Public Information and Breeding Habitat Selection in a Wild Bird Population

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According to the "public information" hypothesis, some animal species may monitor the current reproductive success of conspecifics to assess local habitat quality and to choose their own subsequent breeding site. To test this hypothesis experimentally, we manipulated two components of public information, the mean number of offspring raised locally ("quantity") and their condition ("quality"), in the collared flycatcher *Ficedula albicollis*. Immigration rate decreased with local offspring quantity but did not depend on local offspring quality, suggesting that immigrants are deprived of information regarding local quality. Conversely, emigration rate increased both when local offspring quantity or quality decreased, suggesting that residents can use both components of public information.

Whenever resource quality and/or quantity vary in time and space, individual animals need to gather information on the environment to make optimal choices (*1–3*). Information and decision-making processes are major factors constraining the evolution of behavioral (*4*) and life-history traits (*5*). However, the nature of the information used by individuals in decision-making is poorly understood (*6*, *7*). The task is complicated by the temporal and spatial scales involved [e.g., in breeding habitat selection (*8*)] and by the multiplicity of cues that can be used in a context-dependent way, especially in species with large cognitive abilities [e.g., (*9*)]. Identifying one or several integrative cues explaining a large part of the variance in individual decisions is often a challenge (*10*).

Theoretical (*8*, *11*) and empirical (*5*, *12–14*) evidence exists for the use of public information [in the sense of (*15*), i.e., the performance of conspecifics] in breeding habitat selection, where the mean reproductive success in a breeding patch may function as public information about its quality. Furthermore, prospecting for breeding sites [i.e., gathering information about potential future breeding sites (*7*)] appears to include gathering public information in several species (*4*, *7*, *16*, *17*). However, current evidence that individuals cue on public information in breeding habitat selection is only correlative and thus cannot be used to reject the alternative hypothesis that individuals use some other cues of habitat quality that are linked to reproductive success of conspecifics. Experiments are therefore needed to assess the relevance and generality of the use of public information in breeding habitat selection.

We manipulated local reproductive success of collared flycatchers (*Ficedula albicollis*), a small migratory passerine bird, on the island of Gotland, Sweden (*18*), from 1997 to 1999, by transferring 7-day-old nestlings between nests among breeding plots. Thus we created plots where the mean number of fledglings per breeding pair was increased (I), decreased (D), or left unchanged, by moving nestlings within plots from brood-removed to brood-increased nests (C1) or by no manipulation (C2) (*19*). All plots contained unmanipulated nests. We recorded subsequent movements of individuals to compute immigration and emigration rates. One immigration rate was defined for each age and sex class as the ratio of the number of immigrants (*19*) on the number of nest boxes available to them (*19*), thus accounting for interspecific competition with tits (*Parus* spp.) (*20*) and occupation by residents. Emigration was defined as a change of plot by an individual between one year and the next one(s) (*13*, *19*). Based on the public information hypothesis, we predicted that immigration should increase and emigration decrease when mean reproductive success was experimentally increased, and vice versa (*19*).

As for previous brood size manipulations (*21*), our experiment affected both the mean number of fledglings per breeding pair per plot and their mean body condition at fledging (Fig. 1). Mean fledgling number was increased in I plots and decreased in D plots, compared with control plots; C1 and C2 plots did not differ (Fig. 1A). Mean body condition was decreased in plots containing enlarged broods (plots I and C1), compared with plots where no nest received additional nestlings (plots D and C2, Fig. 1B). These differences in measures of plot reproductive success between treatments were due to the sole effect of the experimental manipulation, because when comparing unmanipulated nests, the mean number and body condition of fledglings in a plot a given year did not differ between treatments [mean number: $F(3,29) = 0.61$, $P = 0.62$; condition: $F(3,29) = 0.87$, $P = 0.47$; accounting for year and replicate].

Both fledgling number and condition have been shown to covary with local recruitment of breeders the following years (*20*, *22*). Thus, individuals could potentially use both local fledgling quantity and quality to predict their expected fitness in various plots in the following year(s). Because our manipulation reversed the natural positive correlation between local fledgling quantity and quality due to individual phenotypic quality [supporting online text (*19*)], it is possible to disentangle their respective roles in breeding habitat selection. If birds use only the quantity of fledglings (or give more weight to this cue), we expect their assessment of breeding plot quality to decrease from I plots to control plots, and from control plots to D plots. If birds use only the quality of fledglings, their assessment of plot quality should increase from I

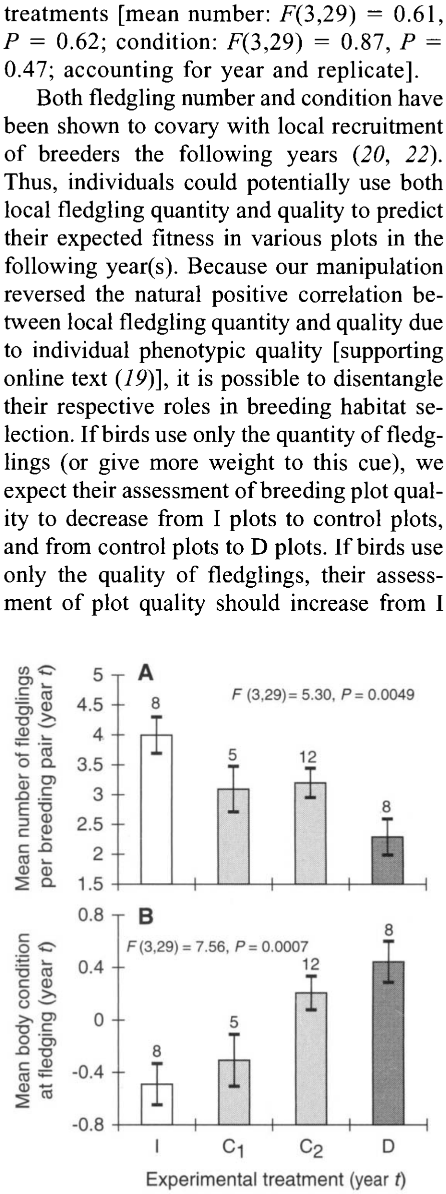

Fig. 1. Effects of the experimental manipulation on two components of local reproductive success in the collared flycatcher: (**A**) mean number of fledglings per breeding pair per plot (±1 SEM); (**B**) mean body condition at fledgling (±1 SEM), computed as the mean value of the residuals of the linear regression of weight on tarsus length both measured at day 13 [$F(1,3937) = 1792.47$, $P < 0.0001$; $R^2 = 0.313$]. Experimental treatments: I: increased plots; C1: control 1 plots; C2: control 2 plots; D: decreased plots. Numbers above bars are sample sizes; the sample unit here is one plot in one year.

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plots to D plots. If birds use fledgling quantity and quality as two separate cues, and if they give more weight to the cue with the highest numerical value, their assessment of plot quality should be higher for both I and D plots than for control plots. Finally, if birds use both fledgling quantity and quality but give more weight to the cue with the lowest numerical value, their assessment of plot quality should be lower for both I and D plots than for control plots.

Local immigration rates strongly differed among treatments (Fig. 2). Immigration was higher in increased (I) plots than control plots, and lower in decreased (D) plots than control plots; it did not differ between C1 and C2 plots (Fig. 2). This pattern is expected if individuals use only fledgling quantity, and not quality, in their settlement decisions.

Adult emigration probability also differed among treatments (Fig. 3). After controlling for the effect of sex and breeding experience (*13*, *23*), we found that adult emigration probability was higher in "increased" (I) and "decreased" (D) plots than in control plots (C1 and C2), whereas it did not differ between I and D plots, or between C1 and C2 plots, respectively (Fig. 3). This pattern suggests that adults use both fledgling quantity and quality when making emigration decisions: when either local fledgling quantity or quality is low, adults assess the quality of their breeding plot as low, and they leave it. The alternative hypothesis that individuals cue on the number of juveniles at independence, which integrates the effect of condition at fledging through early survival (*24*), is not supported by the immigration pattern.

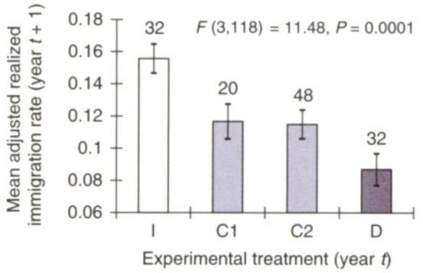

Fig. 2: Immigration rate (±1 SEM) of collared flycatchers in the different experimental treatments. The *y* axis represents values corrected for the effect of sex [$F(1,118) = 17.27$, $P = 0.0001$] and change in the number of nest boxes within plots between years [$F(1,118) = 6.37$, $P = 0.0129$; immigration rate increased with the number of nest boxes in the plot]. Immigration rate was not affected by year [$F(2,118) = 2.47$, $P = 0.09$], replicate within treatment [$F(8,118) = 0.88$, $P = 0.54$], age [$F(1,118) = 1.36$, $P = 0.24$], and breeding density the previous year [$F(1,118) = 0.37$, $P = 0.54$]. Both sexes responded the same to the treatment (interaction treatment by sex: $F(3,115) = 0.05$, $P = 0.98$]. One immigration rate was computed per age (yearling versus older) and sex category, thus giving four values per plot per year.

These results could only be explained by the use of public information, and they imply that flycatchers, like many avian species (*7*), prospect to gather public information (*25*). Observations confirm that prospecting is linked to public information in this species (*26*). The difference in the cues that affect emigration and immigration is likely to reflect constraints in such information-gathering processes. Although information on the current breeding or natal plot is easy to acquire (and thus a mismatch between fledgling quantity and quality is easy to detect) for resident individuals (i.e., potential emigrants), information on the current quality of other breeding plots is probably difficult to gather by breeders and newly fledged juveniles (i.e., potential immigrants) because of spatial and temporal constraints. However, as both quantity and quality of fledglings are positively correlated in nature, each measure brings sufficient information by itself.

Settlement decisions of dispersers also differed according to their previous brood treatment [$N = 108$, $\chi^2(2) = 13.49$, $P = 0.0012$]. After accounting for sex differences, the brood-removed individuals were more likely to disperse to I plots than were unmanipulated individuals [53.8% and 18.7%, respectively; contrast: $n = 93$, $\chi^2(1) = 4.36$, $P = 0.0367$], and brood-increased individuals were less likely to disperse to I plots than were unmanipulated individuals [0% and 18.7%, respectively; contrast: $n = 95$, $\chi^2(1) = 7.12$, $P = 0.0076$], independently from the manipulation on the plot scale [$\chi^2(3) = 3.31$, $P = 0.51$; no difference in the probability to settle in plots C1, C2, or D was observed]. These percentages significantly differ from a random distribution of dispersers among available plots [$\chi^2(3) = 13.97$, $P = 0.0029$]. Thus, individual breeding experience, i.e., "personal information" [in the sense of (*15*)], also influences both departure and settlement decisions, and the meaning of public information cues may differ according to the individual's previous experience.

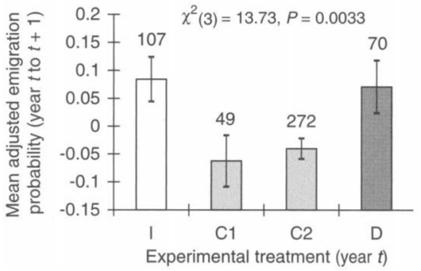

Fig. 3. Adult collared flycatcher emigration probability (±1 SEM) according to experimental treatment. The *y* axis represents residuals from the logistic regression of emigration on sex [$\chi^2(1) = 54.09$, $P \leq 0.0001$ (*13*, *23*)]; interaction treatment by sex [$\chi^2(3) = 2.03$, $P = 0.57$] and previous breeding success [$\chi^2(1) = 40.02$, $P \leq 0.0001$ (*13*, *23*)]. Emigration probability was not affected by year [$\chi^2(2) = 0.26$, $P = 0.88$], replicate within treatment [$\chi^2(7) = 10.35$, $P = 0.17$], density of breeding pairs the previous year [$\chi^2(1) < 0.00$, $P > 0.99$], breeding time [measured by hatching date; $\chi^2(1) = 0.57$, $P = 0.45$], or individual manipulation [brood-removed versus unmanipulated individuals in plots D and C1: $n = 118$, $\chi^2(1) = 0.59$, $P = 0.44$; brood-increased versus unmanipulated individuals in plots I and C1: $n = 155$, $\chi^2(1) = 0.67$, $P = 0.41$]. Thus the perturbation induced by the manipulation per se is not responsible for the observed emigration pattern, whereas individual breeding success strongly affects emigration probability.

Both individual departure and settlement decisions were affected by our manipulation of local reproductive success, providing experimental evidence that birds use public information in breeding habitat selection. The use of public information was particularly expected in species with high breeding densities (*11*, *12*, *14*), high survival prospect (*8*), and open nests (*11*) and for failed breeders or juveniles that cannot rely on their own reproductive success (*12*). Our results, obtained for all breeders of a noncolonial, short-lived, and cavity-nesting species (*18*, *20*), show that the use of public information in breeding habitat selection may be much more widespread than previously thought. In addition, this also shows that birds can use separately fine components of public information.

Our results emphasize the complexity of the cognitive processes involved in the use of public information. Different decisions are based on different cues, and individuals with different phenotypes use these cues differently in relation to their own skills and experience. This complex context-dependent use of public information has implications both in evolutionary ecology [e.g., the evolution of animal aggregation as a consequence of gathering knowledge on all the commodities needed to breed (*27*, *28*)] and conservation biology [e.g., the management of reintroduced populations accounting for individual strategies of breeding habitat selection (*29*, *30*)]. To address such implications, more data are now needed on information-gathering processes (*7*). A recent experimental study in a colonial sea-bird species provided evidence that breeder attendance and presence of prospectors were affected by the manipulation of local reproductive success (*17*). Our results show that varying constraints on information-gathering among phenotypes are likely to shape the use of public information in dispersal.

References and Notes

1. R. A. Johnstone, D. J. D. Earn, *Behav. Ecol. Sociobiol.* **45**, 277 (1999).
2. A. I. Houston, A. Lang, *Anim. Behav.* **56**, 243 (1998).
3. R. D. Gray, M. Kennedy, *Anim. Behav.* **47**, 469 (1994).
4. S. Schjørring, J. Gregersen, T. Bregnballe, *Anim. Behav.* **57**, 647 (1999).
5. M. Frederiksen, T. Bregnballe, *Proc. R. Soc. London Ser. B* **268**, 1519 (2001).
6. L.-A. Giraldeau, in *Behavioural Ecology: An Evolution-*

ary Approach, J. R. Krebs, N. B. Davies, Eds. (Blackwell Science, Oxford, 1997), pp. 42–68.

7. J. M. Reed, T. Boulinier, E. Danchin, L. W. Oring, *Curr. Ornithol.* **15**, 189 (1999).
8. T. Boulinier, E. Danchin, *Evol. Ecol.* **11**, 505 (1997).
9. K. Lahti *et al.*, *Behav. Ecol.* **9**, 122 (1998).
10. J. Clobert, E. Danchin, A. A. Dhondt, J. Nichols, Eds., *Dispersal* (Oxford Univ. Press, Oxford, 2001).
11. E. Danchin, D. Heg, B. Doligez, in *Dispersal*, J. Clobert, E. Danchin, A. A. Dhondt, J. Nichols, Eds. (Oxford Univ. Press, Oxford, 2001), pp. 243–258.
12. E. Danchin, T. Boulinier, M. Massot, *Ecology* **79**, 2415 (1998).
13. B. Doligez, E. Danchin, J. Clobert, L. Gustafsson, *J. Anim. Ecol.* **68**, 1193 (1999).
14. C. R. Brown, M. Bomberger Brown, E. Danchin, *J. Anim. Ecol.* **69**, 133 (2000).
15. T. J. Valone, L.-A. Giraldeau, *Anim. Behav.* **45**, 721 (1993).
16. T. Boulinier, E. Danchin, J.-Y. Monnat, C. Doutreland, B. Cadiou, *J. Avian Biol.* **27**, 252 (1996).
17. T. Boulinier, N. G. Yoccoz, K. D. McCoy, K. E. Erikstad, T. Tveraa, *J. Appl. Stat.* **29**, 509 (2002).
18. L. Gustafsson, W. J. Sutherland, *Nature* **335**, 813 (1988).
19. Materials and methods and supporting text are available as supplementary material on *Science* Online.
20. L. Gustafsson, in *Lifetime Reproduction in Birds*, I. Newton, Ed. (Academic Press, London, 1989), pp. 75–88.
21. R. Pettifor, C. M. Perrins, R. H. McCleery, *J. Anim. Ecol.* **70**, 62 (2001).
22. M. Lindén, L. Gustafsson, T. Pärt, *Ecology* **73**, 336 (1992).
23. T. Pärt, L. Gustafsson, *J. Anim. Ecol.* **58**, 305 (1989).
24. B. Naef-Daenzer, F. Widmer, M. Nuber, *J. Anim. Ecol.* **70**, 730 (2001).
25. T. Slagsvold, J. T. Lifjeld, in *Population Biology of Passerine Birds: An Integrated Approach*, J. Blondel, A. Gosler, J.-D. Lebreton, R. McCleery, Eds. (Springer-Verlag, Berlin, 1990), pp. 441–452.
26. B. Doligez, T. Pärt, unpublished manuscripts.
27. E. Danchin, R. H. Wagner, J. K. Parrish, L. Edelstein-Keshet, *Science* **287**, 804 (2000).
28. E. Danchin, R. H. Wagner, *Trends Ecol. Evol.* **12**, 342 (1997).
29. W. J. Sutherland, *Anim. Behav.* **56**, 801 (1998).
30. T. Caro, *Trends Ecol. Evol.* **14**, 366 (1999).
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Biosynthesis of the Enediyne Antitumor Antibiotic C-1027

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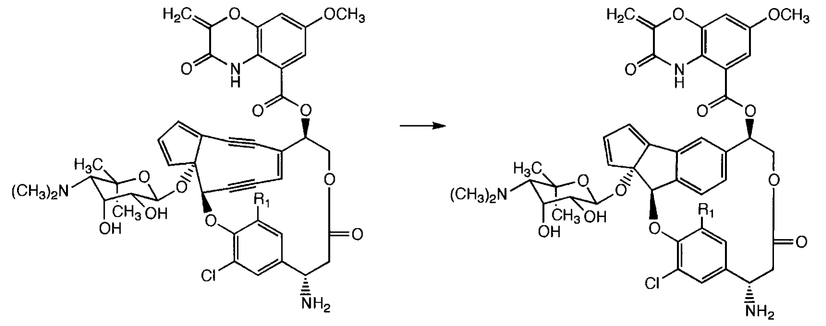
C-1027 is a potent antitumor agent with a previously undescribed molecular architecture and mode of action. Cloning and characterization of the 85-kilobase C-1027 biosynthesis gene cluster from *Streptomyces globisporus* revealed (i) an iterative type I polyketide synthase that is distinct from any bacterial polyketide synthases known to date, (ii) a general polyketide pathway for the biosynthesis of both the 9- and 10-membered enediyne antibiotics, and (iii) a convergent biosynthetic strategy for the C-1027 chromophore from four building blocks. Manipulation of genes governing C-1027 biosynthesis allowed us to produce an enediyne compound in a predicted manner.

C-1027 is a chromoprotein antibiotic produced by *Streptomyces globisporus* and composed of an apoprotein and the C-1027 chromophore (**1**) (Fig. 1) (*1*). It belongs to the enediyne family of antibiotics, structurally characterized by a unit consisting of two acetylenic groups conjugated to a double bond or incipient double bond within a nine- or 10-membered ring, as exemplified by **1** or calicheamicin γ_1^I, respectively [see supporting online material (SOM) (fig. S1)]. The enediyne antibiotics are potent antitumor agents with a previously undescribed molecular architecture and mode of action (*2*–*5*). Although the natural enediynes have seen limited use as clinical drugs mainly because of substantial toxicity, various polymer-based delivery systems or enediyne-antibody conjugates have shown clinical promise and success in anticancer chemotherapy (*4*–*7*). A great challenge will be to develop ways to make new enediynes for mechanistic and clinical studies.

Genetic manipulations of genes governing secondary metabolism offer a promising alternative to preparing complex natural products biosynthetically (*8*–*11*). The success of this approach depends on the cloning and genetic and biochemical characterization of the biosynthetic pathways of the metabolites. The enediynes offer the opportunity to decipher the genetic and biochemical basis for the biosynthesis of structurally complex natural products and to explore ways to make antitumor agents by manipulating genes governing enediyne biosynthesis. Here, we report the cloning, sequencing, and characterization of the complete C-1027 biosynthesis gene cluster from *S. globisporus*, revealing an iterative type I polyketide synthase (PKS) with a previously undescribed domain organization and a convergent biosynthetic strategy for **1** from four biosynthetic building blocks. Manipulation of genes governing C-1027 biosynthesis allowed us to engineer enediyne compounds, as exemplified by deshydroxy–C-1027 (**2**).

We have previously cloned the *sgcAB* genes and demonstrated that they are essential for C-1027 production in *S. globisporus* (*12*). Because antibiotic production genes commonly occur as a cluster in actinomycetes, we set out to identify the C-1027 biosynthesis gene cluster by chromosomal walking from the *sgcAB* locus. An 85-kb contiguous DNA from *S. globisporus* was sequenced and analyzed, revealing 67 open reading frames (ORFs) (see SOM) (Fig. 2A). To determine the boundaries of the C-1027 gene cluster, ORFs at both ends of the sequenced region



1 (R_1 = OH)
2 (R_1 = H)

3 (R_1 = OH)
8 (R_1 = H)

Fig. 1. Structures of the C-1027 (**1**) and deshydroxy-C-1027 (**2**) chromophores and their aromatized products (**3**) and (**8**).

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