THE POPULATION ECOLOGY OF VESPULA VULGARIS (L). VESPIDAE: HYMENOPTERA) AND THE COMPUTER SIMULATION OF COLONIAL SEASONAL DEVELOPMENT

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Population Ecology

Beirne (1940), Fox-Wilson (1946) and Döhring (1960) appear to be the only authors to deal with the abundance and scarcity of social wasps (Vespula spp.) from year to year. All three emphasized the importance of climatic factors. Beirne considered that heavy rainfall in April, May or June decreased, while light rainfall increased, the population later in the season. However, the rainfall hypothesis did not account for all the data and he suggested that some factor, possibly desease, becomes active during a year of abundance which would decrease the population in the following year. This paper suggests that Beirne's unknown factor is exercised by the wasps themselves, as a self-regulating mechanism which operates independently of weather, although weather may alter the speed at which the self-regulation occurs.

The investigation, carried out 1969-1972, was based on a study area of about 151 hectares of farmland and woodland lying 7 miles to the north-east of York, England. During the four year period the sites of 58 nests of V. vulgaris were located in the study area. With the exception of 4 nests, they were situated on field boundaries and were underground. Nest sites tended to be grouped in just under one quarter of the total field boundaries, although the remaining field boundaries seemed equally suitable for nest sites. 1970 with 29 nests was a year of abundance while 1969 with 11 nests and 1971 with 15 nests were years of average abundance, but 1973 with 3 nests was a year of scarcity.

Except for 7 destroyed by other people, the nests were dug up at the end of the season for examination. Supplementary nests dug up outside the study area were also examined throughout the season. During the four years the mature nests seemed to fall into four categories:-

1) NLC (No large cells) nests - These nests were clearly recognisable by the absence of large cells.
2) LCM (Large cells with males) nests - These nests produced large cells, rearing brood that was predominantly male.
3) LCQ (Large cells with queens) nests - These nests produced large cells which only reared queens.
4) LCQM (large cells with queen and males) nests - These nests produced large cells which predominantly reared queen brood, although some males were also reared. Estimates suggest that 76% of the brood was queen and 24% male. Characteristically two or three of the four types of mature nests were collected each year. NLC nests were found in 1969 and 1971, both years of medium abundance, and LCM nests only in 1972, a year of scarcity. LCQ nests were the most common type of mature nest and were found in all four years. LCQM

nests were found in 1970, a year of abundance, and 1972, a year of scarcity.

The mean queen production for LCQ nests was 356 queens (20 nests), for LCQM nests 1461 queens (17 nests) and the overall mean queen production for 37 nests was 868 queens. This is very similar to the mean of 830 queens quoted by Spradbery (1971) and based on 6 nests taken during the second half of September.

The size of the nest built by the founder queen can usually be recognised in the oldest comb of the mature nest by the lighter colour of the pulp. Data from 30 nests gave a mean count of 70 cells (s.d. $\pm$ 19): 16 of the nests came from the study area and thus it is possible to correlate the number of cells in the queen nest with the eventual size of the nest as measured by the number of small cells present in the mature nest. The correlation coefficient was 0.5 and $p < 0.05$, so probable significance is just reached. The coefficient of determination is thus 0.26 and this would indicate that 26% of the variation in the number of small cells between mature nests, was related to the activity or quality of the founder queen, as measured by the number of cells in the queen nest.

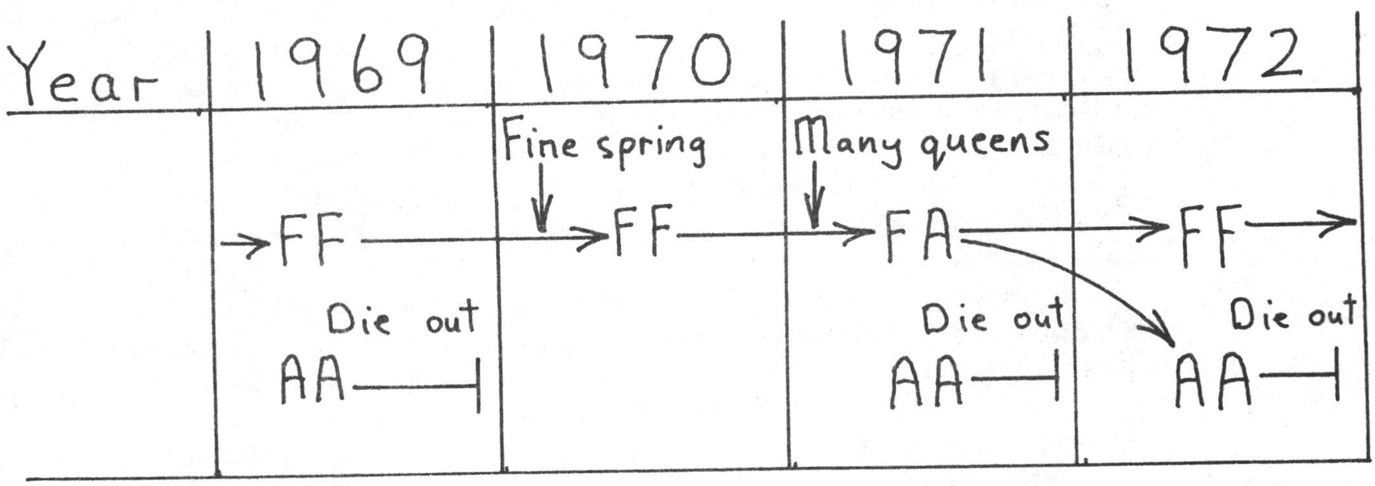
Meteorological readings were obtained from weather station number 2260 at Heslington, York about 10 kilometres from the study area. The weather during May and June 1970 was favourable to wasps: at this time of year there is normally a lower rainfall, higher temperatures and longer periods of sunshine. On the whole, 1969 was less favourable. It is more difficult to make general comments about 1971 and 1972 except that June 1972 was an unfavourable month.

Vertebrate predation in the study area was not recorded while the effect of parasitism on nest populations was considered to be insignificant. 7 nests were removed by man and 2 nests were greatly affected in insecticidal spraying. The number of nests affected by man in each year was not related to nest density.

The foraging activities of the four categories of nests were investigated. Food foraging was either for flesh or liquid containing carbohydrate substances. It is unlikely that flesh was the factor limiting population growth because the real demand for it arose in the autumn, from the presence of larvae in the large cells, and their needs always seemed to be met. NLC nests failed before this autumn demand for flesh developed.

Some attempt can now be made to try and assess the factors that could regulate social wasp abundance from year to year. By regulation is meant the determination of numbers in a population by factors acting in a density dependent fashion mediated through intra- and interspecific relationships. Since weather acts on a wasp population in a density independent fashion, it is unlikely to regulate a wasp population and need not be considered for the moment. Parasites and predators can also be eliminated as regulating factors, because of their rarity. The influence of predators and disease on hibernating queens was not considered. Man's influence also operates in a density independent manner and food is not a limiting factor. The presence of fewer nests in the study area did not necessarily lead to larger nests. Competition between queens in the spring probably occured, but this was not because the queens occupied all available sites but because the queens restricted themselves to only some of the available sites and thus intensified the competition among themselves. Brian and Brian (1952) found queen replacement (usurpation) quite common among <u>V. sylvestris</u> and Nixon (1936) thought there is considerable competition in the spring between founder queens leading to usurpation at least in <u>V. vulgaris</u> and <u>V. germanica.</u>

It has been shown earlier in this paper that the size of a mature nest is dependent on the founder queen's activity when forming the embryo nest. Hence it may be postulated that the size and form of the mature nest is related to the activity and fertility of the founder queen. A nest with an inactive queen fails to produce large cells (NLC nests) while an infertile queen fails to provide fertile eggs for the large cells (LCM nests). More active and fertile queens produce nests that contain large cells which she is able to fill with fertile eggs (LCQ nests), except for the largest nests where even a fertile queen cannot fill all the large cells with fertile eggs (LCQM nests). The problem arises as to why queens producing NLC and LCM nests are able to survive in the population since these colonies leave no or very few offspring; such queens must have other characteristics which make them superior to fertile queens. Perhaps such queens are better able to survive the winter or fair better in the competition for nest sites in the spring; the latter view will be accepted to present the following explanation. It is assumed that the NLC and LCM nests are produced by aggressive queens (AA, in diagram below) and LCQ and LCQM nests by fertile queens (FF). Then in the spring of 1970 fertile (FF) rather than aggressive (AA) queens were present so that many sites were



occupied and many mature nests were possible. The fine spring of 1970 enabled this possibility to be realized. The successful 1970 season resulted in many queens being present in the spring of 1971, resulting in much competition for nest sites so that mainly aggressive infertile queens (AA) established nests with a few queens of mixed aggressive and fertile (FA) characteristics. Only the FA queens produced aggressive (AA) or fertile (FF) queens for 1972. The poor weather in June 1972 did not encourage nest establishment. Thus of the nests surviving in 1972 most were those from the aggressive (AA) queens which died without leaving many queens, while those of the fertile (FF) queens produced most of the queens for spring 1973. On this line of argument the queens of spring 1969 would be similar to those of spring 1972; some would be aggressive (AA) ones forming nests failing to produce queens and some would be fertile (FF) producing the non-aggressive fertile (FF) queens for the following spring.

Thus a population ecology hypothesis is proposed for V. vulgaris which largely revolves around the characteristics of the queen, which can change from one generation to another. At least two characteristics are assumed; one shows itself in increased activity and fertility. The two characteristics function so that activity and fertility act when the population is low, so tending to build up the population while the other characteristic tends to reduce the population when the population is high. The interplay of these two characteristics would result in a cyclic pattern of wasp abundance which was suggested by Beirne (1940). Thus this wasp species would have a self-regulation mechanism of population control where weather could operate to speed or diminish the time taken for the population to move from a high to a low density or vice versa. This is not to say that weather is not an important mortality factor which it probably is, during the winter and spring.

Computer simulation of seasonal development

The social wasp, Vespula vulgaris builds a nest of horizontal combs surrounded by a thick envelope buried in the ground. Workers are very aggressive when their nest is disturbed so that observation of a colony in the field to obtain a day to day description of its development is impossible. The best that can be done is to analyse many colonies taken during different times of the year and try to build up a description of colonial development. However, even with this data to produce a day to day description, incorporating the many relationships of the attributes involved in seasonal development becomes an impossibly lengthy procedure without the help of a high speed computer system. This paper describes an attempt to produce such a computer programme to generate a model of seasonal development. The model was given a large number of atttributes, which are characteristic of colonial development, so that the model will resemble reality.

Briefly the life history of V. vulgaris is as follows. The hibernating queen emerges in the spring and selects a nest site, usually underground. The queen builds the first comb of cells with surrounding envelope and rears the first workers - the queen nest. When the workers emerge they continue to enlarge the queen comb and build successive combs belowt the first, altering and adding to the envelope so as to enclose the enlarging nest - the worker nest. At first workers are produced but later males appear. During August the workers build combs which contain larger cells (=large cells) rather than the smaller cells (=small cells) built earlier in the year. The large cells are used to rear the queen brood and sometimes additional male brood. Later in the autumn the virgin queens and males leave the nest to mate and then the males die and the queens go into hibernation. The founder queen and remaining workers die and the nest disintegrates.

To describe a model for nest development it is necessary to list the attributes or system variables that describe the system at any given time. These are the number of small and large cells present, the number of eggs, larvae or sealed brood or brood present in the small and large cells, the number of adult workers, males and queens present; the males are listed twice, distinguishing between those that are produced from small and from large cells. Eleven ratios between systems variables can also be produced such as the workers to small cells ratio, the larvae to workers ratio, the small cell adults produced to small cells as a measure of small cell used. The forcing functions, or imputs which are not affected by the components of the system, and the parameters or constants can be listed together:

1. The number of cells in the queen nest and the brood content of its cells.
2. The number of days of the vespine season.
3. The length of the developmental stages.
4. The length of worker life which changes during the course of the season.

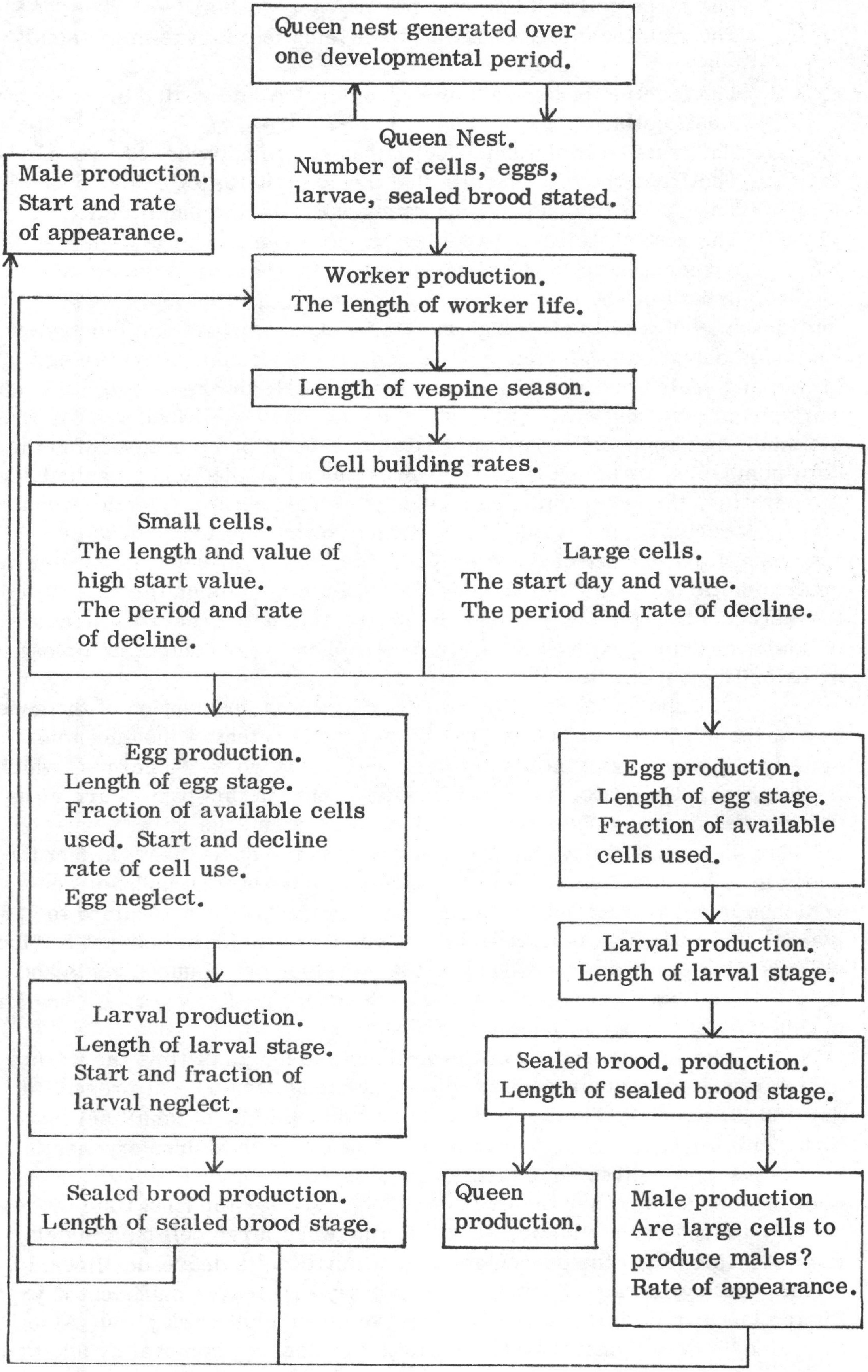
5. The small cell building rate per day per worker.
6. The large cell building rate per day per worker.
7. The fraction of eggs that fail to develop into larvae in the small cells.
8. The fraction of larvae that fail to develop into sealed brood in the small cells.
9. The fraction of the small cells that are actually used to rear brood.
10. The fraction of large cells that are actually used to rear brood.
11. The rate at which adult males appear from the small cells.
12. The rate at which adult males appear from the large cells.
13. A representation of a decision as to whether the large cells will or will not be used to rear male brood.

Interactions between the forcing functions and parameters and the system variables determine the small and large cell additions per day; the egg, larvae and sealed brood additions per day in small and large cells; the adult worker additions and deaths per day, the adult male additions per day from the small and large cells and the adult queen additions per day. Also the total number of workers that have been produced or died can be calculated. In operation, the programme causes to be printed out the systems variables, ratios, forcing function values and products of interactions (transfer functions) for each day of the colony's existence. At present the system is deterministic but could be made stochastic by randomising the rate at which the workers die. Also at present the programme only generates numbers of adults or brood, but could readily be changed to give output in biomass or calorific equivalents.

With the aid of the general flow diagram a description of the generation of the model is now possible. The size and content of the queen nest is stated as it would exist on the day before the first worker emerges, which is the 8th June. This date, as all other dates stated in this paper, are mean dates based on many observations. Since queens emerge in the spring on 5th May there are 35 days in which to generate the queen nest. In fact the queen nest is generated in 25 days (=one developmental period) for convenience in generating the worker nest. Thus the queen is assumed to start to build the first cell on 15th May which is considered as day 1. Since we have almost nil information about the development of queen nests and very little information about the size of the queen nest, as yet, the realism of this part of the output must be very suspect.

With the emergence of the workers the length of time the worker nest exists, to the emergence of the last adult is decided - at present to day 160 (21st Oct.). The workers continue the building of small cells at a high rate for a period of time before the rate begins to drop exponentially to zero, within a given number of days. At first the queen fills 95% of all cells with eggs, whether the cells are being used for the first time or have already reared brood. Later, near the time when large cell building starts (Day 93, 15th Aug.) the percentage use of small cells decreases linearly, so that egg laying rate becomes zero on a day that leaves sufficient days for the last egg laid to develop and emerge as an adult on day 160. Also in the colony's development a facility exists to allow egg removal by adults and

A general flow diagram showing the colonial development of V. vulgaris



immediate replacement. This facility decreases the rate at which larvae appear: otherwise a larva appears 5 days after an egg is laid. Again near the time of the start of large cell building larval neglect begins to operate. In reality this means that the larvae in the upper or older combs are starved so that they fail to become sealed brood. Otherwise, after 10 days (the length of the larval stage) a larva becomes a sealed brood and 10 days later an adult. These adults are usually workers but from day 96 (18th Aug.) male adults emerge at the rate of 1% of emerging adults, but from day 105 (27th Aug.) this rate rapidly grows until day 132 (23rd Sept.) when 50% of emerging small cell adults are males.

Large cell building begins on day 93 (15th Aug.) at a high rate and linearly declines to zero one developmental period before day 160. The percentage use of large cells in which to lay eggs starts at a low value, rapidly increasing to a maximum value by day 110 (1st Sept.). Eggs give rise to larvae and larvae to sealed brood using the same developmental length of time as used for the brood in the small cells. The emerging adults are males or queens; the percentage of adults emerging as males increasing to 25% by day 130 (21st Sept.), but decreasing again to zero by day 145 (6th Oct.), when all emerging adults are queens. Finally on day 160 (21st Oct.) the number of small cells is divided by the number of large cells and if the ratio is above 5, all males produced from large cells are converted to queens, since experience has shown that such nests only produce queens from large cells. If the ratio value is less than 5, the males produced from large cells remain, since such nests produce males and queens from large cells.

To check the output of this programme against actual data, about 150 nests have been examined, 101 in considerable detail. 59 additional nests were examined by Spradbery (1971). Such data was used to estimate a "mean" nest and the programme has been operated so as to agree with this mean nest. Thus a day to day description of colonial development has been obtained. The simulation has generated information which is at present impossible to collect, e.g. the number of males produced per colony, and has thrown up unexpected information, e.g. a periodicity of about 25 days with respect to brood rearing in the model was found, which reflects the developmental period of 25 days that was selected. Observations in the field on the foraging behaviour of workers also showed periodicity in earth removal, pulp and flesh collection, of about 14 days. The model also demands a queen nest far larger than has normally been supposed to be built by a queen. A new method of determining the size of the queen nest from a mature nest taken at the end of the season confirms the model's requirements, and a queen nest of 70 cells is now considered reasonable. The model also allows the possibility of sensitivity analysis, that is, to study the effect on output, on varying input, so that the relative importance of the forcing functions and parameters can be assessed, e.g. the characteristics of the decline of the small cell building rate per day per worker is shown to be very critical.

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