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This Week's Citation Classic

Brown J L & Orians G H. Spacing patterns in mobile animals.
Annu. Rev. Ecol. Syst. 1:239-62, 1970.
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We reviewed the literature on two basic problems, the influence of spacing behavior such as territoriality and coloniality on populations and the ecological selection pressures that favor particular spacing behaviors. [The *SCI*® indicates that this paper has been cited in over 265 publications.]

Rootlets of Behavioral Ecology

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Ecology and behavior interact to determine spatial patterns in the distribution of individuals. Familiar patterns are those created by territoriality or coloniality. The study of these phenomena in the 1960s had been productive, and a review in 1970 in the first issue of the *Annual Review of Ecology and Systematics* seemed appropriate. Our review grew out of Brown's work on territorial behavior[1,2] and Orians's work on coloniality,[3] combined with a long tradition of study of these behaviors among vertebrate biologists.

Our review contained little in the way of new ideas, although a new term, "all-purpose territory," was introduced and became established. The primary cause of its influence may have been simply that it was useful as an accessible review that integrated various concepts of space-related behavior and pointed to key directions of future research.

Twenty years after we wrote this review, it is interesting to look back at our predictions and to compare them with what subsequently happened. First, our predictions:

> Cost-benefit models for the evolution of space-related aggression point to the importance of measuring the temporal and spatial distribution of resources, the costs of exclusion, and the rates of predation on clumped and spaced individuals. Future studies will concern themselves primarily with measuring differences in fitness of individuals of the same species under different conditions and with analyzing changes in spacing patterns in species which exploit a variety of environments. Thus, the study of spacing may rapidly develop into a theoretically rigorous and more experimentally oriented science.

The modern science of behavioral ecology fits this description, and the study of spacing, or social phenomena, still plays a leading role.[4] Shortly after our review, F.B. Gill and L.L. Wolf[5] published a detailed cost-benefit study based on actual measurements of the energy value of resources in and out of territories. These were interpreted using physiological data on energy metabolism and later analyzed by G.H. Pyke[6] within the framework of optimality theory.

The popularity of cost-benefit optimality models increased enormously in the next decades, and they now dominate current textbooks of behavioral ecology. Their roots are in these early studies of territoriality as well as in simple models such as Hamilton's rule and the early optimal foraging models. We expect that such models will continue to be useful, especially when supplemented by newer perspectives resulting from closer attention to genetic and developmental factors.

1. **Brown J L.** The evolution of diversity in avian territorial systems. *Wilson Bull.* 76:160-9, 1964. (Cited 360 times.)
[See also: **Brown J L.** Citation Classic. (Barrett J T, comp.) *Contemporary classics in plant, animal, and environmental sciences.* Philadelphia: ISI Press, 1986. p. 345.]
2. ————. Territorial behavior and population regulation in birds. *Wilson Bull.* 81:293-329, 1969. (Cited 220 times.)
3. **Orians G H.** The ecology of black bird (*Agelaius*) social systems. *Ecol. Monogr.* 31:285-312, 1966. (Cited 220 times.)
4. **Sibley R M & Smith R H.** *Behavioural ecology: ecological consequences of adaptive behaviour.* Oxford, England: Blackwell Scientific, 1985. 620 p.
5. **Gill F B & Wolf L L.** Economics of feeding territoriality in the golden-winged sunbird. *Ecology* 56:333-45, 1975. (Cited 200 times.)
6. **Pyke G H.** The economics of territory size and time budget in the golden-winged sunbird. *Amer. Naturalist* 114:131-45, 1979. (Cited 55 times.)

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