

COMMENTARY

ON BREEDING PERFORMANCE, COLONY GROWTH AND HABITAT SELECTION IN BUFF-NECKED IBIS¹

THIERRY BOULINIER,² *Institut d'Ecologie, CNRS- URA
258 Université Pierre & Marie Curie, 7 Quai St Bernard,
75252 Paris, France.*

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Breeding habitat selection is of prime importance for the fitness of individual birds (Martin 1988). In a given species, nest site quality varies in space and time at different scales due to different environmental factors affecting reproductive success (Wiens 1976). According to the current theory, the distribution of individuals among patches of varying qualities should correspond to an ideal free or an ideal despotic distribution depending on the type of territory competition existing among individuals (Fretwell and Lucas 1970).

An important and neglected assumption behind this hypothesis is that individuals need to assess the quality of the different patches at the time they take their settling decisions to sort themselves in the predicted pattern (Kacelnik et al. 1992). This question underlines the importance of an individual based approach of breeding habitat selection. Rather than concentrating on the distribution pattern of breeding birds in a given environment, it may be productive to infer the processes, notably linked to information gathering, that are operating to generate such patterns. In particular, as for mate selection (Getty 1995), individuals are likely to gather information on potential breeding patches before settling (Klopfer and Ganzhorn 1985). Attendance of non-breeders at the breeding grounds at the end of the breeding season has been recorded in several species (see Danchin et al. 1991 for a review), and these individuals may be gathering information on potential future breeding sites (Reed and Oring 1992).

One source of information for breeding patch selection is the presence of conspecifics (Shields et al. 1988). For individuals that previously bred, another potential source of information is their own reproductive success (Switzer 1993). Moreover the reproductive success of

conspecifics may be another cue used by the birds to choose their breeding habitat (Burger 1982; Boulinier and Danchin, in press). This last hypothesis has been inferred from detailed studies of the fate of individually marked birds of a colonial species, the Black-legged Kittiwake *Rissa tridactyla* (Danchin and Monnat 1992; Danchin and Boulinier, unpubl.), and it provides a set of assumptions and predictions that may be easily tested in other species. In particular, an important prediction of the hypothesis of the use of conspecific reproductive success for breeding patch selection is that the local increase of the number of breeders should be greater for colonies that experienced greater reproductive success the previous year, since they would attract more new breeders and loose less of their own through site infidelity.

Recently, Donazar et al. (1994) reported data on breeding performance of Buff-Necked Ibises (*Theristicus caudatus*) in relation to nest-site substratum with reference to the ideal free distribution. Conversely to what they expected, they found no differences in breeding parameters among colony substrata. They found that brood size varied significantly among colonies and that the main cause of nest and chick losses was predation. Their conclusions were that breeding success varied among colonies independently of the nesting substratum, and that birds would not prefer one substratum over another. Here, I propose another analysis and interpretation of some of the data presented in the light of the hypothesis mentioned above.

Donazar et al. (1994) reported data on the maximum number of active nests observed during the breeding season for five colonies in 1991 and 1992, together with the mean brood size of these colonies in two years (Table 1). From these data, I calculated the rate of growth of each colony (number of active nests in 1992 over the number of nests in 1991; Table 1). If brood size is taken as an indication of the local reproductive success (Donazar et al. 1994), the rate of growth of the colonies between 1991 and 1992 is correlated with their reproductive success in 1991 (Spearman rank correlation, $r_s = 0.89$, $n = 5$, $P = 0.04$), as predicted by the hypothesis that individuals use the reproductive success of conspecifics for their breeding habitat selection. This suggests that the net balance of recruitment was higher for the colonies with higher brood sizes than for those with smaller brood sizes. As age at first reproduction is greater than two, and as the environment is not likely to be highly autocorrelated (see Table 1 of Donazar et al. 1994), this suggests that differential recruitment and dispersal occurred in relation to colony attractiveness due to local reproductive success.

Demography is complex and should be based on parameters estimated separately for different categories of individuals (Clobert and Lebreton 1992). Moreover, knowledge of the behavior of future recruits implies detailed observations that are only available for a small number of species (Cadiou et al. 1994). Nevertheless,

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² Present address: National Biological Service, Patuxent Environmental Science Center, Branch of Migratory Bird Research, 11510 American Holly Drive, Laurel, Maryland 20708-4017, e-mail: boulinier@pandion.pesc.nbs.gov

TABLE 1. Maximum number of nests in 1991, brood size in 1991 and growth rate between 1991 and 1992 of the 5 colonies studied in both years. Growth rates were calculated for each colony by dividing the maximum number of active nests in 1992 by the maximum number of active nests in 1991 (ratio in brackets). For brood size the average \pm SD and sample size (in brackets) are given. Modified from Table 1 of Donazar et al. 1994.

Colony number	Brood size in 1991	Growth rate (1991-1992)
1	2.1 \pm 0.5 (18)	1.1 (30/28)
2	2.1 \pm 0.5 (10)	1.3 (43/32)
5	1.8 \pm 0.6 (10)	0.6 (21/38)
6	1.8 \pm 0.4 (19)	1.0 (40/42)
8	1.3 \pm 0.5 (15)	0.6 (17/30)

the analysis presented here, based on a very small sample of colonies, underlines the importance of looking at the processes that exist at the individual level and may explain the global patterns observed. In this particular case, patch quality may not be directly related to patch substratum, but to the presence of different potential factors that may vary in time and space. Predators, for instance, may be present at one place but not at another. The main cue that may be used by the birds to decide where to recruit may be the local reproductive success of conspecifics or some correlate. In these terms, it would be interesting to look at the spatio-temporal predictability of the bird reproductive success and of the factors affecting it in relation to bird dispersal and recruitment. Such investigations could be carried out on several already existing data sets, notably in colonial breeding species.

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