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Colony Size Selection Determines Adult Survival and Dispersal Preferences: Allee Effects in a Colonial Bird

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ABSTRACT: Avian coloniality traditionally has been investigated by examining how breeding success varies with colony size, but other crucial fitness components rarely have been examined. This may lead to wrong conclusions because unmeasured parameters may change the final fitness balance. We used multistate capture-recapture models to investigate adult survival and dispersal in relation to colony size within a long-term monitored population of lesser kestrels (*Falco naumanni*). Nest predation probability decreases with colony size, and adult survival is predicted to show the same trend because adults are exposed to the same suite of predators. As expected, survival probability was higher in large colonies (0.72 ± 0.015; mean $\pm$ SE) than in medium or small colonies (0.65 ± 0.02). Additionally, dispersal probabilities were higher going from small to large colonies (0.20 ± 0.01) than from large to small (0.08 ± 0.01), as predicted by theory of habitat selection shaped by fitness maximization. These asymmetries are likely to generate size-specific colony population dynamics, so they should be taken into account in studies of colonial birds and other metapopulation-like systems. Allee effects, that is, positive density dependence, appear to be the cause of the evolution of dispersal behavior and may explain the maintenance of coloniality in this species.

Keywords: survival, Allee effect, coloniality, dispersal, *Falco naumanni*, multistate capture-recapture models.

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Many animals form conspecific aggregations for all or part of their lives, and colonies of birds are among the most impressive examples of group-living animals. Therefore, it is not surprising that avian coloniality had long attracted the interest of evolutionary and behavioral ecologists (e.g., Lack 1966) who have devoted a great effort to unravel the selective pressures promoting this kind of conspecific aggregation (e.g., Wittenberger and Hunt 1985; Brown and Brown 1996; Rolland et al. 1998). Yet, the ultimate causative factors of coloniality are controversial and much in dispute, so it remains as a less understood avian social breeding system (Brown and Brown 2001).

Avian colonies usually vary greatly in size even within the same population (Brown et al. 1990). For this reason, classic attempts to explain the evolutionary origin of coloniality focused on the costs and benefits faced by individuals living in colonies of different sizes (e.g. Hoogland and Sherman 1976; Møller 1987; Brown and Brown 1996; Tella 1996). However, this economic approach recently has had critics who argued that it is difficult to distinguish between causative and maintenance factors (Danchin and Wagner 1997; Brown and Brown 2001). Moreover, the identification of all costs and benefits associated with colony size is extremely difficult, so an alternative framework is to use the fitness effects of colony size as an integrative measure of the balance between its advantages and disadvantages (Brown and Brown 1996; Danchin and Wagner 1997; Tella et al. 1998). Research that has addressed the relationship between the number of breeding pairs in a colony and a fitness component has found that there often is an optimal colony size in which individuals experience their highest breeding success (see Brown and Brown 2001 for a review). For this reason, the persistence of colony size variation is doubtless one of the most intriguing features associated with avian coloniality (Brown et al. 1990; Brown and Rannala 1995; Safran 2004; Serrano et al. 2004). In fact, several species may breed both solitarily and in colonies of different sizes (e.g., fieldwares *Turdus pilaris*, Wiklund and Andersson 1994; tree sparrows *Passer montanus*, Sasvári and Hegyi 1994), a phenomenon that

has been interpreted as an evolutionary transitional state from territoriality to coloniality (Siegel-Causey and Kharitonov 1990). Regardless of putative origin, the study of the relationship between fitness and colony size is of great importance in understanding the maintenance and current evolution of this kind of social organization (Brown and Brown 2001).

Empirical evidence of how fitness varies with colony size comes almost exclusively from research focused on breeding performance (e.g., Hoogland and Sherman 1976; Sasvári and Hegyi 1994; Wiklund and Andersson 1994; see Brown and Brown 2001 for a review). However, fitness results not only from breeding success but also from survival parameters. While it has been claimed that we need more information on reproductive success of colonial birds as a parameter integrating all costs and benefits of coloniality (Danchin and Wagner 1997), the relationship between survival and colony size has been largely ignored (but see Spendelow et al. 1995; Brown et al. 2003; Brown and Brown 2004). This deficiency of information could be greatly hindering our interpretation of the consequences of living in different group sizes, and it therefore constitutes one of the major gaps in the knowledge of avian coloniality. Moreover, the relationship between colony size and survival may have serious implications for the understanding of both local population and metapopulation dynamics in colonial birds, especially in medium- to long-lived species in which population persistence is more sensitive to adult survival and dispersal than to fecundity (Sæther and Bakke 2000).

The little effort devoted so far to estimating survival in relation to colony size no doubt is a result of logistical and practical difficulties in collecting high-quality field data and applying appropriate statistical tools. Estimating survival probabilities requires monitoring large numbers of banded individuals through space and time and covering the whole range of colony sizes. Moreover, studies of colonial birds in which every individual that is alive is detected at every sampling occasion are virtually nonexistent, and therefore a statistical approach developed in a capture-recapture context is necessary (Lebreton et al. 1992). Recent development of capture-recapture modeling and its implementation in software packages have allowed for the incorporation of transition probabilities and multiple strata (e.g., Arnason 1972; Brownie et al. 1993; Nichols and Kendall 1995). These multistate models have been used to estimate survival and dispersal of individuals among multiple locations (e.g., Spendelow et al. 1995; Tavecchia et al. 2002; Cam et al. 2004) as well as to estimate survival and transition probabilities among individual states (e.g., Cam et al. 1998; Reed et al. 2003). Similarly, these models constitute an appropriate method to obtain accurate estimates of survival and movement probabilities in relation to colony size (Brown et al. 2003).

In this article, we used multistate capture-recapture models to investigate adult survival and dispersal in a long-monitored population of the facultatively colonial lesser kestrel (*Falco naumanni*) in relation to colony size. Previous research on our studied population has revealed that nest predation, the most important determinant of breeding success (Serrano et al. 2004), decreases with colony size (fig. 1). This density-dependent relationship between breeding success and colony size has been suggested as an important factor affecting individual decisions about dispersal and colony size selection, lending support to the hypothesis that nest predation avoidance is one of the major advantages of coloniality in this species (Tella 1996; Serrano et al. 2001, 2003, 2004). However, adult survival processes are not directly observable in the wild, so the effect of breeding colony size selection on this parameter is unknown.

Our main hypothesis is that adults experience predation-related costs of settling in small colonies, so we expect adult survival probabilities to increase with colony size. In this way, Allee effects, that is, positive density dependence (Allee et al. 1949; see Courchamp et al. 1999; Stephens and Sutherland 1999 for reviews), could be shaping the evolution of behavior. Accordingly, individuals are expected to exhibit adaptive breeding site selection decision rules with regard to the risk of predation to maximize their fitness prospects (e.g., Holt and Barfield 2001) because dispersal probabilities are higher going from small to large colonies than in the opposite direction. Although these predictions are plausible, other factors could be affecting the relationship between adult survival, dispersal, and colony size. Presumably, individuals could also pay survival costs to breed in large colonies. In particular, males settling in large colonies are involved in violent fights that lower their body condition at the beginning of the breeding season (Tella 1996). Moreover, depletion of food resources occurs in the surroundings of the largest colonies during the chick-rearing stage, so adults must travel longer distances to feed their young (Tella 1996). By estimating survival and dispersal probabilities in relation to colony size, we can obtain an integrative measure that weights the costs and benefits of group living and thereby gain insight into current selective pressures related to colony size selection in this facultative colonial bird.

Methods

Study Species and Study Area

Lesser kestrels are small (~150 g), hole-nesting, threatened falcons that prey mostly on invertebrates. They are mi-
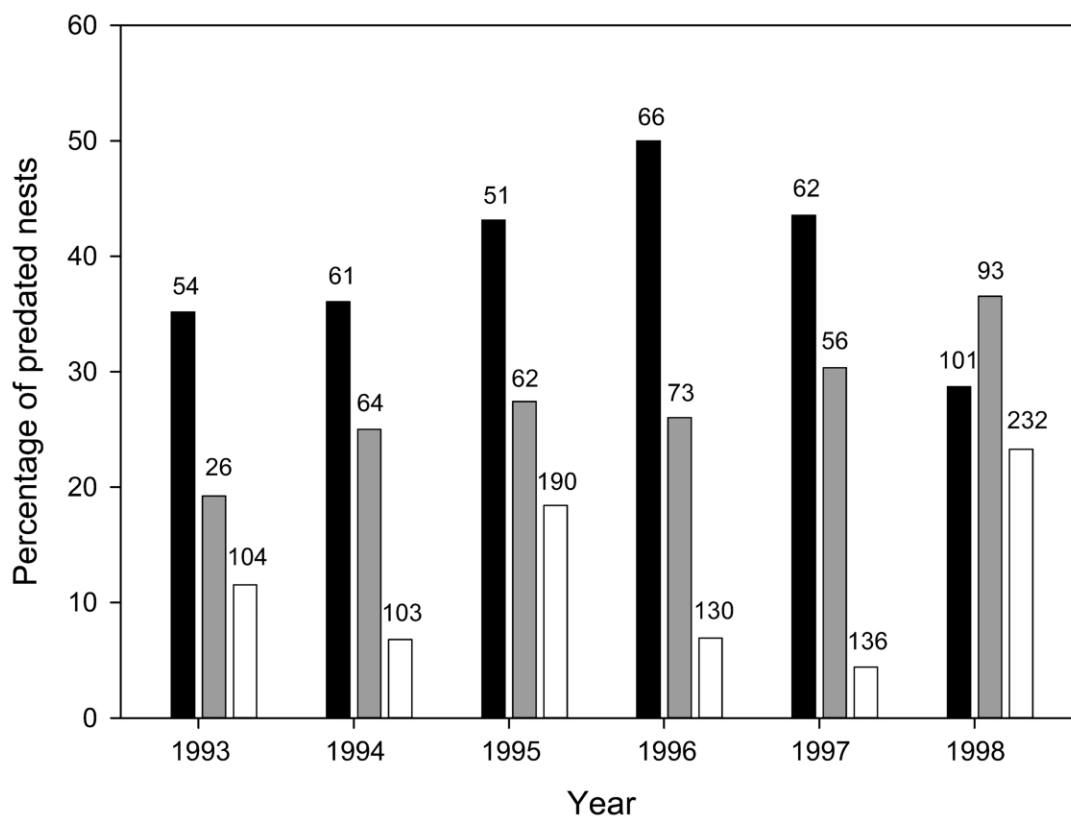
Figure 1: Percentage of nests predated in small (*black*), medium (*gray*) and large (*open*) colonies of lesser kestrels in the Ebro Valley. Sample sizes (number of nests) are indicated above the bars.

gratory birds, and both sexes are easily distinguishable by plumage in the field. At arrival from the wintering quarters, males choose a nest hole and defend it vigorously while displaying to attract a female, but they are otherwise nonterritorial. Males feed females before laying, which occurs in early May. Both sexes roost inside the nest at night before laying and incubate at day, but only females incubate and brood young chicks at night. Lesser kestrels are predominantly monogamous and single-brooded falcons (Negro 1997).

From 1993 to 2000, lesser kestrels were studied in the Ebro Valley, northeastern Spain, where the population was intensively monitored in an area of ~10,000 km². There, they breed under tiled roofs of abandoned farmhouses surrounded by traditionally dry-farmed cereal crops. During the study period, these buildings attracted both solitary pairs and colonies of two to 43 pairs. The number of colonies in the study area has increased from 52 in 1993 to 181 in 2000.

Lesser kestrels are exposed to a large array of predators, mainly red foxes (*Vulpes vulpes*) and brown rats (*Rattus rattus*) in the studied population (Serrano et al. 2004).

These are known to prey both on nestlings and adults, although in many cases of nest predation it was not possible to determine whether adults were killed and removed or had escaped.

Data Collection and Individual Capture-Reencounter Histories

From 1993 to 1999, 4,901 fledglings and 640 adults captured by hand in their nests were each banded with a numbered metal ring and a plastic color band engraved with a two-digit alphanumeric code that could be read with spotting scopes. Each year, regular surveys were carried out to locate colonies and to read bands. Intensive observations of banded kestrels were mostly made during the prelaying period (March–April), but capture-recapture histories were also completed during May and June when we surveyed the colonies directly to record breeding parameters. Because our data set was based on both recaptures and resightings, we use the term "reencounter" for both situations throughout the article. Colony size was defined as the final number of established pairs defending

a nest site, that is, attempting to breed. Further details about field procedures can be found in articles by Serrano and Tella (2003) and Serrano et al. (2004).

As we were interested in adult survival, the capture-recapture data set we used included only breeding birds, that is, adults banded in their nests or birds banded as fledglings that recruited into the breeding population. We were confident in assigning individuals to breeder or non-breeder status because colonies were monitored intensively. Breeders were paired individuals that defended a nest hole where they attempted to breed, while nonbreeders were unpaired floaters that visited several colonies throughout the breeding period. For analytical purposes, we treated individuals banded as chicks as having been marked for the first time when they were first observed as breeders. The data were split into two groups according to sex, and colony sizes were categorized into three classes according to colony size distribution in the population while maintaining enough sample sizes for each colony class (Tella 1996): small (one to three breeding pairs), medium (four to nine pairs), and large (more than nine pairs). This division could seem arbitrary, but our results did not change substantially if we categorized colony sizes in other classes. Although some colonies varied in size across years, transition probabilities were estimated only for changes in colony size, irrespective of whether birds changed between physical colonies. We did not try to separate the two effects for two reasons. First, the number of parameters increases rapidly with the number of states, which may produce problems of stability of estimation, precision of estimates, and identifiability of parameters (Lebreton and Pradel 2002). Second, there was no way of knowing whether a bird was a real disperser in year t if it escaped detection in the previous sampling occasion $t-1$. However, all transitions between small and large colonies implied actual breeding dispersal events (i.e., changes between physical colonies), so we could study actual movement rates between these colony size classes by modeling only changes in colony size.

Estimates of survival probability may be biased by permanent emigration of birds from the study area. In our case, this is unlikely because we intensively monitored a discrete, geographically isolated population occupying a large area (10,000 km^2) and encompassing colonies separated by distances exceeding by far the maximum breeding dispersal distances recorded in this population (Serrano et al. 2001). In addition, 96.4% of adults showed breeding-subpopulation fidelity (i.e., philopatry to clumped aggregations of colonies; see Serrano and Tella 2003), and we monitored all known subpopulations within our studied system each year. Moreover, no case of adult emigration to the nearest populations of lesser kestrels was detected during the study period in spite of intensive mon-

itoring of birds by other research teams (M. Alberdi, C. Gutiérrez, and L. Brun, personal communication). Permanent emigration, if it existed, was therefore negligible, so we are confident that our estimates of survival are very close to real survival.

Statistical Procedures

We used multistate models to estimate survival, reencounter, and transition probabilities via maximum likelihood methods (Nichols and Kendall 1995; Lebreton and Pradel 2002). We started with a general Arnason-Schwarz model, the multistate analogue of the Cormack-Jolly-Seber model with time-specific parameters (see Arnason 1972; Schwarz et al. 1993). This fully time-dependent model makes some fundamental assumptions, so we first tested its goodness of fit using the program U-CARE (Pradel et al. 2003). Then we used program MARK (White and Burnham 1999) to implement the Arnason-Schwarz model, in which all parameters are modeled as a first-order Markovian process (i.e., survival, transition, and reencounter of individuals in year t are conditional on their state in year $t-1$). Survival probability is denoted ϕ, reencounter probability is p, and transition probability is ψ. Colony size, sex, and time variations are specified by using subscripts c, s, and t, respectively. When more than one factor is involved, interaction terms are denoted by asterisks. Our general model had colony size-, sex-, and year-specific probabilities of survival, reencounter, and transition (ϕ_{c*s*t}, p_{c*s*t}, ψ_{c*s*t}). We fitted biologically sensible, constrained versions of this general model that reduced the number of parameters by assuming that ϕ and ψ were constant among colony sizes, among years, and between sexes. However, field effort increased through the years and the sexes differ somewhat in behavior, so we assumed that reencounter probabilities were fully time- and sex-dependent. We used the Akaike's Information Criterion corrected by sample size (AICc; see Burnham and Anderson 1998) to select the most parsimonious model. For model ranking, we report the difference between the best-fitting and other candidate models (ΔAICc) as well as the relative weight of evidence in favor of a particular model (AICc weight). Among the models with greatest support, we also constructed several models in which the effect of colony size, sex, and time were additive (denoted by a plus sign). Model-averaging procedures implemented in MARK were used to obtain model-weighted parameters and unconditional standard errors for the most parsimonious models (Burnham and Anderson 1998). Only the 15 top-ranked candidate models are reported.

Results

After removing birds banded as fledglings that did not recruit as breeders, a total of 662 males and 1,075 females were retained for analysis (table 1). We did not find evidence of lack of fit in the fully parameterized Arnason-Schwarz model (males: $\chi^2 = 94.18$, df $= 98$, $P = .59$; females: $\chi^2 = 128.21$, df $= 111$, $P = .13$). Thus, we did not need to account for transient effects, trap-dependence effects, or other sources of deviation from the general model. We were able to constrain the general model and to obtain models that described the data more parsimoniously. The best model was 3.5 times better supported than the second-ranked model according to AICc weights (table 2).

With regard to reencounter probability, the two initial models with the lowest AICc value (table 2) included colony size, sex, and time as additive effects; that is, the differences were constant among colony sizes and between sexes on a logit scale. The year-specific probabilities of reencounter were higher for medium and large than for small colonies and also higher for males than for females (fig. 2*A*). Model averaging of the two top-ranked models provided probabilities of reencounter ranging from 0.44 (females of small colonies in 1994) to 0.88 (males of large colonies in 1999).

The model we finally selected also included an additive effect of colony size and time on survival probability; that is, the differences in survival among the three colony sizes were constant across years. We calculated average survival per colony size class during the study period as the geometric mean (Cormack 1964) and its standard error with the δ method (Seber 1982). Survival probabilities were very similar for small (0.647 ± 0.019) and medium colonies (0.653 ± 0.018), whereas differences were seen for large colonies (0.72 ± 0.015). The second-ranked model (table 2) showed a very similar structure but included an interaction instead of an additive term between colony size and time. Model-averaging procedures for the two models with highest support provided estimates of survival ranging from 0.56 (SE = 0.04) for small colonies in 1998 to 0.79 (SE = 0.04) for large colonies in 1994 (fig. 2*B*). It is worth noting that survival varied with colony size in the four top-ranked models (table 2), with the first model not including a colony size effect differing greatly from the best-fitting model (ΔAICc = 38.30, AICc weight = 0.00). This provides strong evidence against the null hypothesis of equal adult survival probabilities among colony sizes.

For dispersal probability, the model we finally selected (table 2) indicated that movement among colonies of different size was time- and colony size–dependent. In fact, transition probabilities showed this structure in the 26 top-ranked models (results not shown). This indicates that movement probability among colony sizes varied among years. Transition probabilities between large and small colonies were estimated on the basis of birds changing physical location in all cases. Given that the distribution of colony sizes within the population did not vary among years (mean [range]: small, 72.25 [40–132]; medium, 20.25 [6–42]; large, 13.75 [8–23]; Kruskal-Wallis test: $\chi^2 = 7.0$, df $= 7$, $P = .43$; 55–197 colonies monitored per year), we did not expect time-specific variations in movement between these colony size classes. However, transition between other colony sizes is estimated on the basis of individuals dispersing between colonies and individuals being philopatric to a colony that changed in size, so both effects were confounded. Thus, we tested a model in which transition probabilities between large and small colonies were constrained to be constant among years, maintaining time-specific variations in the remaining combinations of movement between states. This model had overwhelming support (AICc = 8,893.25; AICc weight = 1.00, number of parameters = 48, deviance = 2,115.72), improving substantially the previous best model (ΔAICc of best model in table 2 = 12.01; AICc weight = 0.00). Dispersal probabilities were 0.20 (±0.02) from small to large colonies and 0.08 (±0.01) from large to small colonies.

Table 1: Number of observations of adult lesser kestrels used to fit multistate models of survival and dispersal in relation to colony size

Year	Small		Medium		Large	
	Males	Females	Males	Females	Males	Females
1993	26	44	14	22	52	102
1994	27	32	22	35	68	87
1995	33	48	37	52	93	118
1996	54	85	54	76	114	133
1997	38	49	49	62	127	163
1998	50	81	43	84	161	219
1999	76	131	69	144	112	147
2000	23	35	37	71	97	122

Note: Small = one to three breeding pairs, medium = four to nine, and large = more than nine.

Discussion

This study demonstrates that annual survival of adult lesser kestrels in the Ebro Valley varied with colony size. According to the best-fitting model, adult survival was 8%–14% higher for birds attempting to breed in large than in medium or small colonies. However, our results do not necessarily imply a causal relationship between colony size selection and individual survival. Differential survival patterns could be a consequence of birds of lower quality having a lower probability of survival and settling in the smallest colonies. Contrarily, body condition of males at

Table 2: Multistate models for the effect of breeding colony size (c), time (t), and sex (s) on survival (ϕ), reencounter (p), and dispersal (ψ) probabilities for lesser kestrel in the Ebro Valley

| Model	AICc	ΔAICc	AICc weight	No. of parameters	Deviance
$\phi_{c+t}\, p_{c+s+t}\, \psi_{c*t}$	8,905.25	.00	.78	60	2,102.90
$\phi_{c*t}\, p_{c+s+t}\, \psi_{c*t}$	8,907.72	2.47	.22	72	2,080.35
$\phi_{c+t}\, p_{s*t}\, \psi_{c*t}$	8,926.29	21.04	.00	65	2,113.54
$\phi_{c*t}\, p_{s*t}\, \psi_{c*t}$	8,928.43	23.18	.00	75	2,094.78
$\phi_{t}\, p_{s*t}\, \psi_{c*t}$	8,943.55	38.30	.00	62	2,137.04
$\phi_{t}\, p_{c*s*t}\, \psi_{c*t}$	8,944.03	38.78	.00	76	2,108.27
$\phi_{c}\, p_{s*t}\, \psi_{c*t}$	8,946.76	41.50	.00	58	2,148.55
$\phi_{s*t}\, p_{c*s*t}\, \psi_{c*t}$	8,948.40	43.15	.00	86	2,091.60
$\phi_{.}\, p_{s*t}\, \psi_{c*t}$	8,953.49	48.24	.00	57	2,157.36
$\phi_{c}\, p_{c*s*t}\, \psi_{c*t}$	8,958.35	53.10	.00	75	2,124.70
$\phi_{.}\, p_{c*s*t}\, \psi_{c*t}$	8,967.54	62.29	.00	73	2,138.08
$\phi_{s*t}\, p_{s*t}\, \psi_{c*t}$	8,969.19	63.94	.00	67	2,152.26
$\phi_{s}\, p_{c*s*t}\, \psi_{c*t}$	8,969.71	64.46	.00	72	2,142.34
$\phi_{s}\, p_{s*t}\, \psi_{c*t}$	8,969.82	64.57	.00	57	2,173.69
$\phi_{c*s}\, p_{c*s*t}\, \psi_{c*t}$	8,972.39	67.14	.00	75	2,138.73

Note: Only the 15 top-ranked models are shown.

the beginning of the breeding season was lower in large than in small colonies, and within-age comparisons afterward did not provide evidence of variations in body condition among different-sized colonies (Tella 1996; D. Serrano, unpublished data). However, the proportion of yearlings decreased with colony size (D. Serrano, J. L. Tella, and E. Ursúa, unpublished manuscript), so we tested our most parsimonious model against a model in which two states of individual age (yearling vs. adult) were considered instead. The model of colony size was again supported (colony size: AICc weight = 0.82; age: ΔAICc = 3.05, AICc weight = 0.18), suggesting that breeding colony size was the causative factor. If this is true, survival probabilities could be explained by colony size selection, a behavioral trait occurring during a short time period within the breeding season (Serrano et al. 2004), and Allee effects could be major driving forces behind the maintenance of coloniality in this species. Large colonies persist in buildings inaccessible to foxes and free of brown rats (Serrano et al. 2004). Moreover, predators are detected earlier and an individual's risk of being killed by the predator during mobbing is lower in large than in small colonies (Tella 1996). Accordingly, nest predation rates follows a pattern that agrees with differences in survival estimates between colony size classes (fig. 1). However, this question merits further consideration, and an experimental approach would be desirable to reinforce our results.

Adult kestrels were 2.5 times more likely to move from a small colony to a large colony than in the opposite direction, in agreement with theoretical predictions (Holt and Barfield 2001). This pattern was not influenced by a low availability of small colonies because they were much more frequent than large colonies in the population. Previous studies at the Ebro Valley have demonstrated that adult emigration decisions are strongly determined by breeding success and colony size (Serrano et al. 2001). Furthermore, dispersing individuals appear to select their breeding colony by cuing on the number of previously settled conspecifics (Serrano et al. 2004). The evolution of these decision rules is possible because final colony size is predictable from the beginning of the breeding season (Serrano et al. 2004), guaranteeing not only a higher probability of breeding successfully but also a lower risk of adult mortality via predation.

More generally, this study highlights the necessity of exploring group size–specific survival and dispersal parameters, which might be decisive in drawing valid conclusions with regard to population dynamics and extinction-colonization turnover in colonial nesting birds. Importantly, this problem is also relevant when modeling population trends in metapopulations and in any spatially structured population in which survival and dispersal varies with local population size (e.g. Holmes et al. 1996; Serrano and Tella 2003; Cam et al. 2004). For example, Sæther et al. (1999) showed theoretically that the form of the relationship between emigration and immigration rates and population size strongly affect metapopulation dynamics. In particular, the present study and previous research (Serrano et al. 2004) could explain why the formation of new colonies is relatively low in spite of a high availability of empty buildings, positive population trends, high dispersal rates, and long dispersal distances (Serrano et al. 2003). Moreover, Allee effects are likely to depress early growth rates of newly founded colonies, making
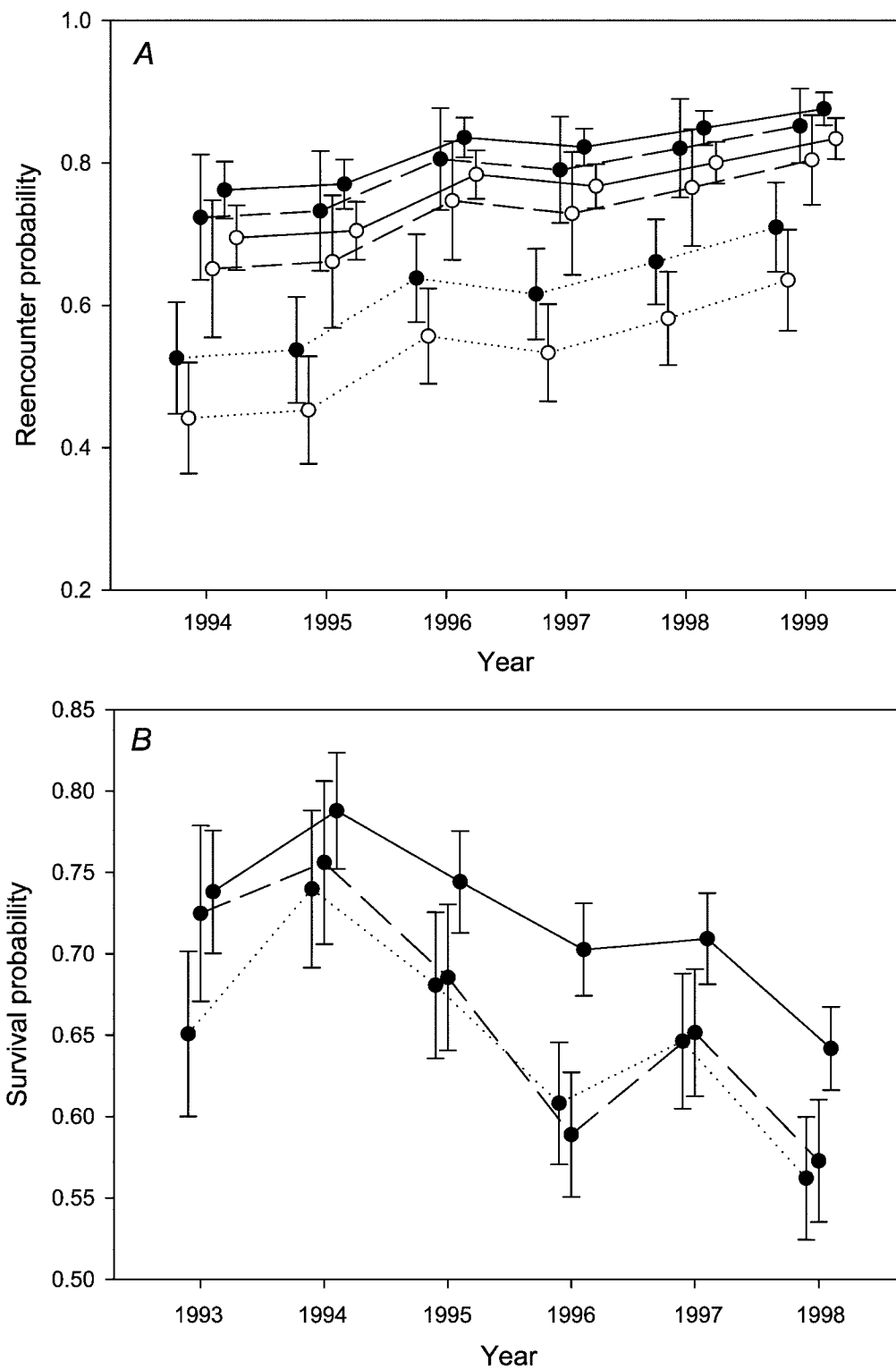
Figure 2: Estimates (±SE) of reencounter (*A*) and survival probability (*B*) of adult lesser kestrels in different-sized colonies. Estimates and unconditional SE of parameters were obtained by averaging of models $\phi_{c+t}p_{c+s+t}\psi_{c^*t}$ and $\phi_{c^*t}p_{c+s+t}\psi_{c^*t}$. *Dotted lines* = small colonies (one to three breeding pairs), *dashed lines* = medium-sized colonies (four to nine pairs), and *solid lines* = large colonies (>nine pairs). *A*, solid dots correspond to males and open dots to females. Note that reencounter and survival probabilities from 1999 to 2000 are not shown because of redundancy in parameter estimation from the finally selected models.

many colonizations ephemeral and reducing rates of spread of the population (Veit and Lewis 1996).

At least several small and medium colonies are likely to yield demographic deficit because of predators causing complete breeding failure, low adult survival, and high emigration rates (see also Serrano et al. 2001, 2004). These demographic sinks would be inevitably doomed to extinction in absence of immigration and "rescue effects" (Brown and Kodric-Brown 1977; Pulliam 1988; Stacey and Taper 1992; Oro et al. 2004). So, from an evolutionary perspective it may be hypothesized that selection should have selected for phenotypes breeding only in large colonies (Holt 1995). As suggested, colony size variability could be maintained by the existence of behavioral mechanisms to prevent first-breeding birds from joining the largest colonies, with many individuals being actively relegated to suboptimal sites (Serrano et al. 2003, 2004). However, despotic distribution alone could not fully explain colony size variability, and other complex demographic mechanisms arising from individual decisions under a scenario of spatiotemporal variations in habitat quality could be involved (Safran 2004; discussed in Oro and Ruxton 2001). For instance, several small and medium colonies in our population perform as well or even better than large colonies (D. Serrano, J. L. Tella, and E. Ursúa, unpublished data), so it appears that there is a large stochastic component in the fitness of these colony sizes. In addition, several massive predation events that decouple colony size from colony quality also have been documented in large colonies in the study area. Spatiotemporal variance in colony quality could therefore have a serious impact on the strength of Allee effects and consequently on emigration-immigration dynamics, demographic stability, and maintenance of colony size variability (see Andreassen and Ims 2001; Oro et al. 2004; Serrano et al. 2004). In this sense, a still-parsimonious model (see the second-ranked model in table 2) included an interaction term between colony size and time on adult survival that could be reflecting, at least in part, a relatively different incidence of predation events on colony size classes across years. Additionally, it should be noted that although movement probabilities between large and small colonies were low, they could represent a relatively high number of individuals for the dynamics of small colonies (Cam et al. 2004).

Failing to consider important components of fitness could lead to mistaken conclusions because any unmeasured parameter could tilt the balance in favor of other colony sizes (Avilés and Tufiño 1998). Studying sociable warblers *Philetairus socius*, Brown et al. (2003) reported that adult survival increased with colony size, although a model without this effect was statistically equivalent. Brown and Brown (2004) found that daily survival probabilities of adult cliff swallows *Petrochelidon pyrrhonota* were lower in small colonies but relatively constant across much of the studied colony size range. Our results suggest that predation could be a cost for adult birds in other colonial species (e.g., Wiklund and Andersson 1994), although it is not always clear how survival should vary with colony size. Since fundamental differences in habitat and life-history traits among species may influence the circumstances affecting the relationship between both parameters, universal patterns are unexpected. Further research on this topic could have far-reaching consequences in our interpretation of net fitness of individuals in different-sized groups, and thus in our understanding of maintenance of colonies and variation in their size.

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