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Public information in selection of nesting colony by lesser kestrels: which cues are used and when are they obtained?

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The use of public information is an important component of breeding habitat selection in birds, especially for colonial species. In this way, individuals can reduce the costs of information acquisition, allowing them to make faster and better settlement decisions based on the quality of breeding sites. We studied the roles of two possible sources of public information on breeding habitat selection in the colonial lesser kestrel, *Falco naumanni*: number of conspecifics settled in the colony (‘the social attraction hypothesis’) and average brood size at fledging in the colony in the previous season (‘the performance-based attraction hypothesis’). Furthermore, we analysed the time at which information is obtained. To attain this we used the rate of occupancy of the colony. We found that average number of fledglings raised in the colony, but not the number of conspecifics breeding the previous year, was correlated with the rate of occupancy, suggesting that public information on conspecific breeding performance may reveal habitat quality and determine colony selection by lesser kestrels. We also found that the number of conspecifics settled at the beginning of the current season did not determine the rate of occupancy of colonies at later stages. Overall, this study provides support for the performance-based attraction hypothesis but not for the social attraction hypothesis. These results may have important implications for management and conservation.

Keywords: breeding habitat selection; coloniality; conspecific attraction; dispersal; *Falco naumanni*; immigration; lesser kestrel; performance-based attraction; public information

The selection of breeding habitat in birds affects fitness, and a large part of the variability in reproductive success among individuals can be attributed to differences in the quality of breeding sites (Dow & Fredga 1985; Martin 1998). Individuals should select habitats that maximize their fitness and this requires time and energy to reduce the uncertainty of habitat choice (Valone & Templeton 2002; Dall et al. 2005). An optimal selection appears possible only if individuals have complete and correct previous information about the quality of all available options. However, evaluating all relevant ecological factors that determine the suitability of habitats may be impossible or too expensive in time and energy invested. Individuals can reduce these costs by using indirect cues that may incorporate most relevant components of habitat quality. The use of these integrative cues for habitat quality assessment may reduce the searching time and improve the quantity and quality of information obtained, allowing individuals to make better and faster decisions that could enhance future fitness benefits (Nordell & Valone 1998).

Ward & Zahavi (1973) suggested that communal roosts or breeding colonies could be used as information centres where individuals enhance their foraging performance by exploring habitat selection of successful foragers (Marzluff et al. 1996; Sonerud et al. 2001; Wright et al. 2003). The use of conspecifics as a source of information about the quality of resources, formally termed ‘public information’ (Valone 1989), has been applied also to other contexts such as mating, opponent assessment and breeding habitat selection (Muller et al. 1997; Danchin et al. 1998; Erwin et al. 1998; Brown et al. 2000; Valone & Templeton 2002; Doligez et al. 2004). This mechanism of aggregation is especially interesting because it may have induced the evolution of coloniality (Danchin & Wagner 1997). With regard to the assessment of breeding habitat selection through public information gathered, two main

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hypotheses have been proposed: the ‘social attraction’ (Stamps 1988) and the ‘performance-based attraction’ (Boulinier & Danchin 1997) hypotheses depending on whether individuals cue on the number of conspecifics present in an area or on their reproductive performance. To distinguish between these two hypotheses is important because both the presence of conspecifics and their productivity have been suggested as stimuli to attract individuals and form aggregations (Danchin & Wagner 1997; Stephens & Sutherland 1999). Moreover, the consequences for spatial distribution, population dynamics and size of colonies may differ if the information used for its selection is the presence of conspecifics or their breeding success. In the absence of other constraining factors, under the social attraction hypothesis, individuals would aggregate in a few very large colonies and the colonies would grow exponentially beyond a critical size in which the costs of colonial breeding override their benefits. In contrast, under the performance-based attraction hypothesis, the size of the colonies would show a temporal variability while tracking environmental changes affecting reproductive output. In this scenario, individuals would gather to form more colonies but not necessarily of large sizes.

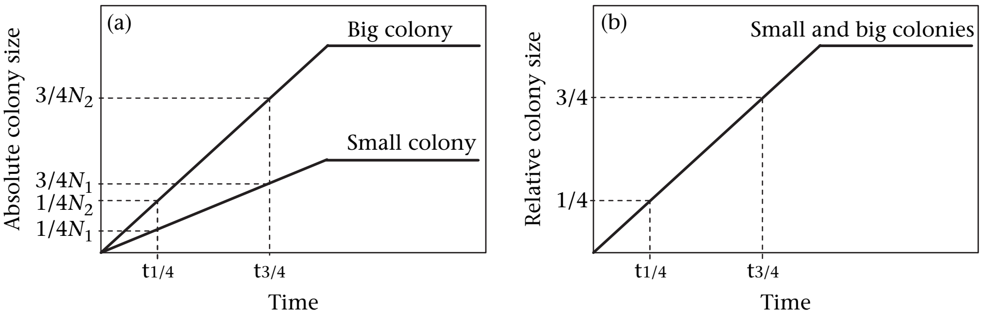
We investigated the use of public information in a lesser kestrel, *Falco naumanni*, population. This colonial and migratory bird is a good model for the study of the use of this information because colonialism provides a context in which public information is highly available and can be transferred at high rate among individuals (Brown et al. 1990). Lesser kestrels, as reported in other avian species (reviewed in Reed et al. 2007), prospect alien colonies, even those located several kilometres from their own, supposedly to obtain information about the quality of breeding habitat for future settlement decisions (Aparicio et al. 2007). Moreover, the lesser kestrel is one of the few species in which the social attraction and the performance-based attraction hypotheses have been simultaneously tested, although contradictory results were obtained (Serrano et al. 2004; Aparicio et al. 2007). The main problem in testing these hypotheses is that breeding success, the number of conspecifics and other factors involved in habitat quality may be correlated (Aparicio et al. 2007). We can experimentally modify the productivity of the colonies (Doligez et al. 2002; Aparicio et al. 2007) to test the performance-based attraction hypothesis. However, we cannot manipulate the size of colonies to test the social attraction hypothesis without incurring ethical violations and thus it could be assessed only by using a correlational approach. Aparicio et al. (2007) manipulated the breeding success of the colonies by enlarging the size of all broods in some colonies and reducing them in other colonies and found that the number of immigrants in a colony was related to mean reproductive success in the previous year. Although the experimental approach used by these authors controlled for other confounding variables involved in habitat quality, they included only small colonies in their study and therefore their results are not easily extrapolated to large colonies. By contrast, Serrano et al. (2004) found that the number of immigrants settled in a given colony was associated with the number of philopatrics at the beginning of the breeding season in a correlational study including a wider range of colony sizes. However, such a correlational approach cannot disentangle the effects of nest site availability and number of philopatrics because both variables are correlated (Aparicio et al. 2007; G. Calabuig, unpublished data). To clarify the mechanism involved in breeding site selection we need a new approach that resolve these issues. We suggest that the rate of occupancy of the colonies at the beginning of the season may provide a useful tool to investigate the use of public information because preferred colonies should be occupied faster. Moreover, we can measure the occupation rate in early settlement phases, when a colony is not saturated and the establishment of new individuals is not constrained by intraspecific competition. Thus, by using this measure of early colony settlement we may overcome those confounding effects, allowing us to distinguish between the two possible sources of public information examined in previous studies.

To derive predictions on occupation rate from the two hypotheses of public information used, let us start from a neutral model of settlement (Fig. 1a), with random arrival order, in which all individuals return to a colony randomly selected or at the same place where they were born or bred in a previous year. If all individuals have identical probability of returning to the breeding area within a given time, the expected number of individuals arriving at a colony up to a certain day as well as the absolute occupation rate of the colonies will depend only on colony size. The relative occupation rate (i.e. absolute settlement rate divided by colony size) would have some advantages over the absolute number because the former is independent of colony size and any other parameter in a neutral model (i.e. in absence of any preference; Fig. 1b). As an alternative to the neutral model, the existence of colony preferences based on public information should be associated with differences in occupation rate. If information was gathered in the previous season, we predict that relative settlement rate at early stages of occupancy will be positively correlated with the estimate used as cue (Fig. 1c). On the other hand, if individuals use public information obtained on the current season (in this case limited to the number of conspecifics present in the colony) we would expect a positive correlation between late settlement rate and the number of individuals settled at earlier occupation stages (Fig. 1d). Furthermore, a consequence of this would be that those individuals arriving for the first time to a colony (dispersers) and requiring information in the current year would settle later than philopatrics who return to their colonies on basis of their own experience, because the current information is available only after the earliest settlements have occurred.

METHODS

The study was carried out in La Mancha, central Spain (600–800 m above sea level), in an area covering approximately 1000 km^2. The climate is meso-Mediterranean with mean temperatures ranging from 24–26°C in July to 4–6°C in January and 300–400 mm of rainfall

Neutral model



Selection based on information acquired in the previous year

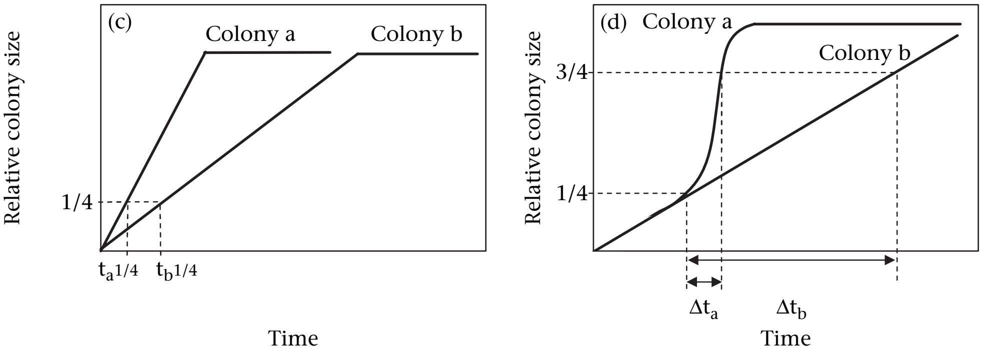


Figure 1. Predictive models of colony occupation rate derived from different hypotheses using public information. Neutral model using absolute (a) and relative (b) number of individuals. Models in which at least some individuals use public information obtained in the previous (c) or in the current (d) year. Colony a is preferred over colony b. Δt_a and Δt_b are the time elapsed between 1/4 and 3/4 of occupation for the colonies a and b, respectively.

concentrated mainly in spring and autumn. The area is extensively cultivated with barley, *Hordeum vulgare*, wheat, *Triticum* spp. and vineyards, *Vitis vinifera*. Other minor habitats include scattered olive groves, *Olea europaea*, some recent pine plantations, *Pinus* spp. and noncultivated areas covered with pastures.

The lesser kestrel is a small insectivorous falcon. In our study area lesser kestrels form colonies of 2–60 pairs located in abandoned farmhouses where they nest under tiled roofs and inside holes in walls. Lesser kestrels normally arrive at this area from their winter quarters in Africa between January and March, depending on the year. Males arrive earlier, take a nest site competing with other males for its possession and try to attract females. Once the pair is formed, the female cooperates with her mate in nest defence. Egg laying lasts from the end of April to the first week of June (Aparicio & Bonal 2002).

General Methods

In 2004, we monitored 17 colonies throughout the breeding season and routinely collected information about breeding performance and adult and chick characteristics (see Aparicio 1997 and Aparicio & Cordero 2001 for more detail of field procedures). The productivity of colonies was calculated as the average number of fledglings produced per pair and surviving to day 30 after hatching. The number of breeding pairs in a colony was measured as the number of females that laid at least one egg.

In 2005 and from early February onwards, we prospected all colonies every 3 days to detect the earliest arrivals. From this date (t0), one of us (G.C.) censused the birds present in each colony. Censuses were performed by recording the number of birds leaving the colony after we approached the building. At the prelaying period, no bird remained perched in colonies with close human presence. Censuses were made early in the morning, when most of the birds remained in the colonies defending their nest (Aparicio et al. 2007). In this period, we identified 56 adults whose arrival date was recorded by their colour rings with the aid of a telescope. These individuals were captured as breeders in the previous year, so we knew their colony of origin.

We analysed colony preference by using data on early and late rate of settlement, assuming that rate of settlement and colony preference are intimately linked (Muller et al. 1997; Martin 1998; Misenhelter & Rotenberry 2000). These rates were measured in each colony at 25 and 75% of its maximum occupancy and were defined as the time elapsed between t0 and 25% (t_{25}) and the time between 25 and 75% of occupancy (t_{75}), respectively. For maximum occupancy we considered the highest number of individuals recorded in all censuses in a given colony. We calculated the day at which these percentages were achieved by interpolating between censuses with a lower and a higher percentage, assuming a lineal growth between two consecutive measures close in time. By using t_{25} and t_{75} we excluded yearlings that arrive much later than adults and that probably follow a different tactic for settlement. Also, we minimized the possible confounding effects that nest site availability and intraspecific competition could exert on preference (rate of settlement). At t_{25} only first-arriving adults have settled in the colonies and there are still plenty of free nest sites that remain unoccupied. Thus, t_{25} is indicative of the promptness of first individuals to select a given colony. By contrast, t_{75} represents a temporal segment of colony occupancy. By using t_{75} we try to measure the possible attraction effect that birds already settled could exert on the subsequently arrived individuals. An association between t_{75} and the number of individuals in the colonies at t_{25} would be indicative of an eventual and current attraction of conspecifics.

Statistical Methods

To test whether individuals used public information from the previous breeding season, we performed a multiple linear regression including t_{25} as dependent variable and mean productivity and number of breeding pairs of colonies in 2004 as independent variables. We also analysed whether previous productivity and/or number of breeding pairs influenced the growth of the colonies in the following year. To attain this, we performed a regression analysis in which the increment of breeding pairs from year $t-1$ to year t, defined as Ln (colony size in year t/colony size in year $t-1$), was dependent variable and average productivity and number of breeding pairs were independent variables. Furthermore, we tested whether conspecific attraction could also be used as public information in the current season. To attain this, we used a linear regression, including t_{75} as dependent variable and number of individuals settled at t_{25} as independent variable. Finally, we analysed differences in arrival dates in philopatrics and immigrants using a Mann–Whitney *U* test. Arrival dates were previously standardized by subtracting each individual arrival date from the average arrival date in its colony. All tests are two tailed and we used a significance level of 0.05.

Ethical Note

The study was done under licence from the Spanish institutional authorities (Environmental Agency of the Community of Castilla-La Mancha and the Ringing Office of the Ministry of Environment) which provided permits for capturing and ringing kestrels. All activities were performed following general ethical guidelines for animal welfare and nature conservation. All 302 breeding adults were caught by hand during incubation and 530 chicks were banded 1 week after hatching. Lesser kestrel is accustomed to human presence, and trapping and handling did not cause any harm or nest desertion or any other damage due to handling or observation of individuals. Human presence is common around the colonies due to agricultural activities and our censuses and monitoring did not provoke any significant alteration for lesser kestrels, which returned to their colonies shortly after.

RESULTS

Use of Information Obtained in the Previous Season

On average, t_{25} was mean ± SD 20.37 ± 6.9 days and ranged 3.5–32.5 days. In a multiple regression t_{25} was inversely related to the productivity of the colony in the previous year ($R^2 = 0.31$, $\beta = -0.55$, $t = -2.57$, $P = 0.022$; Fig. 2) but not to the number of kestrels breeding there ($\beta = 0.27$, $t = 1.26$, $P = 0.229$). This relationship indicates that colonies with higher reproductive success in the previous season attracted lesser kestrels at higher rate at the beginning of the following season independent of the number of breeding pairs and that the latter did not affect occupation rate. We discard the effects of colinearity on the results obtained because independent variables were not correlated ($r = 0.25$, $N = 17$, $P = 0.335$). The increment in breeding pairs between year t_{-1} and t was associated with productivity ($R^2 = 0.29$, $\beta = 0.544$, $t = 2.51$,

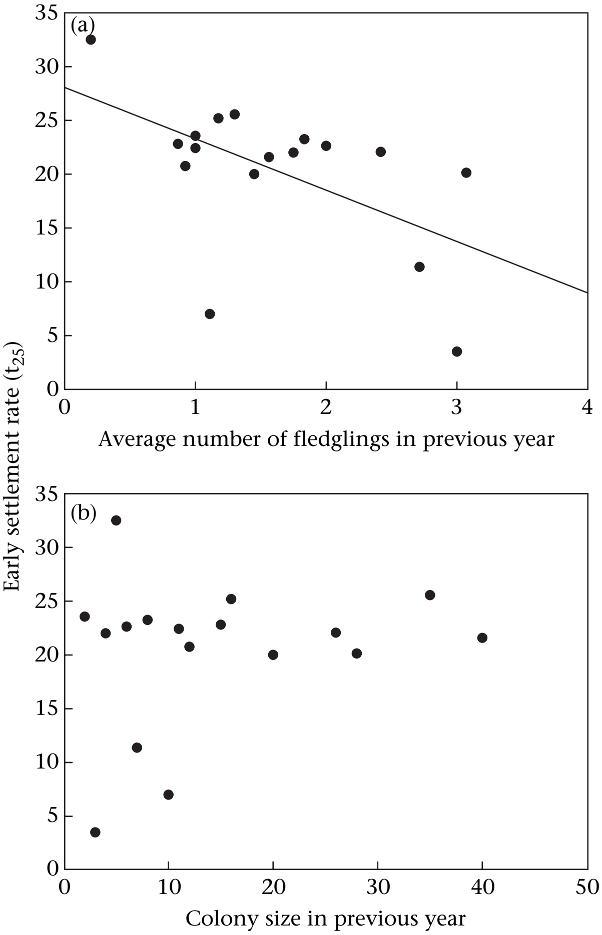


Figure 2. Early settlement rate (t_{25}) in 2005 in relation to (a) average number of fledglings and (b) number of breeding pairs in 2004. Significant regression line is indicated in a.

$P = 0.021$) but not with number of breeding pairs ($\beta = 0.06$, $t = 0.278$, $P = 0.785$).

Use of Information Obtained in the Current Season

We found no significant association between t_{25} and t_{75} ($R^2 = 0.012$, $r = 0.029$, $t = 0.112$, $P = 0.913$; Fig. 3), suggesting that the settlement of individuals arriving later is not explained by the current number of birds present in the colony. Also if immigrants select a colony on the basis of information gathered in the present year we should expect that they settled later than philopatrics. By contrast, lesser kestrels that dispersed and changed breeding site in 2005 settled, on average, earlier than their philopatric counterparts (standardized means ± SE: -14.37 ± 3.34 and -1.84 ± 2.37, respectively; Mann−Whitney U test: $U_{50,6} = 65$, $P = 0.024$).

DISCUSSION

We found that both the rate of occupation in a colony at first stages of settlement (t_{25}) and the growth of the colony from one year to the next were positively correlated with the average number of fledglings raised in that colony but not with the number of breeding birds in the colony the previous breeding season. Assuming that rate of occupation and preference are intimately linked, our results show that preferences are based on colony productivity and not on number of conspecifics in the previous year. This conclusion agrees with that of Aparicio et al. (2007) who performed an experimental study manipulating brood sizes in small colonies (less than 12 pairs) and found that those colonies with enlarged broods received more immigrants the following year than colonies whose brood size were experimentally reduced. However, our results contrast with the conclusions derived from a study performed by Serrano et al. (2004) who found that the number of immigrants was positively correlated with the number of philopatric individuals settled in the current season. Differences between the results of these studies could be due to different methodological approaches used as well as local differences between the study populations. Serrano et al. (2004) used the number of adult immigrants settled in a given colony as a measure of site attractiveness and this approach assumes that all individuals are able to breed in the selected site. Furthermore, in the later study (Aparicio et al. 2007), the effects of colony size could be masked by the greater nest availability of larger colonies. Our study avoids that issue because we measured the settlement rate at t_{25} of occupation, when the number of available nests is high enough to allow new settlements. On the other hand, if kestrels are obtaining public information in the current season, late settlement could be influenced by the presence of conspecifics at the beginning of the settlement period. If so, we would expect a positive correlation between the number of conspecifics at the beginning of the season (e.g. at 25% of occupancy) and the late settlement rate (t_{75}). However, there was no evidence of such association.

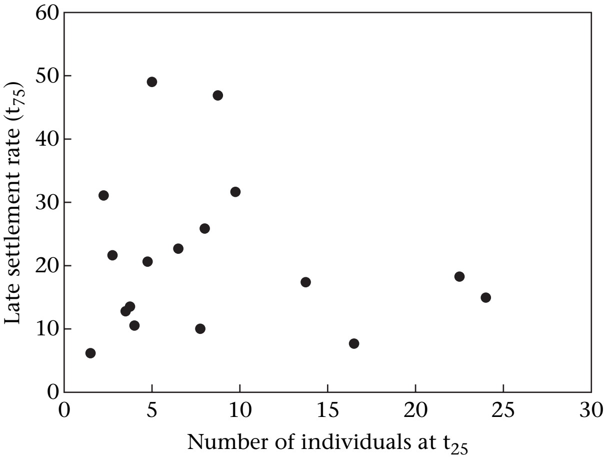


Figure 3. Late settlement rate (t_{75}) in relation to number of individuals already settled at t_{25}.

Alternatively, the positive relationship between the previous productivity and the settlement rate at t_{25} could be spurious if successful individuals were more philopatric and settled earlier than unsuccessful kestrels. However, this spurious relationship seems unlikely because, although dispersal is normally associated with breeding failure (e.g. G. Calabuig, unpublished data), immigrants settled significantly earlier than philopatrics. Thus, it might be difficult for them to use information on the number of philopatrics settled as an indicator of colony quality as suggested by Serrano et al. (2004). Consequently, our results support the performance-based attraction hypothesis (Boulinier & Danchin 1997; Danchin et al. 1998) rather than the social attraction hypothesis (Stamps 1988; Muller et al. 1997; Brown et al. 2000) for colony selection because the rate of settlement in the first stages of occupation of a colony was positively associated with the productivity in the previous year, dispersing kestrels settled earlier than philopatrics and an association between late settlement and the initial colony size was not apparent.

Evidence of the use of public information to select breeding habitat has been reported in at least three other colonial species including black-legged kittiwakes, *Rissa tridactyla* (Danchin et al. 1998), cliff swallows, *Petrochelidon pyrrhonota* (Brown et al. 2000), and black guillemot, *Uria aalge* (Frederiksen & Petersen 1999) and other semicolonial or territorial species such as black kite, *Milvus migrans* (Sergio et al. 2003; Sergio & Penteriani 2005), house wren, *Troglodytes aedon* (Muller et al. 1997), spotted sandpiper, *Actitis macularia* (Reed & Oring 1992), yellow-headed blackbird, *Xanthocephalus xanthocephalus* (Ward 2005), and goldeneye, *Bucephala clangula* (Dow & Fredga 1985). In all these examples the cue used to select a breeding place was breeding performance in the previous year although the use of other related cues such as parental activity has been also suggested (collared flycatcher, *Ficedula albicollis*; Pärt & Doligez 2003).

The acquisition of public information on conspecific breeding success requires prospecting the nests of conspecifics. Prospecting behaviour has been observed in several species. For example, in the great cormorant, *Phalacrocorax carbo sinensis*, new breeders that had been prospecting actively in the previous year obtained breeding sites of higher quality and had higher breeding success than those that had been less active (Schjorring et al. 1999). Also, black-legged kittiwakes appear to prospect conspecific nests at the end of the breeding season, when the information about reproductive success is more reliable (Boulinier et al. 1996). Prospecting behaviour is also very frequent in the lesser kestrel as observed by radiotagging and extensive videotape recordings (G. Calabuig, unpublished), although this behaviour has been neglected by other authors (Serrano et al. 2004). Nest prospecting is normally shown by individuals who failed breeding and become nomadic, visiting different colonies, examining nest sites with chicks and even going into alien nests (G. Calabuig, unpublished data) and could be related to the acquisition of information about breeding sites (Reed & Oring 1992; Boulinier et al. 1996).

The use of public information shown here may have applications for conservation and a detailed understanding of habitat selection mechanisms could be critical to drive conservation measures for endangered species. The lesser kestrel is a vulnerable species (IUCN 2006) that, in central Spain, nests exclusively in farmhouses and other buildings. Most of these buildings are abandoned or scarcely used and show a deteriorated state of conservation. This leads to breeding habitat loss which has been recently aggravated by pillaging of roof tiles (Calabuig et al. 2007). Recent institutional and nongovernmental initiatives include the creation of new breeding sites by conditioning old farmhouses or creating artificial building structures for the establishment of novel colonies. The use of hacking techniques to encourage the colonization of these empty new breeding sites promotes the presence of individuals in subsequent season by natal philopatry. On the basis of the present study, we suggest that an artificial enlargement in nest productivity in the first years of occupation of a colony is possible and may increase the site attractiveness for individuals performing nest prospecting behaviour. This would enhance further occupation of recently founded small colonies located in habitat patches where food is not constrained in the following years. This simple management of artificially enlarged broods could enhance a faster growth than normal at artificially founded colonies or at first stages following foundation, preventing events of environmental stochasticity.

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