while in 1979, 99.3% laid within 7 days of each other.

The average spread of clutch initiation dates within the 7-day synchronous period varied among bunkers (average spread in days among females within a bunker: 2.3 ± 1.1). As the number of nests within a bunker increased, the average spread in laying dates decreased ($\beta = -1.48$, $F_{1,52} = 109.1$, $P < 0.0001$). Bunkers in dense breeding areas showed tighter synchrony; as the number of active nests within 500 m of a bunker increased, the spread in clutch initiation date within that bunker decreased ($\beta = -0.23$, $F_{1,52} = 11.3$, $P = 0.001$; Fig. 2). Additionally, bunker identity ($F_{45,52} = 30.7$, $P < 0.001$) and year of breeding ($\beta = -0.20$, $F_{9,52} = 4.5$, $P = 0.001$)

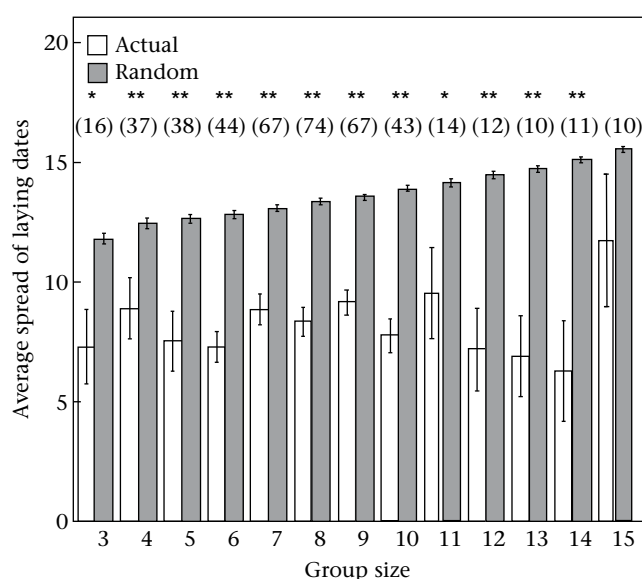


Figure 1. Relationship between group size and breeding synchrony (\pm SE) in European starlings. 'Actual' represents average spread in laying dates of groups of starlings nesting in spatially segregated bunkers. 'Random' represents average spread in laying dates in groups of starlings chosen at random from population. * $P < 0.05$; ** $P < 0.01$.

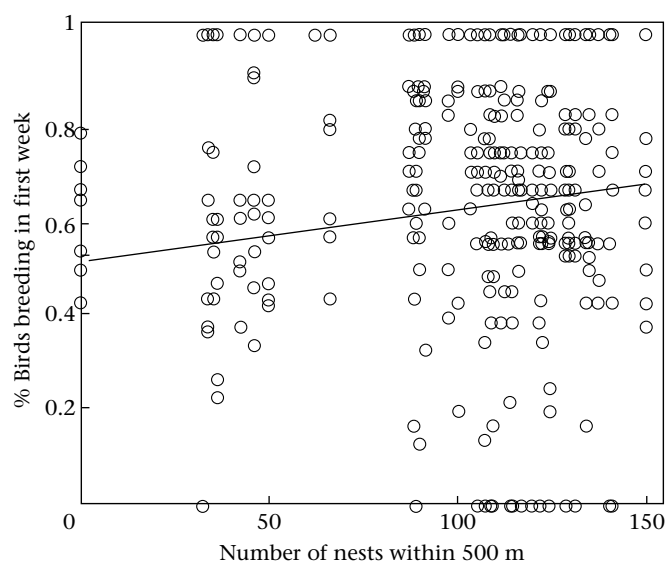


Figure 2. Relationship between density of European starlings within 500 m and breeding synchrony within each site.

significantly influenced breeding synchrony. Clutch size ($F_{1,52} = 0.9$, $P = 0.35$) and air temperature ($F_{1,52} = 0.6$, $P = 0.44$) had no effect.

The density of nests within 500 m was positively related to the proportion of females that bred within the first week ($F_{1,53} = 8.3$, $P = 0.006$). Bunkers with more active nests had a higher proportion of occupied nesting sites ($F_{1,53} = 91.1$, $P < 0.001$). Bunker identity ($F_{46,53} = 1.87$, $P = 0.01$) and increasing clutch size ($F_{1,53} = 6.2$, $P = 0.1$) also predicted early breeding proportion. There was no effect of air temperature ($F_{1,53} = 0.3$, $P = 0.58$) or clutch size ($F_{1,53} = 1.4$, $P = 0.24$).

In bunkers where females showed greater synchrony, females tended to initiate laying earlier ($F_{1,341} = 15.7$, $P < 0.01$; Fig. 3). In addition, average laying date ($F_{52,341} = 8.3$, $P < 0.001$) and average clutch initiation date ($F_{9,341} = 14.2$, $P < 0.001$) differed consistently between bunkers over time. There was no effect of clutch size ($F_{1,341} = 0.84$, $P = 0.36$) or the number of breeding pairs ($F_{13,341} = 1.5$, $P = 0.10$).

Nest Success

Overall, 40.3% of all nests initiated during the study period produced young; the average number of fledglings was 3.2 ± 1.5 . Birds breeding in bunkers with a high degree of synchrony (low average spread in laying dates) reared more fledglings ($F_{86,3734} = 5.0$, $P < 0.001$), even when controlling for clutch size, which also affected breeding success ($F_{5,3734} = 32.1$, $P < 0.001$) and bunker identity ($F_{52,3734} = 2.8$, $P < 0.001$; Fig. 4). Output from the same model revealed that as the breeding season progressed, fledging success decreased ($F_{66,3734} = 1.8$, $P < 0.001$). There was no effect of year ($F_{9,3734} = 1.3$, $P = 0.25$), air temperature ($F_{112,3734} = 1.0$, $P = 0.48$) or the number of active nests: bunkers with more nests were not more successful ($F_{11,3734} = 1.3$, $P = 0.24$).

DISCUSSION

Here we took advantage of a unique spatially-structured population of European starlings to test the role of social stimulation in driving breeding synchrony. We found support for our prediction that groups of females breeding together in spatial units (bunkers) show greater synchrony in clutch initiation dates than equal-sized groups of birds chosen at random from the population as a whole.

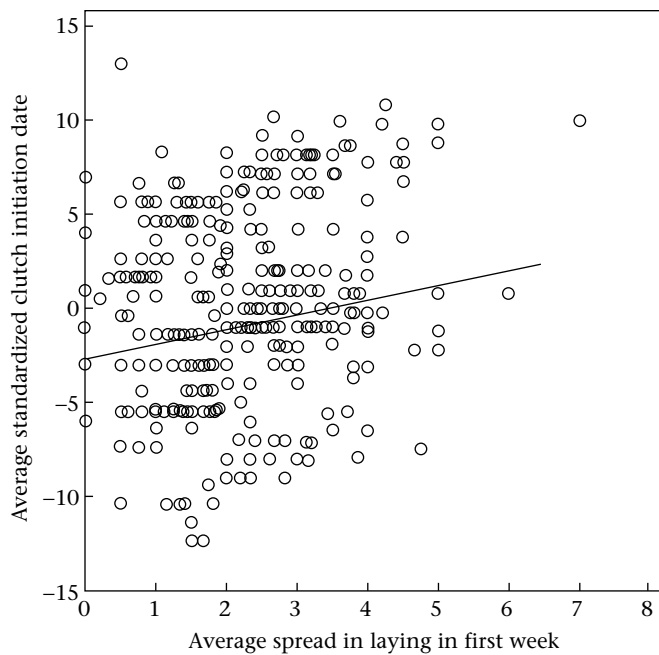


Figure 3. Relationship between average spread in laying dates among female European starlings and standardized average clutch initiation date. Clutch initiation date within each year was standardized to $\bar{X} = 0$.

For group sizes ranging from 3 to 14, we consistently found a tighter spread in laying dates than expected by chance. These differences were not due to environmental effects alone because we controlled for elevation, an important environmental variable at our site, in comparing natural versus random assemblages of laying dates. Taken as a whole, our results suggest that females that nested in the same small-scale spatial unit were more coordinated in their reproductive timing than females in the study site in general.

Female starlings may synchronize breeding purely in response to abiotic or biotic cues, or in response to the presence of

conspecifics (Witter & Goldsmith 1997). We examined the role of conspecific density in driving breeding synchrony, as the tight spread in laying dates within social groups may be due to increased social stimulation that comes through interactions with conspecifics. This supposition was supported by a link between the density of breeding starlings and the tightness of laying spreads. We found that female density was positively correlated with breeding synchrony when densities of breeding conspecifics within 500 m were considered. Because we did not manipulate breeding density explicitly, it is possible that females in our study responded to cues individually, and that increased breeding density is correlated with those cues and, thus, is not causal. However, if the relationship between density represents a link with environmental conditions, then we would expect increasing densities to lead to competition, thus reducing food supplies and leading to greater spread, rather than a tighter spread (Witter & Swaddle 1995). The positive link between density and synchrony reported here is strongly suggestive of a link between social stimulation and timing of breeding. An alternative explanation for this correlation is that later-breeding birds are unable to breed in dense areas, leading to decreased breeding synchrony in less dense locations. However, most bunkers had available nesting sites that were not used, and banding data suggest that most late-laying birds had renested following nest failure (J. E. F. Flux, unpublished data).

The exact physiological and behavioural mechanisms that may drive breeding synchrony are unclear. Larger-scale determinates of breeding timing in starlings, such as yearly variation in the first clutch initiation date at the site appear to be due to variation in environmental factors on a regional (Meijer et al. 1999) and global scale (Tryjanowski et al. 2006), as well as to other non-environmental factors (Flux 1987). However, on the short timescale investigated here (i.e. the beginning of the breeding season), synchrony of timing of egg laying among females probably occurs through ephemeral cues that lead to coordination of reproductive physiology.

One cue that would be common to females using shared breeding locations is song. Male song enhances female mating in starlings (Eens et al. 1993) and increases mating receptiveness in other species (Wasserman & Cigliano 1991; Nowicki & Searcy 2004; Cheng 2008). In addition, in starlings, exposure to conspecific males stimulates follicular development in females (Witter & Goldsmith 1997), and female density stimulates male gonadal development (Burger 1953), leading to a possible feedback loop. Social stimulation also stimulates follicular and gonadal development in food-deprived starlings (Witter & Swaddle 1995; Witter & Goldsmith 1997), providing further evidence that both social interactions and food availability influence reproductive timing. In addition, Meijer & Langer (1995) compared timing of breeding between ad-libitum fed starlings that were and were not in visual contact with food-restricted conspecifics, and they found that birds in visual contact with food-restricted conspecifics bred later. Thus, visual contact with birds whose timing of breeding was suppressed by food restriction slowed the timing of breeding of otherwise high-condition birds; this result is consistent with the idea that social interactions are important in guiding timing of breeding. Further support for the role of food stimulation comes from our finding that females in more synchronous bunkers tended to breed earlier. Jovani & Grimm (2008) proposed that synchrony may minimize detrimental interactions among conspecifics. However, this hypothesis does not predict that synchrony advances laying, whereas a social stimulation hypothesis does.

We report a link between breeding synchrony and individual fledging success, as females breeding in bunkers with tighter synchrony produced more offspring. Without explicitly manipulating synchrony, we cannot differentiate between whether synchrony itself leads to higher fledging success, or whether both

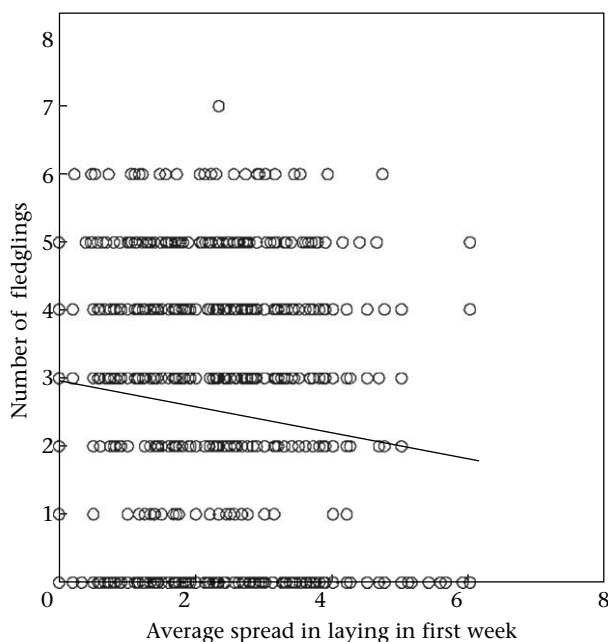


Figure 4. Relationship between the average number of fledgling European starlings produced and the average spread in laying dates among females breeding together in spatially segregated bunkers.

are correlated with a causal agent. Benefits of synchrony are purported to arise after fledging (e.g. reduced predation risk, group foraging; Smith 2004), so these factors cannot explain the pattern reported here. It is likely that all females may seek to nest as early as possible based on environmental conditions (Kallander & Karlsson 1993) and social stimulation, but only some are able to do so. Thus, synchronous assemblages may represent groups of higher-quality females, which have higher breeding success independent of synchrony. Thus, increased fledging success in synchronous assemblages may not arise because of direct benefits of synchrony that occur during the postfledging period.

Our data set encompassed 11 years, and the degree of breeding synchrony fluctuated greatly, ranging from only half of the nests to almost all of the nests in the laying stage during the synchronous period. However, with the exception of 2 years, more than 60% of females bred within 1 week of each other, and in the majority of years, laying occurred within the synchronous period in more than 70% of nests. Therefore, for most breeding seasons, breeding synchrony was rather high, consistent with the high level of breeding synchrony in starlings relative to that in other songbirds (Kessel 1951; Feare 1984).

The functional benefit to starlings of such tight breeding spreads is unclear. Overall, our results reveal a strong effect of social stimulation on breeding synchrony, although average laying dates across densities differed by 1–2 days. The biological relevance of 1–2 days is unclear, although first laying attempts were highly synchronous, with a majority of females laying within 3–4 days of the first female. Naturally forming groups of females showed tighter spread in laying dates than expected from random assemblages of equal size. Furthermore, on a larger spatial scale, we found that synchrony in laying dates was strongly affected by conspecifics, consistent with predictions of social stimulation models (Jovani & Grimm 2008). The next step would be to manipulate breeding density directly to investigate the influence of social stimulation. In addition, further research should investigate whether tight breeding spreads arise as a direct adaptation (e.g. to facilitate foraging by juveniles or to reduce negative interactions between conspecifics), or as a consequence of other factors (e.g. individual quality, male song) that arise as a result of other evolutionary forces.

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