much of a certain time-lag in meeting it, though we should all do our best in our respective ways to help to abbreviate it. We must be careful, too, in making public criticisms, that we get our facts right. It is a sad comment on the quality of public discussion of these matters that, at a time when various publicists are denouncing the poverty in this respect of the public service in general and the Treasury in particular, more than half the top administrators in the Treasury have degrees or similar qualifications as economists.

It is the second problem which worries me more: the problem how to bring it about that the general conduct of public affairs and the state of mind of those who rule over us is sufficiently informed of the relevance of technology and economics and the powerful assistance they can give. I think this problem is very important. If the quality of actual discussion in this respect is compared to what it might be, it is all too painfully obvious what a long way there is to go. But I do not see any simple answer. As I have tried to show earlier, I do not think we shall get anywhere by pitching our claims too high—by contending that either technology or economics holds the key to human destiny. For that would be false, and to rely on that kind of argument would simply provide yet another pretext to the Philistines for not taking us at our true worth. In the long run I should hope much from the presence in *non-specialized* jobs in the public service and business of more persons with a technological or economic educational background; the moral value of that sort of training with its objectivity and its humility *vis-à-vis* the ultimate problems of the universe is still often insufficiently appreciated. I think also that much can be done by patient participation by technologists and economists in the public discussion of questions to which their expert knowledge is germane. The business of politics is much too serious nowadays to be left to the politicians. I hope too that, as time goes on, teaching in schools and universities will come to convey even to those who do not aspire to be experts in these fields some idea of their general relevance and the part they can play in human progress.

But this brings me to the threshold of a subject which at the outset I declared it my intention to avoid. I will conclude, therefore, by expressing my conviction that, in the creation of this broader understanding and this more enlightened outlook, the Imperial College of Science and Technology has a notable part to play, and my firm confidence that it will not fail to rise to the opportunity.

INTERGROUP SELECTION IN THE EVOLUTION OF SOCIAL SYSTEMS

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In a recent book[1] I advanced a general proposition which may be summarized in the following way. (1) Animals, especially in the higher phyla, are variously adapted to control their own population densities. (2) The mechanisms involved work homeostatically, adjusting the population density in relation to fluctuating levels of resources; where the limiting resource is food, as it most frequently is, the homeostatic system prevents the population from increasing to densities that would cause over-exploitation and the depletion of future yields. (3) The mechanisms depend in part on the substitution of conventional prizes, namely, the possession of territories, homes, living space and similar real property, or of social status as the proximate objects of competition among the members of the group concerned, in place of the actual food itself. (4) Any group of individuals engaged together in such conventional competition automatically constitutes a society, all social behaviour having sprung originally from this source.

In developing the theme it soon became apparent that the greatest benefits of sociality arise from its capacity to override the advantage of the individual members in the interests of the survival of the group as a whole. The kind of adaptations which make this possible, as explained more fully here, belong to and characterize social groups as entities, rather than their members individually. This in turn seems to entail that natural selection has occurred between social groups as evolutionary units in their own right, favouring the more efficient variants among social systems wherever they have appeared, and furthering their progressive development and adaptation.

The general concept of intergroup selection is not new. It has been widely accepted in the field of evolutionary genetics, largely as a result of the classical analysis of Sewall Wright[2–4]. He has expressed the view that "selection between the genetic systems of local populations of a species . . . has been perhaps the greatest creative factor of all in making possible selection of genetic systems as wholes in place of mere selection according to the net effects of alleles"[4]. Intergroup selection has been invoked also to explain the special case of colonial evolution in the social insects[5–7].

In the context of the social group a difficulty appears, with selection acting simultaneously at the two levels of the group and the individual. It is that the homeostatic control of population density frequently demands sacrifices of the individual; and while population control is essential to the long-term survival of the group, the sacrifices impair fertility and survivorship in the individual. One may legitimately ask how two kinds of selection can act simultaneously when on fundamental issues they are working at cross purposes. At first sight there seems to be no easy way of reconciling this clash of interests; and to some people consequently the whole idea of intergroup selection is unacceptable.

Before attempting to resolve the problem it is necessary to fill in some of the background and give it clearer definition. The survival of a local group or population naturally depends among other things on the continuing annual yield of its food resources. Typically, where the tissues of animals or plants are consumed as food, persistent excessive pressure of exploitation can rather quickly overtax the resource and reduce its productivity, with the result that yields are diminished in subsequent years. This effect can be seen in the overfishing of commercial fisheries which is occurring now in different parts of the world, and in the overgrazing of pastoral land, which in dry climates can eventually turn good grassland into desert. Damage to the crop precedes the onset and spread of starvation in the exploiting population, and may be further aggravated by it. The general net effect of over-population is thus to diminish the carrying-capacity of the habitat.

In natural environments undisturbed by man this kind of degradation is rare and exceptional: the normal evolutionary trend is in the other direction, towards building up and sustaining the productivity of the habitat at the highest attainable level. Predatory animals do not in these conditions chronically depress their stocks of prey, nor do herbivores impair the regeneration of their food-plants. Many animals, especially among the larger vertebrates (including man), have themselves virtually no predators or parasites automatically capable of disposing of a population surplus if it arises.

It is the absence or undependability of external destructive agencies that makes it valuable, if not in some cases mandatory, that animals should be adapted to regulate their own numbers. By so doing, the population density can be balanced around the optimum level, at which the highest sustainable use is made of food resources.

Only an extraordinary circumstance could have concealed this elementary conclusion and prevented our taking it immediately for granted. Some eight or more thousand years ago, as neolithic man began to achieve new and greatly enhanced levels of production from the land through the agricultural revolution, the homeostatic conventions of his hunting ancestors, developed there as in other primates to keep population density in balance with carrying-capacity, were slowly and imperceptibly allowed to decay. We can tell this from the centrally important place always occupied by fertility-limiting and functionally similar conventions in the numerous stone-age cultures which persisted into modern times[8]. Since these conventions disappeared nothing has been acquired in their place: growing skills in resource development have, except momentarily, always outstripped the demands of a progressively increasing population; there has consequently been no effective natural selection against a freely expanding economy. So far as the regulation of numbers is concerned, the human race provides a spectacular exception to the general rule.

A secondary factor, tending to obscure the almost universal powers possessed by animals for controlling their numbers, is our everyday familiarity with insect and other pests which appear to undergo uncontrolled and sometimes violent fluctuations in abundance. In fact, human land-use practices seldom leave natural processes alone for any length of time: vegetation is gathered, the ground is tilled, treated or irrigated, single-species crops are planted and rotated, predators and competitors are destroyed, and the animals' regulating mechanisms are thereby, understandably, often defeated. In the comparably drastic environmental fluctuations of the polar and desert regions, similar population fluctuations occur without human intervention.

The methods by which natural animal populations curb their own increase and promote the efficient exploitation of food resources include the control of recruitment and, when necessary, the expulsion and elimination of unwanted surpluses. The individual member has to be governed by the homeostatic system even when, as commonly happens, this means his exclusion from food in the midst of apparent plenty, or detention from reproduction when others are breeding. The recruitment rate must be determined by the contemporary relation between population density and resources; under average conditions, therefore, only part of the potential fecundity of the group needs to be realized in a given year or generation.

This is a conclusion amply supported by the results of experiments on fecundity versus density in laboratory populations, in a wide variety of animals including Crustacea, insects, fish and mammals; and also by field data from natural populations[1]. But it conflicts with the assumption, still rather widely made, that under natural selection there can be no alternative to promoting the fecundity of the individual, provided this results in his leaving a larger contribution of surviving progeny to posterity[9]. This assumption is the chief obstacle to accepting the principle of intergroup selection.

One of the most important premises of intergroup selection is that animal populations are typically self-perpetuating, tending to be strongly localized and persistent on the same ground. This is illustrated by the widespread use of traditional breeding sites by birds, fishes and animals of many other kinds; and by the subsequent return of the great majority of experimentally marked young to breed in their native neighbourhood. It is true of non-migratory species, for example the more primitive communities of man; and all the long-distance two-way migrants that have so far been experimentally tagged, whether they are birds, bats, seals or salmon, have developed parallel and equally remarkable navigating powers that enable them to return precisely to the same point, and consequently preserve the integrity of their particular local stock. Isolation is normally not quite complete, however. Provision is made for an element of pioneering, and infiltration into other areas; but the gene-flow that results is not commonly fast enough to prevent the population from accumulating heritable characteristics of its own. Partly genetic and partly traditional, these differentiate it from other similar groups.

Local groups are the smallest racial units capable of continuous existence for long enough to undergo evolutionary differentiation. In the course of generations some die out; others survive, and have the opportunity to spread into new or vacated ground as it becomes available, themselves subdividing as they grow. In so far as the successful ones take over the habitat left vacant by the unsuccessful, the groups are in a relation of passive competition. Their survival or extinction is partly a matter of chance, arising from various forms of *force majeure*, including secular changes in the environment; for the rest it is determined, in general terms, by heritable qualities of fitness.

Gene-frequencies within the group may alter as time passes, through gene-flow, drift (the Sewall Wright effect), and selection at the individual level. Through the latter, adaptations to local conditions may accumulate. Population fitness, however, depends on something over and above the heritable basis that determines the success as individuals of a continuing stream of independent members. It becomes particularly clear in relation to population homeostasis that social groups have highly important adaptive characteristics in their own right.

When the balance of a self-regulating population is disturbed, for example by heavy accidental mortality, or by a change in food-resource yields, a restorative reaction is set in motion. If the density has dropped below the optimum, the recruitment rate may be increased in a variety of ways, most simply by drawing on the reserve of potential fecundity referred to earlier, and so raising the reproductive output. Immigrants appearing from surrounding areas can be allowed to remain as recruits also. If the density has risen too high, aggression between individuals may build up to the point of expelling the surplus as emigrants; the reproductive rate may drop; and mortality due to social stress (and in some species cannibalism) may rise. These are typical examples of density-dependent homeostatic responses.

Seven years of investigation of the population ecology of the red grouse (*Lagopus scoticus*) near Aberdeen, by the Nature Conservancy Unit of Grouse and Moorland Ecology, have revealed many of these processes at work[10]. Their operation in this case depends to a great extent on the fact that individual members of a grouse population living together on a moor, even of the same sex, are not equal in social status. Some of the cock birds are sufficiently dominant to establish themselves as territory owners, parcelling out the ground among them and holding sway over it, with a varying intensity of possessiveness, almost the whole year round. During February–June their mates enjoy the same established status.

In the early dawn of August and September mornings, after a short and almost complete recess, the shape of a new territorial pattern begins to be hammered out. In most years this quickly identifies a large surplus of males, old and young, which are not successful in securing any part of the ground, and consequently assume a socially inferior status. They are grouped with the hens at this stage as unestablished birds; and day by day their security is so disturbed by the dawn aggressive stress that almost at once some begin to get forced out, never to return. By about 8 a.m. each day the passion subsides in all but the most refractory territorial cocks, after which the moor reverts to communal ground on which the whole population can feed freely for the rest of the day. As autumn wears on and turns to winter, the daily period of aggression becomes fiercer and lasts longer; birds with no property rights have to feed at least part of the time on territorial ground defended by owners that may at any moment chase them off. More and more are driven out altogether; and since they can rarely find a safe nook to occupy elsewhere in the neighbourhood, they become outcasts, and are easily picked up by hawks and foxes, or succumb to malnutrition. Females are included among those expelled; but about February the remaining ones begin to establish marital attachments; and at the same time, quite suddenly, territories are vigorously defended all day. Of the unestablished birds still present in late winter, some achieve promotion by filling the gaps caused by casualties in the establishment. Some may persist occasionally until spring; but unless a cock holds a territory exceeding a minimum threshold capacity, or a hen becomes accepted by a territorially qualified mate, breeding is inhibited.

Territories are not all of uniform size, and on average the largest are held by the most dominating cocks. More important still, the average territory size changes from year to year, thus varying the basic population density, apparently in direct response to changes in productivity of the staple food-plant, heather (*Calluna vulgaris*). As yet this productivity has been estimated only by subjective methods; but significant mutual correlations have been established between annual average values for body-weight of adults, adult survival, clutch-size, hatching success, survival of young, and, finally, breeding density the following year. As would be expected with changing densities, the size of the autumn surplus, measured by the proportions of unestablished to established birds, also varies from year to year.

There are increasing grounds for concluding that this is quite a typical organization, so far as birds are concerned, and that social stratification into established and unestablished members, particularly in the breeding season, is common to many other species, and other classes of animals. In different circumstances the social hierarchy may take the form of a more or less linear series or peck-order. Hierarchies commonly play a leading part in regulating animal populations; not only can they be made to cut off any required proportion of the population from breeding, but also they have exactly the same effect in respect of food when it is in short supply. According to circumstances, the surplus tail of the hierarchy may either be disposed of or retained as a non-participating reserve if resources permit.

It is not necessary here to explore in detail the elaborate patterns of behaviour by which the social hierarchy takes effect. The processes are infinitely varied and complex, though the results are simple and functionally always the same. The hierarchy is essentially an overflow mechanism, continuously variable in terms of population pressure on one hand, and habitat capacity on the other. In operation it is purely conventional, prescribing a code of behaviour. When a more dominant individual exerts sufficient aggressive pressure, usually expressed as threat although frequently in some more subtle and sophisticated form, his subordinates yield, characteristically without physical resistance or even demur. It may cost them their sole chance of reproduction to do so, if not their lives. The survival of the group depends on their compliance.

This has been taken as an example to illustrate one type of adaptation possessed by the group, transcending the individuality of its members. It subordinates the advantage of particular members to the advantage of the group; its survival value to the latter is clearly very great. The hierarchy as a system of behaviour has innumerable variants in different species and different phyla, analogous to those of a somatic unit like the nervous or vascular system. Like them, it must have been subject to adaptive evolutionary change through natural selection; yet it is essentially an 'organ' of a social group, and has no existence if the members are segregated.

A simple analogy may possibly help to bring out the significance of this point. A football team is made up of players individually selected for such qualities as skill, quickness and stamina, material to their success as members of the team. The survival of the team to win the championship, however, is determined by entirely distinct criteria, namely, the tactics and ability it displays in competition with other teams, under a particular code of conventions laid down for the game. There is no difficulty in distinguishing two levels of selection here, although the analogy is otherwise very imperfect.

The hierarchy is not the only characteristic of this kind. There are genetic mechanisms, such as those that govern the optimum balance between recombination and linkage, in which the benefit is equally clearly with the group rather than the individual. Without leaving the sphere of population regulation, however, we can find a wide range of vital parameters, the optima of which must similarly be determined by intergroup selection. Among those discussed at length in the book already cited[1] are (1) the potential life-span of individuals and, coupled with it, the generation turnover rate; (2) the relative proportions of life spent in juvenile or non-sexual condition (including diapause) and in reproduction; (3) monotely (breeding only for a single season) versus polytely; (4) the basal fecundity-level, including, in any one season, the question of one brood versus more than one.

These and similar parameters, differing from one species or class to another, are interconnected. Their combined effects are being summed over the whole population at any one time, and over many generations in any given area. It is the scale of the operation in time and space that precludes an immediate experimental test of group selection. An inference that may justifiably be drawn, however, is that maladjustment sufficient to interfere persistently with the homeostatic mechanism must either cause a progressive decline in the population or, alternatively, a chronic over-exploitation and depletion of food resources: in the end either will depopulate the locality.

There still remains the central question as to how an immediate advantage to the individual can be suppressed or overridden when it conflicts with the interests of the group. What would be the effect of selection, for example, on individuals the abnormal and socially undesirable fertility of which enabled them and their hereditary successors to contribute an ever-increasing share to future generations?

Initially, groups containing individuals like this that reproduced too fast, so that the overall recruitment rate persistently tended to exceed the death-rate, must have repeatedly exterminated themselves in the manner just indicated, by overtaxing and progressively destroying their food resources. The earliest adaptations capable of protecting the group against such recurrent disasters must necessarily have been very ancient; they may even have been acquired only once in the whole of animal phylogeny, and in this respect be comparable with such basic morphological elements as the mesoderm, or, perhaps, the cœlom. Once acquired, the protective adaptations could be endlessly varied and elaborated. It is inherently difficult to reconstruct the origin of systems of this kind; but genetic mechanisms exist which could give individual breeding success a low heritability, or, in other words, make it resistant to selection. This could be relatively simply achieved, for example, if the greatest success normally attached to heterozygotes for the alleles concerned, creating the stable situation characteristic of genetic homeostasis[11].

A more complex system can be discerned, as it has developed in many of the higher vertebrates where the breeding success of individuals is very closely connected with social status. This connexion must necessarily divert an enormous additional force of selection into promoting social dominance, and penalizing the less fortunate subordinates in the population that are prevented from breeding or feeding, or get squeezed out of the habitat. Yet it is self-evident that the conventional codes under which social competition is conducted are in practice not jeopardized from this cause: selection pressure, however great, does not succeed in promoting a general recourse to deadly combat or treachery between rivals, nor does it, in the course of generations, extinguish the patient compliance of subordinates with their lot.

The reason appears to be that social status depends on a summation of diverse traits, including virtually all the hereditary and environmental factors that predicate health, vigour and survivorship in the individual. While this is favourable to the maintenance of a high-grade breeding stock, and can result in the enhancement through selection of the weapons and conventional adornments by which social dominance is secured, dominance itself is again characterized by a low heritability, as experiments have shown. In many birds and mammals, moreover, individual status, quite apart from its genetic basis, advances progressively with the individual's age. Not only are the factors that determine social and breeding success numerous and involved, therefore, but the ingredients can vary from one successful individual to the next. A substantial part of the gene pool of the population is likely to be involved and selection for social dominance or fertility at the individual level correspondingly dissipated and ineffective, except in eliminating the sub-standard fringe.

Such methods as these which protect group adaptations, including both population parameters and social structures, from short-term changes, seem capable of preventing the rise of any hereditary tendency towards anti-social self-interest among the members of a social group. Compliance with the social code can be made obligatory and automatic, and it probably is so in almost all animals that possess social homeostatic systems at all. In at least some of the mammals, on the contrary, the individual has been released from this rigid compulsion, probably because a certain amount of intelligent individual enterprise has proved advantageous to the group. In man, as we know, compliance with the social code is by no means automatic, and is reinforced by conscience and the law, both of them relatively flexible adaptations.

There appears therefore to be no great difficulty in resolving the initial problem as to how intergroup selection can override the concurrent process of selection for individual advantage. Relatively simple genetic mechanisms can be evolved whereby the door is shut to one form of selection and open to the other, securing without conflict the maximum advantage from each; and since neighbouring populations differ, not only in genetic systems but in population parameters (for example, mean fecundity[12]) and in social practices (for example, local differences in migratory behaviour in birds, or in tribal conventions among primitive men), there is no lack of variation on which intergroup selection can work.

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GEOMAGNETIC PARAMETERS AND PSYCHIATRIC HOSPITAL ADMISSIONS

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ALTHOUGH the relationship of natural environmental physical forces to human behaviour has always been a matter of general interest and speculation, there has been a paucity of systematic investigations in this connexion among modern scientific workers. Buettner[1], in a critique of the literature bearing on correlations between bioclimatological parameters and human health and behaviour, pointed to the general confusion in the field as well as to the very limited unequivocal findings consisting of the establishment of two 'potentially harmful' weather types. The literature in the field of geomagnetic parameters and human behaviour is more restricted in quantity and in significance of findings.

Possibly the most ambitious pertinent investigation is that of Düll and Düll[2]. In an analysis of approximately 40,000 cases over a period of 60 months they demonstrated graphically a clearly observable relationship between the 67 magnetic storms occurring during this time, and the incidence of nervous and mental diseases and suicides. Their results, however, were not subjected to statistical treatment. Berg[3], reviewing the literature pertaining to the relationships between environmental geophysical parameters and the human population, concluded that firm evidence for or against such relationships is still lacking.

The relative indifference of the behavioural scientists to this problem may possibly be due to the lack of that type of theoretical framework which could permit the interrelationship of the two parameters to be derived as a logical consequence. There has been, however, a growing appreciation of, and body of empirical findings related to, one circumscribed aspect of the overall area, the biological effects of magnetic fields[4–6], particularly with reference to infra-human organisms. A parallel related concern has been the investigations into the electrical organizations of the living organism. Thus, in a review of recent work in the relationship between direct current electricity and living organisms[7], it was suggested that the direct-current electrical system of the organism could be conceived as a control system which could be influenced by external force fields. These considerations led to a pilot investigation[8] which examined the relationship between gross manifestations of extreme human psychological disturbance and natural magnetic field intensity. The psychiatric admissions to two Syracuse, New York, hospitals were correlated with K-index[9] sums as measured at the Fredericksburg Magnetic Observatory, Virginia, for approximately a four-year period. The statistically significant correlation ratios obtained for non-linear relationships, η, of 0·26 and 0·27 suggested that at least some relationship exists between the incidence of psychiatric disturbance and some geophysical parameter associated with the magnetic field.

The investigation reported here is an extension of the pilot work utilizing a larger sample of psychiatric hospital