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Nest aggregation and reproductive synchrony promote Lesser Kestrel *Falco naumanni* seasonal fitness

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Abstract Several factors promote coloniality by enhancing the fitness of colony members. In birds, spatial proximity among nests, breeder abundance and reproductive synchrony have been proposed as primary factors responsible for enhanced colonial defence and foraging success, which, in turn, enhance reproductive success. Whether these factors function synergistically or antagonistically remains, however, an open question due to the absence of an integrated analysis of their effects on fitness. We studied a large population of the Lesser Kestrel, *Falco naumanni*, a facultative colonial species, breeding in colonies of different sizes in their typical pseudo-steppe habitat. We quantified both the singular and interactive effects of nest distance, breeder abundance and reproductive synchrony on kestrel fitness measured as the time to survival of eggs to hatching and nestlings to fledging. Egg survival increased as reproductive stages became more synchronous with the timing of colony breeding, whereas nestling survival benefited from a higher synchrony with most nests in the entire population. Nestling survival was also positively affected by the interaction between nest distance and breeder abundance. Our results suggest that the presence of additional breeders in the colony is not sufficient *per se*, to trigger colonial advantages, but instead,

that synchronised reproduction among multiple breeding pairs nesting in close spatial proximity is necessary to realise those benefits. Our findings provide a novel perspective for future investigations that explore the mechanisms underlying fitness variation among Lesser Kestrel colonies and group-living species in general.

Keywords Lesser Kestrel · *Falco naumanni* · Nest distance · Nest aggregation · Breeding synchrony

Zusammenfassung

Nesterhäufung und reproduktive Synchronie begünstigen die saisonale Fitness beim Rötelfalke *Falco naumanni*

Verschiedene Faktoren begünstigen die Koloniebildung durch die Optimierung der Fitness der einzelnen Kolonienmitglieder. Es wurde angenommen, dass für die Koloniebildung bei Vögeln die räumliche Trennung der Nester, die Anzahl der Brüter, als auch die Synchronisierung der Reproduktion primäre Faktoren darstellen für eine verbesserte Koloniebehauptung und Nahrungssuche und somit auch den Erfolg der Fortpflanzung begünstigen. Ob diese Faktoren synergistisch oder antisynnergistisch wirken bleibt soweit offen, da bisher noch keine integrative Analyse auf deren Effekte auf die Fitness durchgeführt wurde. In dieser Studie wurde eine große Population des Rötelfalken, *Falco naumanni*, untersucht, eine fakultativ koloniebildende Art, die in verschiedenen Koloniegrößen in einem steppenartigen Habitat lebt. Quantifiziert wurden sowohl singuläre als auch interaktive Effekte der Nestdistanz, Brüter Häufigkeit und der reproduktiven Synchronie auf die Fitness der Rötelfalken, gemessen an der Überlebensrate der Eier, der Zeit vom Schlüpfen bis zum Nestling und zum

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Flüggewerden. Weiterhin konnte gezeigt werden, dass die Überlebensrate der Eier mit der Synchronisierung des Nistens in der Kolonie steigt, wohingegen das Überleben der Nestlinge ansteigt mit der Synchronisierung des Nistens der gesamten Population. Das Überleben der Nestlinge war außerdem positiv beeinflusst von der Interaktion zwischen dem Abstand der Nester und der Abundanz der Brüter. Unsere Ergebnisse lassen vermuten, dass die Anwesenheit zusätzlicher Brüter in der Kolonie allein nicht ausreicht, den Erfolg der Kolonie positiv zu beeinflussen, sondern dass stattdessen die synchronisierte Reproduktion vieler Brutpaare die in enger Nachbarschaft nisten, dafür von Nöten ist. Unsere Ergebnisse weisen neue Perspektiven für zukünftige Forschungsansätze auf, die sich mit den Mechanismen der Fitnessvariationen in Kolonien des Rötelfalken und anderen in Gruppen lebenden Arten befassen.

Introduction

The adaptive value of group living has been the focus of several studies (Danchin and Wagner 1997; Rolland et al. 1998; Brown and Brown 2001). Considerable effort has focused on understanding the costs and benefits of coloniality (Danchin and Wagner 1997), although to date, no general model explaining the evolution of coloniality has proven entirely satisfactory (Hoogland and Sherman 1976 but see Hare and Murie 2007). Spatial proximity among nests, breeder abundance and temporal synchrony of nesting stages have been proposed as primary factors underlying enhanced colonial defence and foraging success in colonially-breeding species (Murphy and Schauer 1996; Serrano et al. 2005a; Sachs et al. 2007).

Colonial breeders acquire fitness benefits that must outweigh the costs of both the increased competition for resources (Bonal and Aparicio 2008) and the increased risk of transmission of parasites and diseases (Serrano et al. 2004) associated with group living. Potential offsetting benefits of coloniality include a reduced risk of predation for individuals and their offspring (Bijleveld et al. 2010). An increase in the number of individuals residing in a colony may promote earlier detection of predators (Brown and Brown 1987), reduce individual investment in vigilance (Terhune and Brilliant 1996; Campobello et al. 2012) or serve to confuse or satiate presumptive predators, and therefore lower the predation risk (Oro 1996; Varela et al. 2007; Calabuig et al. 2010a).

Apart from the absolute number of individuals living together, the distance between nests also appears to have positive repercussions on reproductive success (Brown et al. 1990). Colonial individuals nesting close to each other benefit via reduced predation rates, which are

sometimes achieved through enhanced recruitment of individuals to mob predators (Hernández-Matías et al. 2003). A short distance between nests also promotes information transfer, allowing less successful foragers to glean information from neighbouring individuals regarding new food patches (Ward and Zahavi 1973; Weatherhead 1983; Campobello and Hare 2007). Negative effects, however, have been identified, with increased agonistic interactions occurring when neighbour distance shortens below a certain threshold (Serrano and Tella 2007).

Living in groups might be more advantageous when individuals synchronise the timing of breeding. Beyond swamping the capacity of predators to take vulnerable young (Varela et al. 2007), temporal overlap among a high number of breeders promotes heightened efficiency in terms of both vigilance and defence (Murphy and Schauer 1996). Asynchronous breeders, i.e. individuals nesting earlier or later than most colony members, are left by themselves to defend their eggs and nestlings (Hoogland and Sherman 1976; Campobello and Sealy 2010). As a consequence of less efficient individual nest defence in comparison to that by groups, these breeders often suffer decreased hatching and fledging success (Murphy and Schauer 1996; Stokes and Boersma 2000; Sachs et al. 2007). If reproduction of most colony members is also synchronised with the peak of food resource availability, colonial advantages may be enhanced further (Both 2010).

Clustering of nests, an increased number of breeding individuals and reproductive synchrony therefore enhance fitness, although these same factors might also impose fitness costs (Stokes and Boersma 2000). Proximity between breeders promotes extra-pair copulations (Wagner 1993), while a high number of colonial members promotes intense competition for resources (Danchin and Wagner 1997; Sachs et al. 2007; Calabuig et al. 2010b). Whether these three factors function synergistically or antagonistically remains an open question due to the absence of an integrated analysis of their effects on fitness.

In a Mediterranean area, we studied a large population of the Lesser Kestrel *Falco naumanni*, a facultative colonial raptor and a vulnerable species that only recently had its conservation status altered to “least concern” (Collar et al. 1994; IUCN 2011). The core population studied here, breeds in colony buildings surrounded by homogeneous and traditional agricultural crops (Sarà 2010; Triolo et al. 2011; Sarà et al. 2012). Mechanisms that affect population dynamics of this species have been studied in the Iberian peninsula (Negro and Hiraldo 1993; Serrano et al. 2005a; Ortego et al. 2007) but are still virtually unexplored in the remaining part of its Palearctic breeding range. In two different Spanish populations, colony abundance differentially affected the reproductive success of Lesser Kestrels because of different habitat composition surrounding the

different-sized colonies. In heterogeneous habitats, individuals in large colonies tended to produce more young (Serrano et al. 2004) but when colony nest availability was saturated, shorter distances between nests triggered increased agonistic interactions (Serrano and Tella 2007). In contrast, no colony size effect was detected on kestrel breeding performance in more homogeneous habitats (Calabuig et al. 2010b) and it is unknown whether nest distance and breeding synchrony affected kestrel reproductive success. By adopting an innovative approach to quantify distances among nests, we examined whether egg and nestling survival were affected by singular and interactive effects of nest distance, breeder abundance and reproductive synchrony on the fitness of Lesser Kestrels breeding in the Gela Plain (Italy).

Methods

Study species

The Lesser Kestrel is a small raptor that lives in open and dry cereal steppes of the Western Palaearctic (Cramp and Simmons 1980). It is a facultative colonial raptor that breeds in colonies of 2–60 pairs (Forero et al. 1996; Serrano et al. 2004), usually with Jackdaws *Corvus monedula* and Rock Pigeons *Columba livia*. The Lesser Kestrel is a secondary-cavity nester that finds its hole-nests in cliffs or wall crevices and under roof tiles of rural buildings (Negro and Hiraldo 1993). The Lesser Kestrel population in the Gela Plain, the largest in Sicily and one of the most important in Italy (Mascara and Sarà 2007), has grown consistently over the last decade (Sarà 2010).

Study area

The Gela Plain in south-eastern Sicily (Italy, 37°07'N, 14°19'E), is one of the largest plains in Italy (about 474 km²). The area is characterised by gentle slopes up to 200 m a. s. l., limestone and gypsum hills and sand and clay badlands (Mascara and Sarà 2006). Due to limited precipitation (350 mm/year), the agricultural landscape is composed of a mosaic of pseudo-steppes dominated by artichoke *Cynara* spp. fields and non-irrigated, mainly cereal, crops, garigue vegetation, fallow land and pastures. Agriculture has rapidly changed with the intensification of farming practices in some areas of Sicily and populations of Lesser Kestrels have declined because of agricultural shifts, from traditional to woody crop cultivations (Sarà 2010). Contrary to the general Sicilian trend, in the Gela Plain, a more homogeneous agricultural composition and the maintenance of traditional crops, mostly artichokes and wheat (Triolo et al. 2011), have instead represented

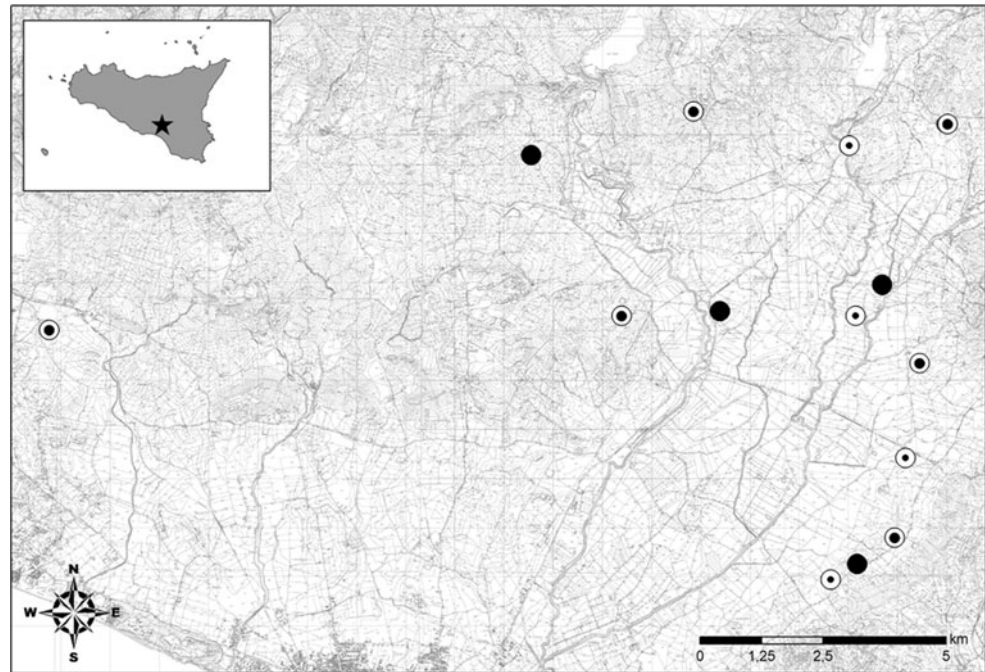
favourable conditions for an increase in the Lesser Kestrel population in the last decade (Sarà 2010). Across the plain, numerous rural buildings, often partially destroyed or abandoned, host Lesser Kestrel nests. Each colony building is usually composed of a single structure, or in rare cases, two or more small houses close to each other (i.e. <30 m apart). Colony buildings are comprised of different sides, representing different faces of the same structure.

Quantification of colony parameters

Investigations were conducted between April and July in 2009 and 2010. Lesser Kestrel nests were first identified by observing colony structures with 10 × 50 binoculars and 20 × 60 spotting scopes. We identified 14 kestrel colonies in 2009 and 12 in 2010, distributed across the plain with a distance of 7 ± 0.5 km (mean \pm SE) between each other (range: 0.6–19 km; Fig. 1). When at least one pair of kestrels showed reproductive behaviour at the observed building (i.e. a male delivering prey to a female, copulation or the inspection of nest chambers; Serrano et al. 2001; Sarà 2010), potential nests inside crevices and under tiles were inspected. Nest checking allowed the quantification of the total number of breeding pairs per colony. We identified 462 nests (18 ± 1.8 per colony per year; range: 5–33) for which we could confirm the presence of at least one laid egg. Other potential nests could not be included in the analyses because of their inaccessibility. Because of the uncertainty about the presence of these nests, it was necessary to exclude some colony sides that potentially but not certainly contained nests. We therefore studied a mean of 2.9 ± 0.4 sides per colony that included 127 nests in 2009 and 123 in 2010. Between years, the number of study nests mirrored the number of total active nests within each colony (Spearman rank order correlation, $r = 0.82$, $P < 0.0001$, $n = 26$) and could therefore be used as an index of colony breeder abundance. Each nest was checked at least three times per season: during egg-laying/incubation and at hatching and fledging times. This schedule allowed the collection of sufficient data to ascertain reproductive success, while simultaneously minimising disturbance at the reproductive sites. During nest checks, we recorded the number of eggs and nestlings inside each nest. As part of a larger investigation, nestlings were marked with numbered aluminium and plastic coloured rings for remote identification of individuals.

The reproductive success of breeding pairs was determined by analyses of the survival time of each egg to hatching and nestling to fledging (Nur et al. 2004). The identification of various reproductive stages was derived from the data collected from nest checks or by a backdating process standardised on 7 days for laying, 29 days for incubation and 29–32 days for fledging periods (Cramp

Fig. 1 Map of the Gela Plain (Sicily, Italy) showing the spatial distribution of Lesser Kestrel colonies. *Small dots* 1–11 pairs; *medium dots* 12–22 pairs; *full circles* 23–33 pairs



and Simmons 1980; Sarà unpubl.). Missing eggs and nestlings and those found with evident signs of predation were recorded as being predated. In some instances of unhatched eggs and nestlings found dead in the nest, we were unable to identify the exact cause of mortality which might have included thermoregulation failure and starvation, due to heavy spring rain and food depletion or inefficient foraging, respectively. Because of such an uncertainty, we could not perform separate analyses per mortality cause. All unhatched or missing eggs and dead or missing nestlings were treated as failed on the day corresponding to the midpoint between the last two consecutive visits (Mayfield 1975; Serrano et al. 2001; Mascara and Sarà 2006).

To determine the role of the number and proximity of conspecifics on reproductive success, we tested the effect of three factors: neighbour index (NI, Campobello and Hare 2007), nearest nest distance (NND, i.e. the shortest distance between the focal nest and its closest neighbouring nest; Negro and Hiraldo 1993) and breeder abundance (i.e. the number of breeding pairs per colony side) on individual fitness. The first index, NI, quantifies the interactive effect between the number of neighbours and their proximity to the focal nesting pair, NND and breeder abundance quantify separately the two variables of nest proximity and number of neighbours, respectively. To quantify both indices, it was necessary to calculate the distances between nests. To do this, colony sides were photographed with a Leica D-Lux 4 and colony photos were uploaded to the software TechDig 2.0. A set of Cartesian axes was assigned to each photo and the length of a reference previously measured in the field (e.g. height of a door, distance

between windows, etc.) was recorded. The position of each nest was marked on the photo, so that x–y coordinates were used to calculate Euclidean distances between each pair of nests (Fig. 2).

The neighbour index was calculated using the formula:

$$NI_{nest_n} = \sum_{i=1}^n (1/dist_{-nest_n})$$

where n is the nest number and $dist_{-nest_n}$, the distance between the nest of interest and each of the other nests on the same colony side (Campobello and Hare 2007). A low value of the index indicates an isolated nest, while a high NI value indicates a nest surrounded by many other active nests in close proximity.

To quantify reproductive synchrony, we adopted the synchrony index (SI) as proposed by Kempnaers (1993) and Class et al. (2011) and applied it to single colonies (Johnsen and Lifjeld 2003; LaBarbera et al. 2010). We estimated three synchrony indices: (1) SI nest/pop as the proportion of fertile females in the population for each day of the focal female's fertile period (Kempnaers 1993; Class et al. 2011); (2) SI nest/col as the proportion of fertile females in the colony for each day of the focal female's fertile period (Johnsen and Lifjeld 2003; LaBarbera et al. 2010); and (3) SI col as the proportion of fertile females within each colony during the fertility period of all colony females (Johnsen and Lifjeld 2003; LaBarbera et al. 2010). The above indices thus quantified the breeding synchrony of each nest with respect to that of the entire population (SI nest/pop) and its colony (SI nest/col), and provided an estimate of the breeding



Fig. 2 Side of one of the colonies that housed Lesser Kestrel nests (red circles). To calculate the distance between nests, a set of Cartesian axes (red lines) and a metric reference (yellow line) previously measured in the field were overlaid onto the digital photograph (colour figure online)

synchrony occurring within each colony (SI col). We considered the fertile period of kestrel females to be from 5 days prior the laying of the first egg (Negro et al. 1992) to the end of the laying period (Mougeot 2004), thus, for a total of 12 days. Although these three indices were correlated with each other (Spearman correlation, $n = 248$, $r = 0.62\text{--}0.70$, $P < 0.001$), they showed a different response as independent factors to egg and nestling survival (see “Results”) and were therefore analysed singly.

Both the variables NND and NI showed a symmetrical and opposite response if correlated with the breeder abundance (Online Resource 1). Thus, as the number of neighbours increased, the nearest distance became shorter, while the mean distance with all the other nests increased. Because of the opposite and symmetrical correlations, distances and number of pairs were maintained as potential predictors to be tested.

Statistical analyses

We determined whether nest distances differed between years with an Analysis of Variance (ANOVA, Zar 1999) where the study year was the orthogonal fixed factor with two levels, one per study year. The survival time of eggs and nestlings was examined using the Kaplan–Meier product limit (Kaplan and Meier 1958; Nur et al. 2004; Bellia et al. 2011). Differences in egg and nestling survival between years were determined using the Gehan–Wilcoxon test, by treating the study year as an independent factor and

survival time as the dependent variable (Cox and Oakes 1984; Fox 2001).

The effect of nest distance, colony size, their interaction effect, and reproductive synchrony was quantified by conducting separate parametric survival tests (Lognormal tests, Dempster et al. 1977) where NI, NND, breeder abundance and SIs were treated as independent factors and egg and nestling survival times were the dependent variable. These models used the expectation maximisation algorithm (Dempster et al. 1977), where the normal distribution of the log-survival times was revealed by points of residual survival times arranged in a straight line. If a regression revealed a statistically significant effect, the survival curve obtained with the minimum and maximum predictor values recorded in the population was projected against the curve obtained with the mean predictor value.

To control for any confounding effect of the first laying day on the nestling survival we calculated the Julian date corresponding to first laying day for each nest and then we conducted a survival test by using Julian dates as independent factor and nestling survival time as dependent variable. Nestling survival was not affected by first laying day (log normal tests, $\chi^2 = 6.45$, $P = 0.096$, $N = 913$), so we excluded a possible effect of the laying date on lesser kestrel nestling survival.

To control for any bias that might have been incurred by determining the survival of each egg and nestling, two separate nested ANOVAs (Underwood 1997), were conducted, using the proportion of eggs hatched and chicks fledged as dependent variables, year and colony size as

independent factors, and colony identity as a random term. Both colony size and identity were nested in year. Results revealed no effect of the year or colony size on either hatching or fledging rates (Online Resource 2), but colony identity did have an effect on both these rates (Online Resource 2). Post hoc tests revealed one single colony to be significantly different from the others in terms of hatching (Newman–Keuls test, between MS = 0.07, $P = 0.023$ for 1 out of 24 pairwise comparisons) and fledging (between MS = 0.06, $P < 0.010$ for all pairwise comparisons) values. Therefore, this colony was removed from the following analyses.

Finally, we tested the relationship between reproductive synchrony and level of nest aggregation by using linear regressions (Zar 1999) between SIs and all NI. All analyses were conducted using STATISTICA 6.0 software (Statsoft Inc. 2001).

Results

Distances between nests did not differ (ANOVA, $F_{1,248} = 2.07$, $P = 0.151$) between 2009 (mean \pm SE: 4.24 ± 0.40 m, $n = 127$) and 2010 (3.31 ± 0.27 m, $n = 123$). The shortest distance between nests ranged from 0.34 to 25.02 m and colony sides hosted 2–11 breeding pairs (5.7 ± 0.08) with 1–23 pairs per colony (10.0 ± 1.10). Nest aggregation measured by the NI ranged from 0.0004 (i.e. isolated nests) to 0.0517 (i.e. nests surrounded by many others within a short distance). Each female overlapped each day of its fertile period with a mean of 39 % (± 0.9 %) of all other fertile females in the population and with 41 % (± 1.2 %) of fertile females in its colony. Single colonies showed 41 % (± 0.7 %) of all nests overlapping their breeding on each day of the kestrel fertility period. This last SI was dependent on nest clumping (i.e. NI), indicating that the more numerous and less distant were the pairs in the colony, the more synchronised was their breeding period (Spearman correlation test: $r = 0.138$, $P = 0.030$, $n = 248$).

The cumulative proportion of eggs that survived to hatching was 0.88 ± 0.01 in 2009 (Kaplan–Meier product limit, $n = 564$) and 0.87 ± 0.01 in 2010 ($n = 583$), while the cumulative proportion of nestlings that survived was 0.69 ± 0.03 ($n = 409$) and 0.77 ± 0.02 ($n = 504$) in 2009 and 2010, respectively. There was no year effect on the survival of eggs (Gehan's Wilcoxon test, $WW = 1666$, $P = 0.80$, $n = 1147$) or nestlings ($WW = -6201$, $P = 0.20$, $n = 913$), allowing data for the two study years to be pooled for further analyses.

Among the independent variables examined, only SI within colonies (SI col) had a significant effect on egg survival to hatching, indicating that more synchronous nests within colonies benefited from a higher hatching rate

Table 1 Effects of neighbour index, nearest nest distance, breeder abundance and breeding SI on the survival time of eggs of Lesser Kestrels breeding in the Gela Plain (Lognormal test, $n = 1147$)

	χ^2	P
Neighbour index	1.50	0.2199
Nearest nest distance	1.56	0.2111
Breeder abundance	3.27	0.0707
SI nest/pop	2.30	0.1292
SI nest/col	4.06	0.0439
SI col	8.43	0.0037

SI nest/pop proportion of fertile females in the population for each fertile day of the focal nest, SI nest/col proportion of fertile females in the colony for each fertile day of the focal nest, SI col proportion of colony fertile females for each day of the kestrel fertility period

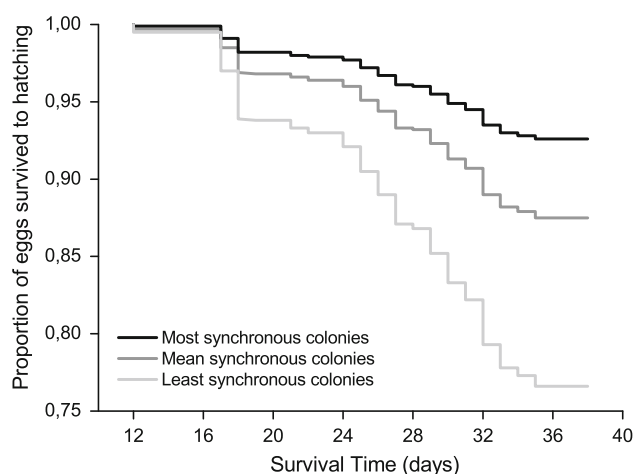


Fig. 3 Survival curves of Lesser Kestrel eggs calculated with minimum, mean and maximum values of breeding SI col values recorded in the population of the Gela Plain (Sicily, Italy)

(Table 1). The positive effect of breeding synchrony on egg survival is shown in Fig. 3, where the survival curve of the population is compared with that resulting from the least or most synchronous colonies. Nestling survival was affected by NI (Table 2). Because neither the NND nor the breeder abundance affected nestling survival (Table 2), these results indicated that proximity and the number of neighbours affected the survival of nestlings via their interaction (i.e., quantified as NI), rather than as individual variables. Contrary to egg survival, nestling survival was also positively affected by population rather than colony breeding synchrony (Table 2). Figure 4 shows the higher survival of nestlings in the most clumped and synchronous nests.

Discussion

In the Gela Plain, nest clumping and reproductive synchrony enhanced the reproductive success of a large Lesser

Table 2 Effects of neighbour index, nearest nest distance, breeder abundance and breeding SI on the survival time of nestlings of Lesser Kestrels breeding in the Gela Plain (Lognormal test, $n = 913$)

	χ^2	P
Neighbour index	12.33	0.0004
Nearest nest distance	0.55	0.4572
Breeder abundance	1.60	0.2065
SI nest/pop	4.86	0.0274
SI nest/col	3.33	0.0682
SI col	0.83	0.3627

SI nest/pop proportion of fertile females in the population for each fertile day of the focal nest, SI nest/col proportion of fertile females in the colony for each fertile day of the focal nest, SI col proportion of colony fertile females for each day of the kestrel fertility period

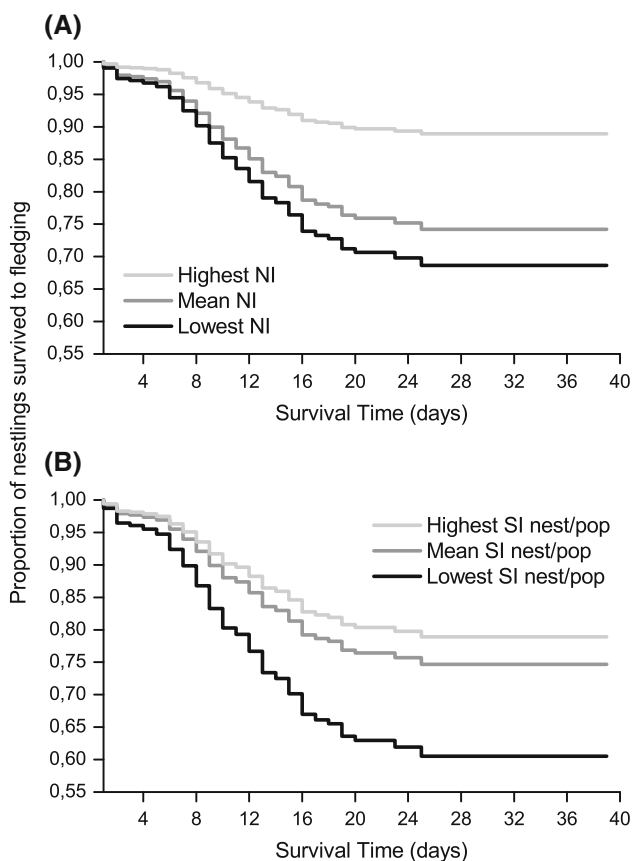


Fig. 4 Survival curves of Lesser Kestrel nestlings calculated with minimum, mean and maximum values of **a** NI and **b** breeding SI nest/pop, both recorded in the population of the Gela Plain (Sicily, Italy). The NI is a measure of nest aggregation that increases with the number of breeding neighbours and decreases with the distance between the focal nest and all conspecifics nesting on a colony side. SI nest/pop: proportion of fertile females in the population for each fertile day of the focal nest

Kestrel population nesting in its typical pseudo-steppe habitat. Breeding individuals surrounded by several conspecifics in close proximity and synchronised in their

reproduction, fledged more young than isolated and relatively asynchronous breeding pairs.

In Lesser Kestrels, colony size is strictly related to breeding experience. Dispersing individuals are often breeders at their first nesting attempt (Jovani et al. 2008; Serrano and Tella 2012). They are prevented from nesting in large colonies by philopatric pairs and then become founders of new small colonies (Serrano and Tella 2007; Calabuig et al. 2010b). Depending on the surrounding habitat, large and small colonies might offer different or similar bases for successful reproduction. In large colonies of one Spanish population occurring in good quality patches, adult kestrels benefited from higher reproductive output than yearlings in small colonies that insisted on habitats rendered suboptimal by a particularly high predation rate (Serrano and Tella 2007). On the contrary, in another population, philopatric individuals and founders nesting in large and small colonies, respectively, enjoyed a similar fitness, probably because of more homogeneous agricultural crops being present near to colony buildings (Calabuig et al. 2010b). The findings of the latter case study are consistent with our results, where a homogeneous land use cover across the Gela Plain (Sarà 2010) might have offered all colonies consistent foraging opportunities and resulted in a similar breeding performances irrespective of the colony size (Mascara and Sarà 2006).

In the Gela Plain, nest clumping and colony abundance did not contribute to higher reproductive success as single factors, but via their interactive effect. An opposite relationship between colony size and nest distance was found in one Spanish kestrel population where the increase of colony size beyond a certain threshold exerted a negative effect because of its repercussions on nest distance (Serrano et al. 2004). Larger colonies implied a shorter distance to the closest breeding neighbour and a consequent increase in agonistic interactions (Serrano and Tella 2007). As the colony became larger, we recorded the same decrease in the closest neighbour distance while the mean distance with the other breeding neighbours increased. This latter event might have compensated for the first effect, resulting in a non-significant single effect of nest distance on reproductive success.

In Spain, the main causes of kestrel nesting failure are predation (Serrano et al. 2004) and nestling starvation (Bonal and Aparicio 2008). Predation was particularly recorded in small colonies that were more accessible to predators (Serrano et al. 2004). In the Gela Plain, 88 % of colony structures are farmhouses with a similar status (i.e. abandoned buildings, partially in ruins with roof still present; Mascara and Sarà 2006; Sarà et al. 2012) which apparently eliminates predator access as a factor that differs between different-sized colonies. Because of their aerial and diurnal activity, Lesser Kestrels might find it

difficult to spot some terrestrial predators, such as Bank Rats (*Rattus rattus*; Serrano et al. 2004); however, the presence of aerial predators might be easier to identify, and the detection, deterrence and defence behaviours by each individual might improve the antipredator efficiency of the group (Brown et al. 1990; Westneat 1992; Arroyo et al. 2001; Campobello and Sealy 2011a, b). Previous findings at the Gela Plain showed that Lesser Kestrels group-mobbed potential aerial predators (Campobello et al. 2012), which is consistent with predation events by European Magpies (*Pica pica*), Jackdaws (*Corvus monedula*) and Common Ravens (*Corvus corax*) recorded during several observation sessions (Campobello et al. 2012, unpubl. data). Accordingly, a valid working hypothesis might test whether enhanced antipredator advantages contribute to the reduced nesting failure among densely clumped breeders found in this study.

The mechanisms underlying our results might also relate to improved foraging efficiency among pairs with many conspecifics breeding in close proximity. In another Spanish population, an important cause of mortality of kestrel nestlings was starvation, mostly recorded in large colonies more exposed to density-dependent food depletion (Bonal and Aparicio 2008). As mentioned above, a more homogeneous habitat composition in the Gela Plain (Sarà 2010; Triolo et al. 2011) might explain the nonsignificant effect of colony size on kestrel reproductive success. Instead, consistent hypotheses worth testing might include improved foraging opportunities and the exchange of information on the whereabouts of good hunting patches (Ward and Zahavi 1973; Campobello and Hare 2007).

In our study population, nest success was also positively correlated with reproductive synchrony. Synchrony at the colony and population level, however, played a different role in egg or nestling survival. Colony synchrony allowed a higher survival of eggs to hatching, while population synchrony increased the survival of nestlings until fledging. In other kestrel populations, age at first breeding has been found to affect synchrony, with yearlings nesting in small colonies being less synchronous and productive than adults (Serrano et al. 2004). A different age composition between differently sized colonies was not observed (M. Sarà unpubl. data), although a more specific study is warranted. Antipredator and/or foraging advantages facilitated by nest clustering would be rendered irrelevant if reproduction among those neighbouring breeding pairs did not overlap temporally. In fact, individuals that start breeding much earlier or later than their neighbours-to-be are effectively isolated breeders and as such, do not enjoy the possible benefits of dilution of predation risk (Varela et al. 2007), enhanced predator detection and deterrence (Wissel and Brandl 1988; Westneat 1992; Murphy and Schauer 1996) or temporal overlap between source peak demand and

habitat availability (Post and Forchhammer 2008; Campobello and Sealy 2009; Rodriguez et al. 2010; Møller et al. 2011).

Our results reveal how colonial factors, typically examined separately, act in concert to affect the fitness of Lesser Kestrels. The abundance of colonial breeders and nest aggregation interact to enhance fitness, although the mechanisms that underlie such benefits are still to be identified as antipredator and/or foraging advantages. Our results, however, revealed no effect of nest clumping on hatching success, which is consistent with the previously reported finding that egg hatchability is independent of colony size (Serrano et al. 2005b). Identifying the putative cause of nestling and egg mortality, including the type of predator, determining colonial age composition and comparing food availability and quality of kestrel diet relative to nestling status would all prove useful in disentangling the potential coloniality benefits provided by synchronous reproduction among tightly clustered breeding pairs.

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