

This Week's Citation Classic

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Patterson I J. Timing and spacing of broods in the black-headed gull *Larus ridibundus*. *Ibis* 107:433-59, 1965.
[Dept. Zoology, University Museum, Oxford, England]

Nesting density in black-headed gulls was determined by an interaction between the territorial aggressiveness of initial residents and pressure from subsequent potential settlers. Birds in the centre of the colony, and those nesting synchronously with others, were most successful. [The SCI® indicates that this paper has been cited in over 120 publications since 1965.]

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"In October 1961, as a new graduate student fresh from training in animal ecology in V.C. Wynne-Edwards's department at the University of Aberdeen, I was anxious for a good grounding in animal behaviour from Niko Tinbergen and his group at Oxford University. My main interest was the social structure and organization of bird colonies, arising from schoolboy studies of the rook *Corvus frugilegus* and later undergraduate work on the kittiwake *Rissa tridactyla*, encouraged by John Coulson of Durham University. With this background, I readily accepted the suggestion that I might join the group of postgraduates working on the black-headed gull and might test some of the ideas on the functional significance of colony-nesting, which Tinbergen had been developing over the previous few years.

"The study was carried out in a very large coastal colony of black-headed gulls at Ravenslass in northwest England. A small field camp provided excellent conditions for research, with frequent small-group discussions of each other's work, greatly enlivened and sharpened during Tinbergen's periodic

visits. Living in close contact with the bird colony for several months, together with others working on closely related research programmes, gave a first-rate opportunity to develop and test hypotheses on colony structure.

"Winters were spent in Oxford, analysing and discussing results, reading, and attending seminars. In this stimulating atmosphere, Tinbergen's outstanding insight into the functional aspects of animal behaviour and his ability to identify and ask the crucial but often apparently (but deceptively) simple questions were to be the major influence on my subsequent approach to research as well as on the success of the gull programme.

"My own study fell into two distinct parts. The first followed my own interests in colony structure, especially how nesting density might be limited through territorial behaviour. I was able to describe the 'aggressive response curve,' the decline in a territory owner's tendency to attack others with increasing distance from the territory centre. This produces an increasing resistance to further settlement as density increases and provides a mechanism for limitation. The second part of the study measured the benefits of nesting in a colony, by examining breeding success in relation to spatial position and laying date.

"The paper is cited for both sections of the work: as a contribution to hypotheses on the limitation of density and as one of the first studies to demonstrate the benefit of nesting synchronously as well as in a dense colony.

"My subsequent research work at Aberdeen has concentrated on aspects of behavioural ecology, especially of rooks and shelducks *Tadorna tadorna*. However, I have recently returned to my early ideas on density limitation and have extended them into a more formal model.¹ I am currently testing this in experiments with cichlid fish, an abrupt but stimulating change of study animal!"

1. **Patterson I J.** Territorial behaviour and the limitation of bird density. *Ardea* 68:53-62, 1981.