

a lot. Whether or not this is so, all foresters with an interest in the effect of vegetation on water yield will find this an essential reference source.

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ANIMAL DISPERSION IN RELATION TO SOCIAL BEHAVIOUR,
by V. C. Wynne-Edwards. Oliver and Boyd. 653 pp., 50 tables,
11 plates.

The general theory of regulation of animal numbers which is taught throughout the world is that individuals of a population (and at the higher level, species) compete with one another in the fight which results in selection and survival of the fittest individuals. And in doing this they use as much of their surrounding resources as possible. All the machinery of population homeostasis — density dependent fecundity, survival, growth, mortality, etc. — is usually considered to act to this end. Professor Wynne-Edwards, however, is completely disenchanted with the theory and has contrived a philosophical Molotov cocktail with which to rend it asunder.

Starting with the observation that in nature starvation is almost never the *proximate* cause of lopping the numbers of a too-numerous population, he proceeds to argue this is evidence that animals cut their numbers before food shortage occurs. To do this, he suggests, the animals must behave in a way by which they voluntarily chop their numbers *before* over-population occurs, that such behaviour must by its nature involve groups of animals, and therefore that group selection (rather than individual selection) must be the basic evolutionary force.

After establishing these points, Wynne-Edwards seeks to consolidate his foothold on the reader's attention with a review (103 pages long) of the paraphernalia by which animals communicate with one another, and brings to the fore evidence of the vast amount of effort animals put into this activity. Calling, roaring, bird-song, sign-posting, swarming, communal roosting, herding, secreting substances into the environment, are considered. Throughout this review he reiterates the point that much of this activity is for display alone (epideictic), and that its purposes are to enable the population to assess its own abundance, disperse its members throughout the habitat in the best possible manner, and by the contacts provided act as a stimulus for the appropriate homeostatic response of increasing or lopping numbers.

These displays are considered to act on the society in many ways. If the signs suggest the society is understocking its environment, the population calls the juvenile, usually unsuccessful breeding "surplus" into breeding action. If there are too many, these socially inferior individuals are denied the right to breed. If after all these social devices fail and recruitment is still too high for safety, the surplus is expelled, exposed to predation, the parents intervene by killing and sometimes eating young, or subordinate individuals are so persecuted by their superiors in the society that they become stressed and die from organic disturbances. Wynne-Edwards sees in all these phenomena evidence that the animals are not just suffering the vicissitudes of the environment and getting along as well as they can, but suggests rather that they act as a

society which governs and responds to the current situation with due prudence.

The key to this is the ritualization of all contests for food to the status of strict conventions which avert and over-ride the undisguised contest: "Conventions lay down codes of law, which have evolved to safeguard the general welfare and survival of society, especially against the antisocial, subversive self-advancement of the individual".

He substantiates and expands his arguments with examples drawn from the literature and fauna of the world, and, in my view, leaves much to be desired in this task. To instance an error of fact (see p. 62): The roar of red deer is a territory-claiming device. As the rutting "season draws near, . . . the sparring and competition that has been going on . . . all summer mounts to a climax. At almost any time stags will . . . mill at each other with their forefeet". (The reviewer has not yet seen this despite several hundred hours' observation.) And soon after: "As Darwin pointed out, the voice of the stag does not serve to call up the hinds, since it is actually the stag that goes after the hinds; and in red deer and moose it is rather the female's voice that draws the male. . . ." (The red deer hind is, so far as the reviewer knows, quite silent except when alarmed.)

In chapter 19 he writes of the importance of tradition in regulating the manner by which animals use their ground, and unfortunately illustrates it with a contradiction. Writing of the rabbit in Britain, he notes that repopulation following decimation by myxomatosis has been "astonishingly slow" (p. 451). Then he "is tempted to conclude that rebuilding a traditional system of dispersion can be a far slower and more deliberate affair than merely producing enough bodies to make good the original loss. . . ." But in the same paragraph he destroys his argument by noting how this same animal has "become a rampant scourge of huge areas of Australia"—without tradition, be it noted. More seriously, he completely ignores the possible influences in Britain of development of a rank vegetation or increase of parasites following the respite from grazing, though these factors have been considered important by several authors.

In chapter 11, Wynne-Edwards deals with communal nuptial displays as a device which enables the population to assess its own abundance and reproduce accordingly. He tests my credulity in this. Thus, when I arrived at the end of the chapter and saw that in lekking birds (those in which the males assemble and compete on traditional sites during the mating season), "The lek remains in session as long as any females could come forward for fertilization . . . and it is inferred that males may withhold coition once a sufficient quota of hens has been fertilized", I was disappointed to find no discussion of the physiological state of these withholding males.

These two examples typify the weakness of the book: The physiology of the case is not adequately considered. The wealth of published information on density-dependent physiological changes, on the occurrence of starvation, on the physiological causation of reproductive loss, on mortality, and so on, receive inadequate treatment in four chapters at the end. They are dismissed as possible proximate causes of population homeostasis.