

This Week's Citation Classic

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Wynne-Edwards V C. *Animal dispersion in relation to social behaviour*.
Edinburgh: Oliver & Boyd, 1962. 653 p. [Univ. Aberdeen, Aberdeen,
Scotland]

The book expounds a general theory that animals can limit their own numbers by social mechanisms. In so doing they avoid depleting their food resources, in the way man has so often done by overexploiting whales, fish, and game; or by overgrazing with livestock. [The SC[®] indicates that this book has been cited over 600 times since 1962.]

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"My hypothesis is that animal numbers can be limited, for prudential reasons, by conventions that generally involve territories or peck-orders or both. Individuals are made to compete for the right to feed, rather than for the food itself. These homeostatic conventions adjust the population density to a level that the food resources can support without being overtaxed. Some individuals succeed in winning the property or rank that gives them the right to feed; the rest are denied it and emigrate, or get killed by predators, disease, or starvation. Quotas of breeding adults are likewise established, and surplus adults are inhibited from breeding.

"The conventional systems are essentially social, and I surmise that this is how sociality originally came to evolve. If so, it gives one a new insight on society, as being inherently competitive and deeply concerned with rank and possessions as status symbols. At the same time societies are brotherhoods, needing collaboration in the observance of conventions and in repelling invaders; they depend on allegiance and the virtues of conformity.

"The idea came as I was writing a review of Lack's book, *The Natural Regulation of*

Animal Numbers, in 1954.^{1,2} It was very exciting and yet seemed so simple that others would surely be drawing the same conclusions any day. My life was already busy and if the hypothesis was to be adequately supported there was a huge literature to survey. In fact it took me seven years to finish the book!

"The topic is interdisciplinary. It relates to a central problem of ecology —the regulation of numbers and 'balance of nature' —and also to the new science of sociobiology. An article I contributed to the *Scientific American* in 1964 ran to 300,000 offprints and reprints.³ I have lectured to audiences in many universities and countries, and have received a medal or two and been elected to the Royal Society. But it has not all been a smooth ride: there is a snag that still makes the subject controversial. Darwin's theory assumes that animals always strive to increase their numbers, and that the fittest are those which leave the most progeny to posterity. But here am I, asserting that animals put prudential restraints on their natural increase. How could such restraints evolve under natural selection which measures success in terms of individual fecundity?

"This is still an impossible question to test or to answer. But a research team I set up in Aberdeen in 1956 has amply confirmed my predictions.⁴⁻⁶ Red grouse have been proved to control their numbers by social behaviour. Experiments in the wild have shown that, though they never overtax their resources, upgrading the food supply leads to an increase in population density and downgrading reduces it; a low plane of nutrition makes the cocks more aggressive (defending bigger territories); an implant of male hormone increases their personal status; and 60% of their number become social outcasts and die in an average year.

"The theory still rings so true and explains so much that it seems almost bound to be correct; and of course prudential adaptations are not the only authentic phenomena that continue to perplex evolutionists."

1. Lack D. *The natural regulation of animal numbers*. Oxford: Clarendon Press, 1954. 343 p.
2. Wynne-Edwards V C. The dynamics of animal populations. *Discovery* (London) **1955**:433-6, 1955.
3. Population control in animals. *Sci. Amer.* **211**:68-74, 1964.
4. Watson A & Jenkins D. Experiments on population control by territorial behaviour in red grouse. *J. Anim. Ecol.* **37**:595-614, 1968.
5. Watson A. Territorial and reproductive behaviour of red grouse. *J. Reprod. Fert.* (Supplement) **11**:3-14, 1970.
6. Miller G R, Watson A & Jenkins D. Responses of red grouse populations to experimental improvement of their food. (Watson A, ed.) *Animal populations in relation to their food resources*. British Ecological Society Symposium No. 10. Oxford: Blackwell Scientific Publications, 1970. p. 323-34.