The political economy of swarming in honeybees: Voting-with-the-wings, decision-making costs, and the unanimity rule*

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Abstract

The political economy of bee swarming offers a fascinating study of collective action in biological systems. Various aspects of the organization of swarming have been explained in this paper as devices bees have evolved to economize on information and decision-making costs associated with the economics and politics of establishing a new nest site.

Introduction

Sociobiology has attracted a great deal of attention in the last decade or so. However, according to biologist Michael Ghiselin, the sociobiological approach has its limitations as it tries to explain all behaviour including altruism, in terms of genetics. As Ghiselin puts it: 'Genes, of course, occur in all organisms, but it is the economic forces that really explain what organisms do.'[1] A 'bioeconomic' approach, incorporating benefit-cost calculations, would better explain biological forms of organization.[2] The bioeconomic approach has been used by Becker (1981), Ghiselin (1978), Hirshleifer (1978, 1982), Tullock (1978), and Wilson (1978) in their work, and will also be used in this paper.

   The paper will explain various aspects of the political economy of swarming in honeybees, focusing especially on the bees' collective choice of a new permanent nest site by unanimous voting rule. The economic analysis draws on the work of Arrow (1974) on organizations, Buchanan and Tullock (1962) on choice of Pareto-optimal voting rule and Schelling (1978) on critical mass phenomena. The paper will describe aspects of the political economy of honeybee swarming in Section 1. Section 2 uses economic

analysis to explain various aspects of swarming in honeybees. Section 3 provides a conclusion and suggests an extension of the line of research in this paper.

1. The political economy of swarming in honeybees

The classic study of swarming in honeybees is by Lindauer (1961). Swarming is the process whereby a bee colony divides itself into two groups: one group staying behind with a new queen, while the other group (the swarm) flies off with the old queen to establish a new colony (Lindauer, 1961; von Frisch, 1967; Wilson, 1971; Michener, 1974; Free, 1977; Seeley, 1982).[3] Among the various causes of swarming such as the presence of disease, poor temperature regulation, etc., over-crowding/congestion appears to be a critical factor. Swarming occurs in late spring to early summer in temperate climates when food supplies are plentiful. The abundance of food supplies facilitates the swarm to establish a new colony before the cold weather sets in.

The swarming process is divided into two stages: one occurring within the nest and the other occurring outside the nest. The first stage is associated with the rearing of additional queens, so that at least one new queen remains in the parent colony. The workers construct queen cells in order to produce new queens. The nurse bees load these cells with large amounts of nutrient gel ('royal jelly'). Before the virgin queens emerge as adults, foraging bees are observed to be shirking from work in response to house bees' increasing unwillingness to accept food from foragers. Some of the foragers, unable to continue foraging, begin to hunt for new nest sites. The former foraging bees have become scout bees, thus providing an example of 'sociogenesis, the procedures by which individuals undergo changes in caste, behavior, and physical location incident to colonial development' (Wilson, 1985: 1490).

The first virgin queen to emerge usually stings her potential rivals to death while they are still in their cells. Should two or more queens emerge more or less at the same time, they fight to the death until one queen is victorious. The victorious queen will leave on a mating flight and will return inseminated for life. She will either take over the parent nest or will participate in an afterswarm herself. Meanwhile, the old queen ceases to be an egg-laying machine as worker bees feed her less and less to ensure that she will be able to fly for some considerable distance to the new nest site.[4] Before departing as a swarm from the parent nest, bees fill their stomachs with honey so that they can postpone foraging for food for a few days while they wait for scout bees to find them a new home.

The actual departure of the swarm occurs about a day or two before the

emergence of the first young queen. In preparation for the actual swarm's flight from the parent nest, worker bees perform buzzing runs (*Schwirr-lauf*). As they dance, bees intentionally touch other bees who, in turn, also begin to do buzzing runs and this spreads rapidly among the bee population until the swarm emerges from the nest and flies off with the old queen. The swarm is approximately half the original bee population of roughly 30,000 or so workers. It is not known how the population sorts itself into two sub-groups since swarm bees are workers of all ages. During the flight from the parent nest, and later during the flight to the new nest site, the queen plays a crucial role, via pheromone odour, in maintaining order and cohesion of the swarm as an organized unit. If the queen is lost, the swarm becomes disorderly and will return to the old nest. The swarm, after emerging from the old nest, will fly a short distance and cluster at a temporary exposed site such as a tree; there they wait for the scout bees to find them a new home.

The second stage of the swarming process is associated with the scout bees searching for potential nest sites and arriving at a unanimous agreement regarding the choice of a particular nest site. It is to be emphasized that only a very small sub-group of the swarm is involved in the searching and voting process – only scout bees constituting about 5% of the swarm. When a scout bee finds a suitable site, it performs a dance on the outside of the surface of the swarm. The tail wagging dance transmits information to other scout bees regarding the distance and direction of the nest site. Many potential nest sites therefore can be announced by scout bees. The scout bees convey information regarding the quality of the potential nest site by the vigour and duration of their dance; the more lively the dance, the better the quality of the potential nest site. A 'democratic' voting process is employed by scout bees in arriving at their choice:

... the agreement appears to take place in a seemingly simple manner; the better the qualities a nesting place exhibits, the livelier and longer will be the messengers' dance after the inspection. In this way new messengers are recruited in the cluster for this place, which then likewise seek out and inspect this nesting place, and then they too solicit by means of the same lively dances. If those scouting bees which at first had only inferior or average dwellings to announce are persuaded by the livelier dances of their colleagues to inspect the other nesting place, then nothing more stands in the way of an agreement. They can now make a comparison between their own and the new nesting place, and they will solicit in the cluster for the better of the two (Lindauer, 1961: 50).

The process of soliciting or 'lobbying' for the best site continues until all conflict and disagreements are democratically resolved as scout bees converge to a unanimous choice. Lindauer has described in detail the actual process whereby a particular swarm arrives at its unanimous decision: 21 nesting places were discovered by scouting bees of this swarm and it took five days before one particular nesting place became the unanimous choice. See Figure 1.
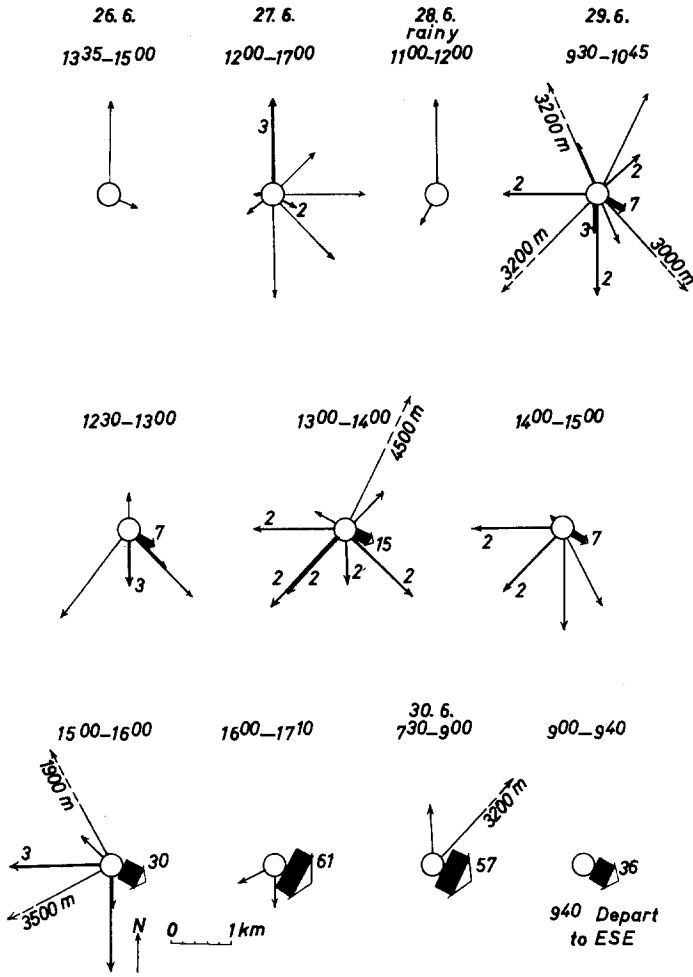
FIG. 20. Example of the recorded announcements of the scouting bees from the moment of swarming at 13:35 on 26 June until the moving into the new dwelling at 9:40 on 30 June. Each arrow represents a newly marked scouting bee that announced a nesting place by means of a dance in the cluster. Direction and length of the arrow give to scale the location of the reported nesting place. First of all nesting places in different directions and distances are announced, but gradually an agreement is reached for the nesting place 350 meters to the southeast.

Figure 1. The process of reaching unanimous agreement among Lindauer's scout bees (Source: Lindauer, 1961: 42)

Lindauer found that the most important reason delaying reaching consensus among the scout bees is that the bees wanted to ensure that the best site, from all possible potential nest sites that have been discovered, will be chosen. Being experienced foragers, scout bees can judge the quality of

nesting sites, and determine the properties which make a particular nesting site the 'best' site. Seeley explains why bees must choose their nesting sites very carefully:

> ... if a colony does survive the critical first winter, it will endure on the average for another five years. In short, a colony has the potential to survive for a long time but faces great risks in moving from an old nest to a new one. Therefore a swarm cannot rely on trial-and-error methods in finding a suitable site. Each colony must make a single, careful decision with which it can live for many years (Seeley, 1982: 168).

Because finding a suitable site is critical for colony survival, it is rare for scout bees not to come to a unanimous agreement. In fact, out of 19 swarms observed by Lindauer, only 2 swarms failed to reach agreement. In the first case:

> ... two groups of messengers had got into competition: one group announced a nesting place to the northwest, the other one to the northeast. Neither of the two wished to yield. The swarm then finally flew off and I could scarcely believe my eyes — it sought to divide itself. The one half wanted to fly to the northwest, the other to the northeast. Apparently each group of scouting bees wanted to abduct the swarm to the nesting place of its own choice. But that was naturally not possible, for one group was always without the queen, and there resulted a remarkable tug of war in the air, once 100 meters to the northwest then again 150 meters to the northeast until finally after half an hour the swarm gathered together at the old location. Immediately both groups began again with their soliciting dances, and it was not until the next day that the northeast group finally yielded; they ended their dance and thus an agreement was reached on the nesting place in the northwest (Lindauer, 1961: 45).

It is possible that in this first case, the swarm did not survive the winter. The second case ended in a totally unexpected way:

> ... for 14 days no agreement had been reached, and then when a period of rain set in, the scouting bees gave up their search for a dwelling and occupied themselves instead with the collection of nectar and pollen. The traveling stores of the swarm bees were apparently used up and it was high time for a replacement of provisions. Thus the activity of the hunters of quarters was completely suppressed, and the swarm made its abode at its first landing place, built honey combs in the bushes, and set up a normal nest for its brood (Lindauer, 1961: 45).

Regarding the first case, what caused the two subgroups of scout bees to disagree on the choice of a particular nest site? Could it be that the failure to agree is due to the fact that the two subgroups were genetically different so that both groups had difficulties in communicating with one another? This may have been the case. Lindauer himself, reporting on research by Boch, pointed out that mixed colonies consisting of different species of bees have communication problems:

If, for example, an Austrian bee receives information from an Italian bee about a food place

100 meters from the nest, she will fly 120 meters, because she interprets the 'Italian dialect' in her Austrian way. And conversely, the Italian bee will fly only 80 meters when given information for 100 meters by an Austrian bee. Similar misunderstandings exist also between other races. It is now clear that each geographic race has its own dialect (Lindauer, 1961: 61).

The idea of a swarm failing to agree on a particular site because of genetic heterogeneity of the swarm has crossed Dawkins' mind:

There is no suggestion here that the two subgroups of bees were genetically different, *though they may have been* [italics mine]. What matters to the point I am making is that each individual follows local behavioural rules, the combined effect of which normally gives rise to coordinated swarm behaviour. These evidently include rules for resolving 'disputes' in favour of the majority. Disagreements over the preferred location for the outer wall of a termite mound might be just as serious for colony survival as disagreements over nesting sites among Lindauer's bees (colony survival matters, because of its effects on the survival of the genes causing individuals to resolve disputes). As a working hypothesis, we might expect that disputes resulting from genetic heterogeneity in termites would be resolved by similar rules (Dawkins, 1982: 206).

Once unanimous decision regarding the choice of a new home is reached, scout bees prepare the swarm to lift-off. They perform zigzag runs accompanied by wing buzzing to break up the cluster. The whole swarm then flies off. Approaching the nest site, scout bees will signal the swarm to stop. Soon the bees will be streaming inside the new home and:

Within 30 minutes of lift-off nearly all the bees are safely inside their new home. Within a few hours they are cleaning out debris, constructing combs and flying off to forage for nectar and pollen. A new colony has been established (Seeley, 1982: 158).

2. Voting-with-the-wings, decision-making costs and the unanimity rule

There are two different voting procedures discussed in public choice theory[5]: traditional voting by ballot, and 'voting-with-the-feet' (Tiebout, 1956). The latter procedure sorts people into homogeneous groups of like tastes by allowing people to leave a community and enter another which has a mix of public goods which satisfy the preferences of the incoming population.

Both kinds of voting procedures are found in the bee society during the two-stage swarming process. The first stage swarming process may be viewed as 'voting-with-the-wings' procedure which sorts the original bee population into two homogeneous subgroups: those who stay and those who exit (the swarm) to establish a new colony (viewed as a public good). The second stage swarming process involves scout bees reaching unanimous agreement regarding the choice of a new nest site. The voting procedure is the traditional voting by ballot (or 'voting by ballet/dancing' in the case of bees).

We will provide answers to the following questions:

1. What are the principles involved in the sorting process by which the original population is divided into two subgroups?
2. Why is voting for a new nest site not conducted within the parent nest, but outside the nest by the swarm?
3. Why is searching for the nest sites and voting for a particular nest site restricted solely to a small subgroup of scout bees?
4. Why do scout bees use the unanimity rule in arriving at their collective choice of a new nest site?
5. What explains the high degree of cooperation and altruism exhibited by scout bees in their search for a new home; why do scout bees not free-ride on the house hunting efforts of other scout bees?

As noted in Section 1, the original bee population sorts itself into two subgroups. But it is not known what principles are involved in the sorting process. Perhaps the dynamics of population division leading to the emergence of the swarm, falls into the class of 'critical mass' phenomena (Schelling, 1978) involving some activity that is self-sustaining once that activity passes a certain minimum level. The swarming process is analogous to the phenomenon of 'tipping-in' and 'tipping-out' (Schelling, 1978) applied to neighbourhood migration, a special case of the critical mass phenomenon:

Not only was the departure of a white population induced by the appearance of minorities, but minorities themselves would be more attracted the larger the minority colony and the faster its growth, with some minimum size required to get a self-sustaining influx started (Schelling, 1978: 101).

As noted earlier, voting for the new site is undertaken only after the swarm has emerged and left the nest. The reason is that if voting for the new nest site is conducted within the parent nest, information must be transmitted to all the bees within the nest and information is costly. It is clearly optimal to reduce the information costs by economizing on internal communication channels (Arrow, 1974). Thus, transmitting information only to members of the swarm, which constitute about half of the original bee population greatly economizes on information costs. The 'voting-with-the-wings' procedure is both a voting and sorting procedure which greatly economizes on information costs because the swarm is the smallest unit consistent with the collective provision of a public good (the new colony).

Since searching for potential nest sites and voting on the choice of a particular nest site are costly activities, it is clearly efficient if such activities are restricted to a small sub-group of specialists who possess the requisite skill and information in assessing the quality of the potential nest site. Scout bees are specialists since they are former experienced foragers. Their foraging skills turns on their ability to find new sources of food and the skill can be

extended to searching for new nest sites. Furthermore, as Adam Smith once suggested, members of the same trade find it easy to communicate with each other because of their shared experiences. Thus it may well be that scout bees, being a highly homogeneous occupational group, can more easily arrive at a consensus regarding the choice of a particular nest site.[6] This may also partly explain why scout bees use the unanimity rule in arriving at their collective choice of a new nest site.[7]

To fully understand why scout bees use the unanimity rule in arriving at their choice, we need to understand the nature of 'external costs' and 'decision-making costs'. According to Buchanan and Tullock (1962), the least costly or the Pareto-optimal decision-making rule is the rule that minimizes both external costs and decision-making costs. From an individual's point of view, external costs are the costs imposed upon the person when an issue is passed by others without the person's consent. The external cost function (C) is downward sloping: when one person imposes his choice upon the group, the expected external costs are very high; external costs decrease as the number of individuals in the group agrees increases and when all members of the group agree on an issue, external costs are reduced to zero. Decision-making costs are the time and effort and direct expenditures involved in persuading others in the group to agree. The decision costs function (D) is upward sloping: when one person is present, decision-making costs are zero, when two persons have to agree, decision costs become positive and these costs increase as the size of the group increases. The Pareto optimal rule is the rule that minimizes the sum of these two costs. There is no a priori reason why simple majority rule is the least costly rule. The optimal rule depends on how high decision-making costs are relative to external costs. Where decision-making costs are extremely high, the one-person (dictatorship) rule is efficient; where external costs are very high relative to decision-making costs, the least costly rule is the unanimity rule. Figure 2 shows that the Pareto optimal rule is a simple majority rule.

Not only the size of the group determines the magnitude of decision-making costs, but also the degree of homogeneity of the group. The more homogeneous the group, the more the individual favours a more inclusive majority rule because both external costs and decision-making costs are lower in a homogeneous group with similar tastes. Clearly, reducing the size of the voting group and increasing the degree of homogeneity of the voting group economizes on decision-making costs. To reduce the size of the voting group, the larger group can delegate its voting rights on a particular issue to a small committee of specialists who represent the larger group's interests. Thus a shift from direct democracy to representative democracy economizes on decision-making costs.

In the context of voting behaviour in bees, restricting voting rights to a small subgroup of scout bees is efficient because: a) the size of the voting
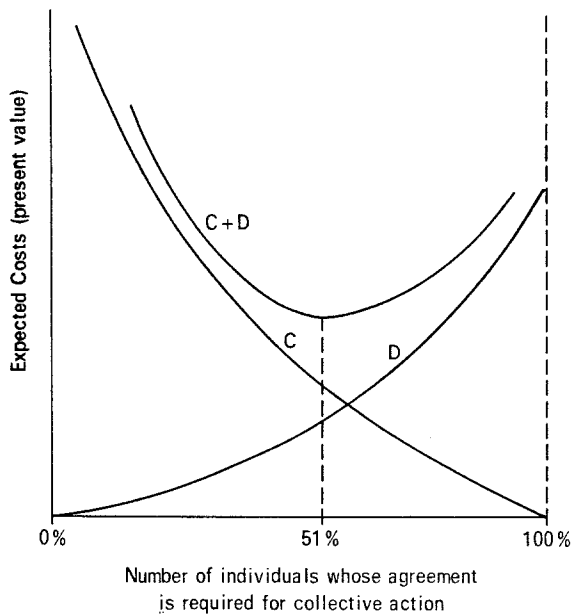
Figure 2. The Buchanan − Tullock model: Simple majority rule as the efficient decision-making rule

group is greatly reduced, since it is about 5% of the swarm; and b) of the high degree of occupational homogeneity of the scout bee subgroup. Thus the reduction in the size of the voting group together with the high degree of homogeneity of group membership means that decision-making costs are low. On the other hand, external costs are extremely high if scout bees use the 'one-bee' (dictatorship) rule in which any one bee can impose its choice of a nesting site on the rest of the group. In the context of bees, the term 'external costs' requires some explanation. Since any bee can gain fitness *only* through the queen, there is really no question of external costs here. As is well known, from a fitness point of view, there is no cost to the individual bee even from suicidal defense of the colony. What corresponds to 'external costs' in this context boils down to a *difference of opinions* about what is best for the queen. The more inclusive the rule, the more certain the bee can be that its own choice of a nest site will not be over-ridden.[8] External costs are still high even when a majority of scout bees agree on a particular nest site since it may well be that the best site is discovered by a scout bee who is not yet in the majority coalition. Because of the high external costs relative to decision-making costs, the use of the unanimity rule by scout bees is efficient.

A key element in the process of arriving at a unanimous agreement is that individual bees are 'programmed' to *change their minds*, when making a binary choice of their own nest sites compared with other nest sites, always

voting for the better quality nest.[9] In this way, a process of proto-coalition formation takes place in which more and more scout bees switch their allegiance and join the majority, voting for the best site until a grand coalition of all scout bees, voting for the best site, emerges.[10] This, together with the fact that each scout bee has only one preferred option, makes it possible for the bee society to avoid the well-known paradox of voting/cyclical majorities problem (Arrow, 1951) connected with any form of pairwise-comparison majority rule.[11]

In their search for a new home, scout bees exhibit a high degree of cooperation among themselves. But because a new colony is a public good in which no bee can be excluded once it is established, a prior question arises: Why do we not observe scout bees exhibiting Prisoner's Dilemma behaviour in choosing to free-ride on the efforts of other scout bees (i.e. observe shirking behaviour in scout bees)? Scout bees have no incentive to free-ride on other scout bees' efforts because the search for a suitable nest site is critical to the survival of the whole swarm, including scout bees. If every scout bee free-rides, then the whole swarm cannot survive in the exposed temporary site. However, in the process of searching for potential nest sites, scout bees may encounter dangers that bring death. Why then do we see altruism in scout bees who, despite occupational hazards, continue to hunt for suitable nest sites?

Here the work of sociobiologists can shed light on the question. Sociobiologists have emphasized the importance of genetic kinship (Hamilton, 1964; Dawkins, 1976, 1982) and reciprocity (Trivers, 1971) as the basis of altruism and cooperation in biological systems. Altruism in scout bees — and even more so in guard bees (Landa and Wallis, 1985) - may be explained as the gene's eye view of natural selection (Dawkins, 1976, 1982).[12] In the words of Axelrod and Hamilton:

A gene, in effect, looks beyond its mortal bearer to the potentially immortal set of its replicas existing in other related individuals. If the players are sufficiently closely related, altruism can benefit reproduction of the set, despite losses to the individual altruist. In accord with this theory's predictions, almost all clear cases of altruism, and most observed cooperation — apart from their appearance in the human species — occur in contexts of high relatedness, usually between immediate family members. The evolution of the suicidal barbed sting of the honeybee worker could be taken as paradigm for this line of theory (Axelrod, 1984: 89–90).

A stronger argument than that provided by Hamiltonian altruism is provided by Tullock: 'The worker bee simply cannot reproduce and hence has no prospect at all of reproducing her own genes directly. It is only by saving the queen that any of her genes may be made to survive.'[13] Wilson (1985), citing the work of West-Eberhard, has argued that as death approaches for insects, the 'optimum strategy for contributing genes to the next generation is to enhance colony welfare through more dangerous occupations such as

defense and foraging, thus producing more brothers and sisters as opposed to personal offspring (p. 1494).' By this criterion, scout bees are engaged in a dangerous occupation which contribute genes to the next generation by enhancing colony survival. And Dawkins has introduced the concept of the 'extended phenotype' defined as 'all effects of a gene upon the world'; more specifically 'the effects [which] influence the survival chances of the gene, positively or negatively (1982: 286). Dawkins gave an example of the beaver building a dam across the stream creating a lake; the lake may be regarded as 'a huge extended phenotype, extending the foraging range of the beaver in a way which is somewhat analogous to the web of the spider (1982: 200).' Viewed in this way, the newly established bee nest site may be regarded as an extended phenotype, allowing the swarm to continue to forage in a new territory, away from the parent nest, thus lessening colonies competing against one another as independent units. The new site, especially when it is a suitable one, increases the survival chances of the new colony.

3. Conclusions and extention of research

The political economy of bee swarming offers a fascinating study of collective action in biological systems. Various aspects of the organization of swarming in honeybees have been explained in this paper as devices bees have evolved to economize on information and decision-making costs associated with the economics and politics of establishing a new nest site that would ensure the swarm's survival, which in turn, would bring forth a new generation of bees.

There are opportunities for extending this line of research. One example is to explain schooling behaviour of fishes.[14] Biologist E. Shaw (1978) has pointed out that schooling fishes remain an exception among vertebrates in that their organization is non-hierarchical, consisting of a 'truly egalitarian state in which all members of the social group are alike in influence and importance. In the school, no fish dominates another and no peck order or hierarchy exists. The fate of a few could well be the collective fate of all because schooling fish act in synchrony behaving as one toward a source of food or away from the engulfing sweep of a predatory trawl' (E. Shaw, 1978: 166). Using the concepts of 'external costs' and decision-making costs, it may be that the egalitarian form of organization is the least costly organizational form in large schools of fish where the cost of establishing leadership is prohibitive.

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NOTES

1. M. Ghiselin (personal communication, June, 1985).
2. The term 'bioeconomic approach' is used by Ghiselin: 'Bioeconomics arose when a number of biologists and economists discovered that they were working on the same basic kind of problem, and that, furthermore, they had a great deal to learn from each other' (personal communication, June, 1985). According to Ghiselin (1982: 132–133) the economic approach to biology goes back to Darwin's work and even further back in time. According to Samuelson, writing on modes of thought in Economics and Biology: 'There is much territory between economics and biology that is still virgin ground. It will be tilled increasingly in the future' (1985: 172). And according to E.O. Wilson: 'I believe that insights from economists can add a great deal in helping even the purest of entomologists to look for new phenomena and theoretical constructions (personal communication, August 3, 1985).
3. For a more detailed description of the socio-economic organization of honeybees, including a brief description of the swarming process, see J. Landa and A. Wallis (1985).
4. Ghiselin has provided an explanation as to why the *old* queen, and not the young queen, leaves the nest: 'The older bee, the mother in the hive, leaves with a swarm of her daughters. Why is this? Well, I think the reason ... is that she is leaving a group of relatives, so she gets something from providing her daughters with a very good place to stay. Also, she is probably an old bee and going to die pretty soon, so she should take the risk. If she were sending out a lot of propagules, as termites do, maybe she would be better off remaining in the hive (1982: 143).
5. Public choice theory is the 'Economics of politics', the application of economics to the study of political processes. For a survey of public choice literature, see D. Mueller (1979).
6. For a theory of the homogeneous occupational group – the Chinese middleman group – as a low cost organization for contract enforcement, see J. Landa (1981), see also J. Carr and J. Landa (1983).
7. B. Grofman has suggested that it may be that bees cannot count, therefore it is easier to use the unanimity rule than the simple majority rule ('how do they know when they have 51% of the vote?'). Also, the fact that bees are swarming on a branch, *exposed* to the elements, gives them an added incentive to converge to an unanimous vote. It is analogous to the sequestration of juries to hasten reaching of unanimous jury decision (personal communication, June 8, 1985).
8. I am indebted to J. Hirshleifer for this insight (personal communication, June 19, 1985).
9. For a view that does not credit bees with rationality, see J. Bennett (1964).
10. For an analysis of a proto-coalition formation process among a network of traders in the 'Kula Ring' gift-exchange system in the Trobriand Islands of Papua New Guinea, see B. Grofman and J. Landa (1983).
11. For a survey of the social choice literature dealing with the voting paradox and related problems of collective choice in democratic societies, see D. Mueller (1979). For an application of social choice theory to voting in corporate law, see F.H. Easterbrook and Daniel R. Fischel (1983). The authors explained why only one class of participants in the corporation (the shareholders) hold dispositive voting rights at one time: 'It is well known, however, when voters hold dissimilar preferences it is not possible to aggregate their preferences into a consistent system of choices ....

The preferences of one class of participants are likely to be similar if not identical. This is true of shareholders, especially for people who buy and sell in the market so that the shareholders of a given firm at a given time are a reasonably homogeneous group with respect to their desires for the firm. So firms with single classes of voters are likely to be firms with single objectives, and single-objective firms are likely to prosper relative to others (p. 405).'

12. However, according to Ghiselin: 'In the *Origin of Species*, Darwin (who knew essentially nothing about genetics) explained the so-called altruism of bees on the basis of each society being selected as a single unit (an extended family). The colonies with the most economically efficient workers out-produce the less efficient colonies, and this occurs in spite of the fact that the workers are sterile. We need not consider such matters from the point of "selfish genes".' (Personal communication, June, 1985).

13. G. Tullock (personal communications, July 15, 1985). For this line of argument, see also G.F. Oster and E.O. Wilson (1978): 'Caste members are programmed to behave altruistically. They surrender most or all of their personal reproductive capacity in favor of the mother queen, undertake risky foraging trips, and sometimes literally throw their lives away in frenzied defense of the nest. What matters is not their personal survival and reproduction, but rather that of the queen (p. 161).'

14. Extending the line of research in this paper to schooling fishes is suggested by Ghiselin (personal communication, June, 1985).

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