# Geometry for the Selfish Herd

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This paper presents an antithesis to the view that gregarious behaviour is evolved through benefits to the population or species. Following Galton (1871) and Williams (1964) gregarious behaviour is considered as a form of cover-seeking in which each animal tries to reduce its chance of being caught by a predator.

It is easy to see how pruning of marginal individuals can maintain centripetal instincts in already gregarious species; some evidence that marginal pruning actually occurs is summarized. Besides this, simply defined models are used to show that even in non-gregarious species selection is likely to favour individuals who stay close to others. Although not universal or unipotent, cover-seeking is a widespread and important element in animal aggregation, as the literature shows. Neglect of the idea has probably followed from a general disbelief that evolution can be dysgenic for a species. Nevertheless, selection theory provides no support for such disbelief in the case of species with outbreeding or unsubdivided populations.

The model for two dimensions involves a complex problem in geometrical probability which has relevance also in metallurgy and communication science. Some empirical data on this, gathered from random number plots, is presented as of possible heuristic value.

*leading to disadvantageous genes.*

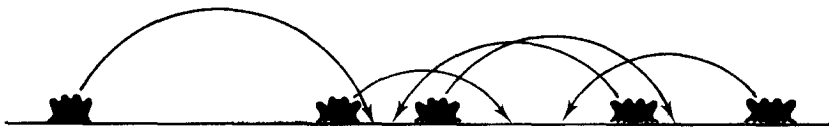## 1. A Model of Predation in One Dimension

Imagine a circular lily pond. Imagine that the pond shelters a colony of frogs and a water-snake. The snake preys on the frogs but only does so at a certain time of day—up to this time it sleeps on the bottom of the pond. Shortly before the snake is due to wake up all the frogs climb out onto the rim of the pond. This is because the snake prefers to catch frogs in the water. If it can't find any, however, it rears its head out of the water and surveys the disconsolate line sitting on the rim—it is supposed that fear of terrestial predators prevents the frogs from going back from the rim—the snake surveys this line and snatches *the nearest one*.

Now suppose that the frogs are given opportunity to move about on the rim before the snake appears, and suppose that initially they are dispersed in some rather random way. Knowing that the snake is about to appear, will all the frogs be content with their initial positions? No; each will have a better chance of not being nearest to the snake if he is situated in a narrow gap between two others. One can imagine that a frog that happens to have climbed out into a wide open space will want to improve his position. The part of the pond's perimeter on which the snake could appear and find a certain frog to be nearest to him may be termed that frog's "domain of danger": its length is half that of the gap between the neighbours on either side. The diagram below shows the best move for one particular frog and how his domain of danger is diminished by it:

But usually neighbours will be moving as well and one can imagine a confused toing-and-froing in which the desirable narrow gaps are as elusive as the croquet hoops in Alice's game in Wonderland. From the positions of the above diagram, assuming the outside frogs to be in gaps larger than any others shown, the following moves may be expected:

What will be the result of this communal exercise? Devious and unfair as usual, natural justice does not, in general, equalize the risks of these selfish frogs by spacing them out. On the contrary, with any reasonable assumptions about the exact jumping behaviour, they quickly colleet in heaps. Except in the case of three frogs who start spaced out in an acute-angled triangle I know of no rule of jumping that can prevent them aggregating. Some occupy protected central positions from the start; some are protected only initially in groups destined to dissolve; some, on the margins of groups, commute wildly from one heap to another and yet continue to bear most of the risk. Figure 1 shows the result of a computer

10° segments of pool margin (degrees)

| Position number | 0 | | | 90 | | | 180 | | | 270 | | | 360 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 3 3 3 | 6 1 3 3 | 4 1 3 5 | 1 3 4 5 2 9 4 | 5 6 3 5 4 | 1 2 2 | 4 3 |
| 2 | 5 2 2 | 8 3 2 | 6 1 1 7 | 2 4 7 11 2 | 7 5 2 5 5 | 3 2 | 4 4 |
| 3 | 6 1 2 | 8 3 1 | 8 9 | 4 9 11 | 9 4 1 7 5 | 2 2 | 4 4 |
| 4 | 6 1 | 9 3 | 9 8 | 4 11 10 | 10 3 8 6 | 1 2 | 4 5 |
| 5 | 7 | 9 2 | 9 8 | 5 12 8 | 12 1 9 6 | 3 | 4 5 |
| 6 | 7 | 9 | 9 8 | 5 14 7 | 13 9 5 | 5 | 3 6 |
| 7 | 8 | 7 | 9 8 | 5 16 5 | 15 9 3 | 6 | 3 6 |
| 8 | 9 | 5 | 9 9 | 4 18 3 | 17 9 1 | 6 | 5 5 |
| 9 | 10 | 4 | 8 10 | 3 20 1 | 19 8 | 6 | 7 4 |
| 10 | 12 | 3 | 7 11 | 2 22 | 20 6 | 6 | 9 2 |
| 11 | 13 | 2 | 6 12 | 1 22 | 22 4 | 7 | 9 2 |
| 12 | 14 | | 6 13 | 22 | 24 3 | 7 | 9 2 |
| 13 | 14 | | 5 13 | 22 | 26 2 | 8 | 8 2 |
| 14 | 15 | | 3 13 | 22 | 28 1 | 9 | 7 2 |
| 15 | 16 | | 1 13 | 22 | 30 | 10 | 6 2 |
| 16 | 17 | | 12 | 22 | 32 | 9 | 6 2 |
| 17 | 17 | | 11 | 22 | 33 | 8 | 7 2 |
| 18 | 18 | | 9 | 22 | 35 | 6 | 8 2 |
| 19 | 19 | | 7 | 22 | 37 | 5 | 9 1 |

FIG. 1. Gregarious behaviour of 100 frogs is shown in terms of the numbers found successively within 10° segments on the margin of the pool. The initial scatter (position 1) is random. Frogs jump simultaneously giving the series of positions shown. They pass neighbours' positions by one-third of the width of the gap. For further explanation, see text

simulation experiment in which 100 frogs are initially spaced randomly round the pool. In each "round" of jumping a frog stays put only if the "gap" it occupies is smaller than both neighbouring gaps; otherwise it jumps into the smaller of these gaps, passing the neighbour's position by one-third of the gap-length. Note that at the termination of the experiment only the largest group is growing rapidly.

The idea of this round pond and its circular rim is to study cover-seeking behaviour in an edgeless universe. No apology, therefore, need be made even for the rather ridiculous behaviour that tends to arise in the later stages of the model process, in which frogs supposedly fly right round the circular rim to "jump into" a gap on the other side of the aggregation. The model gives the hint which I wish to develop: that even when one starts with an edgeless group of animals, randomly or evenly spaced, the *selfish avoidance of a predator can lead to aggregation.*

## 2. Aggregations and Predators

It may seem a far cry from such a phantasy to the realities of natural selection. Nevertheless I think there can be little doubt that behaviour which is similar in biological intention to that of the hypothetical frogs is an

important factor in the gregarious tendencies of a very wide variety of animals. Most of the herds and flocks with which one is familiar show a visible closing-in of the aggregation in the presence of their common predators. Starlings do this in the presence of a sparrowhawk (Baerends & Baerends-van Roon, 1950; Hostman, 1952; Lorenz, 1966; Tinbergen, 1951); sheep in the presence of a dog, or, indeed, any frightening stimulus (Scott, 1945). Parallel observations are available for the vast flocks of the quelea (Crook, 1960), and for deer (Darling, 1937). No doubt a thorough search of the literature would reveal many other examples. The phenomenon in fish must be familiar to anyone who has tried to catch minnows or sand eels with a net in British waters. Almost any sudden stimulus causes schooling fish to cluster more tightly (Breder, 1959), and fish have been described as packing, in the presence of predators, into balls so tight that they cannot swim and such that some on top are thrust above the surface of the water (Springer, 1957). A shark has been described as biting mouthfuls from a school of fish "much in the manner of a person eating an apple" (Bullis, 1960).

G. C. Williams, originator of the theory of fish schooling that I am here supporting (Williams, 1964, 1966), points out that schooling is particularly evident in the fish that inhabit open waters. This fits with the view that schooling is similar to cover-seeking in its motivation. His experiments showed that fish species whose normal environment afforded cover in the form of weeds and rocks had generally less marked schooling tendencies. Among mammals, similarly, the most gregarious species are inhabitants of open grassy plains rather than of forest (Hesse, Allee & Schmidt, 1937). With fish schools observers have noted the apparent uneasiness of the outside fish and their eagerness for an opportunity to bury themselves in the throng (Springer, 1957) and a parallel to this is commonly seen in the behaviour of the hindmost sheep that a sheepdog has driven into an enclosure: such sheep try to butt or to jump their way into the close packed ranks in front. Behaviour of this kind certainly cannot be regarded as showing an unselfish concern for the welfare of the whole group.

With ungulate herds (Galton, 1871; Sdobnikov, 1935) with bird flocks (Tinbergen, 1951; Wynne-Edwards, 1962) and with the dense and sudden-emerging columns of bats that have been described issuing at dusk from great bat caves (Moore, 1948; Pryer, 1884) observations that predators do often take isolated and marginal individuals have frequently been recorded. Nor are such observations confined to vertebrate or to mobile aggregations. Similar observations have been recorded for locusts (Hudleston, 1958), for gregarious caterpillars (Tinbergen, 1953a) and, as various entomologists have told me, for aphids.

For the aphids some of the agents concerned are not predators in a strict

sense but fatal parasites. Insect parasites of vertebrates are seldom directly fatal but, through transmitted diseases or the weakening caused by the activities of endoparasitic larvae, must often cause death indirectly nevertheless. Thus escape from insect attack is another possible reward for gregarious instincts. From observations in Russia, V. M. Sdobnikov (1935) has stated that when reindeer are standing in dense herds only the outermost animals are much attacked by insects. Among the species which he observed attacking the reindeer, those which produced the most serious affliction were nose flies and warble flies, larvae of which are endoparasites of the nasal passages and the skin respectively. Recently Espmark (1968) has verified and extended most of Sdobnikov's information. His work reinforces the view that such oestrid flies are important and ancient enemies of their various ungulate hosts, as is suggested by the fact that their presence induces a seemingly *instinctive* terror. Reindeer seem to be almost as terrified of them as they are of wolves, and cattle react as though they feared the certainly painless egg-laying of warble flies far more than they fear the painful bites of large blood-suckers (Austen, 1939).

The occurrence of marginal predation has also been recorded for some of the aggregations formed by otherwise not very gregarious animals for the purpose of breeding. The best data known to me concerns nesting Black-headed gulls. The work of Kruuk (1964) has been reinforced by further studies, summarized by Lack (1968). The latter seem to have shown that *all* marginal nests failed to rear young, mainly due to predation. Perhaps, nevertheless, the gulls that could not get places in the centre of the colony were right in nesting on the edge rather than in isolation where, for a conspicuous bird like a gull, the chances would have been even worse.

It is perhaps worth digressing here to mention the *temporal* aspect of marginal predation. The "aggregation" in timing already alluded to for bats issuing from bat caves parallels the marked synchrony in breeding activities which is seen in most aggregations and which has been called the "Fraser Darling effect". In explanation of this, Lack (1968) points out that late and early breeders in terns and the black-headed gull do worse in terms of young raised than those best-synchronized with the mass, and he implies that this is mainly due to predation. Individuals coming into breeding condition late or early may also have a problem in sexual selection—that of finding a mate. This point will be touched on later. There are similar influences of temporal selection for flowering plants.

The securing of a nest site in the middle of a colony area is certainly likely to be an achievement of protected position in a sense related to that explained in the story of the frogs, but in the relative immobility of such positions the case diverges somewhat from the initial theme. In all the

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foregoing examples, except perhaps that of the insect parasites of vertebrates, close analogy to that theme has also been lost through the assumption that the predator is likely to approach from outside the group. This is difficult to avoid.†

When a predator habitually approaches from outside it is comparatively obvious how marginal pruning will at least maintain the centripetal instincts of the prey species. Whether predation could also initiate gregariousness in an originally non-gregarious species is another matter. As mentioned before, this will begin to seem likely if it can be shown that when predators tend to appear within a non-aggregated field of prey geometrical principles of self-protection still orientate towards gregarious behaviour. So far I have only shown this for one highly artificial case: that of jumping organisms in a one-dimensional universe. For the case in two dimensions a more realistic story can be given. The most realistic would, perhaps, take reindeer and warble flies as its subject animals, but in order to follow an interesting historical precedent, which has now to be mentioned, the animals chosen will be cattle and lions.

In 1871 Francis Galton published in *Macmillan's Magazine* an article entitled "Gregariousness in Cattle and in Men". In it he outlined a theory of the evolution of gregarious behaviour based on his own observations of the behaviour of the half wild herds of cattle owned by the Damaras in South Africa. In spite of the characteristically forceful and persuasive style of his writing, Galton's argument is not entirely clear and consistent. Some specific criticisms will be mentioned shortly. Nevertheless it does contain in embryo the idea of marginal predation as a force of natural selection leading to the evolution of gregarious behaviour. The main predators of the Damaraland cattle, according to Galton, were lions, and he states clearly that these did prefer to take the isolated and marginal beasts. The following passage shows sufficiently well his line of thought. After stating that the cattle are unamiable to one another and do not seem to have come together due to any "ordinary social desires", he writes:

> "Yet although the ox has so little affection for, or individual interest in, his fellows, he cannot endure even a momentary severance from his herd. If he be separated from it by strategem or force, he exhibits every sign of mental agony; he strives with all his might to get back again and when he succeeds, he plunges into its middle, to bathe his whole body with the comfort of closest companionship."

† Cannibalism in gregarious species raises different problems and may help to explain why the nests of gulls do not become very closely aggregated [see "the gull problem" in Tinbergen (1953b)]. Insects have another kind of "wolf in sheep's clothing": the predator mimicking its prey (Wickler, 1968).

## 3. A Model of Predation in Two Dimensions

Although as Galton implies, lions, like most other predators, usually attack from outside the herd, it is possible to imagine that in some circumstances a lion may remain hidden until the cattle are feeding on all sides of it. Consider therefore a herd grazing on a plain and suppose that its deep grass may conceal—anywhere—a lion. The cattle are unaware of danger until suddenly the lion is heard to roar. By reason of some peculiar imaginary quality the sound gives no hint of the whereabouts of the lion but it informs the cattle of danger. At any moment, at any point in the terrain the cattle are traversing, the lion may suddenly appear and attack the nearest cow.

As in the case of the "frog" model, the rule that the predator attacks the nearest prey specifies a "domain of danger" for each individual. Each domain contains all points nearer to the owner of the domain than to any other individual. In the present case such domains are polygonal (Fig. 2). Each polygon is bounded by lines which bisect at right angles the lines which join the owner to certain neighbours; boundaries meet three at a point and an irregular tesselation of polygons covers the whole plane. On hearing the lion roar each beast will want to move in a way that will cause its polygonal domain to decrease. Not all domains can decrease at once of course: as in the case of the frogs, if some decrease others must grow larger; nevertheless, if one cow moves while others remain stationary the one moving can very definitely improve its position. Hence it can be assumed that inclinations to attempt some adaptive change of position will be established by natural selection. The optimal strategy of movement for any situation is far from obvious, and before discussing even certain better-than-nothing principles that are easily seen it will be a cautionary digression to consider what is already known about a particular and important case of such a tesselation of polygons, that in which the "centres" of polygons are scattered at random. Patterns of a more concrete nature which are closely analogous to the tesselation defined certainly exist in nature. In two dimensions they may be seen in the patterns formed by encrusting lichens on rocks, and in the cross-sectional patterns of cracks in columnar basalt. The corresponding pattern in three dimensions, consisting of polyhedra, is closely imitated in the crystal grains of some metals and other materials formed by solidification of liquids. The problem of the statistical description of the pattern in the case where centres are distributed at random was first attacked with reference to the grain structure of metals (Evans, 1945). More recently the $N$-dimensional analogue has been studied by E. N. Gilbert (1962) on the incentive of a problem arising in communication science. Yet in spite of great expertise many simple facts about even the two-dimensional case remain
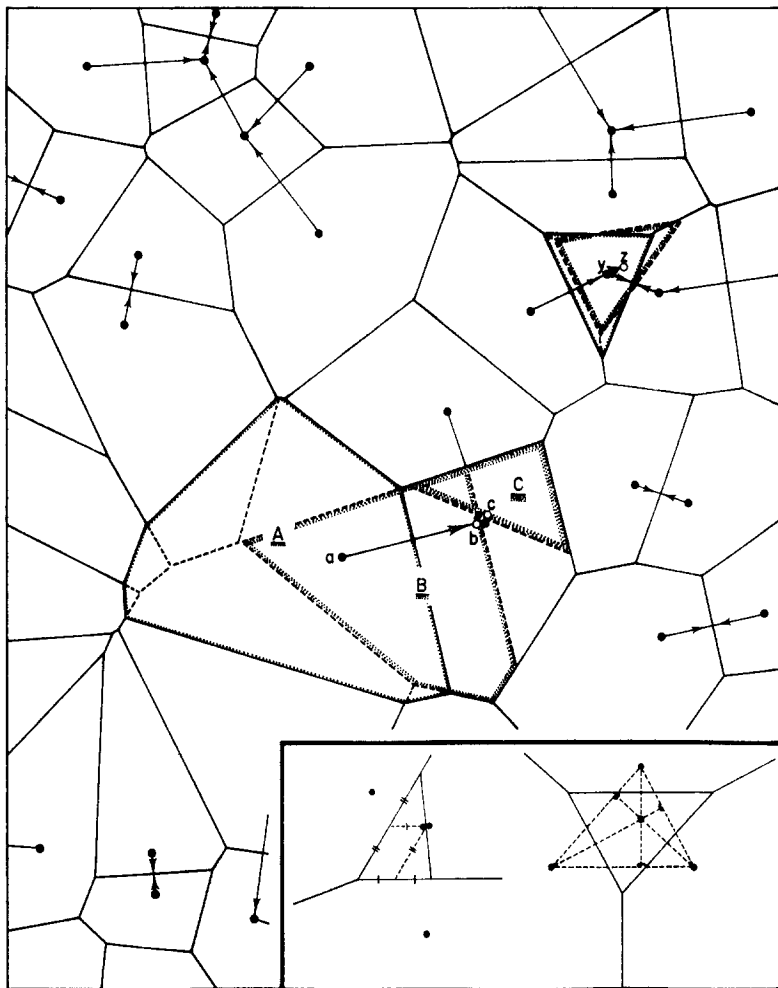
FIG. 2. Domains of danger for a randomly dispersed prey population when a hidden predator will attack the nearest animal. Thin arrowed lines indicate the nearest neighbour of each prey. Thicker arrowed lines show supposed movements of particular prey. Position of prey is given a lower case letter and the domain obtained from each position is given the corresponding upper case letter. The pattern underlining the domain letter corresponds to the pattern used to indicate the boundary of the domain in question. Dashed lines are used for the boundaries of domains that come into existence after the first movement.

Approach to a nearest neighbour usually diminishes the domain of danger (as a → b), but not always (as y → z). On reaching a neighbour the domain may, in theory, be minimized by moving round to a particular side (as b → c). The inset diagram shows geometrical algorithms for minimum domains attainable by a (on reaching c), and by y. In the case of y the minimum domain is equal to the triangle of neighbours and is obtained from the orthocentre of that triangle.

unknown. The distribution of the angles of the polygons is known (J. L. Meijering, personal communication); something is known of the lengths of their sides, and Gilbert has found the variance of their areas.† Nothing, apart from the fairly obvious value of six for the mean, is known of the numbers of sides. Since a biologist might be interested to know whether, in the ideal territory system of these polygons, six neighbours is the most likely number, or whether five is more likely than seven, some data gathered from plots of random numbers is given in Table 1.

TABLE 1

*Distribution of the number of sides of 376 polygons constructed from random number plots*

| No. of sides | | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|
| No. observed | | 3 | 38 | 97 | 123 | 70 | 29 | 11 | 4 | 1 |
| Total no. observed | 376 | | | | | | | | | |

Data for 100 of these polygons were received from E. N. Gilbert. The rarity of triangles indicates that the sample area chosen for Fig. 2 is not quite typical.

After glancing at Gilbert's paper a non-mathematical biologist may well despair of finding a theory of *ideal* self-protective movement for the random cattle. Nevertheless experimentation with ruler and compasses and one small evasion quickly reveal a plausible working principle. As a preliminary it may be pointed out that the problem differs radically from the linear problem in that domains of danger change continuously in size with movements of their owner. (In the linear case no change takes place until an individual actually passes his neighbour; this was the reason for choosing organisms that jump.) Now suppose that one cow alone has sensed the presence of the lion and is hastily moving through an otherwise motionless herd. In most circumstances such a cow will diminish its domain of anger by approaching its nearest neighbour. A direct approach can seldom be the path it would choose if it requires that every step should bring the maximum decrease of danger, and when the nearest neighbour is a rather isolated individual it may even happen that a domain increases during approach to a nearest neighbour (Fig. 2, y → z). Such increases will tend to be associated with polygons with very low side number. When an individual is enclosed in a ring of others and consequently owns a many-sided domain, decrease in area is almost inevitable (Fig. 2, a → b). Since the average number of sides is six and triangles are rare (Table 1), it must be a generally useful rule for a cow to approach its nearest

† Recently R. E. Miles (1970) has greatly extended analysis of this case (*Math. Biosci.* **6**, 85) (footnote added in proof).

neighbour. This is a rule for which natural selection could easily build the necessary instincts. Behaviour in accord with it has been reported in sheep (Scott, 1945). The evasion, then, is to imagine that these imaginary cattle are too slow-witted to do anything better. Most readers will agree, I hope, that there is no need to call them stupid on this account.
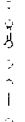
If the rest of the herd remains stationary and the alarmed cow reaches its nearest neighbour it will usually further decrease its domain of danger by moving round to a side that gives it a minimal "corner" of the neighbour's now enlarged domain (Fig. 2, b → c; left inset diagram shows the principle for finding such a minimal "corner" domain. In this position the cow of the story may be supposed to reach equilibrium; it is some sort of equivalent, albeit not a close one, of the stable non-jump positions that sometimes occur with the frogs. Even more than with the stable positions of the frogs, how-ever, the stable positions of this model must be almost impossible to attain. As in the case of the frogs this is seen as soon as we imagine that all the other cows are moving and have similar aims in view.

Nearest-neighbour relationships connect up points into groups (Fig. 2). Every group has somewhere in it a "reflexive pair"; that is, a pair for which each is the nearest neighbour of the other. A formula for the frequency of membership of reflexive pairs when the points are randomly dispersed has been derived by Clark & Evans (1955). It is $6\pi/(8\pi+\sqrt{27})$. Halving and inverting this expression gives us the average size of groups as $3\cdot218$. No further facts are known mathematically about the relative frequencies of different sizes of groups, but a summary of the forms and sizes found in the random number plots is given in Table 2.

Clearly, if randomly dispersed cattle condense according to the statistical pattern indicated in Table 2, the groups so formed can hardly be described as herds. Nevertheless there is undoubtedly a gregarious tendency of a kind, and once such primary groups have formed the cattle in each group will see a common advantage in moving through the field of groups using the same principles as before. Thus an indefinite series of such condensations will take place and eventually large herds will appear. Condensation is not prevented by having the points initially more evenly spaced than in the random dispersion. For example, when the points are initially in some lattice formation the inherent instability of the system is actually easier to see than it is for the random dispersion: every point, if moving alone, can definitely diminish its domain of danger by approaching any one of its equidistant neighbours. Thus even for the most unpromising initial condi-tions it remains evident that predation should lead to the evolution of gregarious behaviour.

No story even as poorly realistic as the foregoing can be given for the

TABLE 2

| No. in group | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|
| No. of cases found | 46 | 37 | 24 | 8 | 5 | 1 |
| Configurations found | 46 | 37 | 9 2 4 | 4 2 1 | | |

| Mean $N$ in group | observed: 3·107 |
|---|---|
| | expected: 3·218 |

The nearest neighbour relation allocates points of a random dispersion to groups (see arrowed lines on Fig. 2). Here the configurations found in 121 groups formed by 376 points are recorded together with their frequencies of occurrence. Double connecting lines indicate the reflexive nearest neighbour relationship.

case of predation in three dimensions. In the air and in water there is still less cover in which the predator can hide. If there were a hiding place, however, for what it is worth the argument can be repeated almost exactly and we arrive at 3⅝ for the mean size of primary groups. For celestial cattle in a space of infinitely many dimensions the mean group size attains only to 4.†

Whether or not marginal predation is, as I believe it to be, a common primary cause of the evolution of gregariousness, it is surprising that the idea of such a cause has received so little attention from biologists. The reason for the neglect of Galton's views cannot lie in the non-scientific nature of the journal in which it was originally published. Galton repeated them in his book *Inquiries into Human Faculty* (1883), and this is one of

† The general formula, where $n$ is the number of dimensions, is

$$\frac{4n}{n+1} + \frac{2}{(n-1)\pi^{\frac{1}{2}}}\left(\frac{3^{\frac{1}{2}}}{2}\right)^{n-1}\frac{\Gamma\{n/2\}}{\Gamma\{(n-1)/2\}}.$$

his best known works. Yet both the hints of the present hypothesis in writings on the schooling of fishes and the admirable study and discussion of this hypothesis by G. C. Williams (1964) were completely independent of Galton's publications. Galton himself is certainly largely to blame for this. With one exception he did not relate his idea to species other than cattle and sheep, and the one exception was man. Something of the tenor of his views on the manifestations of gregariousness in man may be gathered from the fact that the relevant passage in the book mentioned above is headed: "On gregarious and slavish instincts". Needless to say his analogy between human and bovine behaviour now seems somewhat naive. His views remain, as always, interesting and evocative, but their dogmatic and moralizing tone and their obvious connection with their author's widely distrusted line on eugenics can be imagined to have scared off many potentially interested zoologists. Another probable reason for the neglect of Galton's idea is that he himself presented it mixed up with another really quite separate idea which he treated as if it were simply another aspect of the same thing. This was that every cow, whether marginal or interior, benefited by being part of a herd, and that therefore herding was beneficial to the species. His supporting points are undoubtedly forcible; he mentions mutual warning and the idea that by forming at bay in outward-facing bands the cattle can present a really formidable defence against the lions. However, whether or not the cattle actually do, in the last resort, overcome their centripetal inclination and turn to face the predator (as smaller bands of "musk ox" certainly do), these points raise a different issue, as do the mass attacks on predators by gregarious nesting birds. My models certainly give no indication that such mutualistic defence is a necessary part of gregarious behaviour. Moreover, mutual defence and warning can hardly be described as "slavish" behaviour and so seem not to be covered by Galton's heading. There is no doubt, of course, that mutual warning and occasional unselfish defence of others are sometimes shown by gregarious mammals and birds, but where such actions occur they are probably connected on the one hand with the smallness of the risk taken and, on the other, with the closeness of the genetical relationship of the animals benefited (Hamilton, 1963). With the musk ox, for example, the bands are small and clearly based on close family relationships. Sheep and cattle also take risks in defending their young (as Galton pointed out), but this is based on recognition of their own offspring. Apart from the forced circumstances, and the unnatural dispositions engendered by domestication, females usually do not associate with, still less defend, young which are not their own (Williams, 1966). The ability to recognize particular individuals of the same species is highly developed in mammals and birds and there is no difficulty either practical or theoretical

in supposing that the mutualistic behaviour of the adult musk oxen, for instance, is an evolutionary development from the altruism involved in parental care. Positive social relations between members of family groups probably exist submerged in most manifestations of mass gregariousness in animals higher than fish. For example the flock of sheep driven by a shepherd owes its compactness and apparent homogeneity to the presence of the sheep dogs: when it is left undisturbed on the mountain it arranges itself into a loosely clustered and loosely territorial system. The clusters are usually based on kinship and the sheep of a cluster are antagonistic to any strange sheep that attempts to feed on their ground (Hunter, 1964). It accords well with the present theory that the breeds of sheep that are most readily driven into large flocks are those which derive from the Merino breed of Spain (Darling, 1937), which is an area where, until very recently, predation by wolves was common. Galton likewise gave the relaxation of predation as the reason for European cattle being very much less strongly gregarious than the cattle he observed in Africa. He noted that the centripetal inclinations evolved through predation would be opposed continually by the need to find ungrazed pasture, so that when predation is relaxed gregarious instincts would be selected against. This point has also been made by Williams.

Most writers on the subject of animal aggregation seem to have believed that the evolution of gregarious behaviour must be based on some advantage to the aggregation as a whole. Many well known biologists have subscribed, outspokenly or by implication, to this view. At the same time some, for example Hesse *et al.* (1937), Fisher (1953) and Lorenz (1966), have admitted that the nature of the group advantage remains obscure in many cases. On the hypothesis of gregarious behaviour presented here the apparent absence of a group benefit is no cause for surprise. On the contrary, the hypothesis suggests that the evolution of the gregarious tendency may go on even though the result is a considerable lowering of the overall mean fitness. At the end of our one-dimensional fairy tale, it will be remembered, only the snake lives happily, taking his meal at leisure from the scrambling heaps of frogs which the mere thought of his existence has brought into being. The cases of predators feeding on apparently helpless balls of fish seem parallel to this phantasy: here gregariousness seems much more to the advantage of the species of the predator than to that of the prey. Certain predators of fish appear to have evolved adaptations for exploiting the schooling tendencies of their prey. These cases are not only unfavourable to the hypothesis of a group advantage in schooling but also somewhat unfavourable to the present hypothesis, since it begins to seem that there must be an advantage to fish which do not join the school. The thresher shark is said to use its much elongated tail to round up fish into easily eaten schools (Williams, 1964).

Even worse, the swordfish is recorded as feeding on schools by first im-mobilizing large numbers with blows from its sharp-edged sword. This may be its usual method of feeding, and the sawfish may use its weapon similarly. Such predators presumably do best by striking through the middle of a school; lone fish might fail to attract them. It is obvious, however, that such cases should not be assessed on the assumption that a particular predator is the only one (Bullis, 1960). At the time of attack by a swordfish there may be other important predators round about that are still concentrating on the isolated and peripheral fish. In the case of locusts the occurrence of such contrary influences from predation is recorded (Hudleston, 1957): large bird predators (ravens and hornbills) attacking bands of hoppers of the desert locust did tend to disperse the bands, and to decimate their central members, by settling in their midst, but at the same time smaller birds (chats and warblers) captured only marginal hoppers and stragglers.

Adaptations of the predator to exploit the gregariousness of its prey certainly suggests the possibility of a changeover to a disaggregating phase of selection. In terms of the earlier story, if the snake evolves such a lazy preference for taking its prey from a heap that it comes to overlook a nearer lone frog, then it may come to be the mutant gregariphobe which survives best to propagate its kind. There are in fact many examples of species which are gregarious in only part of their range or their life cycle and possibly this may reflect the differing influences of different predators.

A surprising number of discussions of animal aggregation have mentioned the occurrence of marginal predation and yet shown apparently no apprecia-tion of its possible evolutionary significance. Whether marginal predation or similarly orientated pressure of selection on individuals is sufficiently powerful to account for the gregariousness observed in any particular case cannot be decided by any already existing body of data. Nevertheless it can be claimed that for none of the cases so far discussed does the data exclude the possibility. It can also be claimed that all the rival theories based on the idea of "group selection" are theoretically insecure. Consider for example the theory of Wynne-Edwards (1962) which, from this basis, attempts to bring many facts of animal aggregation under a common explanation. This theory suggests that aggregations serve to make individuals aware of the current level of population density and that this awareness reacts on repro-ductive performance in a way that holds off the possibility of a disastrous crash due to over-exploitation of the food supply or other limited resources. Except in cases where groups are exclusive and mutually competitive for territory it is very difficult to see how there can be positive selection of any tendency by an individual to reproduce less effectively than it is able (Hamilton, 1971). Wynne-Edwards's cases of massive aggregations, even those

having a kin-based substructure as in the gregarious ungulates, are unlikely candidates for the class of exceptions. The alternative theory supported here has no parallel difficulty as to the underlying processes of selection since it can rest firmly on the theory of genetical natural selection.

Certain other versions of the idea of a group benefit, unlike the Wynne-Edwards theory, do not require the concept of self-disciplined restraint by individuals. With such versions, statements that aggregation has evolved because it aids the survival of the species may be treated as merely errors of expression, in which a possibly genuine effect is given the status of a cause. The factor of communal alertness, for instance, may really make life more difficult for a predator and safer for a gregarious prey, especially if the predator is one which relies on stealth rather than speed. In Galton's perhaps over-persuasive words,

> "To live gregariously is to become a fibre in a vast sentient web over-spreading many acres; it is to become the possessor of faculties always awake, of eyes that see in all directions, of ears and nostrils that explore a broad belt of air; it is to become the occupier of every bit of vantage ground whence the approach of a lurking enemy might be overlooked."

But there is of course nothing in the least altruistic in keeping alert for signs of nervousness in companions as well as for signs of the predator itself, and there is, correspondingly, no difficulty in explaining how gregariousness on this basis could be evolved.

Returning to the more interesting and controversial postulate of a population regulatory function for mass aggregation, consider, as a point of detailed criticism, the problem presented by aggregations in which several species are mixed. All the main classes of aggregation that have so far been mentioned —fish schools, bird flocks (both mobile and nesting) and grazing herds— provide numerous examples of species mixture. The species involved may be as widely related as ostriches and antelopes (Hesse *et al.*, 1937). If it is difficult to see how the supposed group selection can work within a species it is certainly even more difficult when the groups are mixed. On the other hand the theory that gregariousness is essentially due to the need for cover finds no difficulty over this point provided that the species which mix have at least one important predator in common. None of the vertebrate predators that have been mentioned as possible agents for the moulding of gregarious inclinations in their prey seem so specialized in their hunting as to make it improbable that individuals of one prey species could expect to gain some protection by immersing themselves in an aggregation of another species.

Perhaps most of the examples of mixed aggregation lie outside the class for which Wynne-Edwards and his supporters would claim a population regulatory function. The examples which have been cited in support of the

theory are, in general, more directly concerned with reproduction. Apart from the case of nest aggregations, which has been discussed, there remain Wynne-Edwards's numerous citations of nuptial gatherings. With these the case for the effectiveness of marginal predation is admittedly weaker. Marginal predation seems somewhat less likely on general grounds and there is little evidence. However, there are other ways in which selection is likely to favour individuals which are in the nuptial gathering (or at least on its margin) over those that are isolated. Such selection may be sexual; it may work through differences in the chances of obtaining a mate. As one example, consider the swarms of midges that are so common in damp, still, vegetated places in summer. Many species of nematocerous flies have the habit of forming such swarms. Each swarm usually consists of males of a single species and tends to hover in a fixed spot, often near to some conspicuous object. Females come to the swarm and on arrival each is seized by a male. Passing over possible stages in the initiation of such habits, it is at least clear that as soon as proximity to the swarm itself becomes a key to the female's further co-operation in copulation there is likely to be little chance of mating for the male which does not join the swarm. In such a case the optimal position for a male is probably, not, as it is under predation, at the centre of the throng, and considering how males might endeavour to spend the maximum time in relatively favoured positions, downwind or upwind, above or below, possible explanations for the dancelike motion of such swarms become apparent.

I wish to thank Dr I. Vine for the stimulus to publish this paper: his paper (*J. theor. Biol.* **30,** 405), treating the influence of predation from a different point of view and showing one way in which gregariousness may be beneficial to the group as a whole, was sent to me in manuscript.

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