

Testing the effect of conspecific reproductive success on dispersal and recruitment decisions in a colonial bird: design issues

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ABSTRACT Factors affecting dispersal and recruitment in animal populations will play a prominent role in the dynamics of populations. This is particularly the case for subdivided populations where the dispersal of individuals among patches may lead to local extinction and 'rescue effects'. A long-term observational study carried out in Brittany, France, and involving colour-ringed Black-legged Kittiwakes (*Rissa tridactyla*) suggested that the reproductive success of conspecifics (or some social correlate) could be one important factor likely to affect dispersal and recruitment. By dispersing from patches where the local reproductive success was low and recruiting to patches where the local reproductive success was high, individual birds could track spatio-temporal variations in the quality of breeding patches (the quality of breeding patches can be affected by different factors, such as food availability, the presence of predators or ectoparasites, which can vary in space and time at different scales). Such an observational study may nevertheless have confounded the role of conspecific reproductive success with the effect of a correlated factor (e.g. the local activities of a predator). In other words, individuals may have been influenced directly by the factor responsible for the low local reproductive success or indirectly by the low success of their neighbours. Thus, an experimental approach was needed to address this question. Estimates of demographic parameters (other than reproductive success) and studies of the response of marked individuals to changes in their environment usually face problems associated with variability in the probability of detecting individuals and with non-independence among events occurring on a local scale. Further, very few studies on dispersal have attempted to address the causal nature of relationships by experimentally manipulating factors. Here we present an experiment designed to test for an effect of local

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reproductive success of conspecifics on behavioural decisions of individuals regarding dispersal and recruitment. The experiment was carried out on Kittiwakes within a large seabird colony in northern Norway. It involved (i) the colour banding of several hundreds of birds; (ii) the manipulation (increase/decrease) of the local reproductive success of breeding groups on cliff patches; and (iii) the detailed survey of attendance and activities of birds on these patches. It also involved the manipulation of the nest content of marked individuals breeding within these patches (individuals failing at the egg stage were expected to respond in terms of dispersal to the success of their neighbours). This allowed us to test whether a lower local reproductive success would lower (1) the attendance of breeders at the end of the breeding season; (2) the presence of prospecting birds; and (3) the proportion of failed breeders that came back to breed on the same patch the year after. In this paper, we discuss how we dealt with (I) the use of return rates to infer differences in dispersal rates; (II) the trade-off between sample sizes and local treatment levels; and (III) potential differences in detection probabilities among locations. We also present some results to illustrate the design and implementation of the experiment.

1 Introduction

Using individually colour marked birds, most studies have either estimated survival and related it to covariates using capture–recapture methodology, or experimentally tested hypotheses related to life history evolution using return rates of individuals as a surrogate for survival rate (Clobert, 1995). Relatively few experimental studies have accounted for potential differences in detection probabilities among individuals despite clear potential for bias (Martin *et al.*, 1995; Boulinier *et al.*, 1997). Individuals may differ in their probability of being detected for many reasons, and notably because they may disperse or skip breeding. These reasons can have important biological significance, and experimental studies designed to test what factors affect these processes are needed.

Factors affecting dispersal and recruitment in animal populations are likely to play a prominent role in the dynamics of populations (Pulliam, 1996; Clobert *et al.*, 2001). This is particularly the case for subdivided populations where the dispersal of individuals among patches may lead to local extinction and ‘rescue effects’ (Hanski & Gilpin, 1997). If patches of breeding habitat differ in quality and if the quality of these patches is temporally predictable, then it may be particularly valuable for individuals to use information that can be sampled at the end of a breeding season to decide where to settle for the next season (Boulinier & Danchin, 1997). A long-term observational study carried out in Brittany, France, and involving colour-ringed Black-legged Kittiwakes (*Rissa tridactyla*) suggested that the reproductive success of conspecifics (or some social correlate) could be one important factor affecting dispersal and recruitment decisions (Danchin *et al.*, 1998). By dispersing from patches where the local reproductive success was low and recruiting to patches where the local reproductive success was high, individual birds could track spatio-temporal variation in the quality of breeding patches (quality related to factors that can vary in space and time at different scales such as food availability, the presence of predators or ectoparasites). Such a process was also suggested by the fact that the timing of prospecting on colonies by failed breeders and young individuals corresponded to the period during which the best information was available on the relative quality of breeding patches (Boulinier *et al.* 1996) and that prospecting individuals were attracted to successful breeding cliffs (Cadiou, 1999). Other recent studies have reported patterns consistent with

the use of conspecific reproductive success for breeding patch selection and dispersal (Doligez *et al.*, 1999; Schjørring *et al.*, 2000; Brown *et al.*, 2000). Such observational studies may nevertheless confound the role of conspecific reproductive success with the effect of a correlated factor (e.g. the local activities of a predator). In other words, individuals may have been influenced directly by the factor responsible for the low local reproductive success or indirectly by the low success of their neighbours. Relatively few studies on dispersal have attempted to address the causal nature of relationships by experimentally manipulating factors. Here, we present an experiment designed to test for an effect of local reproductive success of conspecifics on behavioural decisions of individuals regarding dispersal and local recruitment. We discuss the principle of this experiment, its implementation in the field and the series of design issues it has raised.

2 Principle of the experiment and basic design

It is well known in many species that lower site fidelity is observed following breeding failure than following breeding success (Switzer, 1997). Nonetheless, few studies have addressed whether this was due to differential responses associated with individual experiences or to differences in individual quality—lower quality individuals being more likely to fail their reproduction and to die. A recent experiment tested this; the reproductive success of a set of randomly chosen marked individuals was decreased (by removing their eggs), and their return rate was subsequently compared to the return rate of control individuals (Haas, 1998). In the current experiment, we have applied the same type of approach. However, as we were interested in testing for an effect of conspecific reproductive success on the decisions of individuals regarding recruitment and fidelity to local breeding patches, we manipulated not only the reproductive success of individually colour-marked birds, but also of groups of their neighbours on the same breeding patches.

The experiment was carried out on Kittiwakes within a large seabird colony in northern Norway. It involved (i) the colour ringing of several hundreds of birds; (ii) the manipulation (increase/decrease) of local reproductive success of breeding groups on cliff patches; and (iii) the detailed survey of attendance and activities of birds on these patches. It also involved the manipulation of the nest content of marked individuals breeding within these patches. This was done because we predicted that individuals failing at the egg stage would respond in terms of dispersal to the success of their neighbours. This experiment allowed us to test whether a reduced local reproductive success would lower (1) the attendance of breeders at the end of the breeding season; (2) the presence of prospecting birds; and (3) the proportion of failed breeders that returned to breed on the same patch the year after.

3 Design issues

3.1 Using return rates to compare dispersal rates

The basis for testing the main prediction of this experiment is that return rates to local breeding plots can be used to infer differences in the proportion of individuals that will be site-faithful *versus* individuals that will disperse (or not breed), and that this response depends on the two different treatments. As return rates are strongly linked to survival rates (Martin *et al.* 1995), for such a comparison to make sense,

survival rates of birds submitted to the different treatments should be assumed to be the same, or at least the survival rate of birds from unsuccessful plots should not be lower than that from successful plots. Survival rates of individuals from the two treatment groups should not differ if they are affected in the same way by the same series of factors. In our case, it was planned that the nest content of all colour-marked individuals would be manipulated at the egg stage, thus this should not have differentially affected the survival of individuals between the two treatment groups. In a recent experiment on the costs of reproduction in Kittiwakes, Golet *et al.* (1998) removed egg clutches to reduce the cost of reproduction for individuals with the prediction that these individuals would survive better than control individuals. Thus, in our case, removing eggs should not have decreased the survival of manipulated birds due to differential breeding efforts. The only difference between the two treatment groups in our experiment is that their neighbours were, or were not, put in failure at the egg stage. This could have affected survival in two ways: (1) the mortality risk on breeding patches could have varied due to differences in the local attendance of individuals (group size effect), and/or (2) the difference in the activities of the two groups could have exposed them to different mortality risks outside breeding patches (for instance, prospecting for a new site on different patches may expose individuals to higher predation risks or parasitism). Regarding the first, it should be noted that successful and unsuccessful patches within each plot pair were situated a maximum of 100 m away from each other, and thus it is quite unlikely that exposure to adult mortality risk varied at that scale. Regarding the second, difference in attendance and prospecting activities are part of the predictions of the experiment. If these different activities lead to differential exposure to mortality risks, then this can be interpreted as part of the different costs and benefits of attempting to disperse. In other words, it is not a problem for our prediction that a potential increase in mortality risk associated with prospecting is confounded with 'dispersal' in determining the return rate of individuals. One important advantage of such a design is that it requires the monitoring of the activities of individuals on the study plots, but not outside, where individuals are difficult to locate and may vary dramatically in the probability of being detected.

3.2 Accounting for detection probability

The fact that the probability of detecting marked individuals in the field is rarely 1 and that it can differ depending on the treatment is a critical issue to consider in such an experiment. As explained above, in order to compare dispersal rates, we have compared the proportion of marked birds that returned to breed (i.e. built a nest) on their plot the year after manipulation for individuals put in failure on successful plots and individuals put in failure on unsuccessful plots. Thus, the experiment did not rely on the probability of finding individuals that dispersed or did not breed in the year following the treatment, but conversely relied on the ability to detect any breeding attempt by marked birds on the study plots during the season following the treatment. Study plots were thus surveyed on regular occasions (every three days) during the entire breeding season, and the presence and behaviour of any marked bird was recorded. The probability of detecting individuals involved in breeding is likely to vary among individuals (e.g. difference in the proportion of time spent brooding such that colour rings are hidden in the nest, or in the proportion of time spent at sea), but also with the timing of the

season (e.g. nest building period versus brooding period) and the knowledge of the observer (e.g. expectation of seeing a marked bird on a site where one has already been recorded several times). In this context, Pollock's robust design (Pollock, 1982) applied between two primary sampling periods, the season of the experimental manipulation and the following season, provided a way to estimate a rate of 'locally surviving and renesting' while accounting for the probability of detecting individuals using the pattern of detection versus non-detection of individuals over the series of secondary sampling occasions within the second primary period. As we were primarily interested in the proportion of individuals that had been recorded as breeders and put in failure in the first year and that came back and bred the second year, we computed the ratio of the estimated number of individuals that came back and bred the second year, estimated using a closed population model accounting for individual detection probability using the pattern of detection of individuals over the second breeding season, over the number of individuals that had been recorded as breeders and put in failure in the first year. This application of the robust design is an analogue to the use of the design proposed recently for estimating the rate of species extinction in animal communities between two points in time (Nichols *et al.*, 1998). We used the jackknife estimator of Burnham & Overton (1979) for estimating the number of breeders, as this estimator permits heterogeneity in the probability of detecting individuals (model M_h), is relatively robust to departures from assumptions, and the estimates and their associated standard errors and 95% confidence intervals can be computed directly using software COMDYN (Hines *et al.*, 1999; <http://www.mbr-pwrc.usgs.gov/comdyn.html>). This was done independently for the group of failed individuals on successful plots versus failed individuals on unsuccessful plots in the first year. Exploratory analyses using program CAPTURE to test for which closed population model was fitting best the data were carried out (Rexstad & Burnham, 1991). We did not attempt to use capture-recapture models for open populations over several years following the manipulation as our main interest was in what had happened in the year following the manipulation on plots that could be heavily monitored.

3.3 Trade-off between sample sizes and treatment levels

On plots where all individuals were put in failure, the sample size can be made of a relatively large number of marked individuals. Conversely, on plots where the treatment involved putting individuals in failure surrounded by successful individuals, the sample sizes were directly constrained by the level of success to be maintained locally: the higher the sample size, the lower the local success, and thus the lower the level of the treatment applied within a given patch. In the case of our experiment, the trade-off between sample sizes and treatment levels had to have been taken into account when considering what sample sizes would be required to have the ability to detect an effect of the treatment. We discuss below this issue by considering the relationship between the variance of the coefficient of association between the treatment and the return rate, the sample size and the level of treatment.

In a simple linear regression model, the variance of the regression coefficient is given by $(\sigma^2/n\sigma_x^2)$, where σ^2 is the variance of the response variable Y (the residual variance), n is the number of observations and σ_x^2 the 'variance' of the predictor variable X (if X is fixed, i.e. not a random variable, as in an experiment with fixed treatments, it is not a true variance, but a measure of the variability of the treatments). This expresses the fact that the variance of the regression coefficient

will decrease as the sample size n increases and as σ_x^2 (the variability of the treatments), increases, and that these have identical effects on the variance of the regression coefficient.

Here, however, we are dealing with a binomial response variable and must consider a logistic regression model. In a logistic regression model, the main difference comes from the fact that the variability of the response variable is now dependent on the expected proportion π_i and the number of birds in each treatment group m_i : the binomial variance is equal to $m_i\pi_i(1 - \pi_i)$, $i = 1, \dots, n$ being the different groups of birds.

The logistic regression model is written as $\text{Logit}(\pi) = \beta_0 + \beta_1 x$, and the approximate variance-covariance matrix of the regression coefficients is given by (McCullagh & Nelder, 1989):

$$\text{cov}(\beta) = (X^T W X)^{-1}$$

where X is the design matrix and W a diagonal matrix containing the weight associated with the binomial variance:

$$W = \text{diag}\{m_i\pi_i(1 - \pi_i)\}$$

In the simplest case of two proportions, π_1 and π_2 , corresponding to two values of the predictor variable x_1 and x_2 and the number of birds m_1 and m_2 in each group, we have:

$$\begin{aligned} X = & (1 x_1) \\ & (1 x_2) \end{aligned}$$

A bit of algebra leads to a simple formula for the variance of the regression coefficient β_1 :

$$\text{var}(\beta_1) = (w_1 + w_2)/[w_1 w_2 (x_1 - x_2)^2]$$

where w_i are the binomial weights equal to $m_i\pi_i(1 - \pi_i)$.

Whereas the term $(x_1 - x_2)^2$ is common to the linear regression case, the weights w_i reflect the fact that the precision of the regression coefficient will get lower when observed proportions get close to 0 or 1. This is illustrated in Fig. 1.

What can be seen from Fig. 1 is that the ability to detect an effect (i.e. a decreasing function of the variance of the regression coefficient) is much affected by the expected effect of the treatment (compare Fig. 1(a) with 1(b)), and by the sample size and treatment level. When the expected effect of the treatment is weak, several combinations of sample size and treatment levels provide the same ability to detect an effect with the constraint that there is a trade-off between increasing sample size and increasing treatment level (which can take the form, for instance, of the dotted line in Fig. 1(a)). In that case, a low treatment level and large sample size would do as well as a high treatment level and low sample size. When the expected effect of the treatment is strong, the combinations of sample size and treatment level that provide a good ability to detect an effect are when the level of the treatment takes a relatively minimal value; sample sizes required an increase on either side of this treatment level (Fig. 1(b)). Another element to be considered when implementing such an experiment in the field is that the 'treatment' level can be modified by natural causes, e.g. predation on the successful plots, which cannot always be compensated for (for example by replacing with eggs from manipulated nests).

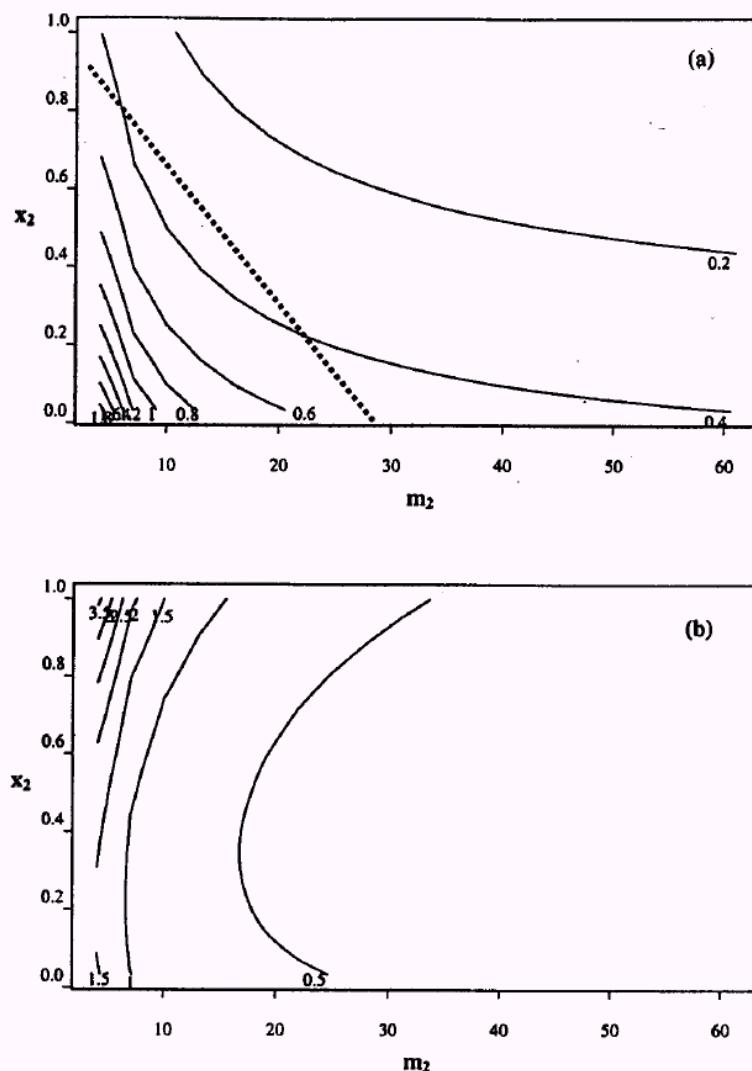


FIG. 1. Variance of the regression coefficient β_1 for different combinations of the treatment value (x_2) and the number of observations (m_2). Figures (a) and (b) illustrate two contrasting cases: (a) weak treatment effect $\beta_1 = -0.5$; (b) strong treatment effect $\beta_1 = -3$. x is assumed to be equal to 0, the intercept is taken as 2 giving a return rate for the control group equal to $1/(1 + \exp(-2)) = 0.88$. A strong treatment effect would result for $x = 1$ in a return rate equal to $1/(1 + \exp(-2 + 3 \times 1)) = 0.27$, a weak treatment effect in a return rate equal to 0.82. Dotted line: possible shape of the trade-off between increasing sample size and increasing treatment level.

3.4 Experimental unit and non-independence among individuals

In this study, the experimental unit is a plot, and not the individuals within a plot. With treatments applied following a randomized block design, one plot per pair of plots being put in failure and the other being left/maintained in success, analyses can be done using hierarchical generalized linear models (e.g. Lindsey, 1999). There will be evidence for an effect of the local reproductive success on the attendance of individuals on failed sites, the number of prospecting birds or the probability of returning to breed if there is a consistent effect of the treatment among plots.

4 Implementation in the field

4.1 Study population

The study was conducted on the island of Hornøya ($70^{\circ}22'N$, $31^{\circ}10'E$), in the north-east of Norway, where more than 20 000 pairs of Kittiwakes breed (Erikstad *et al.*, 1995). In the first year of study (1998), we colour marked individually more than 400 adult birds on a series of breeding cliffs. The cliffs were split into a series of paired plots that were surveyed to assess the local reproductive success, the attendance of birds on built and non-built sites, and the presence and activities of marked individuals throughout the breeding seasons (visit to each plot every three days). The experimental manipulation of the local reproductive success was carried out in 1999, and in 2000 a special effort was made early in the season (March–April) to determine which individuals came back and bred on the plots.

4.2 Experimental treatment

Within each pair of study plots, one plot was randomly chosen to be put in failure and the other was left/maintained in success. Manipulations of nest contents were performed at the egg stage, where we expected the strongest response (Danchin *et al.*, 1998). Within plots to be put in failure, eggs were removed from all nests. Within plots to be left in success, only a limited number of nests with colour marked breeders were put in failure. If birds in failed nests laid a replacement clutch, these eggs were also removed. Eggs were either used to maintain success in other 'successful' nests or kept for analyses of yolk content as part of a parallel study on maternal investment in eggs (Gasparini *et al.*, 2001). Care was taken to spend the same amount of time at each plot within a plot pair so that disturbance would be comparable. By moving eggs into nests that had just failed, usually due to heavy local predation by ravens *Corvus corax*, it was possible to cancel local failures and maintain relatively high success on some plots. Natural failures at different stages lead nevertheless to different local levels of success on 'successful' plots (the average number of chicks produced per nest on 'successful' plots varied from 0.4 [plot 11_R] to 1.2 [plot 3_E]). These levels were comparable to natural levels observed in cliffs 'in success'.

5 Preliminary results

The results presented here are preliminary and are given as an illustration of the above discussion. They are not presented as definitive evidence for the patterns that may appear, but need to be confirmed by a more complete analyses of the data from the described experiment. In particular, results presented concern only five of the nine pairs of study plots.

5.1 Attendance of failed breeders on successful and unsuccessful plots

The attendance of individuals during the chick rearing period (after day 180) on failed nest sites was lower on plots put in failure than on plots left/maintained in success (ANOVA, randomized block design analysis, with plot pair as a random factor, treatment as a fixed effect: $F_{1,203} = 500.23$, $P = 0.001$). We verified that such a difference did not occur before the egg removal treatment was applied

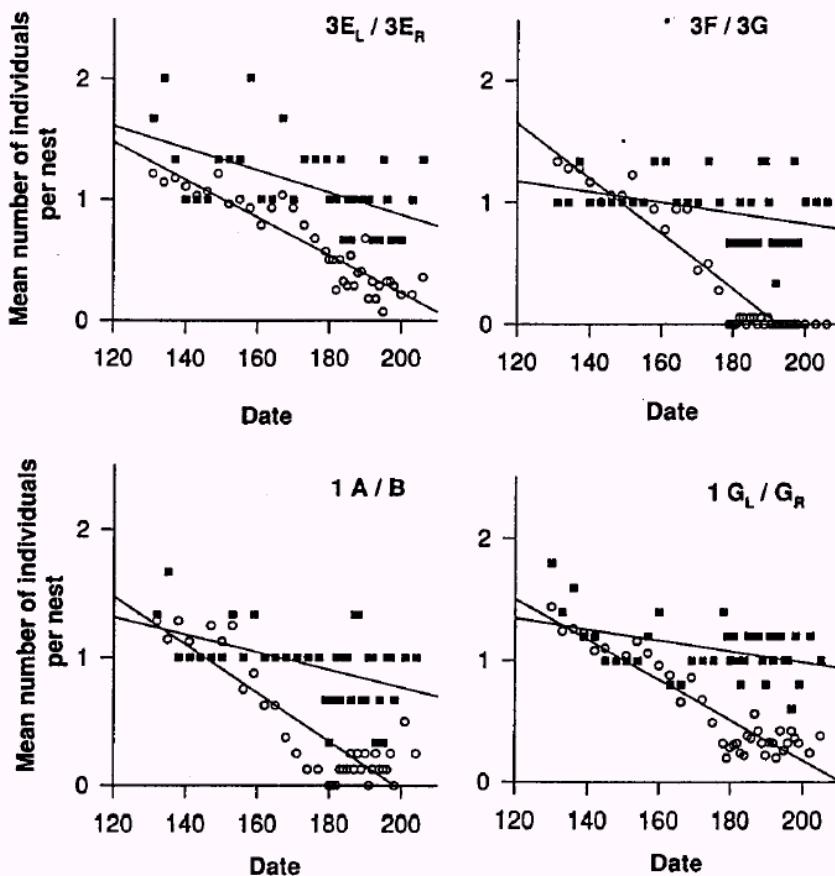


FIG. 2. Average number of individuals attending failed nest sites for four pairs of plots during the 1999 breeding season (pairs '3E_L/3E_R', '3F/3G', '1A/1B', and '1G_L/1G_R'). Nest contents were manipulated after day 145. ■ are for successful plots and ○ are for unsuccessful plots.

($F_{1,63} = 2.73$, $P = 0.1033$). These results are illustrated in Fig. 2, where the average number of individuals attending a failed nest site is given for four pairs of plots during the 1999 breeding season.

5.2 Number of prospecting birds on successful and unsuccessful plots

The number of birds attending non-built nest sites during the 1999 season gives an indication of the temporal and spatial pattern of prospecting: for the two pairs of plots taken as examples, prospecting on non-built sites was highest during the chick rearing period and occurred mostly on successful plots (Fig. 3). Observations of the behaviour of ringed birds showed that most birds on non-built sites were prospecting birds and not off-duty birds resting on a site close to their nest. These results are fully consistent with the observations reported by Boulinier *et al.* (1996) regarding the timing of prospecting, and by Cadiou (1999) regarding the apparent attraction of prospecting individuals to successful plots at the time of chick rearing.

5.3 Return rates of breeding birds on successful and unsuccessful plots

Using program CAPTURE, it appeared that model M_{th} , which makes the assumption of a heterogeneity among individuals in the probability of being detected and

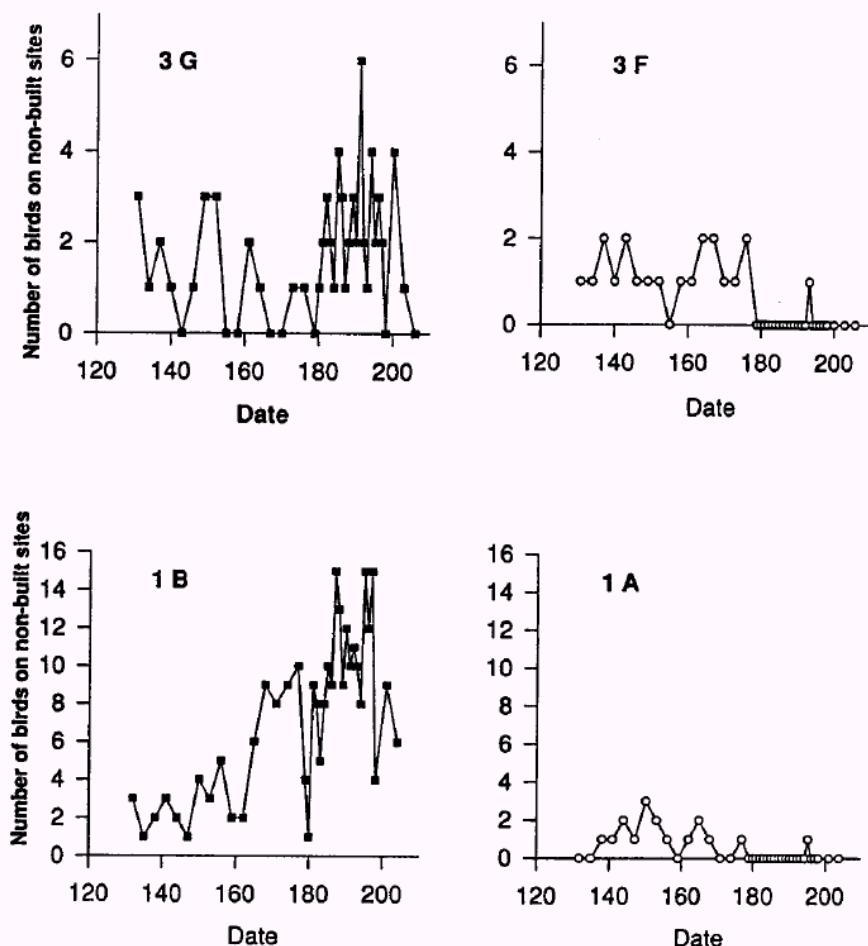


FIG. 3. Prospecting: number of individuals attending non-built sites during the breeding season for two pairs of plots (pair '1A/1B' and pair '3G/3F'). Nest contents were manipulated after day 145. Most prospecting occurred during the chick rearing period (i.e. after day 170). ■ are for successful plots and ○ are for unsuccessful plots.

a time effect on the probability of being detected, would be the most appropriate, even when considering only observations carried out over the beginning of the season. Results were nevertheless very similar when using model M_h , which is the estimator implemented in program COMDYN. Using the corresponding jackknife estimator, the estimated probability of detecting a breeding individual returning as a breeder in 2000 did not differ between the two groups, as it was 0.951 (95% c.i. = 0.847 – 1.00) and 0.932 (95% c.i. = 0.820 – 1.00) for the series of unsuccessful and successful plots, respectively. Accounting for that probability of detection, the overall proportion of experimentally failed individuals that returned to breed on unsuccessful plots was 0.49 (95% c.i. = 0.36 – 0.67) compared to 0.77 (95% c.i. = 0.55 – 1.0) on successful plots. Looking within each plot pair (Table 1), we see a trend suggesting a higher proportion of individuals returning to breed on the successful plot (observed in four of the five plot pairs). Several individuals that did not return to breed on their plot were recorded prospecting or breeding on other plots. This observation suggests that, indeed, a portion of birds that did not return to breed on the same plot may have been in the process of dispersing.

TABLE 1. Proportion of marked failed individuals that returned to breed on the same plot the year after. Results are presented for five plot pairs, with the proportion on the plots that were left/maintained in success on the left, and the proportion on the plots that were put in failure on the right.

| Plot pair | Proportion of failed individuals that returned to breed on the same plot | |
|----------------------------------|--|------------------|
| | Unsuccessful plots | Successful plots |
| 1A/1B | 5/10 | 3/3 |
| 2A/2B | 9/13 | 2/4 |
| 1G _L /1G _R | 10/18 | 4/5 |
| 3E _L /3E _R | 13/27 | 2/3 |
| 3F/3G | 1/13 | 2/3 |
| Total | 38/81 | 13/18 |

6 Discussion

Despite the importance of dispersal in evolutionary ecology and for understanding the dynamics of subdivided populations, very few experimental studies have attempted to test what factors may affect dispersal in birds. The current work shows that, at least at some spatial scales, it may be possible to use an experimental approach to study factors affecting dispersal. Such studies need specific designs involving multi-sites. The advance in capture–recapture methodology clearly should help analysing data on dispersal in such settings, but it should be stressed that specifically designed observational and experimental studies are required to answer such questions (Nichols & Kendall, 1995). The description of our experimental approach testing the role of conspecific reproductive success (or some social correlate) for breeding habitat selection shows that such experiments are not obvious to carry out, but may provide crucial information on a wide array of important biological processes linking the behaviour of individuals to the dynamics of subdivided populations in ecological landscapes (Lima & Zollner, 1996). Regarding the specific questions addressed by our experiment, a confirmation of the preliminary results presented here would have implications for our understanding of factors affecting the dynamics of individuals in space and time in relation to environmental changes. This would have, in turn, implications for the understanding of evolution ecology questions, such as the evolution of colonial breeding in birds, but also for studies on the conservation of species living in fragmented habitats.

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