The Genetical Evolution of Social Behaviour. II

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Grounds for thinking that the model described in the previous paper can be used to support general biological principles of social evolution are briefly discussed.

Two principles are presented, the first concerning the evolution of social behaviour in general and the second the evolution of social discrimination. Some tentative evidence is given.

More general application of the theory in biology is then discussed, particular attention being given to cases where the indicated interpretation differs from previous views and to cases which appear anomalous. A hypothesis is outlined concerning social evolution in the Hymenoptera; but the evidence that at present exists is found somewhat contrary on certain points. Other subjects considered include warning behaviour, the evolution of distasteful properties in insects, clones of cells and clones of zooids as contrasted with other types of colonies, the confinement of parental care to true offspring in birds and insects, fights, the behaviour of parasitoid insect larvae within a host, parental care in connection with monogyny and monandry and multi-ovulate ovaries in plants in connection with wind and insect pollination.

1. Introduction

In the previous paper (Hamilton, 1964) a genetical mathematical model was used to deduce a principle concerning the evolution of social behaviour which, if true generally, may be of considerable importance in biology. It has now to be considered whether there is any logical justification for the extension of this principle beyond the model case of non-overlapping generations, and, if so, whether there is evidence that it does work effectively in nature.

In brief outline, the theory points out that for a gene to receive positive selection it is not necessarily enough that it should increase the fitness of its bearer above the average if this tends to be done at the heavy expense of related individuals, because relatives, on account of their common ancestry, tend to carry replicas of the same gene; and conversely that a gene may receive positive selection even though disadvantageous to its bearers if it causes them to confer sufficiently large advantages on relatives. Relationship alone

never gives grounds for *certainty* that a person carries a gene which a relative is known to carry except when the relationship is "clonal" or "mitotic" (e.g. the two are monozygotic twins)—and even then, strictly, the possibility of an intervening mutation should be admitted. In general, it has been shown that Wright's Coefficient of Relationship r approximates closely to the chance that a replica will be carried. Thus if an altruistic trait is in question more than $1/r$ units of reproductive potential or "fitness" must be endowed on a relative of degree r for every one unit lost by the altruist if the population is to gain on average more replicas than it loses. Similarly, if a selfish trait is in question, the individual must receive and use at least a fraction r of the quantity of "fitness" deprived from his relative if the causative gene is to be selected.

For a more critical explanation of these ideas and of the important concept of "inclusive fitness", which will be freely referred to in what follows, the reader is referred to the previous paper.

2. The Grounds for Generalization

It is clear that in outline this type of argument is not restricted to the case of non-overlapping generations nor to the state of panmixia on which we have been able to base a fairly precise analysis. The idea of the regression, or "probabilistic dilution", of "identical" genes in relatives further and further removed applies to all organisms performing sexual reproduction, whether or not their generations overlap and whether or not the relatives considered belong to the same generations.

However perhaps we should not feel entirely confident about generalizing our principle until a more comprehensive mathematical argument, with inclusive fitness more widely defined, has been worked out. But even from this point of view there does seem to be good reason for thinking that it can be generalized—reason about as good, at least, as that which is supposed to give foundation to certain principles of the classical theory.

Roughly speaking the classical mathematical theory has developed two parallel branches which lie to either side of the great range of reproductive schedules which organisms actually do manifest. One is applicable to once-and-for-all reproduction (e.g. Kingman, 1961); and this form is actually exhibited by many organisms, notably those with annual life-cycles. The other is applicable to "continuous" reproduction (e.g. Kimura, 1958). This involves a type of reproductive process which is strictly impossible for any organism to practice, but which for analytic purposes should be approximated quite closely by certain species, for example, some perennial plants. Our model is a generalization in the former branch and there seems little reason to doubt that it can be matched by a similar model in the latter.

Even in the classical theory itself difficulties still face generalization

between the two branches, and yet their continuance does not seem to cause much worry. For instance there does not seem to be any comprehensive definition of fitness. And, perhaps in consequence of this lack, it rather appears that Fisher's Fundamental Theorem of Natural Selection has yet to be put in a form which is really as general as Fisher's original statement purports to be (Fisher, 1930, p. 37, see points raised by Moran, 1962, pp. 60, 66). On the other hand, the clarity of Fisher's statement must surely, for general useful-ness, have far out-weighed its defects in rigour.

3. Valuation of the Welfare of Relatives

Altogether then it would seem that generalization would not be too foolhardy. In the hope that it may provide a useful summary we therefore hazard the following generalized unrigorous statement of the main principle that has emerged from the model.

> The social behaviour of a species evolves in such a way that in each distinct behaviour-evoking situation the individual will seem to value his neighbours' fitness against his own according to the coefficients of relationship appropriate to that situation.

The aspect of this principle which concerns altruism seems to have been realized by Haldane (1955) as is shown in some comments on whether a genetical trait causing a person to risk his life to save a drowning child could evolve or not. His argument, though not entirely explicit and apparently restricted to rare genes, is essentially the same as that which we have outlined for altruism in the Introduction.

Haldane does not discuss the question which his remarks raise of whether a gene lost in an adult is worth more or less than a gene lost in a child. However, this touches an aspect of the biological accounting of risks which together with the whole problem of the altruism involved in parental care is best reserved for separate discussion.

The principle was also foreshadowed much earlier in Fisher's (1930, p. 177 *et seq.*) discussion of the evolution of distastefulness in insects. That this phenomenon presents a difficulty, namely an apparent absence of positive selection, is obvious as soon as we reject the pseudo-explanations based on the "benefit to the species", and the problem is of considerable importance as distastefulness, construed in a wide sense, is the basis not only of warning coloration but of both Batesian and Mullerian mimicry. The difficulty of explaining the evolution of warning coloration itself is perhaps even more acute here; *a priori* we would expect that at every stage it would be the new ultra-conspicuous mutants that suffered the first attacks of inexperienced predators. Fisher suggested a benefit to the nearby siblings of the distasteful,

or distasteful and conspicuous insect, and gave some suggestive evidence that these characters are correlated with gregariousness of the larvae. He remarked that, "the selective potency of the avoidance of brothers will of course be only half as great as if the individual itself were protected; against this is to be set the fact that it applies to the whole of a possibly numerous brood." He doubtlessly realized that further selective benefit would occur through more distant relatives but probably considered it negligible. He realized the logical affinity of this problem with that of the evolution of altruistic behaviour, and he invokes the same kind of selection in his attempt to explain the evolution of the heroic ideal in barbaric human societies.

Another attempt to elucidate the genetical natural selection of altruistic behaviour occurring within a sibship was published by Williams & Williams in 1957. Although their conclusions are doubtlessly correct the particular form of analysis they adopted seems to have failed to bring out the crucial role of the two-fold factor in this case.

A predator would have to taste the distasteful insect before it could learn to avoid the nearby relatives. Thus despite the toughness and resilience which is supposed to characterize such insects (qualities which the classical selectionists may have been tempted to exaggerate), the common detriment to the "altruist" must be high and the ratio of gain to loss (k) correspondingly low. The risks involved in giving a warning signal, as between birds, must be much less so that in this case, as indicated in the previous paper, it is more credible that the condition

$$k > \frac{1}{r}$$

is fulfilled even when cases of the parents warning their young and the young each other up to the time of their dispersal are left out of account. The average relationship within a rabbit-warren is probably quite sufficient to account for their "thumping" habit (for relevant observations see Thompson & Worden, 1956, pp. 104, 217). Ringing experiments on birds indicate that even adult territorial neighbours must often be much closer relatives than their powers of flight would lead us to expect (e.g. Lack, 1953, pp. 114–16); a fact that may be of significance for the interpretation of the wider comity of bird behaviour.

The phenomena of mutual preening and grooming may be explained similarly. The mild effort required must stand for a diminution of fitness quite minute compared to the advantage of being cleansed and cleared of ectoparasites on parts of the body which the individual cannot deal with himself. Thus the degree of relationship within the flocks of birds, troupes of monkeys and so on where such mutual help occurs need not be very high before the condition

for an advantage to inclusive fitness is fulfilled; and for grooming within actual families, of monkeys for instance, it is quite obviously fulfilled.

An animal whose reproduction is definitely finished cannot cause any further self-effects. Except for the continuing or pleiotropic effects of genes which are established through an advantage conferred earlier in the life-history, the behaviour of a post-reproductive animal may be expected to be entirely altruistic, the smallest degree of relationship with the average neighbour being sufficient to favour the selection of a giving trait. Blest (1963) has recently shown that the post-reproductive behaviour of certain saturnid moths is indeed adaptive in this way. His argument may be summarized in the present terminology as follows. With a species using cryptic resemblance for its protection the very existence of neighbours involves a danger to the individual since the discovery of one by a predator will be a step in teaching it to recognize the crypsis. With an aposematic species on the other hand, the existence of neighbours is an asset since they may well serve to teach an inexperienced predator the warning pattern. Thus with the cryptic moth it is altruistic to die immediately after reproduction, whereas with the warningly-coloured moth it is altruistic to continue to live at least through the period during which other moths may not have finished mating and egg-laying. Blest finds that the post-reproductive life-spans of the moths he studied are modified in the expected manner, and that the cryptic species even show behaviour which might be interpreted as an attempt to destroy their cryptic pattern and to use up in random flight activity the remainder of their vital reserves. The selective forces operating on the post-reproductive life-span are doubtless generally weak; they will be strongest when the average relationship of neighbours is highest, which will be in the most viscous populations. It would be interesting to know how behaviour affecting gene-dispersion correlates with the degree of the effects which Blest has observed.

4. Discrimination in Social Situations

Special case (b) of the previous paper has shown explicitly that a certain social action cannot in itself be described as harmful or beneficial to inclusive fitness; this depends on the relationship of the affected individuals. The selective advantage of genes which make behaviour conditional in the right sense on the discrimination of factors which correlate with the relationship of the individual concerned is therefore obvious. It may be for instance, that in respect of a certain social action performed towards neighbours indiscriminately, an individual is only just breaking even in terms of inclusive fitness. If he could learn to recognize those of his neighbours who really were close relatives and could devote his beneficial actions to them alone an advantage to inclusive fitness would at once appear. Thus a mutation causing such

discriminatory behaviour itself benefits inclusive fitness and would be selected. In fact, the individual may not need to perform any discrimination so sophisticated as we suggest here; a difference in the generosity of his behaviour according to whether the situations evoking it were encountered near to, or far from, his own home might occasion an advantage of a similar kind.

Although this type of advantage is itself restricted to social situations, it can be compared to the general advantage associated with making responses conditional on the factors which are the most reliable indicators of future events, an advantage which must for instance have been the basis for the evolution of the seed's ability to germinate only when conditions (warmth, moisture, previous freezing, etc.) give real promise for the future survival and growth of the seedling.

Whether the trend implied could ever spread very far may be doubted. All kinds of evolutionary changes in behaviour, especially those subject to the powerful forces of individual advantage, are liable to disrupt any *ad hoc* system of discrimination. This is most true, however, for discrimination in the range of distant relationships where the potential gains are least. The selective advantage when a benefit comes to be given to sibs only instead of to sibs and half-sibs indifferently is more than four times the advantage when a benefit of the same magnitude is given to cousins only instead of to cousins and half-cousins indifferently.

Nevertheless, if any correlate of relationship is very persistent, long-continued weak selection could lead to the evolution of a discrimination based on it even in the range of distant relationships. One possible factor of this kind in species with viscous populations, and one whose persistence depends only on the viscosity and therefore may well be considerably older than the species in question, is familiarity of appearance. For in a viscous population the organisms of a particular neighbourhood, being relatives, must tend to look alike and an individual which used the restrained symbolic forms of aggressive behaviour only towards familiar-looking rivals would be effecting a discrimination advantageous to inclusive fitness.

In accordance with the hypothesis that such discriminations exist it should turn out that in a species of resident bird, strongly territorial and minimally vagrant, the conflicts which proved least readily resolved by ritual behaviour and in which consequent fighting was fiercest were between the rivals that had the most noticeable differences in plumage and song. Whether much evidence of this nature exists I do not know. The rather uncommon cases of interspecific territory systems in birds, as recently reviewed by Wynne-Edwards (1962, p. 391), seem to be contrary. If differences between interspecific and conspecific encounters were noticed by the original observers

they are not mentioned by Wynne-Edwards; and in any case, the very exis-
tence of these situations, taken at face value and assumed to be stable and of
long standing, is as contrary to the present theory as it is to Gause's principle.
Likewise, the positive indications I can bring forward are rather few and feeble.
Tinbergen (1953, p. 49) has observed a hostile reaction by Herring Gulls
towards members of their colony forced to behave abnormally (caught in
a net) and states that a similar phenomenon is sometimes observed with
other social species. Personal observations on colonies of the wasps *Polistes
canadensis* and *P. versicolor* have shown a very strong hostility when a wasp
taken off a nest, is returned to it in a wet and bedraggled condition. This type
of reaction after a member of the colony has been much handled seems to be
quite common in the social insects. It is perhaps specifically aroused by certain
acquired odours, or these combined with the odour of venom. That bird-
ringers, who would surely have noticed any social stigma that fell upon
birds carrying their often very conspicuous rings, usually report that the rings
were no apparent inconvenience to the birds is a counter-indication whose
force is slightly reduced by the fact that in passerines and most other common
birds the legs are unimportant in social communication. It is similarly
fortunate for the insect ethologist that spots of fresh oil-paint by themselves
on bees and wasps seem to provoke very little reaction. Butterflies of the
family *Lycaenidae*, especially males, are often to be seen jostling one another
in the air, sometimes in groups of more than two. The function of this
behaviour is obscure; the species do not seem to be at all strongly territorial.
According to Ford (1945, p. 256) lepidopterists find that a bunch of jostling
butterflies is rather apt to contain an unusual variety.

   With the higher animals we may perhaps appeal to evidence of discrimina-
tion based on familiarity of a more intimate kind. Animals capable of forming
a social hierarchy presumably have some ability to recognize one another as
individuals, and with this present it is not necessary for the discrimination
to be on the basis of "racialistic" differences of appearance, voice or smell.
An individual might look extremely like certain members of a group and lie
within the group's range of variation in every one of his perceptible charac-
ters and yet still be known for a stranger. Speaking from a wide knowledge
of just such social animals Wynne-Edwards (1962, p. 136) refers to "the
widespread practice of attacking and persecuting strangers and relegating
newcomers to the lowest social rank" and gives several references. The
antagonistic nature of this discrimination is of course just what we expect.

   As might be expected the evidence in the cases of closest relationship is
much more impressive. Tinbergen (1953, p. 224 *et seq.*) investigated the ability
of Herring Gulls to recognize their own chicks by observing the reaction to
strange chicks placed amongst them. He found that during the first two or

three days after hatching strange chicks are accepted, but by the end of the first week they are driven away. Herring Gulls will sometimes form the habit of feeding on the live chicks as well as on the eggs in their own breeding colony when they can catch them unattended, but Tinbergen records no case where an intruded chick was killed although this probably sometimes happens; the hostile behaviour he observed was half-hearted at first but became more definite as the age of the gull's own brood advanced. During the days which follow hatching, the chicks become progressively more mobile and the chance that they will wander into neighbouring nest-territories must increase. Therefore it seems a reasonable hypothesis that the ability to discriminate "own young" advances in step with the chance that without such discrimination strange chicks would be fostered and the benefits of parental care wasted on unrelated genes. Supporting this hypothesis are the findings quoted by Tinbergen (p. 228) of Watson and Lashley on two tropical species of tern: "The Noddies nesting in trees do not recognize their young at any age, whereas the ground-nesting Sooties are very similar to Herring Gulls in that they learn to recognize their own young in the course of four days." House Sparrows will accept strange young of the right age placed in the nest but after the nestlings have flown "they will not, in normal circumstances, feed any but their own young." (Summers-Smith, 1963, p. 50). Not all observations are as satisfactory for the theory as these however; we may mention the positive passion for fostering said to be shown by Emperor Penguins that have lost their own chick (Prevost, 1962). This and some other similar anomalies will be briefly discussed in the last section.

Tinbergen showed that Herring Gulls discriminate eggs even less than chicks, the crudest egg-substitutes being sufficient to release brooding behaviour providing certain attributes of shape and colour are present. This is what we would expect in view of the fact that eggs do not stray at all. It is in striking contrast with the degree of egg-discrimination which is shown by species of birds subject to cuckoo parasitism.

The theoretical principle which these observations seem largely to support is supplementary to the previous principle and we may summarize it in a similar statement.

> *The situations which a species discriminates in its social behaviour tend to evolve and multiply in such a way that the coefficients of relationship involved in each situation become more nearly determinate.*

In situations where relationship is not variable, as for example between the nestlings in an arboreal nest, there still remains a discrimination which, if it could be made could greatly benefit inclusive fitness. This is the discrimination of those individuals which do carry one or both of the behaviour-

causing genes from those which do not. Such an ability lies outside the conditions postulated in the previous paper but the extended meaning of inclusive fitness is obvious enough. That genes could cause the perception of the presence of like genes in other individuals may sound improbable; at simplest we need to postulate something like a supergene affecting (a) some perceptible feature of the organism, (b) the perception of that feature, and (c) the social response consequent upon what was perceived. However, exactly the same *a priori* objections might be made to the evolution of assortative mating which manifestly has evolved, probably many times independently and despite its obscure advantages.

If some sort of attraction between likes for purposes of co-operation can occur the limits to the evolution of altruism expressed by our first principle would be very greatly extended, although it should still never happen that one individual would value another more highly than itself, fitness for fitness. And if an individual can be attracted towards likes when it has positive effects—benefits—to dispense, it can presumably be attracted the other way, towards unlikes, when it has negative effects to dispense (i.e. when circumstances arise which demand combat, suggest robbery, and so on).

5. Genetical Relationship in Colonies

In this section we discuss a small selection of the biological problems relating to life in colonies, choosing particularly those which the theory we have developed is able to illuminate in a simple and novel manner and those concerning which discussions in the existing literature are often unsatisfactory.

CLONES

According to considerations advanced so far the coefficient of relationship between all members of a clone should be unity. If this is so our theory predicts for clones a complete absence of any form of competition which is not to the overall advantage and also the highest degree of mutual altruism. This is borne out well enough by the behaviour of the clones which make up the bodies of multicellular organisms. However, when we consider populations of free-living asexual organisms there appears to be a discrepancy in that competitive adaptation is hardly less conspicuous than it is for most wholly sexual populations and altruism if it exists, is not easily detected. To account for this discrepancy three points may be made.

In the first place it may be doubted how many apparently asexual populations are really as they seem. Repeated discoveries of sexual or recombinative processes in species formerly thought to possess none may cause a suspicion that pure clonal populations of any considerable size are uncommon; and

taking into account the well-known generalization that asexual reproduction tends to give place to sexual with the onset of adverse conditions, it may be argued that fully competitive (i.e. stationary or declining) pure clonal populations must be less common still. In a mixed sexual-asexual population the levels of competition and altruism should, neglecting mutation, be appropriate to the average relationship.

Secondly, as regards the appearance of competitive adaptations, we may repeat what was noted in the previous paper, namely that to the new mutant all individuals have zero relationship (for the locus in question); any selfish mutation must therefore have an immediate advantage and its progress will be merely slowed down, not completely arrested, by the self-destruction it comes to work in the later stages of its spread.

Thirdly, as regards the absence of co-operation and altruism, we may note an adjustment to the metric of relationship which we have so far found it convenient to neglect but which will have a slight effect in reducing the relationship between in a clonal population. This again involves mutation. Each step in the path of mitotic connection between two asexual organisms corresponds to a constant chance of mutation (m). The chance that a mutation does not occur ($1-m$) can be multiplied along these paths just as is the factor $\frac{1}{2}$ along paths of meiotic connection in the ordinary calculation of r, and the grand product is likewise the expectation of replica genes in the relative. The number of generations for a given value of r to be reached is approximated by the formula

$$\frac{1}{2m} \log_e \frac{1}{r}.$$

This would apply to the minimum relationship but it is that borne to an individual by half the population and the average relationship is very close to it. With normal mutation rates the decrease in relationship will be slow. Thus if $m = 10^{-5}$ the number of generations for asexual descendants of a common ancestor to become as widely related as full-sibs or the gametes of a single sexual individual is about 39,660. A bacterium with continuously favourable growth conditions so that it divided once every 20 minutes would take $1\frac{1}{2}$ years to run through this many generations whilst a unicellular green alga such as *Chlorella*, dividing once every 15 hours, would take 68 years.

However, taking all three points together and especially considering the fact that a population will normally be started by many sexually produced spores, our apparent discrepancy is largely removed. Such obvious differences in co-operation and altruism as are apparent between a "*colony*" of *Volvox* and a *population* of *Chlamydomonas*, or, to present the contrast another way, within and between colonies of *Volvox*, are at least plausibly accounted for.

The co-operation of the cells in the *Volvox* colony, or coenobium as it is perhaps better called, can be regarded as due to the closeness of their relationship, a mere 14 cell generations being necessary to produce the 10,000 or so cells concerned (*V. globulina*).

Thus the classical "evolutionary" series in the *Chlorophyceae*, starting with temporary cohesion of mitotic daughter-cells of a free-living unicellular form like *Chlamydomonas* and ending with forms with a large and highly differentiated soma is well in accord with our theory.

FUSION OF INDIVIDUALS OR CLONES

If on the contrary such integrated colonies were found to be formed by the coming together of random members of the population or even by the cohesion of meiotic daughter-cells, there would be some cause for surprise, especially if a soma were formed without any sign of discord among the cells.

Something like this has in fact been noted in the *Rhodophyceae* (Jones, 1956). The sporelings developed from either carpospores or tetraspores of *Gracillaria verrucosa* were found to fuse readily when they grew into contact. Jones suggested that the compound sporelings so formed might have an advantage over solitary ones in nature in being less likely to be smothered by sand in the littoral situations in which they grow since he had observed that they sent up fronds sooner and more strongly; but about four out of five of the component sporelings must nevertheless have been total losers by the arrangement to judge by the numbers of fronds sent up. Jones does not state whether the spores in question were from a single parent thallus, but he states that he has seen young plants resembling his compound sporelings in the wild.

Fusion of plasmodia is known in the Myxomycetes (e.g. Martin, 1940; a detailed description for *Dictostelium discoideum* is given in Bonner, 1949). But again, if the cultures in which this has been observed were made up from spores taken from a single sporulating plasmodium, as seems quite likely, the congregating cells or fusing plasmodia cannot be regarded as unrelated, and they could be segregants which happened to have received like combinations of the incompatibility genes normally effective in preventing fusion.

Knight-Jones & Moyse (1961) give an interesting summary of the known facts concerning fusion in marine colonial animals (including reference to the above-mentioned case of *Gracillaria*). It seems that fusion of adjacent colonies does sometimes occur naturally in sponges and corals when contact is made in the early stages of growth; but old colonies tend to develop a line of demarcation where they meet and the same is true of the Bryozoa and the colonial ascidians, fusion even in the early stages being unknown in these groups.

The theoretical considerations which the present theory would apply to the cases of the three preceding paragraphs may be gathered from the discussions that will be given in the next section concerning fighting and co-operation. In general, it is fair to state as a matter of fact that the sexually produced individuals of a species do not, and usually will not, fuse with one another. Of course from such a statement, a large exception must be made for the fusion of haploids in the normal sexual cycle; but here it will be noted that except in respect of certain unusual types of chromosomes the discipline of the meiotic process must generally assure equal reproductive expectations for the two co-operating genomes.

Knight-Jones and Moyse emphasize the contrast between the mutual behaviour of zooids of a single colony and that occurring between the members of the dense clusters that arise from the gregarious settling of larvae: "Such systems are strikingly more economical than is a barnacle population, in that the crowded and smothered barnacles die wastefully, but unsuccessful zooids are resorbed and their materials presumably transferred to help growth elsewhere." According to the present view, clonal colonies of zooids are things of a very distinct kind from colonies of sexually produced organisms such as oysters or barnacles, and the co-operation of zooid individuals, which comes to reach such remarkable complexity in some of the pelagic Siphonophora, should in itself cause no surprise.

COLONIES OF SOCIAL INSECTS

The colonies of the social insects are remarkable in having true genetic diversity in the cooperating individuals.

Caution is necessary in applying the present theory to Hymenoptera because of course their system of sex-determination gives their population genetics a peculiar pattern. But there seems to be no reason to doubt that the concept of inclusive fitness is still valid.

(a) *A hypothesis concerning the social tendencies of the Hymenoptera*

Using this concept it soon becomes evident that family relationships in Hymenoptera are potentially very favourable to the evolution of reproductive altruism.

If a female is fertilized by only one male all the sperm she receives is genetically identical. Thus, although the relationship of a mother to her daughters has the normal value of $\frac{1}{2}$, the relationship between daughters is $\frac{3}{4}$. Consider a species where the female consecutively provisions and oviposits in cell after cell so that she is still at work when the first of her female offspring ecloses, leaves the nest and mates. Our principle tells us that even if this new adult had a nest ready constructed and vacant for her use she would prefer,

other things being equal, returning to her mother's and provisioning a cell for the rearing of an extra sister to provisioning a cell for a daughter of her own. From this point of view therefore it seems not surprising that social life appears to have had several independent origins in this group of insects or that certain divisions of it, represented mainly by solitary species which do more or less approximate the model situation (e.g. most halictine bees), do show sporadic tendencies towards the matrifilial colony.

It may seem that if worker instincts were so favoured colony reproduction could never be achieved at all. However, this problem is more apparent than real. As soon as either the architectural difficulties of further adding to the nest, or a local shortage of food, or some other cumulative hindrance, makes the adding of a further bio-unit to the colony $1\frac{1}{2}$ times more difficult than the creating of the first bio-unit of a new colony the females should tend to go off to found new colonies. Of course, in a more advanced state with differentiated workers, the existing workers would be expected to connive at the change-over to the production queens, which is, so to speak, the final object of their altruism. That in actual species the change-over anticipates the onset of adverse conditions is not surprising since they must be to a large extent predictable. In Britain where winter sets the natural termination the vespine wasps round off their colony growth at about the time one would expect but some bumble-bees begin rather surprisingly early. If climatic termination were not in question and queen-production tended to come a little late so that the worker population had already risen above the number that could work efficiently on the nest workers might best serve their inclusive fitness by going off with the dispersing queens, despite the fact that in this case the special high relationship of workers to the progeny of the queen no longer holds. Descriptively this is roughly what happens in the meliponine bees (Moure, Nogueira-Neto & Kerr, 1956) and, apart from the serious complication of the swarms having many queens each, it seems to be what happens in the polybiine wasps. In *Apis*, as is well known, it is the old queen who goes off with some of her daughters, *leaving* a young queen together with sister workers. This oddity cannot be so easily derived in the imagination from semi-social antecedents in colony reproduction (it could come more readily from the habit of the whole colony absconding under adverse conditions) and like other peculiar features in honeybees it hints at a long and complicated background of social evolution. Of course as attempts to represent the actual course of evolution and its forms of selection the above outlines are in any case thoroughly naïve; they are merely intended to *illustrate* certain possible courses which would accord with our principles.

The idea that the male-haploid system of sex-determination contributes to the peculiar tendency of the Hymenoptera towards social evolution is
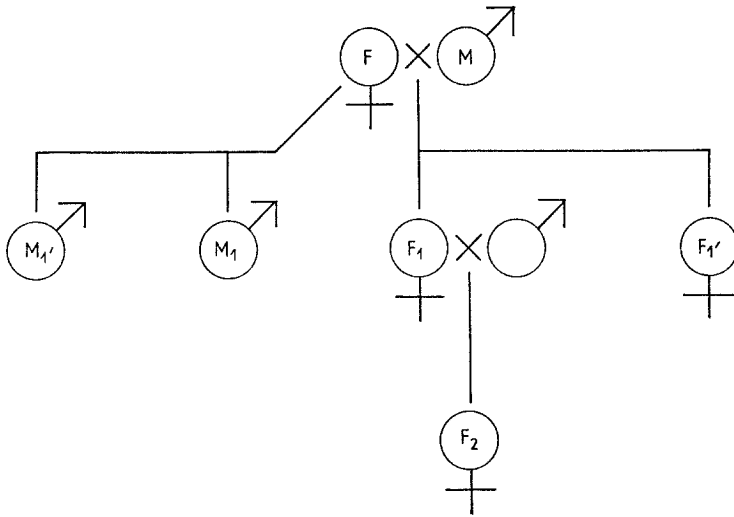
Fig. 1. A hymenopteran pedigree.

Fig. 2. Coefficients of relationship for the pedigree of Fig. 1. Asterisks indicate the coefficients that would diminish in cases of polyandrous insemination assuming the fathership of particular offspring to be unknown.

somewhat strengthened by considering other relationships which may be relevant.

Figure 1 shows a hymenopteran pedigree and Fig. 2 shows the co-efficients of relationship between the individuals lettered on the pedigree.

The relationships concerning males are worked out by assuming each male to carry a "cipher" gene to make up his diploid pair, one "cipher" never being considered identical by descent with another. For all male relationships we then have

$$r = \tfrac{1}{2}c_1$$

where c_1 is the chance that the two have a replica each. The convenience of this procedure, which is arbitrary in the sense that some other value for the fundamental mother-son and father-daughter link would have given an equally coherent system, is that it results in male and female offspring having equal relationships to their mother which matches with the fact that when the sex-ratio is in its equilibrium condition individuals of opposite sex have equal reproductive values (see Bodmer & Edwards, 1960).

The relationships whose values are affected by polyandrous insemination of the female are indicated in Fig. 2 by asterisks. It will be seen that among those unaffected, because fertilization is not involved, are the relationships of a female to her son, $r = \tfrac{1}{2}$, and to her brother, $r = \tfrac{1}{4}$. According to our theory these values indicate that workers should be much less inclined to give up their male-producing in favour of the queen's than they are to give up their female-producing in favour of a singly-mated queen. Laying by workers is known to occur in each of the main social groups, bees, wasps and ants. The extent to which the practice occurs in normal colonies remains largely obscure; but in some species it is so prevalent that observers have been led to suggest that all the male members of the population are produced in this way (Wheeler, 1928, p. 220; Richards, 1953, p. 81). In fairness however, rather than emphasize this apparently detailed fit of our hypothesis, it should be pointed out that male-egg production by workers is in any case the simplest possible manifestation of an incipient selfish tendency since it does not require the complicated preliminary of mating.

Males are related to their brothers as well as to their sisters with $r = \tfrac{1}{4}$; their relationship to their daughters is $\tfrac{1}{2}$. Hence the favourable situation for the evolution of worker-like instincts cannot ever apply to males, and in conformity with this, working by males seems to be unknown in the group. Again however, it must be admitted that another explanation of the fact could be advanced: except for the faintest ambiguous suggestion in one genus (*Trypoxylon*, see Kirkpatrick, 1957, p. 254) there is not even any parental care by males even in the solitary nesting species, so that the evolution of worker behaviour would have difficulties of initiation in this sex.

While this point must be fairly taken, nevertheless it may be that the male-haploid system is still the prime cause of the very different behaviour of males. It can be shown that it causes a selection pressure towards a sex-ratio which is markedly female-biassed. This may be seen as due to the fact that in the replacement of the gene pool in each generation the females have a bigger contribution to make than the males, so that, so long as the numerical deficiency of males has not gone too far, it is more profitable to produce females than males. And if a chronic deficiency of males does occur it is clear that the male sex will tend to evolve adaptations for polygamous mating which must be almost completely incompatible with the evolution of male parental care. The argument concerning the sex-ratio must properly take into account the relative expensiveness of producing the two sexes. Thus if individuals all incur the same expenditure irrespective of sex, which must be the case for instance with a bee which provisions a series of cells with equal amounts of food, the ratio is the well-known ratio $1 : 1 \cdot 618$; only when a male is merely half as expensive as a female does the ratio sink to the usual $1 : 1$. The argument does not apply, however, if there is thelytoky, polyembryony, etc. and it does not apply once a worker caste has come into existence. If worker laying takes place a more male-biassed ratio should prevail.

(b) *Multiple-mating and multiple-insemination in Hymenoptera*

Following these considerations of sex-ratio, however, it is not surprising to find in most solitary and even moderately social Hymenoptera that the male carries more sperm than is necessary to fill the spermatheca of a single female. Generally it seems that he carries far more than enough. Possibly only in some very highly social species is multiple-insemination *necessary* to fill the spermatheca. This is an important point in favour of our hypothesis since it pre-disposes to the production of the production of the very highly intra-related families which the male-haploid system makes possible. But to what extent, over the range of groups and species, the females actually produce such families remains a large question. The literature contains many references to multiple matings by female Hymenoptera, spread over many of the major groups of the order. How frequently such multiple mating is accompanied by a significant degree of multiple insemination, and how the phenomena are distributed with respect to incipient, advanced or retrogressing social life are matters too wide and complex to be reviewed here. For the present it must suffice to quote the very small amount of work known to the author which bears directly on multiple insemination.

Concerning female wild bees in general, Michener, Cross, Daly, Rettenmeyer & Willie (1955) state that: "Spermathecas with only a few sperms have not been found, in spite of some search, although specimens with the

spermatheca only half-full are known". But in a survey of some Australian halictines, Michener (1960) found that on the whole the number of sperms in spermathecas was small in comparison with his experience of American halictines. Without knowledge of the quantity of sperms which the male can provide or of mating behaviour, one cannot be sure what this argues about multiple-insemination, but it suggests that it may be uncommon. Taken together with Michener's notable failure to find any small-ovaried worker-type bees, which according to him are a feature of most common halictines of other continents, this observation seems, therefore, against our hypothesis. But Michener notes as another general feature, the short adult life-span of the Australian bees and concludes that, "There is no evidence that any female lives long enough to encounter her adult progeny", which at least offers another possible reason why worker behaviour has failed to appear. Plateaux-Quénu (1959) thought queens of the quite highly social *Halictus marginatus* were probably multiply inseminated because she found some queens towards the beginning of the period of fertilization with only partially filled sperma-thecae. Michener & Lange (1958a) present evidence that a female of the solitary (though gregarious-nesting) anthophorine bee (*Paratetrapedia oligo-tricha*) in Brazil, taken in copula, was engaged in receiving her second in-semination, this apparently being the only direct evidence of such a thing in a primitive bee known to them at the time.

   Multiple insemination of a high order effectively producing a progeny of multiple paternity seems to be firmly established for the honeybee (e.g. Taber & Wendel, 1958; Kerr, Zucchi, Nakadaira & Butolo, 1962). On the other hand, it would seem not to occur in the Meliponinae (Kerr *et al.*, 1962). It occurs in the socially very advanced fungus-growing ants, e.g. *Atta sexdens* (Kerr, 1961). But in another myrmicine of a different tribe I found no evi-dence but of single inseminations, using Kerr's sperm counting methods.

   Suppose a female is mated by n males and they are respectively responsible for proportions

$$f_1, f_2, \ldots f_s, \ldots f_n, \ (\sum_s f_s = 1),$$

of her female progeny. The average relationship between daughters is then

$$\tfrac{1}{2}(\tfrac{1}{2} + \sum_s f_s^2).$$

In particular, if all males contribute equally we have

$$\bar{r} = \tfrac{1}{2}\left(\tfrac{1}{2} + \frac{1}{n}\right),$$

which is the lowest average relationship for a given value of n. If two males contribute equally we have $\bar{r} = \tfrac{1}{2}$ as for normal full-sibs. Clearly multiple-insemination will greatly weaken the tendency to evolve worker-like altruism

and $n > 2$ in the model situation described above should prevent its incipience altogether. Using Taber & Wendel's estimate (1958) of $\bar{n} = 8$, which Kerr's different method roughly confirmed, we get $\bar{r} = \frac{5}{16}$, which doubtless should be raised a little to allow for inequality in the contributions of the drones. It does seem at first rather surprising that altruism towards sisters so much *less* related than full sisters can be maintained at its observed pitch of perfection. But even the limiting value of $\bar{r}$ is no lower than $\frac{1}{4}$ and we may well imagine that once established the biological advantage of the social mode of reproduction, which is evidenced by the success of the social insects in general, proves sufficient to outweigh even a twofold higher value in personal offspring. It may also be argued that the firm establishment of highly differentiated trophogenic worker castes creates a gulf which a sexualized mutant is unlikely to cross successfully, especially when as in honeybees so much depends on the behaviour of the other workers. For example, a mutant sexualized worker of the honeybee will eclose from a worker cell and will therefore be small. Even if it secretes queen-substance it is unlikely to be as attractive as a proper queen and is likely to be killed. If it escapes it cannot found a colony on its own. Thus, if the trend to multiple insemination occurs after the firm establishment of the worker caste, its threat to colonial discipline is a rather remote one.

In species of social Hymenoptera which found their colonies through single fertilized females the difficulties and dangers of seeming to be royal are less important; but the mutant will still suffer handicaps from its probable small size and lack of food-reserves. In ants it will be further handicapped by its lack of wings. Nevertheless with ants there are strong indications that trends of worker sexualization have occurred in the evolution of the group (Haskins & Haskins, 1955; Michener & Michener, 1951, p. 126; Wheeler & Chapman, 1922; Wheeler, 1928, pp. 173–4). It may be remarked that the sexualized worker is likely to have a smaller spermatheca and so to restore single insemination, which will, according to our theory, restore the basis for re-evolving strong worker altruism.

An ability of females to lay unfertilized eggs which develop into females would open another possible avenue for selfish selection. Again, the menace will be greatest when multiple insemination of queens occurs, for then when a worker had inherited the causative gene from its father there would be a better chance, especially when the gene frequency was low, that it would have some normal worker sisters to help rear its offspring. In general, whether we are concerned with parthogenetic production of males or females we need only follow Sturtevant's (1938) argument and visualize the drastic or fatal over-production of sexual or egg-laying forms which would occur in the "son" or "daughter" colonies due to an egg-laying worker to see the potent counter-selection to which a fully penetrant causative gene will

become exposed. Clearly the situation is worse for the gene when it is common than when it is rare so that an equilibrium is possible.

Female-to-female parthogenesis by workers does occur sporadically in honeybees and shows geographical variation in its incidence. In the South African race, *Apis mellifera capensis* Esch., it seems that worker eggs always develop into females (see Kerr & Araujo, 1958)†. But whether this is explicable as a selfish trait is rather doubtful. To be such the laying-workers would have to try to get their eggs cared for in queen-cells. Despite what Flanders (1962) seems to quote Onions as having stated—that in queenless hives "Uniparental workers do not construct either queen cells or drone cells", and that "a queenless colony gradually disintegrates"—Dr. Kerr informs me that these bees do eventually construct queen cells in an emergency and can thereby secure the perpetuation of their colony; but he found that they did so somewhat tardily compared to queenless colonies of the familiar honeybees. Of course for them, possessing this unusual ability, the need to initiate queen-rearing at once is not so urgent. Also in some other races diploid eggs laid in queen cells by workers in hopelessly queenless hives may sometimes be reared and so save their colonies from extinction (Butler, 1954, p. 58).

Female-to-female parthenogenesis is also present in various species of ants. For example in the ant *Oecophylla longinoda*, parthenogenesis of a clonal type seems to have become a normal mode in the reproduction of the colony (Ledoux, see Wilson, 1963). Here the workers and not the mother queen produce the new generation of queens, which is suggestive at least that the situation had its origin through the selection of a selfish trait.

(c) *Termites*

The special considerations which apply to the Hymenoptera do not seem to have been noticed by Williams & Williams (1957). The discussion which they base on their analysis of the full-sib relationship would, however, be applicable to the termites where this relationship is ensured in the colony by having the queen attended by a single "king". Termites of both sexes have an equal relationship ($r = \frac{1}{2}$) to their siblings and their potential offspring. Thus the fact that both sexes "work" is just what we expect; we need only a bio-economic argument to explain why restriction of fertility to a few members has proved most advantageous to the sibship as a whole. On this point the present theory can add little to previous discussions.

When either king or queen dies the worker castes rear a substitute or "neotene" from the eggs or young nymphs already present. The neotene mates

† Other interesting peculiarities reported for this race are its mild temperament and the presence in workers of large queen-like spermathecae. However Dr. Kerr tells me that he has checked that laying-workers do not have sperm in their spermathecae.

with the surviving parent. The progeny which come from such a mating will still be related to the old workers with $r = \frac{1}{2}$. They will be related among themselves by $r = \frac{5}{8}$. They will also tend to be highly homozygous and such matings are in fact said to be somewhat infertile.

It is surprising, however, if increasing the tendencies to social cohesion by such close inbreeding can ever pay off as a long-term policy against the disadvantages of decreasing adaptive flexibility. That it may be a successful short-term policy for a species is perhaps indicated by the frequency of mention of brother-sister mating in the literature on social insects; but these statements are not always based on very firm evidence.

(d) *Pleometrosis and association; population viscosity in the social insects*

However it does seem necessary to invoke at least a mild inbreeding if we are to explain some of the phenomena of the social insects—and indeed of animal sociability in general—by means of this theory. The type of inbreeding which we have in mind is that which results from a high viscosity of population or from its actual subdivision into small quasi-endogamous groups.

In some ants (e.g. *Iridomyrmex humilis*), at least one species of stingless bee (*Melipona schencki*, see Kerr, 1949 and orally) and apparently most species of wasps of the sub-family Polybiinae it is normal to have at least several "queens" engaged in egg-laying in each nest. This phenomenon is known as pleometrosis. Colony reproduction is by swarming with several or many fertilized females—potential queens—in each swarm. Clearly this social mode presents a problem to our theory. Continuing cycle after cycle colonies can come into existence in which some individuals are almost unrelated to one another. Such situations should be commoner the higher the number of founding queens, but less common in so far as there is any positive assortment of true sisters in the swarms. They would be very favourable to the selection of genes causing selfish behaviour and this in turn would be expected to lower the efficiency of social life and to reduce the species. Yet though selfish behaviour is certainly not absent—witness the large proportion of unfertilized wasps in egg-laying condition (Richards & Richards, 1951), and the common occurrence of dominance behaviour—it does not seem to do the colonies much harm and the species concerned are highly successful in many cases. For example, the genus *Polybia* includes several very abundant species in the Neotropics and has obviously undergone considerable speciation with the whole system in working order.

Wasps of the widespread genus *Polistes*, doubtfully placed in a separate sub-family from the Polybiinae, present a rather similar problem. In this case it seems that there is usually or always only a single principal egg-layer on the nest; she dominates the others and they succeed in laying only a few eggs if

any (e.g. Gervet, 1962). But with many of the species and races that inhabit warmer lands it is common for the initial building of the nest to be the work of two or more fertilized queen-sized wasps. This phenomenon has been called "association" (Richards & Richards, 1951). Even at this stage the dominant wasp does least work and probably all the egg-laying, and, probably due to their more arduous and dangerous lives, the auxiliaries (as the subordinate queen-like wasps are called) tend to disappear in the course of time so that a queen assisted by her daughter workers becomes the normal situation later on. Here it is the ready acceptance of non-reproductive roles by the auxiliaries that we have difficulty in explaining. There is good reason to believe that the initial nest-founding company is *usually* composed of sisters (Rau, 1940; personal observations on *Polistes versicolor*), which brings the phenomenon closely into line with the pleometrosis of the polybiines. But it is doubtful if the wasps have any personal recognition of their sisters and if a wasp did arrive from far away it is probable that it would be accepted by the company provided it showed submission to the one or two highest ranking wasps. Dominance order does sometimes change and an accepted stranger has before it the prospect of rising in rank and ultimately subduing or driving off the queen. Thus an innocent rendering of assistance is not always easy to distinguish from an attempt at usurpation as Rau has pointed out, so that the readiness to accept "help" is really just as puzzling as the disinterested assistance which some of the auxiliaries undoubtedly do render.

The geographic distribution of the association phenomenon in *Polistes* is striking (Yoshikawa, 1957). We may state it as a general, though by no means unbroken, rule that northern species approximate to the vespine mode of colony foundation and tropical species to the polybiine to the extent above described. The single species *Polistes gallicus* illustrates the tendency well. At the northern edge of its range in Europe its females usually found nests alone. In Italy and Southern France the females found nests in companies; while in North Africa the species is said to found colonies by swarming with workers (see Richards & Richards, 1951). We here suggest two hypotheses which could bring these facts into conformity with our general theory.

The first posits a general higher viscosity of the tropical populations. This will cause, through inbreeding, all coefficients of relationship to have higher actual values than we would get taking into account only connections through the past one or two generations. And it will also increase the tendency for casual neighbours to be related, which is clearly of potential importance for the association phenomenon.

Populations of *Polistes* certainly are very viscous. Generally the wasps have a strong attachment to their place of birth (Rau, 1940), and like to found nests near the parental nest. They are weak flyers. And they do show a very

pronounced tendency to local variation. But whether these remarks apply any more strongly to tropical than to temperate populations I do not know. Polybiine wasps seem to be weaker flyers than vespines and also have indications of a tendency for swarms to build not far from the parent nest. Polybiines also show much geographical variation.

By its very nature the so-called temperate climate may tend to force a greater degree of vagrancy on the insects inhabiting it, both through its pronounced seasons and its seasonal irregularities. A discussion of this idea from a similar biological point of view can be found in Wynne-Edwards (1962, p. 463). As one further factor relevant at least to *Polistes* we suggest that if, as seems probable, the genus is of tropical origin the northern species will be derived from former races which themselves tended to be made up of vagrant colonist wasps which had flown north. Thus there would have been selection for wasps willing and able to found nests alone; and in general, in the course of such a spreading colonization, a species would be expected to shed some of its co-operative adaptations. But if the spread was very slow, as it may well have been, these factors would hardly apply.

The second hypothesis appeals to the lack of marked seasons in the tropics causing a lack of synchronism in the breeding activity of insects. This will tend to cause inbreeding because it scarifies the mating population. Thus a Polybiine nest may be in active production of sexual wasps when its nearest neighbours are not and its progeny may therefore be more inclined to mate among themselves. The same doubtless applies to *Polistes* in a really equable tropic environment and with *Polistes* we again have an important correlative effect that when a nest-founding wasp accepts an adventive helper the chance that she is a sister is also increased. However, with *Polistes*, multiple-queen nest founding does occur even where the wasps are constrained by the climate to follow a definite seasonal cycle. Queens may come together in the spring after hibernation to found their colonies. Rau (1940) records some interesting observations on *P. annularis* in the United States showing the variability of its nesting behaviour and he mentions his general experience that the hibernated queens return to the old nest for a short time before going off to found nests. Such behaviour should help to ensure that in cases of associative founding the co-foundresses are sisters. The cases of hibernating yet associating *Polistes* would seem to dismiss any hypothesis that the differences we have noted between northern and tropical wasps is due solely to factors following from the necessity for hibernation. In *Vespula*, queens do often hibernate in the parental nest and yet do not show association in nest-founding.

To the extent that they are valid, the above hypotheses would also help to extenuate previously discussed difficulties concerning the maintenance

of reproductive altruism despite multiple insemination of queens. It may be remarked that although modern work rather indicates that its breeding system is far from viscous the honeybee does seem to maintain local races quite readily. With *Atta sexdens* I have noticed that males and females come to earth from their nuptial flight in local concentrations, but whether these are associated each with an established colony or represent some wider nuptial gathering is not clear.

(e) *Aggressiveness*

The aggressiveness of the workers of social insects towards disturbers of their nest is one of the most conspicuous features of their altruism. The barbed sting and the function of sting autotomy are physical parallels of the traits of temperament. The correlation of these characters with sterilization does seem to hold very well throughout the social Hymenoptera. Queens are always timid and reluctant to use their stings compared to workers. In *Polistes*, workers, unless very young, are more aggressive than auxiliaries, and auxiliaries more than the reigning queen. Races of honeybees in which laying workers occur more frequently or appear more readily when the hive becomes queenless are generally milder than the races where they are less prevalent (Sakagami & Akahira, 1958, 1959; Kerr & Araujo, 1958). Polybiine wasps, pleometrotic and lacking pronounced caste differences, are generally somewhat less fierce than vespines.

However, aggressiveness is also clearly a function of the size of the colony, or perhaps even more of the worker: queen ratio. This applies not only to particular colonies as they grow larger but also in a general way to variation in mature colony size between species. This effect too is not very surprising, for, to take the extreme case, we can see that it is only when its nest is overpopulated and its services in other directions superfluous that the worker can afford to throw its life away. Typically the vespines have the higher worker: queen ratio, so that from this point of view as well, it is not surprising that the polybiines are generally speaking milder wasps. It is interesting to learn that even in the limited north-south range covered by the islands of Japan, *Polistes* shows in this respect as well its previously noted tendency to bridge the two types. Yoshikawa (1962) gives an interesting comparison of northern and southern Japanese species and it is seen that northern species are both fiercer and have the larger colonies. Iwata (quoted by Yoshikawa) believes that the fierceness is a function of the colony size. Although no properly associative *Polistes* occur in Japan, Yoshikawa (1957) has found a case of temporary association in a southern species, suggesting a slight or vestigial tendency. Perhaps this factor may play a part in the difference in fierceness. Existence of auxiliaries would seem incompatible with a high degree of

worker differentiation and will therefore tend to counter the development of high worker altruism. But just why it appears to be also incompatible with higher worker : queen ratios is not entirely clear.

(f) Usurpation

Its made or half-made nest is obviously a valuable property to a queen bee, wasp or ant. If it is ready provisioned or staffed by workers and set for the rearing of sexual brood it is even more valuable. It is therefore not surprising that usurpation has become a major evolutionary and behavioural issue with the nesting Hymenoptera.

On the one hand we have the great array of parasites. Often, especially in bees and wasps, the host and parasite species seem to be closely related, suggesting that the habit arose out of petty intra-specific usurpation. But the present theory indicates considerable difficulties for the sympatric emergence of a parasitic race. Unless the evolving complex of characters could include a strong tendency to vagrancy the usurper would in too many cases destroy the genes on which its own behaviour was founded. One allopatric race invading the territory of another with at least partial reproductive barriers already present should create a more promising situation for progress in usurper-instincts. A situation like this, involving occasional parasitism, is suggested for two species of *Bombus* in Britain (Free & Butler, 1959, p. 77). Plateaux-Quénu (1960) has observed a half-provisioned nest of *Halictus marginatus* being used by a female of *H. malachurus*. Both these species are social on about the same level as *Bombus*.

On the other hand, we have the sensitivity about adventive females which is so widespread in the nesting Hymenoptera, including the parasites themselves. According to Plateaux-Quénu, conspecific usurpation is frequently attempted, albeit before the appearance of the workers, in the nest aggregations of *Halictus malachurus* and sometimes succeeds. A successful conspecific usurpation, strongly resisted, has actually been observed in *Polistes fadwigae* by Yoshikawa (1955) and I have observed what was probably an attempt, persistent but unsuccessful, in *P. versicolor*. Something similar seems to have been seen by Kirkpatrick (1957, p. 277) with *P. canadensis*[†]. And with the same species I have found that if a dominant wasp is transferred from one nest to another a mortal fight, usually with the reigning dominant, begins immediately; whereas a young worker similarly transferred may sometimes be accepted and, perhaps because of its submissiveness, seldom

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† In the light of observations of Sakagami & Fukushima (1957) an alternative interpretation that one is concerned with an attempt to thieve larvae for food in these cases, should be borne in mind. But I have not seen thieving in either *P. versicolor* or *P. canadensis* even in artificial situations that should encourage it. It would in any case be normally very difficult to perform in associative species.

receives so severe an attack. Extreme suspicion concerning wasps which approach the nest in a wavering uncertain manner sometimes prevents a genuine member of the colony from rejoining it, at least for some time, in *P. canadensis*. This is especially apt to happen with young wasps, perhaps returning from their first flight; and it may be a rather paradoxical result of such a reception that they sometimes end up working on a nearby nest not their own. Possibly it is the danger of usurpation, joint with that of para- sitoids, that keeps so large a proportion of a *Polistes* colony idle on the nest when one would have thought they could be much more usefully employed out foraging.

As the very existence of association necessitates, antagonistic behaviour is not so marked in the very early stages of nest-founding: then, with *Polistes versicolor*, a considerable amount of swapping of wasps may take place from week to week within a local group of initiated nests—for example all those located around the buildings of a household and usually not far from a last year's abandoned nest from which very likely all or most of the wasps are derived. The same sort of thing has been noted by Ferton (1901) for *P. gallicus* and by Rau (1940) for *P. annularis*. But even at this stage fights are sometimes seen severe enough for the combatants to fall off the nest.

In these associative *Polistes* the great variation in the degree of association —from lone nest-founding to companies of 12 or more crowded on and about a tiny nest-initial—the frequent abandonment of young nests, the quarrels, the manifest concern about adventive wasps, combine to create an impression which is very reminiscent of the breeding affairs of the South American cuckoos *Crotophaga ani* and *Guira guira* as described by Davis (1940 a, b). In their broad features the situations are indeed so similar as to suggest similar trends of selection must be at work in populations similarly patterned with respect to relationship. In these birds, much as in *Polistes*, we have a basic ability to rear young independently complicated by a tendency of some birds to assist altruistically (perhaps most marked in *Crotophaga*) and of others to play the cuckoo (most marked in *Guira*, which also sometimes parasitises other birds). A striking difference from *Polistes* of course is the presence of males, playing parts in close parity with those of females. And the systems also differ in that usually several birds succeed in laying in the com- munal nest, which is more like what is found with certain primitively social xylocopine bees (see, e.g. Michener, 1958) than like *Polistes*. When the clutch becomes very large through this cause a large proportion of eggs may fail to hatch. Eggs are sometimes taken out and dropped. Such action by a particular bird might serve to increase the proportion of its own eggs in the clutch. For all the seeming confusion and inefficiency these birds are, like *Polistes versicolor* and *P. canadensis* in the same area, widespread and apparently successful.

(g) *Pleometrosis in Halictinae*

The social halictine bees closely parallel the systems found in *Polistes*. Worker populations are of comparable size. The state of affairs found in *Augochloropsis sparsilis* (Michener & Lange, 1958b) and in *Lasioglossum inconspicuum* (Michener & Wille, 1961) shows that these species have a class closely corresponding to the auxiliaries of warm-climate *Polistes*. But since at least some of the halictine nests are pleometrotic it seems more probable that some of their auxiliaries become layers later on rather than dying young as workers as they tend to do in *Polistes*. Probably only a minority of the species of Halictinae have any trace of a worker caste and the group also differs in the wide range of types of sociability which their tunnel-nesting encourages. For instance, quite a common situation with burrowing bees, both Halictinae and others, is for several females to be using a common entrance tunnel while each owns a separate branch tunnel further back.

Michener (1958) has recently suggested that the road to sociability and the development of a worker caste has lain in this group through a stage like this followed by a stage like that found in *Augochloropsis sparsilis*. This we are inclined to doubt since even if the nest-system users are for some reason always sisters the genetic relation of sister eggs will always be twice that of niece eggs irrespective of multiple insemination, so that on the present theory social evolution via the matrifilial colony always offers the easier route to worker altruism. Hymenopteran societies in which the queen (or queens) have auxiliaries but not, later, filial workers, seem in fact to be unknown. The classical theory concerning the evolution of the social insects has always posited a wide overlap of generations allowing mother and daughters to co-exist in the imaginal state as one of the preconditions for the evolution of this kind of sociability, and it is surely significant that it is never observed where this condition is lacking, as it might well be if genetic interest in nieces were sufficient to encourage reproductive altruism†. That such altruism could arise through genetic interest in the offspring of unrelated bees sharing the same excavation, as Michener actually suggests, seems to me incredible.

(h) *Tunnel-guarding by bees*

There is however another important type of social behaviour to which Michener has re-drawn attention which might well arise on the basis of much

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† As regards the traces of similar sociability that exist in birds, with *Crotophaga* and *Guira*, present evidence suggests the possibility of both aunt-like and sister-like altruism, although just how widely genetical relationship may range within groups is not known. Other recorded cases in birds suggest *immature* progeny helping the mother to rear subsequent broods (Skutch, 1935). These immatures would doubtless reproduce normally later on.

lower relationships. One of the potential advantages when two or more females share a common entrance tunnel is that the entrance can be defended against parasites by a single bee, leaving the others free to forage. Instincts for guarding a narrow entrance seem to be widespread in the nest-excavating bees and also occur in Meliponinae (Michener 1958). Michener has seen females of *Pseudogapostemon divaricatus*, a workerless but entrance sharing species, apparently taking turns at the duty and he and other observers have seen guard bees of this and other species repulse mutillids (Michener, 1958, 1960; Michener & Wille, 1961) and parasite bees (Michener & Wille, 1961). The menace of intruding parasites may give such co-operation a very high advantage. But it would seem that once established the system should give an even higher advantage to the sporadic "shirker", so that it is a little difficult to see how guarding could become perfect. Perhaps it is not. One may however construct a simple imaginary system that would render it so: the bees could evolve an instinct which allowed them to leave duty at the nest entrance only on the stimulus of another recognized tenant coming in, or better, of another bee coming up from behind; this would ensure that there was always a bee on duty or at least somewhere in the nest system. By going out when supposed to be on duty, a bee would jeopardize her own brood as much as, if not more than, the broods of the others, so that selection would tend to stabilize the instinct. Interestingly Claude-Joseph and Rayment both have claimed to have observed guarding on this system, but Michener (1960) is inclined to doubt these claims because his careful observations on *P. divaricatus* in Brazil had revealed that the be-haviour was more irregular than might appear at first sight, bees remaining on guard for some time and allowing others to go out past them. In a highly pleometrotic nest-system, shirking might be relatively easier and safer for the isolated social deviant but the spells of guard-duty demanded would also be much shorter and therefore the selective incentive to shirking much less. Nevertheless, even if it is possible to account for the evolution of guard-instincts without a basis of relationship between the bees, it is hard to see how other socially disruptive practices, such as robbing within the nest-system, could fail to evolve unless a bee's co-tenants were also usually the carriers of some part of its inclusive fitness.

6. Equal-Status Situations

By an equal-status situation we simply mean a social situation where there is no obvious and regular difference in age, caste or sex between the individuals concerned. Several apparently of this nature have already been mentioned, including the nest-system of independently working solitary bees discussed

just previously. Now, using other examples, we indicate some other kinds of argument which it may be useful to apply to these situations.

CO-OPERATION

In certain ants, notably *Lasius flavus* and *L. niger* (Waloff, 1957), it is known that companies of several queens will cooperate in excavating the initial nest. Since these have just come to earth from a vast mating-flight they are un-likely to be close relatives. According to Waloff, the queens of *L. flavus* usually cohabit peacefully in the nest-chamber and even keep their eggs in a common pile, but about the time cocoons are first formed they tend to separate, some taking a portion of the brood (not necessarily a very fair one it seems) to a particular corner of the nest. There is evidence that the queens so separated tend to control distinct sectors in the developing nest, each having its own worker population; and whether by death of queens—by fighting or otherwise—or by migration of a "sector", most nests of *L. flavus* end up haplo-metrotic. In *L. niger* fighting between the queens is regular and generally only one survives in the initial nest chamber.

If we imagine a situation where, of the queens which succeed in co-opera-tively establishing an initial nest, only one is allowed to survive and use it, rather as happens with *L. niger* except that the survivor is chosen at random and not according to fighting prowess, we see that unrelated queens will evolve instincts to co-operate as a group of n if the chanceth at they succeed in establishing the chamber is more than n-times the chance that one would succeed if alone. When engaged in digging the queens are very helpless and it is not difficult to imagine that a team gets itself underground so much more quickly than an individual that this criterion is met. As to the continued amity once the chamber is made Waloff's observations on experimental multi-queened initial nests showed that for some reason the queens survive better and rear their first workers sooner when in a group than when alone; if sufficiently marked in a state of nature such an effect could explain the continued amity. With the appearance of the first workers the queen and her brood tend to become more independent and we expect behaviour to change accordingly.

It will be seen that in essentials this situation has much in common with that previously described concerning the fusion of sporelings of *Gracillaria verrucosa*.

In both cases we have a strong presumption that a stage in which selection very strongly favours the united group over the lone individual gives place to conditions where the individual would be better off in the absence of its close companions. According to our theory whether these new conditions will bring on an overt struggle or fighting will depend very largely on the

degree of relationship in the group in question, or rather on the degree of relationship that has held on average in the multitude of similar situations which have occurred during the evolutionary development of the behaviour.

<div align="center">FIGHTS</div>

The argument to be applied to fights is merely another form of the argument applied above to co-operation. If two evenly matched unrelated animals holding one unit of reproductive potential each are in a typical situation which holds out the prospect of a fight, and if their instincts have been nicely adjusted by natural selection to suit the average outcome, then they will fight only if the expectation of reproductive potential for the winner is more than one unit. If they are sibs they will fight only if the expectation of "winner's r.p.$+\frac{1}{2}$ loser's r.p." is greater than $1\frac{1}{2}$. Thus if one inevitably dies in the fight the winner must normally gain by more than 50% or the two will prefer to co-exist. In the case of a "hymenopteran full-sistership" they will not fight to the death unless the expected gain to the winner is more than 75%. But with the honeybee, with the amount of multiple-insemination discussed previously, about a 40% increase will be enough. In this case we may put it that unless the presence of an extra young queen can increase the growth of the colony by more than 40% the reigning young queen will prefer to do without her. Thus the mutual animosity of young queens is not very surprising. The "piping" by a still imprisoned queen incidentally would seem to have the characteristics of altruism. The females of various species of Hymenoptera (in *Vespula Halictus*, etc.) are said to fight in spring for the possession of the maternal nest in which they hibernated together. But in these cases we do not know about multiple-mating and anyway there is probably no question of a fight to the death, beaten females are usually expelled and presumably go off to discover or excavate other nest sites.

It may be noted that the larvae of "gregarious" parasitoid Hymenoptera in whose case there is normally no question of "going off" do not fight even if overcrowded (Salt, 1961). "Gregarious" refers to species where the adult normally lays several eggs per host. In "solitary" species, which lay only one egg per host, the first instar larva is adapted for fighting and always attempts to kill any other larvae in the same host; normally there is only one survivor. The gregarious larvae in a host are not necessarily "hymenopteran full-sisters" however, even apart from the question of polyandrous insemination. In cases of polyembrony they will be clonal. The same would be true if the mother reproduces by thelytoky, and, as Dr. Salt has reminded me, this certainly occurs in some ichneumon-flies; and female-to-female parthenogenesis of one kind or another is wide-

spread throughout the parasitoidal Hymenoptera. In such cases the comparison to the batch of females competing for the nest is still less valid, although in itself the difference in social behaviour between these two types of parasitoid according to relationship remains very striking. In the parasitoidal Diptera with normal sexual reproduction our theory predicts that the competition between gregarious larvae should be fiercer; whether this is observed I have been unable to ascertain, but gregarious cases are certainly much less common in Diptera and this at least is what we expect.

PARENTAL BEHAVIOUR TO MINIMIZE SIBLING COMPETITION

Of course the above argument is of potentially much wider application. It may be applied to broods of insect larvae feeding under circumstances where the exigencies of competition are not so inflexible as with parasitoids, for example to broods feeding on plants. Competition within such broods should according to our theory be fiercest in species where the female is inseminated by many males. Fierce competition will waste the energies of the brood and the ovipositing behaviour of adult females should tend to evolve so as to minimize this wastage which spells a lowering of total surviving progeny. Hence over a range of species the habit of laying eggs in batches should correlate with monandrous insemination of females. The correlation should be stronger for cases where the larvae are also gregarious.

This reminds us of Fisher's suggestions concerning the evolution of distastefulness and warning-coloration and we note that he appears to have tacitly assumed that the broods he discusses would be of full sibs. Probably this is fair for his cases of Lepidoptera. But as regards the sawfly larvae which he also cites, we have all the diverse hymenopteran possibilities already mentioned, both those dependent on multiple mating and, for some species, those due to female-to-female parthenogenesis. Since we know polyandrous insemination to be a distinct possibility for the Hymenoptera it is of interest to note that D'Rozario (1940) found evidence for the gooseberry sawfly, *Nematus ribesii*, that though the males are readily polygynous the female ceases to be attractive after one mating. *N. ribesii* is a good Dzierzon-rule species and concerning the sex-ratio it is said that "females predominate" (Imms, Richard & Davies, 1957). If we assume equilibrium sex-ratio and equally costly males and females the average relationship is actually a little under one-half†. In accordance with Fisher's suggested correlation the eggs are laid close together and the larvae are aposematic and fairly gregarious. However to the counter-instance admitted by Fisher—the butterfly *Anosia*

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† The equilibrium ratio assuming the cost of male and female to be equal is $\frac{1}{2}(3 - \sqrt{5})$: $\frac{1}{2}(\sqrt{5} - 1)$. Using the coefficients given in Fig. 2 we get the average relationship $1 - \sqrt{5}/4 = 0 \cdot 44$.

plexippus which "scatters her eggs although she has solitary, inedible, conspicuous, larvae"—it will be fair to add another; the case of the moth *Panaxia dominula* which also scatters her eggs although her larvae are conspicuous and presumably distasteful. In the vegetation they tend to be found concentrated on the preferred food plants but are probably not truly gregarious. I have noticed in the wild that the female moth ceases to be attractive as soon as she enters copulation; thus females are probably only once mated, and the case is contrary to my suggested correlation as well as to Fisher's. But of course, though these few instances help to outline the situation, they carry little weight for or against the hypothesis.

When a brood is still under parental care the parent or parents involved will be concerned to minimize the wasteful effects of sibling competition. Their disciplinary task will be easiest if the brood is of full-sibs. In the vast majority of cases it is so, either due to monogamy or to polygamy combined with parental care by the female alone. In the unusual cases of birds where polyandry is combined with male parental care it seems that the male is always mono-gynous and broods a clutch given him by a single female (Wynne-Edwards, 1962, pp. 237–8). But in some Ratites male parental care for polymaternal broods does seem to occur (Kendiegh, 1952); and in lekking birds there would seem to be a distinct possibility of polypaternal clutches. Doubtless many more exceptions could be found. The notable case of the polyandrous social insects has already been discussed; we merely note here that the method of rearing larvae in cells is ideal for preventing direct competition and where this method is not adopted, as in *Bombus* and the social xylocopine bees, we have added reason for expecting that the queens are effectively monandrous. Nevertheless larval competition seems to be severe in some species of *Bombus* (Free & Butler, 1959, pp. 16, 19–21). Although the cases where full-sibships are not the rule cannot amount to much numerically compared to the vast array of cases where they are, we do not intend to suggest that diminishment of sibling competition is the sole evolutionary *raison d'etre* of permanent mating ties and bi-parental broods. The cases where the tie continues, as in many birds, from brood to brood and even sometimes until one of the mates dies are sufficient to show that other factors must be operating as well.

There are some rather puzzling cases where the parent seems deliberately to provoke competition in the brood, for example by associating more eggs with a food-supply than it could ever fully support. As just one example we have the case of *Bombus* just mentioned: in *B. agrorom* it has been found that only 30 to 40% of the eggs laid become eventual adults. Mortality is greatest in the late egg and early larval stages and cannibalism among the larvae is suggested (p. 16). However, the habit of many hawks of having one more nestling than it is normally possible to rear is fairly obviously a special

strategy allowing for the chance that the breeding season will turn out a good one; and explanations of a like nature may appear for the other cases eventually.

The strong tendency of plants to produce seeds of standard sizes irrespective of the size of the plant shows that how available food-reserves are apportioned between seeds is not a matter of indifference to the fitness of a plant. This is indeed just what we would expect provided the situations into which the seeds disperse are not too varied. Thus for one seed to expand selfishly at the expense of its neighbours may or may not be advantageous to the inclusive fitness of its genotype but it is almost certainly not in the interest of that of the parent plant. Wind-pollination will tend more to produce half-sibships among the seeds in an ovary than will insect-pollination. Hence according to our theory if seeds in general have genotypic control of their own growth, as they surely must to some extent, wind-pollinated plants will tend to have the more pressing difficulties in respect of uniform seed production. Hence it is rather to be expected that the situation which most lays itself open to this type of competition, the ovary with numerous closely placed ovules, will be uncommon in wind-pollinated plants. By comparison with entomophilous plants this is certainly the case, although there do seem to be a few anomalous genera, e.g. *Populus* and *Juncus*. In a great many anemophilus genera carpels or gynoecia originally with two, three or four ovules end up, through more or less regular abortions, as one-seeded "fruits". But sometimes the seeds may nevertheless be quite closely placed, as in the pine cone, the birch "catkin", the maize cob, etc.

The remarks at the end of Section 3 of the previous paper apply to this case as well as to the above problems of animal parental care. We note again that the selfish genes for seed growth tend to waste their powers a little not only because of the assortation due to relationship but also because of the purely chance occurrence of extreme situations where gene-replicas are largely in competition with one another. But this extra effect can only be of importance when the number of seeds in the ovary is very small. A much more important contrary factor must be the tendency of wind-borne pollen grains to arrive one by one rather than all at once as with insect pollination, so exacerbating the disciplinary problem of the wind-users. But on this point, even more than on others in the above discussion, our ideas are as yet rather unclear.

7. Anomalies

Here and there in the literature are found records of behaviour where relationship is conspicuously disregarded, or harms or benefits are dispensed apparently in contravention of our principles.

However, in every case known to me it seems possible to claim either that the situation has been misinterpreted or that the observation concerns a biological error; that is, a rare occurrence in an unusual situation or something of the kind.

The latter would seem to be the case for instance with the unusual cases of adult birds feeding the young of other species (e.g. Summers-Smith, 1963, p. 50).

Where apparently gratuitous inter-species assistance is recorded more regularly, misinterpretation must be suspected. A non-apparent return benefit signifying a symbiosis, or some degree of positive deception signifying some sort of cuckoo-parasitism, are possibilities that should be borne in mind. For instance, it has been reported that different species of xylocopine bees of the genus *Exoneura* in Australia will sometimes pool their broods in a common nest (Rayment, quoted by Sakagami, 1960). The finding by Michener (1961a) of a seemingly very similar situation in the related genus *Allodapula*, together with signs of adaptation to parasitism by one of the species, strongly suggests that the situations Rayment has observed contain at least some mild element of parasitism. And Michener's (1961b) further finding of two species parasitic on *Exoneura*, clearly derived from the genus itself and hardly separable from it taxonomically, point the same way. These two species are not adapted for pollen-collecting and hence must be fully dependent, but at least one of the supposed parasites in *Allodapula* does collect pollen and so presumably does contribute something to the nest.

Among birds the Cuculidae are a thoroughly anomalous family as regards parental care. We have already mentioned *Guira* and *Crotophaga*. Kendiegh (1952) gives a summary of knowledge of reproductive behaviour in other genera. *Geococcyx californicus* also seems to have many females laying in each nest. The two North American species of *Coccyzus* show a situation rather like that which Rayment has found in *Exoneura*. The species are reported sometimes to lay in each other's nests. But both have brooding instincts and a case has been recorded where both species incubated on the same nest.

At the level of single species we may instance the occasional exceptions to the rule that nesting Hymenoptera know their own nests and do not, even if they safely could, transfer to others. As regards the transference of workers, which seems to be not uncommon in some wasps, some cases are perhaps errors due to the powers of visual recognition not being equal to the situation. A strong basis of relationship between neighbour nests, which I believe is usual with the species of *Polistes* in which I have observed worker transference (*canadensis* and *versicolor*), would greatly reduce the selection against such errors. Then there may be situations in which transferral is

really in the interests of inclusive fitness, for example if a colony is dying out
(Deleurance, 1955), or happens to find itself with more workers than can use-
fully be employed on it, or if a wasp brings in food when all the larvae on its
own nest are completely sated. This last explanation may perhaps apply to the
cases of cross-provisioning by solitary wasps in a dense nest aggregation
observed by Tsuneki (quoted by Sakagami, 1960), and to the cases which
Deleurance (1952) has observed in *Polistes* in the wild where a worker pays
visits to two nests. In birds there is a parallel of a sort in a practice of nesting
guillemots and razorbills (Fisher & Lockley, 1954, p. 283). It seems that
parent birds will sometimes feed the hungriest chicks in the dense nest aggre-
gation rather than their own.

As regards the already mentioned fostering passion shown by Emperor
Penguins that have lost their chicks, some doubt as to whether the observa-
tions have been correctly interpreted would seem to remain (Kendiegh, 1952).
But taking the statements at their face value we might suggest for instance, that
it has something to do with heat-conservation. Perhaps the parent penguin
is so closely adapted to living with its offspring that it is, at the stage in ques-
tion, at a positive disadvantage without a chick nestling in the brood-pouch.
But such a situation would hardly come into being unless there were strong
general relationship within the flock. We seem to need to postulate this in any
case to explain some other social behaviour of penguins, for example, the way
Adelie Penguins parents are said to leave their young in the care of only a few
adults while they go off on long fishing expeditions. On the other hand, some
apparently social behaviour such as the formation of the crèche in severe
weather is easily interpretable as being almost entirely selfish.

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