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CLIMATIC CLUSTERS OF THE INDIAN REGION

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ABSTRACT

In this paper we derive climatic clusters of the Indian region using data on monthly mean profiles of the precipitation, the moisture index (defined as the ratio of precipitation and potential evapotranspiration) and of the minimum temperature. The delineation of regions over which the patterns of profiles of important climatic factors such as precipitation are similar is necessary for the determination of meteorological zones over which prediction can be made as well as for understanding the distribution of vegetation cover. The latter has been the major aim of the studies of climatic classification. In the traditional approach to this problem, the meteorological stations in the region are assigned to predetermined categories such as arid, semi-arid etc. on the basis of the values of the climatic factors (or of the bulk parameters derived therefrom) characterizing these stations.

Here the variation of the climatic patterns over the Indian region has been analysed to obtain climatic clusters, which represent natural grouping of the patterns and hence of the meteorological stations at which they occur, as well as the climatic boundaries separating these clusters. This analysis is facilitated by an initial reduction of dimensionality in the description of the patterns achieved by using principal component analysis. Sixteen clusters of the mean monthly profiles of the moisture index have been obtained. It is found that there is a close correspondence between these clusters and the distribution of the vegetation types in the country.

KEY WORDS Climatic classification Clustering Empirical orthogonal functions Indian climatic clusters Rainfall analysis Moisture index

1. INTRODUCTION

The identification of the spatial scales associated with the temporal scales of significant variation of climatic factors is an essential prerequisite for the determination of the subregions over which meteorological predictions for the various time-scales can be given. It is also necessary for determining the optimum network of meteorological stations over the region. At present over the Indian region, the short and medium range forecasts are issued for the meteorological subdivisions (Figure 1) whereas for the long range forecasts, the country is divided into much larger zones—northwest India, northeast India and Peninsula (Rao and Ramamurthy, 1958). Ideally, the subregions should be chosen so as to satisfy two conditions. First, the meteorological stations within any region must be characterized by similar climatic patterns. Secondly, the temporal variation over scales beginning with the subseasonal must be in phase for the stations within the subregion. In this paper we derive the climatic subregions for the Indian region which satisfy the first condition.

The delineation of the subregions which are homogeneous with respect to the values or patterns of the important climatic factors is the problem of climatic classification. Traditionally this problem has been of concern to plant geographers who sought to understand the distribution of vegetation types in terms of the variation of the climate. Consequently the climatic factors generally chosen have been the ones considered to be critical in determining the vegetation cover. In this approach, climatic zones such as arid, semi-arid etc. are specified in terms of the values of the critical climatic factors, or bulk parameters derived from them. The problem of classification then involves assigning the meteorological stations of the region to one of these predetermined categories. The result is naturally sensitive to the

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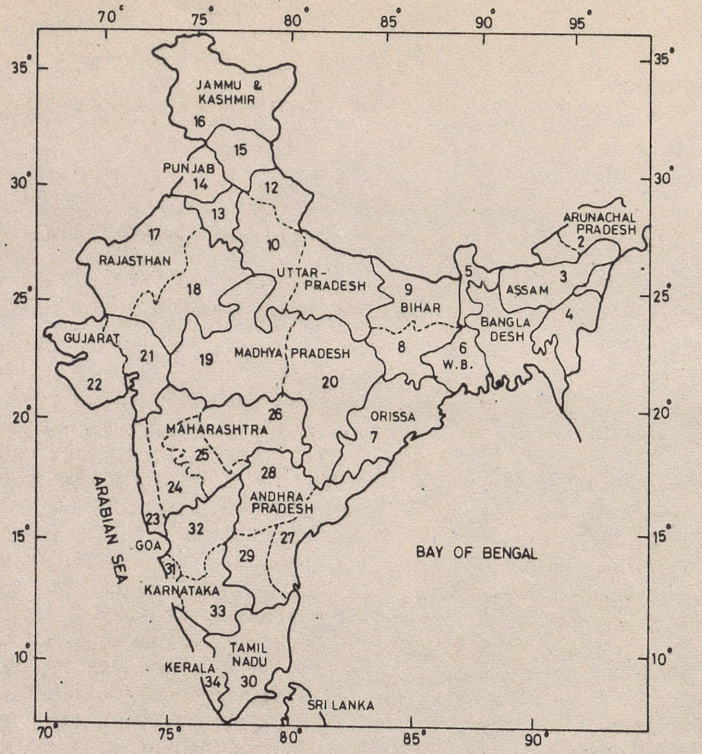

Figure 1. Meteorological sub-divisions of India (after Rao (1976))

specific choice of the climatic boundaries adopted, which are based on the observations of the vegetation types in a few regions. The more general validity of this choice for other regions of the world under the sway of different climatic conditions cannot be taken for granted. Hence the scheme of climatic classification appropriate for any given region has to be selected with reference to the vegetation cover of that region.

The subjectivity involved in the choice of climatic boundaries in such a classification scheme can be avoided by treating the problem as one of clustering of the climatic patterns rather than of classification. The aim then is to obtain natural groups or clusters of the patterns and hence of the meteorological stations at which they occur. The boundaries between these clusters are arrived at from the analysis and are not specified *a priori*.

The most significant climatic factor determining the nature and productivity of the plant cover in the tropics is the availability of moisture, and moisture availability is chosen as the major criterion in most of the climatic classifications, for example Thornthwaite and Mather (1955) and Budyko (1974). The availability of moisture depends primarily on the rainfall pattern and, not surprisingly, the most important climatic factor to be forecast is also the rainfall. This suggests that a cluster analysis of the patterns of rainfall and moisture index should provide critical information for the determination of the climatic zones for the purpose of prediction as well as for the interpretation of the distribution of vegetation types. For a large region such as India, the appropriate strategy in agriculture or forestry in terms of the choice of plant species and schedules of cultural operations can be experimentally determined at only a few field stations. In order to determine the optimum network of such stations it is necessary to have quantitative estimates of the similarity between the climatic patterns at different stations and the climatic clusters based on these estimates.

It is well known that the nature of the vegetation depends not only on the seasonal or annual means of the rainfall or the moisture index but also on its distribution within the season. For the Indian region, this was pointed out more than two thousand years ago by Kautilya, when he designated the pattern with two-thirds of the rainfall concentrated in the second month of the rainy season as the golden regime for agriculture (Kaugle, 1969). The classifications proposed by Troll (1965) and Hargreaves (1971) are also based on the distribution of the moisture index within a year. Many authors have derived a climatic classification of the Indian region based on criteria suggested by Thornthwaite (1948) and Thornthwaite and Mather (1955) (Subramanyam, 1956; Subramanyam *et al.*, 1965; Krishnan, 1968; Rao *et al.*; 1971). On a comparison of the results of several climatic classification schemes for the tropics, Virmani *et al.* (1978) concluded that the distribution of the moisture availability within a year is the most important criterion for climatic classification for agricultural applications. Thus the minimum information necessary for a useful classification appears to be the information about monthly mean patterns of moisture availability.

In this study we analyse the variation of the monthly mean patterns of moisture availability defined as the ratio of the precipitation to the potential evapotranspiration at several stations over the Indian region using the method of empirical orthogonal functions. The patterns are represented in the plane of the amplitudes of the two leading components which together explain more than 80 per cent of the variance. Thus an adequate measure of the difference between any patterns is the Euclidean distance between the points representing these patterns in this plane. An analysis of the distribution of the points representing the patterns of moisture availability by a procedure similar to that used by Gadgil and Iyengar (1980) has yielded 16 moisture index clusters for the Indian region. Since the minimum temperature is also known to be a limiting factor for plant growth (Blasco and Legris, 1973) the mean monthly profiles of the minimum temperature have also been analysed in a similar manner to obtain the thermal clusters.

The data base and the methodology are described in Sections 2 and 3. Clusters obtained by analysis of temporal profiles of rainfall and moisture index are discussed in Section 4, and by analysis of the minimum temperature profiles in Section 5. The climatic clusters so obtained are compared with the distribution of the vegetation types and with the meteorological subdivisions in Section 6.

2. DATA

The mean monthly profiles of the precipitation (P) and the minimum temperature (T) at 119 stations distributed uniformly throughout India (Figure 2), obtained from the climatological tables published by the India Meteorological Department (1967), and the mean monthly potential evapotranspiration (P_E), given by Rao *et al.* (1971) using Penman's (1948) formula, are the basic data for this study. Thus the climate at every station is specified in terms of 12 values each of the precipitation (P), the moisture index (P/P_E) and of the minimum temperature (T) implying a data matrix of the order 119 × 36.

3. METHODOLOGY

3.1. *Reduction of dimensionality*

The first step in the analysis is the reduction of the dimensionality of the specification of the climate at every station to the minimum possible, without significant loss of information. Since the 12 monthly mean values in the profiles of any element (such as rainfall) at a station are likely to be correlated, a more economical representation which is maximally powerful in bringing out the difference between the profiles at the different stations can be obtained by using the method of empirical orthogonal functions (Lorenz, 1956). The value of any element (say precipitation P) at a station i, in the month j can then be expressed as

$$P(i, j) = \sum_{n=1}^{12} A_n(i) B_n(j)$$

where $B_n(j)$ is the nth eigenvector of the covariance matrix and $A_n(i)$ the corresponding amplitude or

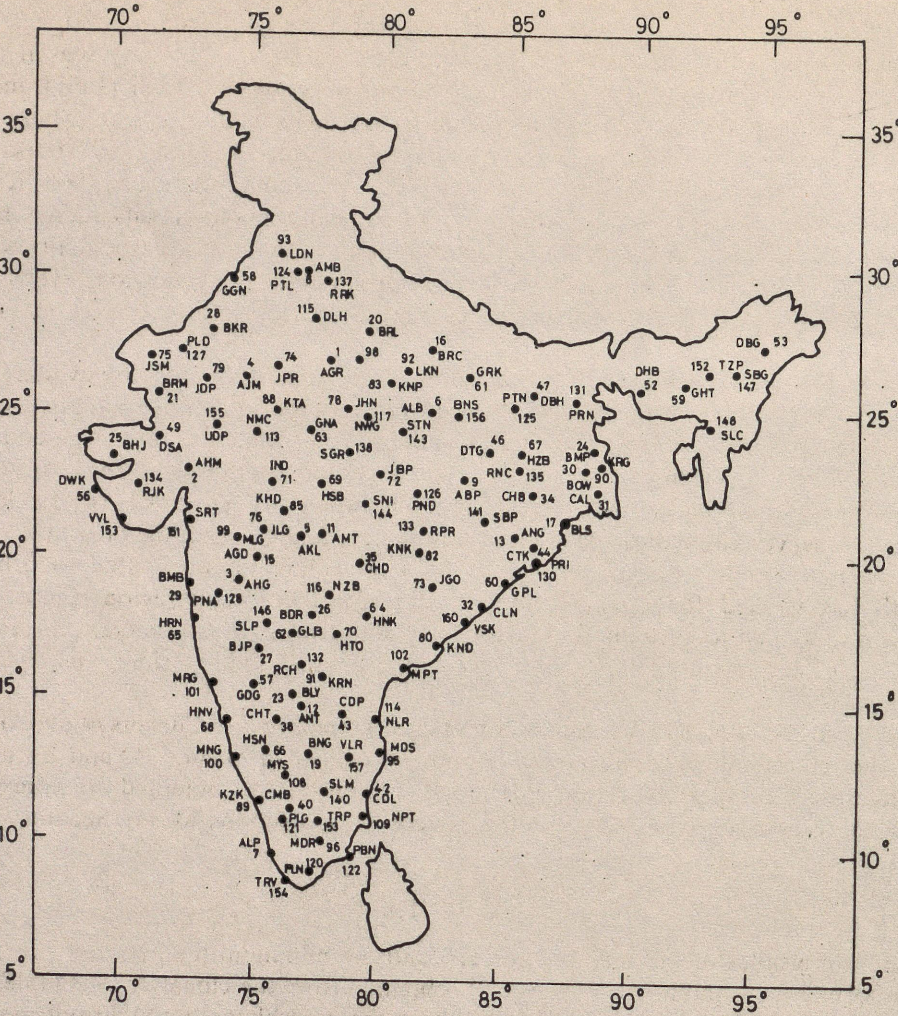

Figure 2. Meteorological stations used in the analysis

coefficient. Given the eigenvectors $B_n(j)$, every station can be represented as a point in the n-dimensional space of the amplitudes A_n.

We have analysed separately the profiles of (i) precipitation P, (ii) the moisture index P/P_E, (iii) minimum temperatures T, for all the stations. We find that in each case, the first two principal components explain more than 80 per cent of the variance. Thus the profiles of these climatic parameters at the different stations can be adequately represented as points in the plane of the amplitudes A_1, A_2 of the first two components. The Euclidean distance between points representing two stations in this plane is a direct measure of the difference between the two profiles. A small distance between two points on this plane implies that the profiles at the stations which they represent are similar and further that annual or seasonal totals have similar values. A large distance between two points can arise either from disparity in profiles or in the annual totals or a combination of both.

3.2. *Analysis of climatic patterns*

In general the points representing the patterns of any climatic element, such as rainfall, in the 12-dimensional space of their monthly values (or in any other co-ordinate space such as that of the principal components), may be assumed to form a continuum. When this distribution is either uniform or random, the logical way of classifying the patterns is by division into unit cells in this 12-dimensional space, the length of the cell being chosen appropriately.

If, on the other hand, the distribution is patchy or clumped, one can fruitfully seek clusters of these patterns. For a patchy distribution, there are clear gaps between neighbouring patches with a relatively large number of points within each patch or cluster. If the geographical distribution of the stations chosen is almost uniform (as is the case in this paper), such patchiness of the distribution of the actual patterns indicates that all the possible patterns within the observed limits are not equally probable. The probability is large within the patches and very small in the gaps between them. This suggests that natural climatic boundaries may be identified with such gaps. A classification based on climatic boundaries located in these gaps will not be unduly sensitive to the choice of the boundaries.

There are three scales which characterize a clumped or patchy distribution: (i) The typical nearest neighbour distance within a cluster, i.e. a scale which specifies the grain of the cluster; (ii) A scale measuring the separation between neighbouring clusters, i.e. the minimum distance between a point belonging to one cluster and another belonging to the neighbouring cluster; (iii) The extent of the cluster, i.e. the maximum distance between two points in a cluster.

If the grain-scale as well as the extent of the cluster are smaller than the separation scale, the clusters are not only well separated but also compact. Then the similarity is high between any two patterns within a cluster and low between patterns belonging to different clusters. Several methods, such as the nearest centroid method, are effective in delineating the clusters in this case (Anderberg, 1973).

However, we find that very often for meteorological patterns, even when the distribution is patchy with clear gaps between the neighbouring clusters, the extent of the patches is greater than the separation scales. This means that the clusters are sprawling rather than compact (cf. Fig. 5.1 in Anderberg, 1973). In such a case the degree of similarity between any two patterns in a cluster is not necessarily high. However, such points can be linked by a series of intermediate points within the cluster such that the degree of similarity is high between successive points. This is not true of disparate points belonging to different clusters. To identify clusters when their extent may be comparable to the separation scale, we suggest the use of grain-scale to specify a threshold value for the separation scale. Specifically we consider the clustering acceptable if and only if (i) the nearest neighbour of every point within a cluster belongs to the same cluster, (ii) the minimum distance between two points of neighbouring clusters is larger than twice the value of the smaller of the two grain-scales of these clusters.

The search for clusters satisfying the above conditions is enormously simplified because of the initial reduction of the data set to two dimensions. Because of this two dimensional representation, the human capacity for recognition of patterns (which is known to surpass, by far, that of automatic pattern recognition) can be effectively used to make an initial guess at the number and locations of the clusters. The procedure adopted here involves the following steps. First, nuclei of prospective clusters are identified by visual inspection. Then their nearest neighbours are added and initial clusters formed and their grain-scales determined. This procedure is continued until clusters satisfying the two conditions are obtained.

Finally a test is performed to ensure that the distance between any point in a cluster and its nearest neighbour is within a certain threshold. In this test the nearest neighbour distances of points in a cluster are assumed to be a sample from a normal population. The null hypothesis that the points with the highest values of nearest neighbour distances belong to the same population as the others in the cluster is tested at the 95 per cent level by the ratio test (Crow, *et al.*, 1960). Those samples for which the hypothesis is rejected, are removed from the cluster and treated as isolated points.

Having obtained this basic clustering, it may be worth while for some applications to further subdivide the clusters so as to ensure that the differences between two patterns belonging to the same group are less than an appropriate threshold. Then clear climatic boundaries would exist only between the original clusters, but the patterns would possess the desired degree of similarity within any subcluster.

4. CLUSTERS OF PROFILES OF PRECIPITATION AND MOISTURE INDEX

4.1. *First sorting*

Contours of the mean annual precipitation and moisture index are shown in Figures 3 and 4. On applying principal component analysis to the profiles of mean monthly precipitation, we find that the first two eigenvalues account for 74 and 14 per cent of the variance respectively. The first eigenvector (Figure 5) with a maximum in July and a mild trough in November can be considered to represent the southwest monsoon component. Similarly the second eigenvector with peaks in May–June and October–November and trough in July–August can be taken to represent the pre-monsoon and post-monsoon (or the northeast monsoon) component. The first two eigenvectors obtained from the monthly mean profiles of the moisture index are similar (Figure 5) to those obtained from the precipitation profiles, and the first two eigenvalues, in this case, account for 73 and 14 per cent of the variance respectively.

The distribution of the points representing the different stations in the plane of the two leading principal components for profiles of the precipitation is shown in Figure 6. Note that although the distribution of the stations is almost uniform, the distribution of the precipitation patterns is not uniform and apart from isolated points, five distinct clusters emerge. The distribution of points representing moisture index profiles is similar (Figure 6). Thus the variation in the profiles of the moisture index arises mainly from that in the precipitation, and rainfall clusters are not significantly different from moisture index clusters. Apart from isolated point clusters, there are four (five) clusters of the moisture index (precipitation) profiles. For both cases, clusters I to III (IV) consist of stations from the high rainfall region, viz. west coast and northeastern parts, whereas the large dense cluster IV (V)

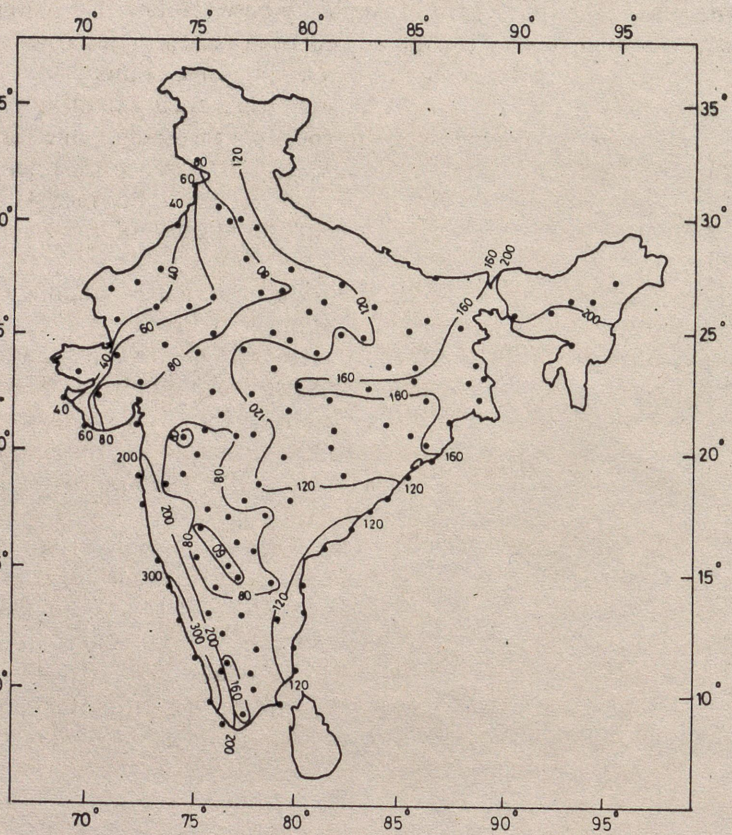

Figure 3. Mean annual rainfall (*P*) in cm

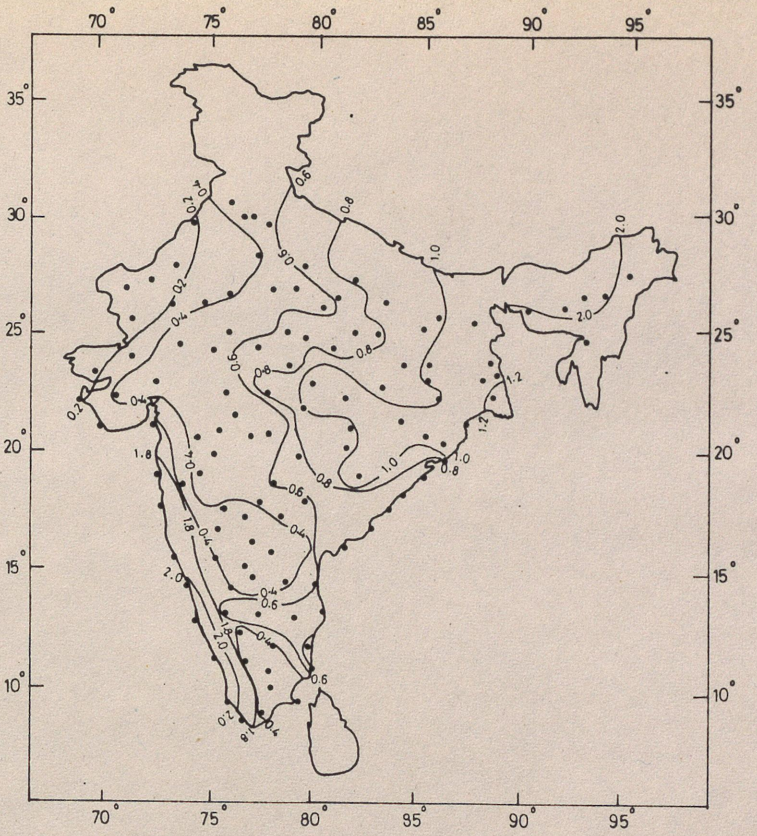

Figure 4. Mean annual moisture index (P/P_E)

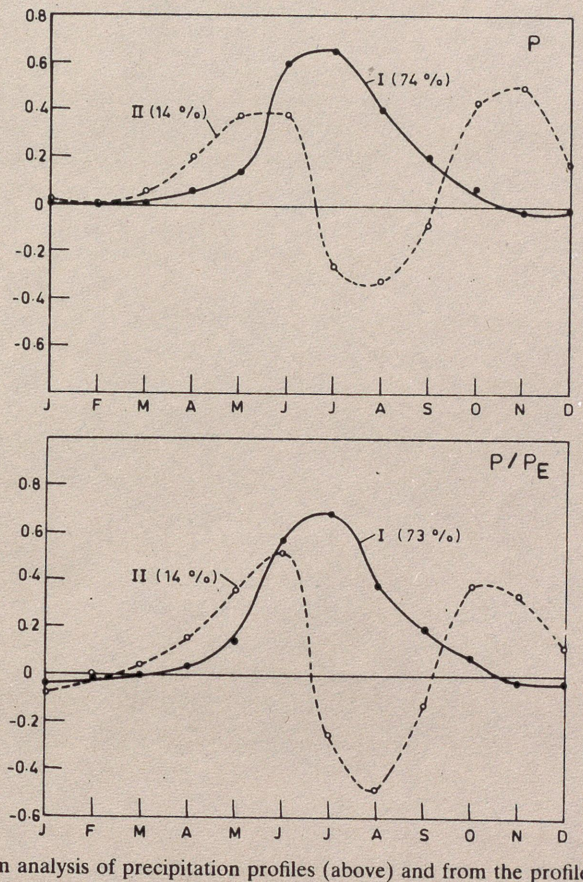

Figure 5. Eigenvectors from analysis of precipitation profiles (above) and from the profiles of moisture index (below).

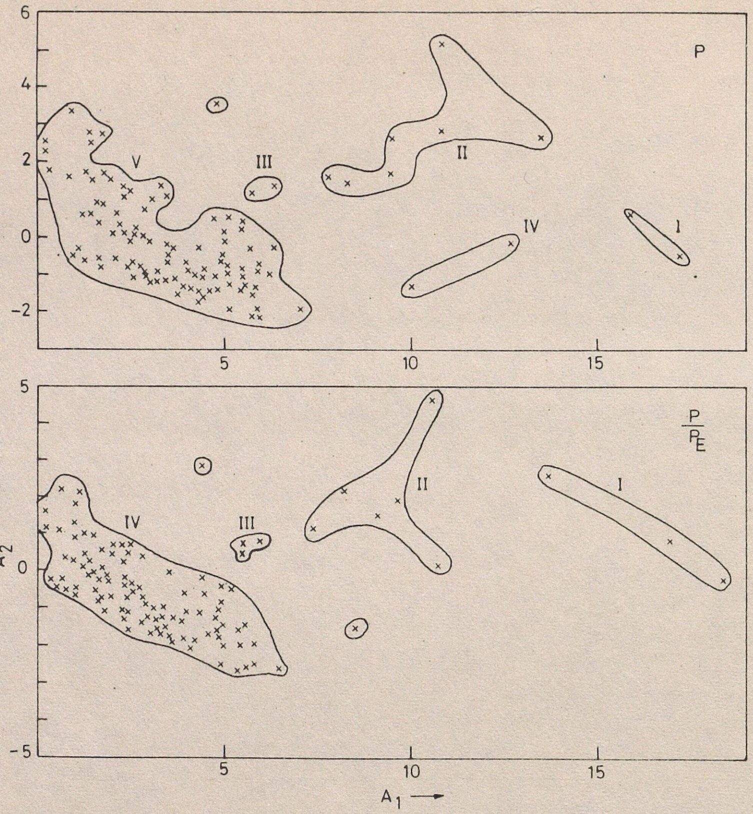

Figure 6. Distribution of the profiles at the different stations in the amplitude space A_1–A_2 of the leading eigenvectors in Figure 5 for precipitation (above) and for moisture index (below)

consists of stations from the rest of India. The high rainfall regions have prominent orographic features and, over some parts, there is considerable variation of the profiles of the moisture index even over distances comparable to the typical separation between stations. Hence the clusters obtained are sensitive to the choice of the grid of stations, and we expect more clusters to emerge and existing clusters to become better-defined if a finer grid is used. The geographical location of the clusters of Figure 6 is shown in Figure 7. The mean moisture index profiles are shown in Figure 8. It is seen from the figure that for any month, the ratio of the standard deviation to the mean is much higher in the dense cluster, compared to the other clusters. This indicates that the dense cluster is less homogeneous, and the moisture index patterns of the stations in it may differ considerably from each other.

4.2. *Second sorting*

In order to bring out the differences, if any, between the stations belonging to the dense cluster of stations spread over most of India, we repeated the principal component analysis separately for this dense cluster, after omitting the other stations. The first two eigenvectors for this second sorting of the profiles of the precipitation as well as of the moisture index are shown in Figure 9. Again the first eigenvector represents the southwest monsoon component and the second the northeast component with the two leading eigenvalues together accounting for at least 85 per cent of the variance. The distribution of the points representing the profiles of the moisture index at different stations in the plane of the amplitudes of the leading components and the clusters that emerge are shown in Figure 10. As in the first sorting, this is similar to the result obtained from rainfall profiles. The geographical locations of the clusters of Figures 7 and 10 are shown in Figure 11. It is important to note that all the clusters are

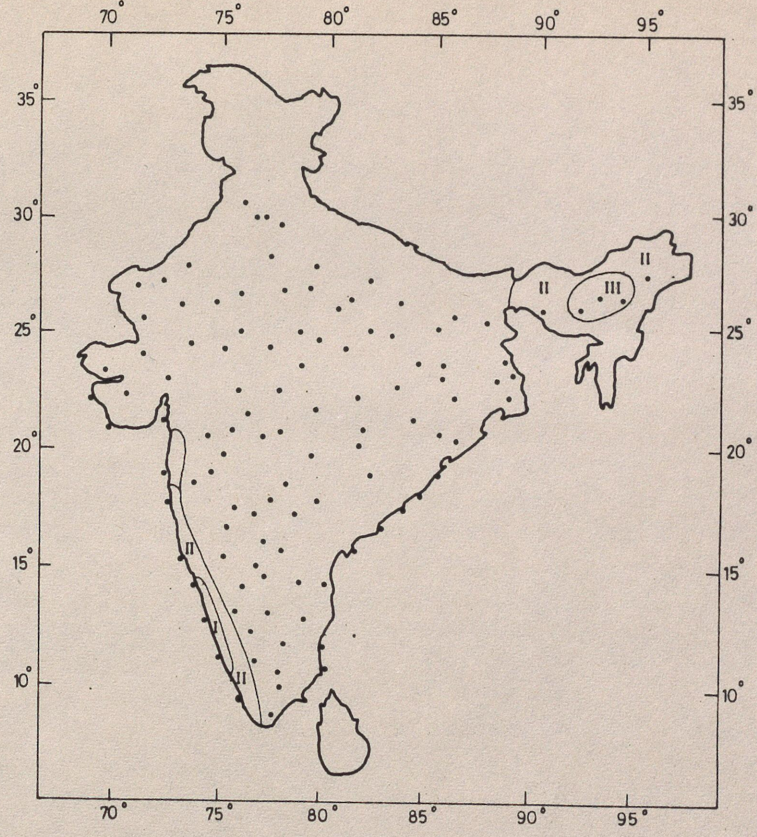

Figure 7. Geographical location of the moisture index clusters of Figure 6

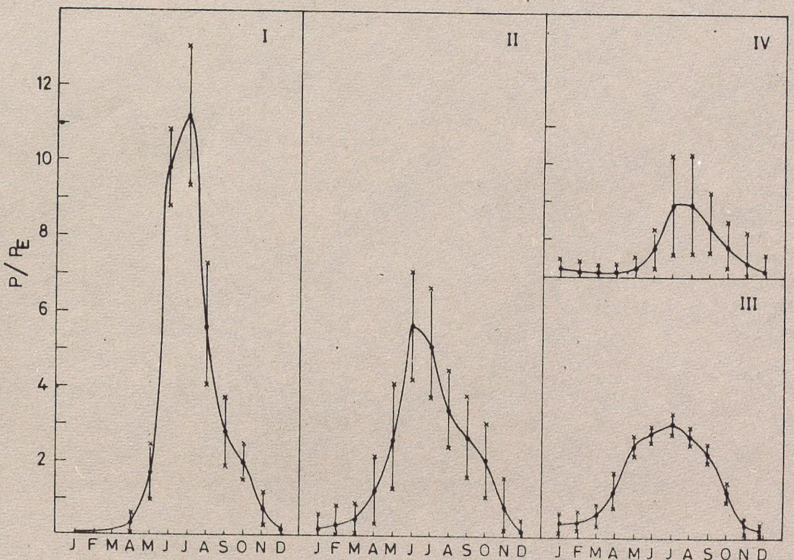

Figure 8. Mean moisture index profiles of the clusters in Figure 6. The standard deviations for each month are also shown

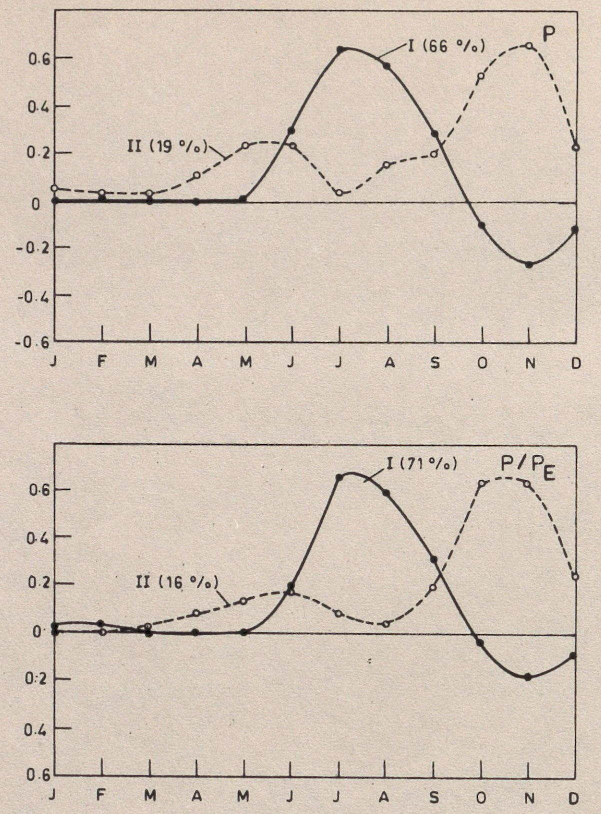

Figure 9. Eigenvectors from analysis of precipitation profiles (above) and for moisture index (below) for the second sorting

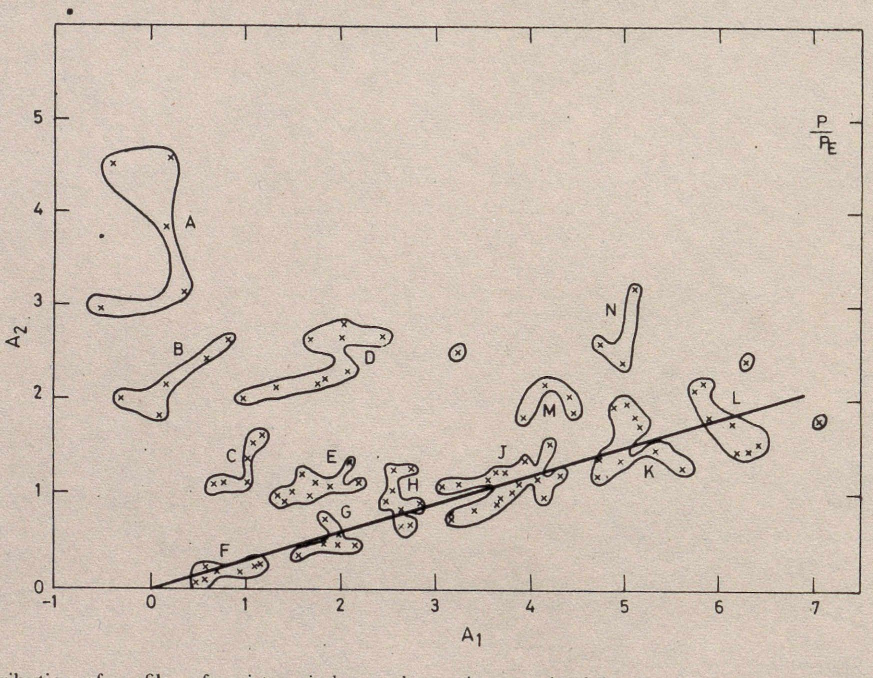

Figure 10. Distribution of profiles of moisture index at the stations retained for second sorting in the amplitude space of the eigenvectors shown in Figure 9

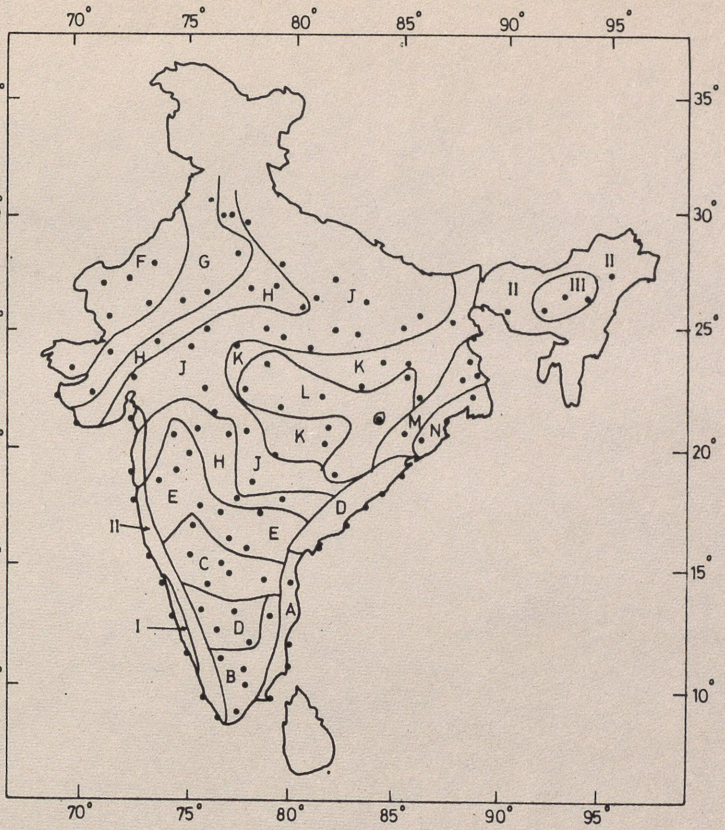

Figure 11. Geographical locations of the clusters of profiles of moisture index from the first and the second sorting

geographically contiguous although no information about geographical location of the stations was used in the analysis.

The peninsular clusters A–E are similar to those obtained by Gadgil and Iyengar (1980). The mean moisture index profiles of these clusters are shown in Figure 12. Note that the contribution of the southwest monsoon increases with increasing latitude along the east coast as well as in the central part of the peninsula.

The most remarkable feature of the distribution of the clusters of moisture index profiles shown in Figure 10 is the alignment of the clusters F–L about the line

$$A_2 = 0{\cdot}3A_1$$

Consequently the mean profiles of these clusters are similar (Figure 13) and the clusters differ mainly in the quantum of rainfall received. The clusters M and N have a disproportionately large amplitude of the second component relative to these clusters.

4.3. *Meteorological interpretation*

As pointed out by Gadgil and Iyengar (1980), the amplitude of the second principal component (representing the pre-monsoon and northeast monsoon) decreases monotonically with latitude north of about 10°N over the peninsula. This suggests that the second component is a manifestation of some system located equatorward of 10°N. It is interesting to note in this context that the ITCZ is located in this equatorial region in the pre-monsoon and post-monsoon seasons. Further, even in the summer monsoon an ITCZ appears intermittently over this region (Sikka and Gadgil, 1980). Thus the pattern of

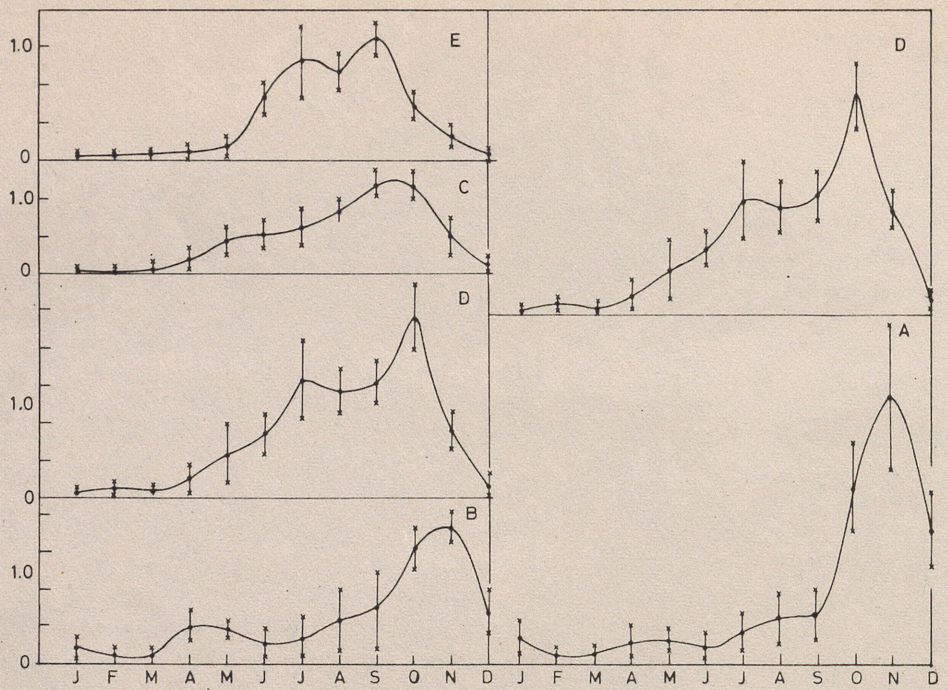

Figure 12. Mean moisture index profiles for the peninsular clusters along the east coast (to the right) and along a central longitude. Standard deviations for each month are also shown

the second component may be looked upon as an empirically derived rainfall pattern associated with the oceanic ITCZ.

In the monsoon trough zone, the rainfall pattern in the clusters F–L has been shown to be similar with the amount of rainfall increasing from F to L. Thus as one moves southeastward in the trough zone from the arid region in the northwest, the amplitude increases and the pattern remains the same along the monsoon trough until the coastal clusters with a disproportionately large amount of rainfall in the

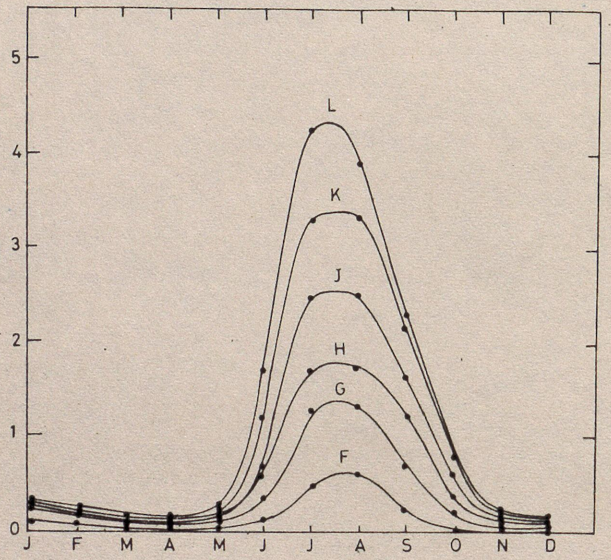

Figure 13. Mean moisture index profiles for the clusters in the monsoon trough zone

pre- and post-monsoon season are encountered. The pattern of the clusters along the trough zone, obtained by a linear superposition of the first two eigenvectors in the proportion implied by the equation in Section 4.2, can thus be interpreted as the empirically derived rainfall pattern associated with the monsoon trough or the continental ITCZ.

5. THERMAL CLUSTERS

The first two eigenvectors obtained from principal component analysis of the monthly mean of the minimum daily temperature are shown in Figure 14, and the distribution of stations in the amplitude space of the two leading components is shown in Figure 15. It is seen that the first component with a maximum during the winter explains 81 per cent of the variance whereas the second one with a maximum in the summer explains about 14 per cent. The amplitude associated with the second

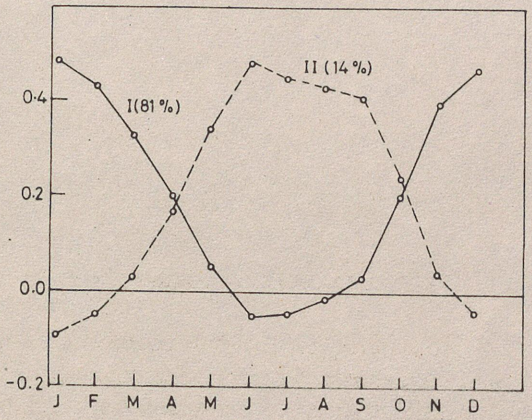

Figure 14. Eigenvectors obtained from the analysis of profiles of mean monthly minimum temperature

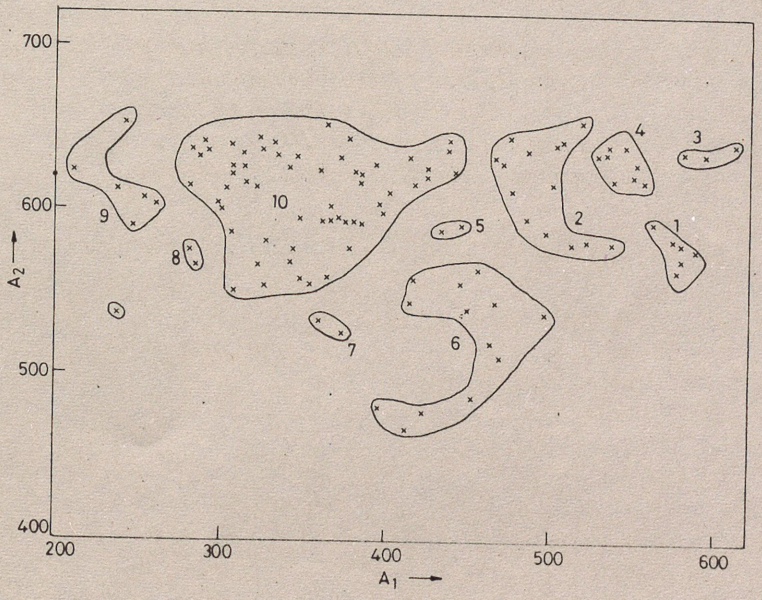

Figure 15. Distribution of the minimum temperature profiles at the different stations in the amplitude space A_1–A_2 of the eigenvectors of Figure 14

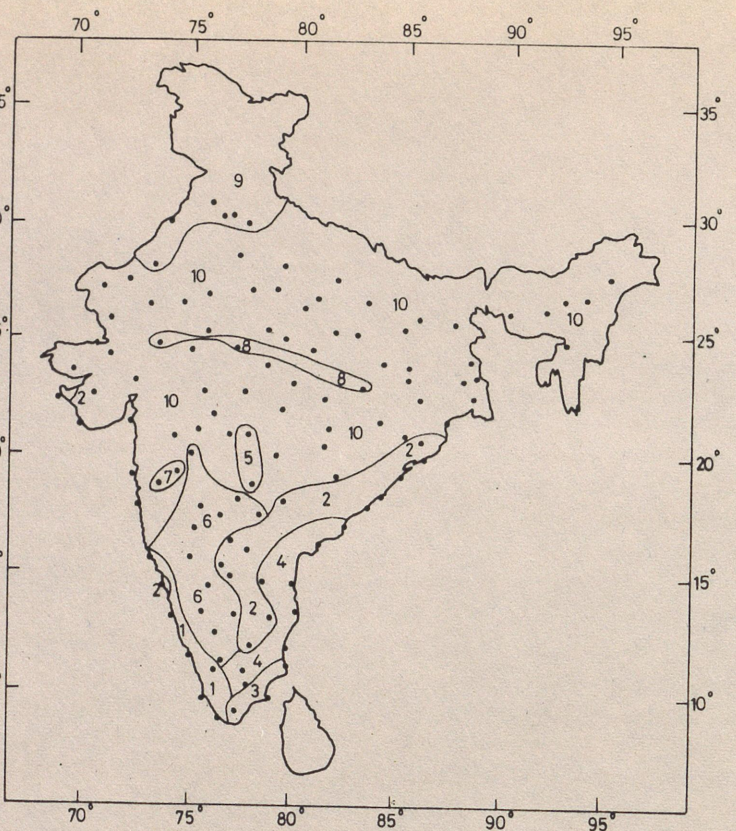

Figure 16. Geographical locations of the clusters of Figure 15

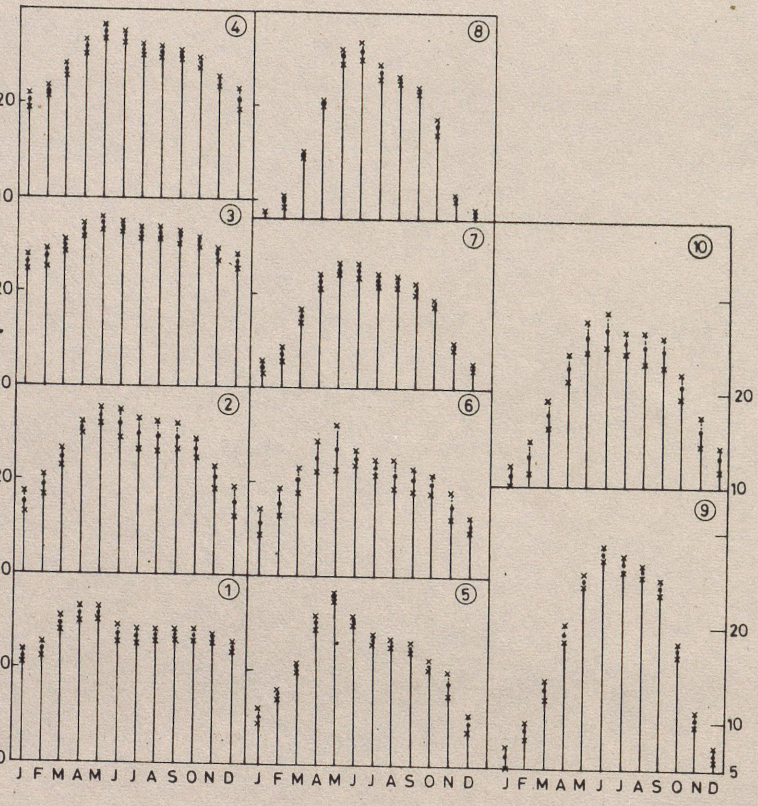

Figure 17. Mean minimum temperature profiles for the clusters of Figure 16. The standard deviations for each month are also shown

component is larger than that with the first for most of the stations, yielding the familiar temperature profiles with a maximum in the summer. The geographical locations of the clusters of Figure 15 are shown in Figure 16. It can be seen from Figure 15 that a vast majority of the clusters occur along a line parallel to the A_1 axis, with the value of A_1 varying from a minimum in the northeasternmost region, to a maximum in the coastal regions of the peninsula. As expected, the value of A_1 is largely determined by the latitude. The mean profiles of the clusters are shown in Figure 17.

Rao's (1972) analysis of the thermal regime on the basis of the annual values of the potential evapotranspiration yielded only two classes. Most of the country came under the megathermal type. Mesothermal regions were confined to the western Himalayas and a few pockets in the northeast. However, our analysis of the mean monthly profiles of minimum temperature has yielded ten thermal clusters. Where the minimum temperature is known to be also important for determining the nature of the vegetation, the temperature clusters obtained here can be used in conjunction with the moisture index clusters.

6. DISCUSSION

Our analysis has two major advantages over the earlier classifications. First, the classification criteria are objectively determined. Secondly, we have been able to use the detailed distribution of the moisture index and the minimum temperature within a year (instead of bulk parameters derived therefrom) owing to the efficiency of principal component analysis in the reduction of the dimensionality. With this, clusters which are homogeneous not only with respect to the seasonal or annual totals but also with the detailed shape of the profile have been obtained. As a result, marked variations within zones deduced

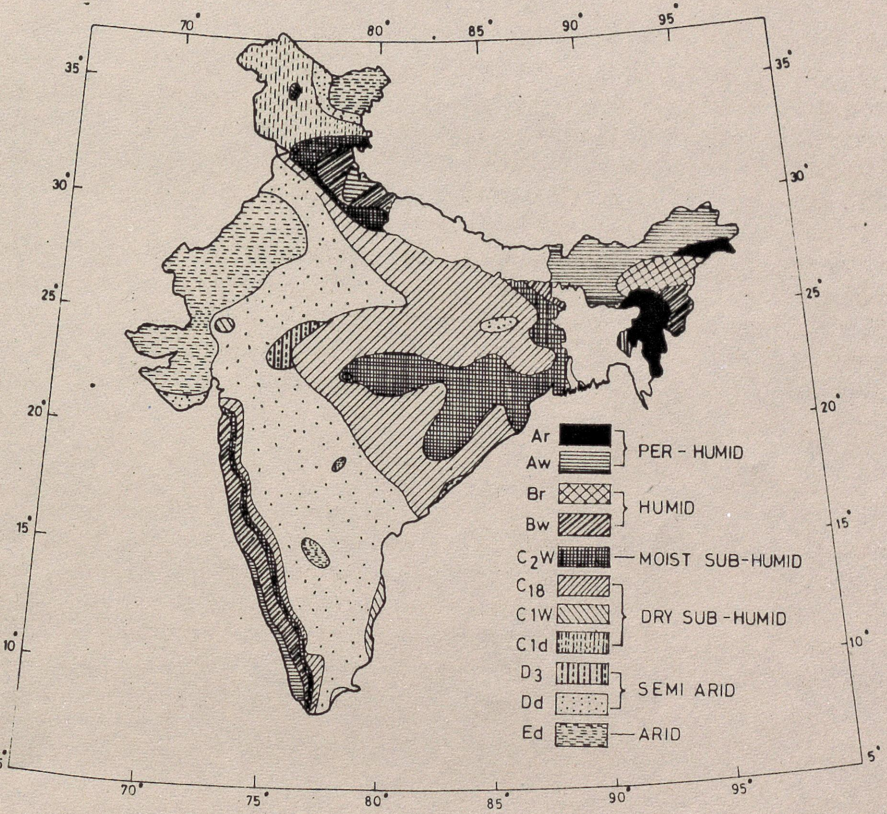

Figure 18. Moisture regimes after Rao (1972)

to be homogeneous in earlier classifications have become manifest. For example in the classification of the moisture regime obtained by Rao *et al*. (1972) based on Thornthwaite's method (Figure 18), there is a prominent semi-arid zone extending from the northwest down to the peninsula. However, as expected, the mean monthly moisture index profiles vary considerably in this zone, and about eight distinct clusters emerge from our analysis in this zone alone (Figure 11). Given the sensitivity of the vegetation to the detailed distribution of the moisture index within a year, the clusters obtained here are likely to be more pertinent for understanding the distributions of vegetation.

Indeed, there is a close correspondence between the climatic clusters based on moisture index profiles and the distribution of vegetation types (Meher-Homji, 1980; Gadgil and Meher-Homji, 1982). The nature of the vegetation types characterizing each climatic zone is given in Table I.

A comparison of the meteorological subdivisions of India (Figure 1) and the climatic clusters of Figure 11 indicates that they are generally similar, although there are some important differences. For example, the cluster A along the southern part of the coast is clubbed with the interior cluster B and part of D in the meteorological subdivision Tamilnadu (30). Similarly the three clusters C, E and H are clubbed in the subdivision North interior Karnataka (32). Since the division into the various states is necessary for administrative convenience, we suggest that the climatic divisions for India be obtained by a superposition of the statewise map on the climatic cluster map.

Table I

Climatic clusters	Vegetation types
First sorting	Vegetation containing evergreen plant species
West coast region I	*Dipterocarpus–Mesua palaquium* evergreen forest of Malabar
West coast region II	Other wet evergreen forest types of Malabar
Northeastern region II	Tropical moist deciduous forest of eastern Himalayas and northeastern Hills
Northeastern region III	Wet evergreen forest of northeastern Hills
Second sorting (Cluster IV)	Vegetation lacking evergreen plant species
A	*Manilkara–Chloroxylon* zone of Coromandal coast
B	*Albizzia amara–Acacia* zone
C	*Hardwickia binata–Anogeissus latifolia* zone
D	*Anogeissus latifolia–Chloroxylon–Albizzia amara* zone
E	*Acacia–Anogeissus latifolia* zone + part of *Anogeissus latifolia–Terminalia–Tectona* zone
F	*Prosopis–Capparis–Ziziphus* zone of Indian desert
G	*Acacia–Capparis* zone of Indian desert
H	*Anogeissus pendula* zone of Rajputana + part of *Anogeissus latifolia–Terminalia–Tectona* zone
J	*Tectona–Terminalia* zone + part of *Anogeissus latifolia–Terminalia–Tectona* zone
K L M	*Shorea robusta* zone
N	*Shorea–Dillenia–Pterospermum* zone

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QUANTITATIVE ETHOLOGY OF SOCIAL WASPS: TIME–ACTIVITY BUDGETS AND CASTE DIFFERENTIATION IN *ROPALIDIA MARGINATA* (LEP.) (HYMENOPTERA: VESPIDAE)

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Abstract. Time–activity budgets of several individually identified members of *Ropalidia marginata* colonies have been constructed with the aim of studying caste differentiation in social wasps that show no morphological differences between individuals. Analysis of these data by multivariate statistical techniques including principal components analysis and hierarchical cluster analysis has demonstrated the presence of three different behavioural castes which we have named Sitters, Fighters and Foragers. The Sitters in a colony consist of the queen and also some non-egg-laying individuals. The Fighters are non-egg-layers that show alarm reactions in response to disturbances and also fight with other individuals on the nest to a very large extent. The Foragers are also non-egg-layers and they spend a large proportion of their time making trips to places away from the nest to collect food, building material etc.

The social insects comprising ants, bees, wasps and termites are remarkable in that they exhibit extreme degrees of social organization and division of labour within members of a social group or colony. The present day species of bees and wasps exemplify a series of stages in the spectrum of social organization and caste differentiation from solitary to eusocial. In insect societies, a caste is defined as a set of individuals that are both morphologically distinct and specialised in behaviour (Wilson 1971). By this definition, the caste systems of social wasps (Vespidae) are often not as highly developed as those of the other social insects (West-Eberhard 1969; Jeanne 1972; Litte 1977). Morphological differentiation is not common and when present has a simple nutritional basis (Wilson 1971).

However, even in the complete absence of morphological differentiation, there could be behavioural differences between the members of a colony. At a very primitive level of division of labour, it is probable that the behavioural repertoire of all the individuals would be similar and the differences quantitative rather than qualitative. Such differences could be best detected by studying how each individual allocates its time between the different possible behaviour patterns. Hence, we have constructed time-activity budgets for individually identified members of *R. marginata* colonies and looked for evidence of behavioural caste differentiation.

Ropalidia marginata is a common paper wasp in India that builds small open nests on the eaves of undisturbed buildings or on the twigs of cypress bushes (*Cupressus sempervirens*) (Gadagkar 1980). The nests contain up to 100 adults, although smaller nests (< 10 adults) are more common. Small nests have a single egg-layer whereas large nests tend to have several egg-layers. No morphological differences are noticeable between egg-layers and non-egg-layers or between any of the adults on a nest, though individuals with well-developed ovaries tend to be among the heavier individuals (Gadgil & Mahabal 1974; Gadagkar et al., unpublished observation).

In this paper we show that analysis of the time–activity budgets of the adults of *R. marginata* colonies yields three distinct behavioural castes which we have named Sitters, Fighters and Foragers after their distinguishing attributes.

Subjects and Methods

A. Study Animal

The study was conducted on two small post-emergence nests of *R. marginata* (the total number of adults per nest varied between four and 40 during the period of study) built on cypress bushes (*Cupressus sempervirens*) in Cubbon Park in the city of Bangalore (13°00′ N and 77°32′ E), India, between November 1979 and April 1980. All the adults in the colonies were individually labelled by marking them with one or more spots of aeroplane paint of different colours on different parts of the body. The marking was done immediately after the emergence of an adult. A census of all the wasps present at the nest was taken at about 0700 hours since none of them was ever seen to leave the colony before this time during preliminary ad libitum observations. Both the colonies had a single egg-layer (queen) each during the entire period of study. Males disappeared from the colony within a few days after emergence. Thus all the data in this paper pertain to the females.

B. Sampling Methods

Four kinds of sampling methods were used in the study (Altmann 1974).

(1) **Ad libitum sampling** was employed for constructing an ethogram, i.e. we compiled a descriptive catalogue of the behavioural repertoire of the species to get preliminary information on the basis of which subsequent sampling methods were chosen.

(2) **Instantaneous scanning** of the behavioural states of all animals in a colony was performed at 134 randomly chosen times during the period of study.

(3) **All occurrences of rare behaviours** were noted. Some behaviours that appeared to be relatively rare on the basis of ad libitum sampling were recorded in 100 separate 5-min sessions during which all occurrences of each such behaviour by every animal in the colony were recorded. Here every behaviour was treated as an event and no information on its duration was recorded.

All sampling sessions were begun and terminated by time-contingent rules using a stop watch accurate to 0.1 s. Observations were made for a total of 160 h. Ad libitum observations showed that the wasps were relatively inactive between 1800 and 0900 hours. Hence all sampling sessions were randomly chosen between 0900 and 1800 hours. All data were recorded on coding sheets in an 80-column format ready to be punched on computer cards. The data were analysed using a DEC 1090 computer at the Indian Institute of Science, Bangalore, India.

C. Analysis of Data

(1) **Behavioural repertoire.** The behavioural repertoire of *R. marginata* was classified into 37 distinct behavioural categories (Gadagkar, unpublished data; Gadagkar and West-Eberhard, in preparation). However, data on the following 11 categories alone were analysed in this study.

(i) **Sit and Groom.** By sitting is meant simply sitting quietly without doing anything in particular and without being alert to any external disturbance. In this position the wasps sit with their bodies held compactly in one plane and their legs and wings drawn close to the body with the antennae lowered. Grooming is always self-grooming and no allogrooming has been observed. The most frequent forms of grooming involve rubbing posterior legs against each other and against wings and abdomen, anterior legs against mouth parts, antennae and head, and antennae against mouth parts.

(ii) **Raise Antennae.** This involves sitting with wings drawn close to the body but the antennae raised above the body plane. There is a transition from Sitting to Raising Antennae when there is any disturbance.

(iii) **Raise Wings.** This involves sitting with both antennae and wings raised above the body plane. The legs are either folded or stretched so as to raise the body above the substratum. Raising Antennae is followed by Raising Wings if the disturbance continues.

(iv) **Walk.** The wasps walk from the face of the nest and back; when they walk they sometimes reach different cells in the nest and sometimes reach other adults sitting on different parts of the nest.

(v) **In Cells.** The wasps get inside the cells with only their head or the entire body either simply 'inspecting' the contents or receiving secretions from the larvae or transferring liquid to larvae.

(vi) **Absent from Nest.** Absence from the nest is considered here as one category although a wasp temporarily absent from the nest may return with food, building material, liquid or nothing.

(vii) **Bring Food.** As mentioned earlier the wasps sometimes bring back food, building material or liquid.

(viii) **Attack.** The wasps fight with each other. Attacking involves climbing over the opponent and sometimes chewing the dorsal part of its body, but more often bending itself over the head of the opponent and biting its mouth parts.

(ix) **Attacked.** The wasp that is being attacked is very subdued and keeps its body stiff with antennae, legs and wings all drawn close to the body.

(x) **Snatch Food.** This is the act of acquiring solid food from another individual. The other individual is said to **(xi) Lose Food.**

(2) **Time–activity Budgets.** With the data available it was possible to calculate the time–activity budgets of 20 wasps derived from the two

colonies for the six activities, Sit and Groom, Raise Antennae, Raise Wings, Walk, In Cells and Absent from Nest.

(3) **Frequencies of rare behaviour.** For behaviour that tended to occupy a very small proportion of time as observed from the scans, and for behaviours that are better treated as events rather than states, frequencies were computed from the all-occurrences recording sessions. These behaviours included Bring Food, Attack, Attacked, Snatch Food and Lose Food.

(4) Principal components analysis. From the time-activity budgets, every individual can be characterized by the proportion of time it spends in each of the six different behaviours. The method of principal components analysis (Frey and Pimental 1978) yields a new set of uncorrelated variables. Moreover, the new variables are maximally powerful in bringing out the differences between individuals in the sense that, of all the possible linear combinations, the proportion of total variance accounted for by each of the new variables is maximal (Anderberg 1973). It is often possible that only a small number of these new variables account for almost all the variance between the individuals.

(5) Hierarchical cluster analysis. Using the proportion of time spent in the six activities by different individuals as input data, Pearson product moment correlation was obtained as an index of similarity between pairs of individuals. Using these indices of similarity, a hierarchical cluster analysis was performed with the single linkage algorithm (DeGhett 1978).

Results

Time–activity budgets calculated for 20 individuals reveal that adults of *R. marginata* spend 85–100% (mean ± SD = 95.9 ± 4.4) of their time in the six activities Sit and Groom, Raise Antennae, Raise Wings, Walk, In Cells and Absent from Nest. However, the manner in which a given wasp allocates its time among these six activities is highly variable. For example, the queens (individuals 1 and 14) spend no time at all in Absence from Nest and among the other individuals; the time allotted to this activity varies from 4–69%. Similarly, the time spent in Sit and Groom varies from 7–56%, with the queen representing the highest value.

The results of principal components analysis performed using data on the time–activity budgets of 20 wasps are presented in Table I. The first principal component accounts for 72.3% of the total variance with Absence from Nest as its dominant term (weightage = 0.8289). The second principal component, whose dominant term is Raise Antennae (weightage = 0.8219), accounts for 20.2% of the total variance. Since the first two components together account for 92.5% of the total variance, we have represented each individual as a point in the coordinate space of the associated amplitudes of these two principal components. As seen from Fig. 1, the points fall into three obvious clusters. This has been confirmed by the method of nearest centroid; the distance between any individual and the centroid of the cluster to which it belongs is less than its distance from the other two centroids. Individual 13 alone does not fall into any of the three clusters. This we believe is because most of the data on this animal was collected when the nest was in the process of being abandoned because of extensive predation by *Vespa tropica*, a common predator of *R. marginata* colonies.

It must be emphasized here that the three clusters have emerged as a result of an objective analysis of the data in as much as no prior

Table I. Eigenvectors of Principal Components, Eigenvalues, Percentage of Variance, and Cumulative Percentage of Variance

	Principal components			
Behaviour	1	2	3	4
Sit and Groom	−0.5305	−0.5025	0.0118	0.5835
Raise Antennae	−0.1056	0.8219	−0.1701	−0.4060
Raise Wings	0.0152	0.1012	0.9052	0.1252
Walk	−0.1343	−0.0690	−0.2960	0.6004
In Cells	−0.0457	−0.0524	−0.2357	0.1169
Absent from Nest	0.8289	−0.2328	−0.0917	−0.3238
Eigenvalue	1.27×10^4	3.54×10^3	7.33×10^2	4.34×10^2
Variance (%)	72.30	20.20	4.18	2.48
Cumulative variance (%)	72.30	92.50	96.68	99.16

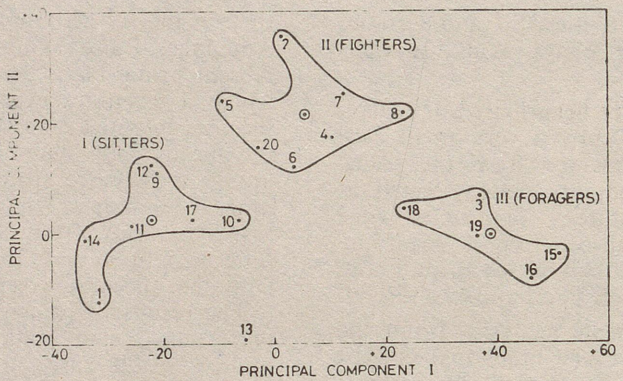

Fig. 1. Behavioural castes of *R. marginata*. Twenty wasps are shown as points in the coordinate space of the amplitudes associated with the first two principal components. The points fall into three clusters (or castes) by the criterion of nearest centroid. Circled dot = centroid.

assumptions were made regarding the criteria to be used for classification or the number of clusters required.

Absence from Nest is the dominant term in the first principal component, and clusters I and III thus represent two extremes for this activity, while cluster II is intermediate. Similarly, Raise Antennae is the dominant term in the second principal component and the members of cluster II are thus different from those of clusters I and III in the time spent with Raised Antennae. An independent method of classification, namely hierarchical cluster analysis using the Pearson product moment correlation as an index of similarity between individuals also gives identical clusters (Fig. 2). Individual 13 is again separated from all the others and one can recognize three clusters with the same composition as the clusters obtained from the principal components analysis. Although this method does not permit us to identify the distinguishng features of each cluster, we would like to interpret the complete concurrence of the two methods as an indication of the robustness of the clusters.

The mean profiles of the three clusters with reference to the six activities used in the classification are shown in Fig. 3A. Figure 3B shows the mean profiles of the sàme three clusters using the frequencies of the five other activities not used in the classification. Although it is not necessary for any one activity alone to show significant differences between the clusters (as the clusters have been obtained by the consideration of six activities simultaneously), it is obvious from Fig. 3A that the time spent in Sitting and Grooming, Raised Antennae, and Absence from the Nest are the most distinguishing attributes of clusters I, II and III respectively. The difference in the time spent in Raised Antennae between clusters I and II is rather small. On the other hand if we look at Fig. 3B, a high frequency of Attacking emerges as a very conspicuous attribute of cluster II. Moreover, there is a significant positive correlation between the time spent by an individual with Raised Antennae and its frequency of attacking

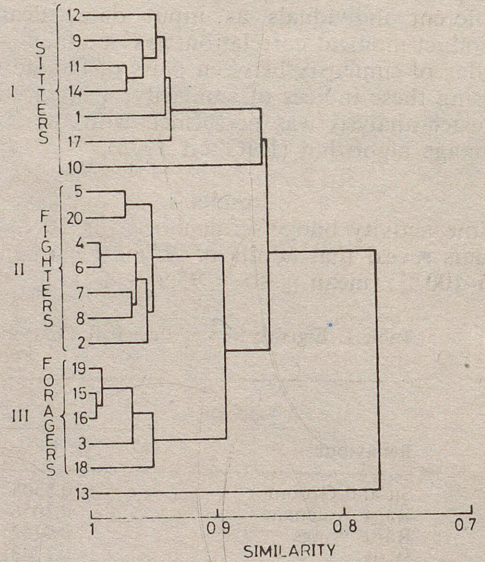

Fig. 2. Hierarchical cluster analysis of 20 adults of *R. marginata* numbered as in Fig. 1. The similarity between individuals shown in the Pearson product moment correlation calculated using the percentage of time spent in six activities as input data. The method of single linkage algorithm has been used in clustering.

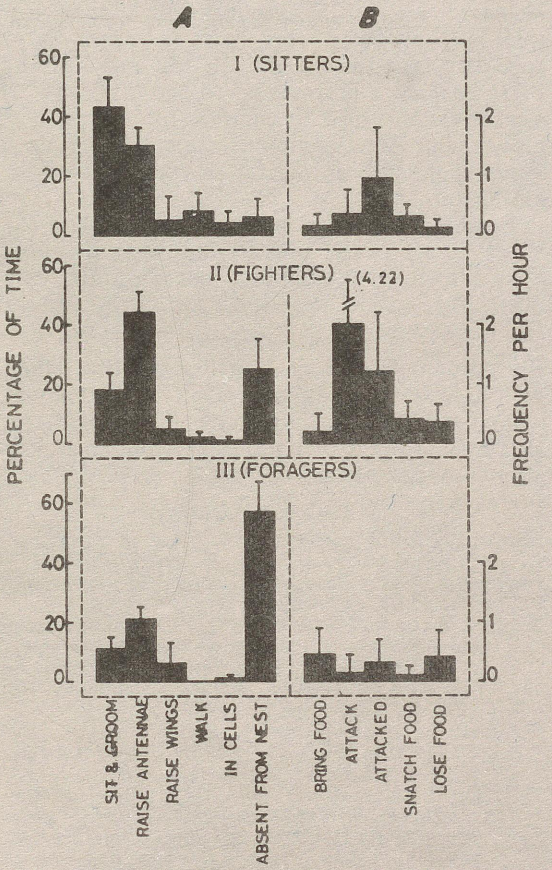

Fig. 3. Mean behavioural profiles of the clusters obtained in Figs 1 and 2. A, mean percentages of time spent in each of the six activities that were used in obtaining the clusters are shown for Sitters, Fighters and Foragers. B, mean frequencies per hour of the five activities that were not used to obtain the clusters are shown for Sitters, Fighters and Foragers.

other individuals ($P < 0.01$). Hence we wish to consider Attacking or Fighting as the distinguishing attribute of cluster II. Wasps in cluster III spend a great deal of time being Absent from the Nest. Because these wasps often bring back food loads or building material (confirmed by casual observations on wasps away from their nests), we consider Foraging as the distinguishing attribute of cluster III. Thus we see that the adults of R. *marginata* colonies can be classified into three behavioural castes which can be called Sitters, Fighters and Foragers.

Discussion

Multivariate analysis of data on time–activity budgets of individually identified members of colonies of the social wasp *Ropalidia marginata* reveals the presence of three behavioural clusters despite the absence of any obvious morphological caste differentiation. These three behavioural clusters have been named Sitters, Fighters and Foragers on the basis of their most distinguishing features.

Sitters are those that spend much more time Sitting and Grooming than others. They do little or no foraging and seldom fight either with members of their own group or those of other groups (Fig. 4). It is important to note that the queens of both the colonies (individuals 1 and 14) belong to this group. However, there are other non-egg-laying members of this group. Whether these are 'hopeful queens' who may still have some chances or reproducing on their own (see West-Eberhard 1978), or naive workers yet to be recruited into the worker force, is not clear at present. These questions are being investigated by queen removal experiments.

Fighters are individuals that spend a large proportion of their time with Raised Antennae, and they also Attack other individuals frequently. They show the highest frequency of attacking other members of their own group and a lower frequency of attacking a Sitter or a Forager (Fig. 4). Sitting with Raised Antennae probably serves the function of guarding the nest and its brood against parasites and predators. This is supported by the fact that wasps remain in this position for extended periods of time if the nest is disturbed either by the investigator or by tachinid flies known to parasitize their brood (unpublished observations). It is conceivable that Attacking induces the other

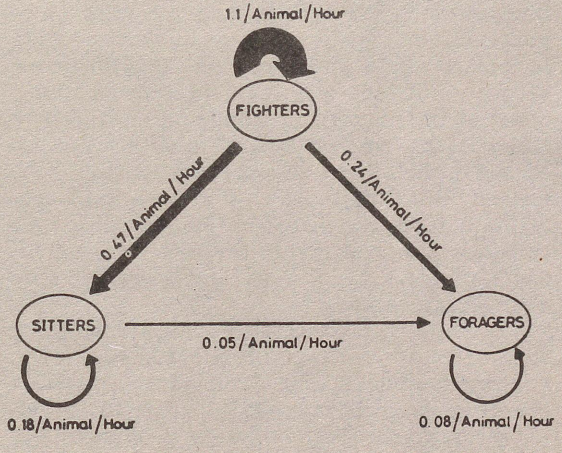

Fig. 4. Mean attacking frequencies within and between Sitters, Fighters and Foragers.

members of the colony to work. We have sometimes observed wasps leave the nest as a result of repeated attacks from nest mates and later return with food or building material. Further support for this idea comes from the observation that Fighters also snatch food from other individuals to a large extent; there is a significant positive correlation between the frequency of Attacking and that of Snatching Food ($P < 0.01$) (see also Gadagkar 1980). Fighters may also have some chance of becoming egg-layers if the colony becomes large and polygynous or if some accident were to befall the queen. In *Mischocyttarus mexicanus*, for example, the next most dominant individual becomes the egg-layer if the queen is removed (Litte 1977). This is one possible reason why Fighters show the highest frequency of attacking another Fighter (Fig. 4). By means of attacking, a linear dominance hierarchy can be recognized among the members of a colony (Gadagkar 1980). In one instance we observed that a queen had disappeared from a nest and the most dominant individual of the remaining wasps immediately began to lay eggs (unpublished observations).

Foragers constitute the principal worker force of a colony. They show the lowest frequencies of Sitting and Grooming, Attacking and being Attacked (see also Fig. 4). Thus, they do not seem to be involved in reproductive competition with their nest mates and we suggest that they have the least chance of becoming egg-layers.

It should be pointed out that egg-laying itself was not used as one of the activities in the present analysis. This is because egg-laying occupies an extremely small proportion of the time available to a wasp and we were more interested in classifying individuals according to the manner in which they allocated their time between different activities. Moreover, differentiation into reproductive and non-reproductive castes is very well established in all eusocial insects. On the other hand, the fact that both the queens fall in the same cluster in spite of egg-laying not being included in the analysis can be considered as evidence of the biological significance of the kind of behavioural classification we have attempted.

The results of this study are remarkably similar to those of the only other similar study concerning social insects. Brothers and Michener (1974) collected behavioural data on the primitively social bee *Lasioglossum zephyrum* and subjected them to principal components analysis. Their results show that the bees can also be clustered into three groups which they call queens, guards and workers. It is interesting to speculate that the queens, guards and workers of *L. zephyrum* correspond to the Sitters (with queens as some of their members), Fighters (that also spend the maximum time with Raised Antennae) and Foragers respectively of *R. marginata*.

Further work is in progress to elucidate the effects of age of the animals and stage of colony development on such a behavioural caste differentiation.

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On the Moulding of Population Viscosity by Natural Selection

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In this paper, we explore the conjoint evolution of dispersal and social behaviour. The model investigated is of a population distributed over a number of sites each with a carrying capacity of two adults and an episode of dispersal in the juvenile stage. The fertilities are governed by whether an individual and its neighbour are selfish or co-operative. It is shown that the best dispersal strategy for the co-operative genotype always involves lower levels of dispersal; and further that ecological conditions favouring low levels of dispersal increase the selective advantage of a co-operative genotype. Given this positive feedback, we suggest that in any taxon viscosity and co-operativity will tend to be correlated and bimodally distributed. Hence we predict the existence of two kinds of animal societies; viscous and co-operative (e.g. quasi-social wasps such as *Mischocyttarus*), and non-viscous and selfish (e.g. communal sphecid wasps such as *Cerceris*), and relatively few social groups with intermediate levels of co-operativity and viscosity. We also suggest that when one of the two sexes disperses, it will be the sex with lower potential for co-operative behaviour.

1. Introduction

The patterns of dispersal of living organisms have important implications for the evolution of their social behaviour. Thus, in a viscous population, i.e. in a population in which an individual's neighbours are its close relatives, altruistic and co-operative interactions will be favoured (Hamilton, 1964). Investigations of the evolution of dispersal behaviour carried out so far suggest that high rates of dispersal will be favoured by (a) high rates of survival of dispersives, (b) high probability of extinction of demes, (c) small deme sizes, and (d) out of phase fluctuations in the carrying capacity of the habitats occupied by the different demes. However, some dispersal is favoured even under conditions of constant carrying capacity of the habitats and high mortality of the dispersives (Gadgil, 1971; Hamilton & May, 1977; Comins, Hamilton & May, 1980). We suggest that the dispersal rates will also be affected by the selection pressure for reducing the chances

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of competitive interactions and for enhancing the chances of altruistic and co-operative interactions between closely related individuals. Hence, we expect high rates of dispersal and low levels of viscosity to be favoured in populations in which the social interactions are preponderently of a competitive nature and low rates of dispersal and high levels of viscosity to be favoured in populations in which they are largely of an altruistic or co-operative nature. High levels of viscosity in turn create conditions under which the evolution of altruistic or co-operative behaviour is favoured. It is our contention that such a positive feedback system must lead to the evolution of two modes of animal societies: viscous societies with high levels of altruism/co-operation, and non-viscous ones with high levels of competitive interactions. The purpose of the present paper is to explore this conjoint evolution of dispersal and social behaviour.

2. The Model

(A) THE BASIC ASSUMPTIONS

We propose to investigate these problems within the framework of a generalization of the Hamilton & May (1977) model. Consider an asexual population distributed over n sites. The carrying capacity of each site is two adult individuals, and this remains constant in time. The juvenile stage is the dispersive stage. The fertility of an adult depends on its own genotype i and that of its neighbour j on the same site and is specified by X_{ij}. Of the X_{ij} offspring produced by an individual of the i-th genotype, a fraction d_i disperses; while the rest remain on the same site. All the offspring dispersed are subject to the same level of mortality, so that a fraction α of these survives. All the surviving dispersives are distributed uniformly amongst all the sites. At each site, the parents and the offspring remaining at the parental site compete with the juveniles arriving from the pool of the dispersives, on an equal footing, and finally only two of these survive to the next breeding season.

Consider a population comprising two genotypes with frequencies p_1 and p_2. For the carrying capacity of two per site, there are three types of sites: two homogeneous with both individuals of type 1 or 2 and the third heterogeneous with one individual of each genotype. The frequencies of these three site types are denoted by f_{11}, f_{22} and f_{12} respectively. The dynamics governing the evolution of these site frequencies and hence the genotypic frequencies is described in Appendix A. The model as formulated here is a reasonable representation of species with fertilities of the order of 25 or more and with either non-overlapping generations or those in which generations overlap but the parents do not have a marked edge over the juveniles. The model is thus evidently applicable to the temperate zone species of the primitively social wasps mentioned in the concluding section.

(B) COEFFICIENT OF VISCOSITY

In the fully viscous case, with $(d_1 = d_2 = 0)$, an arbitrary distribution of site frequencies evolves until all the heterogeneous sites have been converted into homogeneous ones and eventiually the distribution

$$f_{11} = p_1, \qquad f_{12} = 0, \qquad f_{22} = p_2 \tag{1}$$

is attained. On the other hand, in the completely non-viscous case in which all the offspring born are dispersed (i.e. $d_1 = d_2 = 1$), any initial distribution of site frequencies will attain, within one generation, the stationary distribution

$$f_{11} = p_1^2, \qquad f_{12} = 2p_1p_2, \qquad f_{22} = p_2^2 \tag{2}$$

if there is no differential reproduction or survival. Hence an appropriate measure of the viscosity of the population is the extent to which the frequencies of the homogeneous sites exceed those obtained in a fully non-viscous population given by equation (2).

We find that irrespective of the initial conditions, within a few generations, the site frequencies attain a quasi-steady distribution specified in terms of the genotypic frequencies in most cases. However, no such quasi-steady distribution is attained when selection occurs extremely rapidly with large changes in genotypic frequencies over time scales of less than ten generations. The quasi-steady site frequency distribution attained under moderate selection can be represented as

$$f_{11} - p_1^2 = f_{22} - p_2^2 = \beta p_1 p_2 \tag{3}$$

enabling us to define a parameter β as:

$$\beta = \frac{f_{11} - p_1^2}{p_1 p_2} = \frac{f_{22} - p_2^2}{p_1 p_2}. \tag{4}$$

The site frequency distribution goes from equation (2) to equation (1) as β changes from zero to unity. The definition (4) for the parameter β can be readily generalized for the case of a population comprising several genotypes.

The attainment of the quasi-steady distribution of site frequencies which implies the attainment of a constant value of β is illustrated in Fig. 1. If there are large changes in genotypic frequencies during the course of

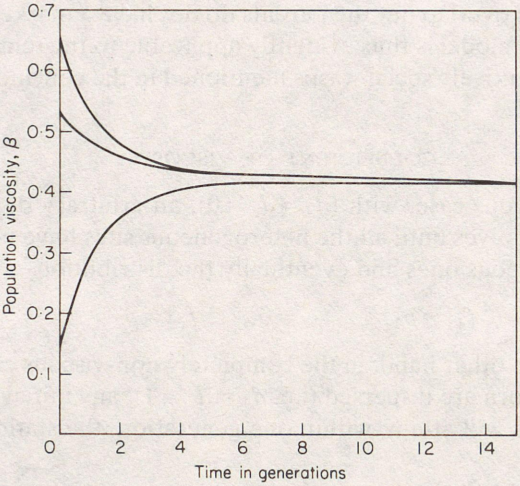

FIG. 1. The population viscosity β as a function of time for three widely differing initial distributions of site frequencies. Note that β approaches a constant value by about ten generations $\alpha = 0{\cdot}3$, $d_1 = 0{\cdot}2$, $d_2 = 0{\cdot}7$, $X_{11} = X_{12} = X_{21} = X_{22} = 1$, $p_1 = 0{\cdot}9$.

evolution, such as when an invader ultimately takes over the population, the value of β also changes slowly over the selection time-scale. However, the rate of chnage in β is much smaller than that in the genotypic frequencies. Hence β can be taken as an appropriate measure of viscosity.

The coefficient of viscosity β depends upon the dispersal rates d_1, d_2 and survival α. In addition, it is weakly dependent on the genotypic frequencies as well as on the differential fertilities (Figs 2, 3). The contours

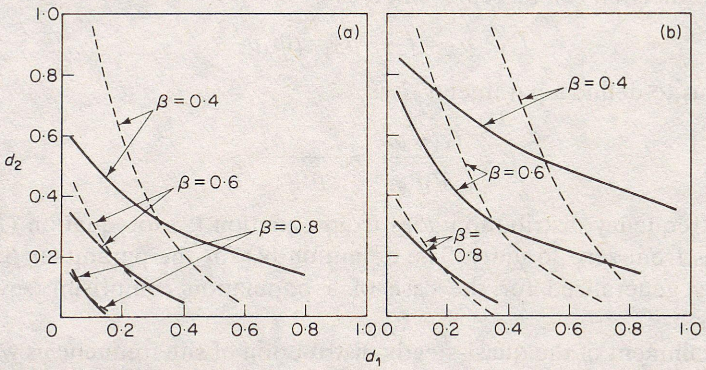

FIG. 2. Contours fo β for 0·4, 0·6 and 0·8 in the $d_1 - d_2$ plane. $X_{11} = X_{12} = X_{21} = X_{22} = 1$. - - - - - $p_1 \sim 0$, —— $p_1 \sim 1$. (a) $\alpha = 0{\cdot}7$, (b) $\alpha = 0{\cdot}3$.

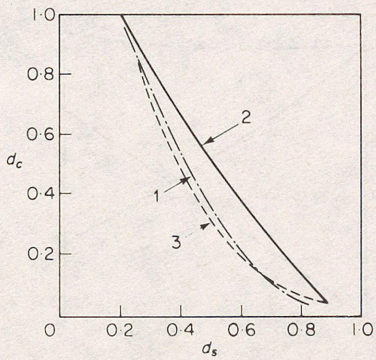

FIG. 3. Contours of $\beta = 0{\cdot}5$ in the $d_s - d_c$ plane, for $p_s \simeq 0$; $\alpha = 0{\cdot}3$. (1) – · – · – $X_{sc} = X_{cc} = X_{ss} = X_{cs} = 1{\cdot}0$. (2) —— $X_{sc} = 1{\cdot}8$, $X_{cc} = 1{\cdot}4$, $X_{ss} = 0{\cdot}6$, $X_{cs} = 0{\cdot}2$. (3) - - - - - $X_{sc} = 1{\cdot}2$, $X_{cc} = 1{\cdot}1$, $X_{ss} = 0{\cdot}9$, $X_{cs} = 0{\cdot}8$.

of β in Fig. 2 indicate that β is more sensitive to changes in the dispersal rate of the invader relative to those for the native genotype.

(C) DISPERSAL AND COMPETITION MORTALITY

Some dispersal of offspring away from the parental site is favoured even under unfavourable conditions, such as high mortality of dispersives and constant carrying capacity of the sites. This is because, unlike a sedentary genotype, a dispersing genotype has a chance of taking over new sites (Hamilton & May, 1977; Comins, Hamilton & May, 1980). While some dispersal will always be favoured, there will be selection against very high levels of dispersal due to the higher levels of mortality suffered by the dispersives. The optimal level of dispersal will therefore depend on the relative magnitudes of the mortality suffered by dispersives and the subsequent mortality due to competition at the sites. The Malthusian parameter, or the rate of change in total numbers, characterizing any genotype is obtained by deducting the total mortality suffered during dispersal and competition at the sites from the total number of births (see Appendix B).

An increase in d, the fraction of the offspring dispersed, leads to an increase in the mortality suffered during dispersal and a decrease in the mortality due to competition at the sites. There is therefore some value of d between zero and unity for which the total mortality is minimum and the Malthusian parameter is maximum (Fig. 4). This is the optimal dispersal rate for the genotype for the given set of Xs and α, and for the particular dispersal rate and frequency of the competing genotype. What is more pertinent, however, from an evolutionary point of view, is an unbeatable

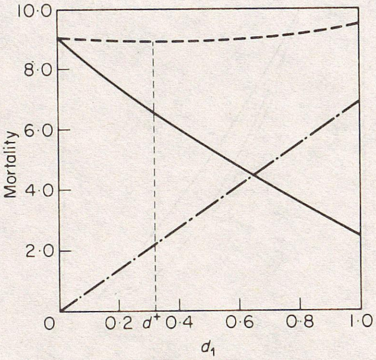

FIG. 4. Mortality of dispersives (– · – · –) competition mortality at sites (——), and total mortality (- - - - -) as a function of dispersal rate d_1. The optimal dispersal rate d^+ for this parameter set is 0·32. $p_1 \simeq 0{\cdot}99$. $\alpha = 0{\cdot}3$, $d_2 = 0{\cdot}6$, $X_{11} = X_{12} = X_{21} = X_{22} = 10$.

or evolutionary stable dispersal strategy (ESS), i.e. a dispersal rate such that a genotype possessing that strategy will always invade a population of a genotype possessing any other dispersal rate while a population with that dispersal rate will not be invaded by a mutant possesing any other dispersal rate.

3. Dispersal Strategies

(A) UNBEATABLE STRATEGY

To begin with, consider the case when all the fertilities are equal, i.e.

$$X_{11} = X_{22} = X_{12} = X_{21}. \tag{5}$$

The difference in the Malthusian parameters of the two genotypes $m_1 - m_2$, depends, in general on the dispersal rates d_1 and d_2, the survival α, as well as the site frequencies. When the quasi-steady distribution of the site frequencies has been attained, $m_1 - m_2$ depends only on the dispersal rates, the survival and the genotypic frequencies. The dynamics of the interactive system studied in that case is best represented as a fate-map in the parameter space of the dispersal rates of the competing genotypes (Fig. 5). This parameter space gets divided into three types of regions by the curves $m_1 = m_2$, along which fitnesses of the two genotypes are equal. These regions are characterized by: (a) m_1 exceeding m_2 irrespective of genotypic frequencies, (b) m_2 exceeding m_1 irrespective of genotypic frequencies, and (c) m_1 exceeding m_2 only when p_1 is sufficiently large.

Of the curves on which $m_1 = m_2$, one is the straight line $d_1 = d_2$ along which the competing genotypes are identical in every repect. This line always separates regions of the first two types. For a given set of genotypic

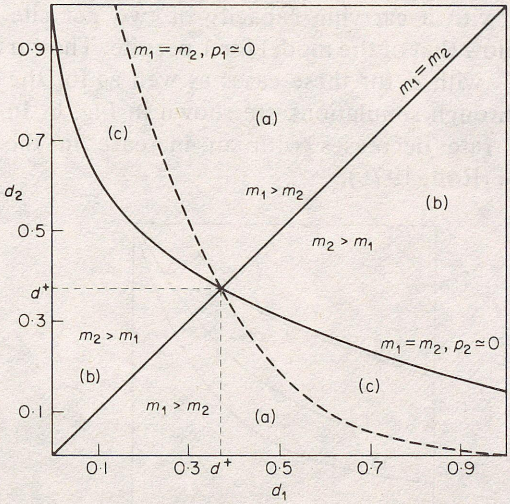

FIG. 5. A fate-map in the $d_1 - d_2$ plane depicting the relative magnitudes of m_1 and m_2. The space is divided into three regions: (a) $m_1 > m_2$ at all frequencies, (b) $m_2 > m_1$ at all frequencies, and (c) $m_1 > m_2$ or $m_1 < m_2$ depending on the frequency. $d_1 = d_2 = d^+$ represents the ESS. $\alpha = 0{\cdot}4$, $X_{11} = X_{12} = D_{21} = X_{22} = 1$.

frequencies, there is another curve along which m_1 equals m_2. On this curve, both the ds are suboptimal, but in different directions, one genotype dispersing far too much and the other too little such that the total mortality suffered through competition and dispersal deaths by each is the same. The set of such curves corresponding to the whole set of possible genotypic frequencies occurs within the region bounded by the two curves for the extreme genotypic frequencies, namely $p_1 \simeq 0$ and $p_1 \simeq 1$ shown as region C in Fig. 5 (Appendix C, Section 1). Note that the whole set of these curves intersects the line $d_1 = d_2$ at a single point $d = d^+$.

This point $d = d^+$ in fact represents the unbeatable strategy. Thus if $d_1 = d^+$, that population cannot be invaded by a genotype with any other d whereas this genotype can always invade a population with any $d \neq d^+$. The same argument holds for $d_2 = d^+$. The unbeatable strategy can also be derived analytically (Appendix C, Section 3).

When the fertilities are equal, the optimal dispersal rate d^+ depends only on α, the probability of survival of the dispersives and increases with α. For a carrying capacity of one per site, Hamilton & May (1977) show that

$$d^+ = \frac{1}{2-\alpha}$$

so that $d^+ = \frac{1}{2}$ even when $\alpha = 0$, increasing to $d^+ = 1$ at $\alpha = 1$.

For our model with a carrying capacity of two per site the optimal dispersal rate is below that of the model for 1 per site. The curves depicting the variation of d^+ with α for these cases as well as for the case of four per site derived through simulations are shown in Fig. 6. In general, the optimal dispersal rate decreases with an increase in the number of individuals per site (Roff, 1975).

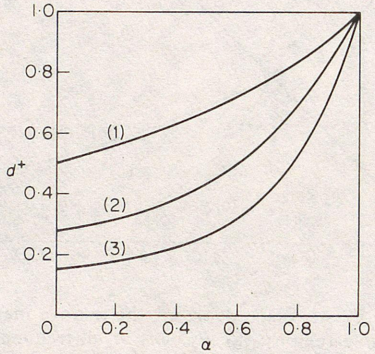

FIG. 6. The evolutionarily stable dispersal strategy d^+ as a function of survival of dispersives α for models with carrying capacities of one, two and four adults per site. $X_{11} = X_{12} = X_{21} = X_{22} = 1$.

(B) OPTIMAL VISCOSITY

The shape of the curves of $m_1 = m_2$ $(d_1 \neq d_2)$ in the $d_1 - d_2$ plane is similar to that of the contours of constant β, and for any set of genotypic frequencies the curve of $m_1 = m_2$ $(d_1 \neq d_2)$ nearly coincides with a contour of β (Figs 2 and 5). In fact, we find that the variation of β on the entire set of $m_1 = m_2$ $(d_1 \neq d_2)$ curves is negligible and to a first approximation, the value of β

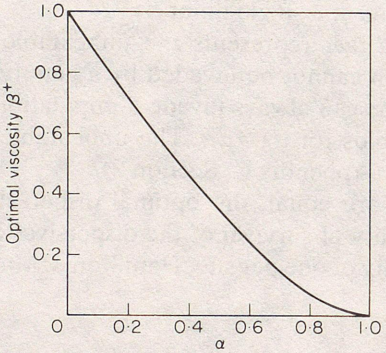

FIG. 7. Optimal viscosity β^+ as a function of survival of dispersives α. $X_{11} = X_{12} = X_{21} = X_{22} = 1$.

on this set of curves is equal to a constant, say β^{+}, irrespective of the genotypic frequencies. It is interesting to note that if the population viscosity β is less than β^{+}, then the genotype with a lower rate of dispersal is selected for; on the other hand, if the population viscosity is greater than β^{+} selection favours the genotype with a higher rate of dispersal. Hence β^{+} may be interpreted as the optimal level of viscosity for the population. Figure 7 depicts the variation of β^{+} with α, deduced from the expressions derived in Appendix C, Section 2.

4. Social Interactions

(A) PAY-OFF MATRICES

We may now generalize our model further to incorporate social interactions. Let the two competing genotypes be selfish (s) and co-operative (c). The effects of their behavioural traits will be manifest in their fertilities which will depend on who their neighbours are. When two co-operatives are neighbours they both do well, while, when a selfish individual is a neighbour of a co-operative it does well at the cost of the co-operative. When two selfish are neighbours, they both do only moderately well. Our main interest is to note how optimal d_s differs from optical d_c and how the optimal dispersal rate specified by other conditions, namely, the probability of survival of dispersives α, in turn affects the selection for selfish or co-operative traits.

While the outcome of competition betwen s and c will be determined primarily by their fertilities Xs it will be modulated by dispersal. These fertilities may be thought of as the pay-off matrices in a game, (Maynard Smith, 1976; Gadgil, Nanjundiah & Gadgil, 1980). Four classes of fertility matrices emerge for the conditions postulated above.

(*a*) $$X_{sc} > X_{cc} > X_{ss} > X_{cs}$$

Since $X_{sc} > X_{cc}$, a selfish genotype can invade a population of co-operatives, but since $X_{cs} < X_{ss}$ a co-operative cannot invade a population of selfish. Selfish is therefore an ESS for this payoff matrix.

(*b*) $$X_{cc} > X_{sc} > X_{ss} > X_{cs}$$

Since $X_{sc} < X_{cc}$ a selfish genotype cannot invade a population of co-operatives; also since $X_{cs} < X_{ss}$, a co-operative cannot invade a population of selfish. There is therefore a frequency dependence; and the final outcome depends on initial conditions.

(*c*) $$X_{cc} > X_{sc} > X_{cs} > X_{ss}$$

Since $X_{cs} > X_{ss}$ a co-operative can invade a population of selfish, but since $X_{sc} < X_{cc}$, a selfish cannot invade a population of co-operatives. Hence co-operative is the ESS.

(*d*) $$X_{sc} > X_{cc} > X_{cs} > X_{ss}$$

Since $X_{sc} > X_{cc}$, selfish can invade a population of co-operative and since $X_{cs} > X_{ss}$ co-operative can invade a population of selfish. Hence the final outcome is a stable co-existence of both types.

Note that in every case $X_{cc} > X_{cs}$ but $X_{sc} > X_{ss}$. Thus the co-operative genotype is always better off when its neighbour is like itself, but the selfish genotype is always better off when its neighbour is unlike itself.

(B) MINIMAX STRATEGIES

The outcome of the competitive process now depends on the dispersal strategies adopted, as well as differential fertilities arising from the social interactions. The effect of these social interactions can best be understood by studying the stability with respect to invasions by the other genotype (Appendix D) and comparing the resultant fate-maps in the $d_s - d_c$ plane (Fig. 8) with those obtained by assuming equal fertilities of the competing genotypes (e.g. Fig. 5). The regions in the fate-maps are no longer symmetric. The X_{ij} values govern the details of these regions, so that when the selfish geonotype is favoured as in case (a), the region where $m_s > m_c$ is much larger than the region where $m_s < m_c$. Furthermore, in this case, an evolutionarily stable dispersal strategy is available only to the selfish genotype (Fig. 8(a)). However, it is worth noting that even in this case there are combinations of $d_s - d_c$ values for which the co-operative genotype is favoured.

It is useful here to introduce the concept of a minimax dispersal strategy $\hat{d}$. Thus $\hat{d}_i$ is the minimax strategy for i if it serves to maximize $m_i - m_j$ given that j assumes the dispersal strategy which tends to minimize $m_i - m_j$. It is then the dispersal strategy under which i is doing the best it can, while j, its competitor is also doing the best it can. This concept holds even if $m_i - m_j < 0$, i.e. ith genotype is being eliminated even when it does its best. The minimax dispersal strategy $\hat{d}_i$ in that case will serve to reduce the rate at which i is eliminated to the lowest possible value.

For any given d_j, we can determine that $\hat{d}_i$ which maximizes $m_i - m_j$ (which also implies minimizing $|m_i - m_j|$ if $m_i < m_j$), and similarly for any given d_i we can determine that $\hat{d}_j$ which maximizes $m_j - m_i$. If these two curves intersect, they do so at a saddlepoint. The dispersal rates at this saddlepoint correspond to the minimax strategy for the two genotypes. For

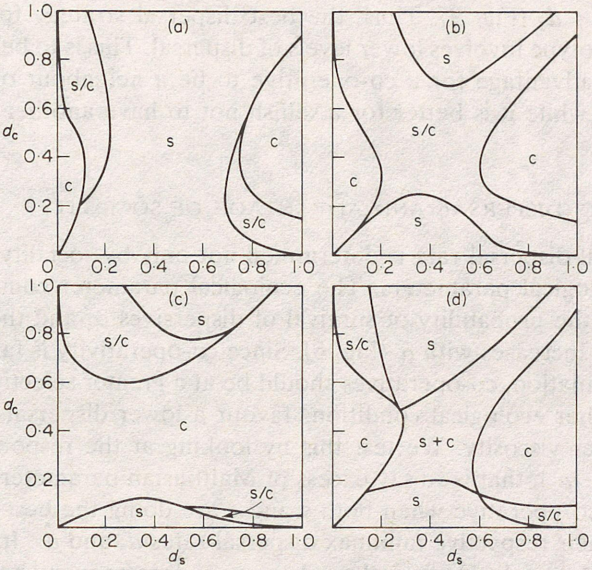

FIG. 8. Fate maps for the four classes of X_{ij} matrices for $\alpha = 0\cdot4$. (*a*) $X_{\mathrm{sc}}=1\cdot2$, $X_{\mathrm{cc}}=1\cdot1$, $X_{\mathrm{ss}}=0\cdot9$, $X_{\mathrm{cs}}=0\cdot8$, (b) $X_{\mathrm{cc}}=1\cdot2$, $X_{\mathrm{sc}}=1\cdot1$, $X_{\mathrm{ss}}=0\cdot9$, $X_{\mathrm{cs}}=0\cdot8$, (c) $X_{\mathrm{cc}}=1\cdot2$, $X_{\mathrm{sc}}=1\cdot1$, $X_{\mathrm{cs}}=0\cdot9$, $X_{\mathrm{ss}}=0\cdot8$, (d) $X_{\mathrm{sc}}=1\cdot2$, $X_{\mathrm{cc}}=1\cdot1$, $X_{\mathrm{cs}}=0\cdot9$, $X_{\mathrm{ss}}=0\cdot8$. The regions are marked as follows: S = selfish wins at all frequencies; C = co-operative wins at all frequencies; S/C = selfish or co-operative wins depending on initial frequency; S + C = selfish and co-operative co-exist stably.

our model such saddlepoints can be identified for every case. We consider the results of such an analysis for the matrix (a).

We find that although the exact values of $\hat{d}_{\mathrm{s}}$ and $\hat{d}_{\mathrm{c}}$ depend primarily on the probability of survival of the dispersives and on the fertility values, in

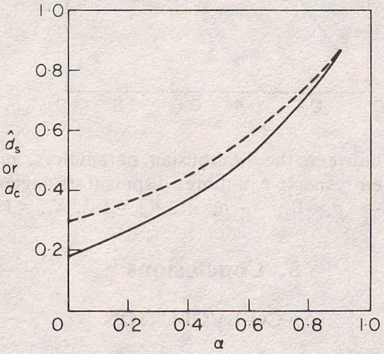

FIG. 9. The minimax strategies $\hat{d}_{\mathrm{s}}$ (– – –) and $\hat{d}_{\mathrm{c}}$ (——) as functions of survival of dispersives α. $X_{\mathrm{sc}}=1\cdot2$, $X_{\mathrm{cc}}=1\cdot1$, $X_{\mathrm{ss}}=0\cdot9$, $X_{\mathrm{cs}}=0\cdot8$, $p_{\mathrm{c}}\sim1$.

every case $\hat{d}_c < \hat{d}_s$ (Fig. 9). Thus, the best dispersal strategy for the co-operative genotype involves lower levels of dispersal. This is to be expected since it is of advantage for a co-operative to be a neighbour of another co-operative, while it is better for a selfish not to have another selfish as a neighbour.

(C) DISPERSAL AND ADVANTAGE OF SOCIALITY

The optimal dispersal rate is determined not only by sociality, but also by other ecological parameters. The ecological parameter considered in our model is the probability of survival of dispersives α, and the optimal dispersal rate increases with α (Fig. 6). Since co-operativity is favoured in a viscous population, co-operatives should be at a greater selective advantage when other ecological conditions favour a lower dispersal rate, and hence a higher viscosity. We test this by looking at the response of the value of $(m_s - m_c)$, that is to say excess of Malthusian parameter of selfish over that of co-operative when both s and c are doing the best they can, i.e. possess their respective minimax dispersal rates $\hat{d}_s$ and $\hat{d}_c$. In fact, our calculations (Appendix D) show that wherever α decreases and hence lower dispersal is favoured, the co-operative genotype has an increased selective advantage (Fig. 10).

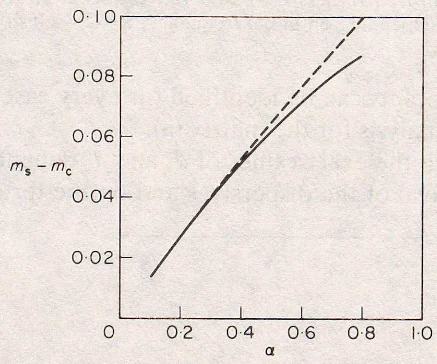

FIG. 10. The difference between the Malthusian parameters, $m_s - m_c$, when both the competitors have adopted their respective minimax dispersal strategies $\hat{d}_s$ and $\hat{d}_c$ as a function of survival of dispersive α. —— $p_s \sim 0$; - - - $p_s \sim 1$, $X_{sc} = 1{\cdot}2$, $X_{cc} = 1{\cdot}1$, $X_{ss} = 0{\cdot}9$, $X_{cs} = 0{\cdot}8$.

5. Conclusions

(A) CO-EVOLUTION

We have thus demonstrated with our model that (a) co-operativity favours higher levels of viscosity, and (b) higher levels of viscosity favour co-operativity. This implies a positive feedback between the evolution of greater co-operativity or altruism and the evolution of high levels of population viscosity. Thus, when ecological conditions favour high (low) levels of viscosity, the evolution of high (low) levels of co-operativity will be favoured. Whereas, when ecological conditions favour high (low) levels of co-operativity the evolution of high (low) levels of viscosity will be favoured. Given this positive feedback, a population initially below a threshold of co-operativity/viscosity will be expected to evolve in the direction of higher dispersal and lower co-operativity, while a population above the threshold should evolve in the direction of hgher co-operativity and viscosity (Fig. 11). We therefore expect that (a) viscosity and co-operativity will tend to be correlated, rather than distributed independently of each other, and (b) viscosity and co-operativity will be bimodally distributed.

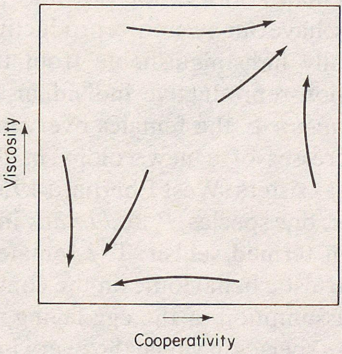

FIG. 11. Expected course of conjoint evolution of co-operativity and viscosity. A positive feedback should result in most animal societies evolving to the two expected modes of low co-operativity and low viscosity or high co-operativity and high viscosity depending on the initial conditions.

Hence we predict the existence of two kinds of animal societies—viscous and co-operative groups or non-viscous and selfish associations with few social groups exhibiting intermediate levels of co-operativity and viscosity.

The primitively social wasps provide interesting instances of these two kinds of societies showing the expected correlation between the dispersal and co-operative behaviour within a set of related species. Thus conspecific individuals of many species of Sphecid wasps nest in aggregations despite the availability of suitable nesting sites elsewhere. In one set of species there is much conflict amongst individual members of such aggregations which are often known to include unrelated females (Eickwort, 1981). This conflict may take the form of usurpation of nests and robbery of prey as in *Cerceris simplex* (Alcock, 1975). On the other hand there is little conflict especially in terms of prey stealing in another Sphecid *Trigonopsis cameronii* (Eberhard, 1972). These Sphecid wasps in fact provide excellent material to test our prediction of the existence of two kinds of animal societies with few intermediates. We expect that in this taxon one set of species has evolved along the communal mode with nest mates expected to be unrelated and in considerable conflict (e.g. *Cerceris simplex* and *Lindenius columbianus erranus*) and others to have evolved along the quasisocial or even eusocial mode with nest mates closely related and co-operative or altruistic (e.g. *Trigonopsis cameronii* and *Microstigmus comes*) (Eickwort, 1981; Matthews, 1968).

Another striking example of the correlation between the evolution of viscosity, co-operativity/altruism is furnished by species of the primitively eusocial wasp genus *Polistes*. In the temperate zone species of this genus several overwintering females born in the previous fall establish a colony together. Such colonies have many non-reproductive workers, although these are morphologically indistinguishable from the egg layer. In the species in which such non-reproductive individuals behave altruistically, e.g. *P. fuscatus* and *P. metricus* the females overwinter near their colony of birth and the foundresses of a new colony in the spring are closely related individuals such as sisters (West Eberhard 1969, Ross and Gamboa, 1981). There is, however, one species, *P. exclamans* in which the association of foundresses has been termed selfish. The females at a colony exhibit little co-operative or altruistic behaviour; on the contrary, there is tremendous conflict over the assumption of the egg laying role. As expected this is the only known *Polistes* species in which the overwintering females appear to disperse very widely (MacCormack, 1982). The polistine wasps are therefore another taxon in which our predictions may be tested. Finally while our model is too simple to directly apply to mammals, it would be worthwhile examining the distribution of co-operativity and viscosity in a taxon such as ungulates. In this animal group the viscous, co-operative mode is exemplified by species like the African elephant (*Loxodonta africana*) and the non-viscous selfish mode by species like the wildebeest (*Connochaetes taurinus*) (Douglas-Hamilton, 1972; Estes, 1974).

(B) MALE AND FEMALE

Our results are also likely to be applicable to the patterns of dispersal and social behaviour within two sexes of a given animal species. If we assume that inbreeding imposes a high enough cost, there will be selection for the dispersal of at least one of the sexes. Then the sex that indulges less in co-operative behaviour, and more in competitive behaviour is more likely to disperse than the sex that engages less in competitive and more in co-operative behaviour.

This prediction is borne out by primitively eusocial polistine wasps of the genus *Mischocytharus*. In these wasps males exhibit no co-operative/altruistic behaviour and are presumed to disperse widely, while females which develop altruistic sterile caste are known to remain close to their birthplace (Jaenne & Bermudez, 1980; Little, 1981). Amongst the social insects there is no known instance of males co-operating more strongly than the females and also no known examples of males staying together while females disperse. It is therefore tempting to quote possible instances from mammals although admittedly our simple model does not cover this case. Female dispersal seems to characterize species such as *dhole*, the Indian Wild dog (*Cuon alpinus*) where only one of the pack females breeds excluding others while males co-operate regularly in hunting (Johnsingh, 1982). Male dispersal on the other hand characterizes species such as elephant in which males compete greatly for access to females, while females show high levels of co-operative and altruistic behaviour (Douglas-Hamilton, 1972).

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APPENDIX A

The site frequencies of the three types of sites 1-1, 1-2, 2-2 are f_{11}, f_{12}, f_{22} respectively. The genotypic frequencies are then given by

$$p_1 = f_{11} + \tfrac{1}{2} f_{12}, \qquad p_2 = f_{22} + \tfrac{1}{2} f_{12}.$$

Given f_{ij} and p_i at any point of time, those at the subsequent generation can be computed as follows:

The number of offspring of the genotype i are

$$n_i = 2 f_{ii} X_{ii} + f_{ij} X_{ij}, \qquad i = 1, 2 \text{ with } j \neq i$$

The numbers dispersing are $n_i d_i$ and of these, $\alpha n_i d_i$ survive the dispersal mortality. The pool of the dispersives consists of $\alpha n_1 d_1$ individuals of genotype 1 and $\alpha n_2 d_2$ of genotype 2. Of these a portion f_{11} settle on sites which were origninally of type 1-1, f_{12} on sites 1-2 and f_{22} on sites 2-2 respectively.

The numbers competing at a site type ij after the arrival of the dispersives is $2D_{ij}$ where

$$D_{ij} = [1 + X_{ij}(1 - d_i) + X_{ji}(1 - d_j) + \alpha(n_1 d_1 + n_2 d_2)]/2. \tag{A2}$$

The frequencies of the two genotypes at the different sites involved in this competition can be readily evaluated. The frequency of the first genotype at the three types of sites is

$$\eta_{11} = \frac{2 + 2X_{11}(1 - d_1) + \alpha d_1 n_1}{2D_{11}}; \qquad \eta_{12} = \frac{1 + X_{12}(1 - d_1) + \alpha d_1 n_1}{2D_{12}};$$

$$\eta_{22} = \frac{\alpha d_1 n_1}{2D_{22}}. \tag{A3}$$

Note that at the 1-1 and 1-2 sites the residents as well as a part of the dispersive pool are of genotype 1 whereas at the 2-2 site, only the dispersive pool contains individuals of this type.

Since the individuals at any site compete on an equal footing, the frequency of the site type 1-1 in the next generation is

$$f_{11}(t+1) = \eta_{11}^2(t) f_{11}(t) + \eta_{12}^2(t) f_{12}(t) + \eta_{22}^2(t) f_{22}(t) \tag{A4}$$

and the genotypic frequency is

$$p_1(t+1) = \eta_{11}(t) f_{11}(t) + \eta_{12}(t) f_{12}(t) + \eta_{22}(t) f_{22}(t). \tag{A5}$$

The equations (A4) and (A5), which are appropriate for sampling with replacement, can be used for our model provided that the numbers competing at a site are sufficiently large. Henceforth, we assume that this condition is satisfied. For example, for d_1, $d_2=\frac{1}{2}$, $\alpha=0{\cdot}2$ and p_1, $p_2=\frac{1}{2}$, this assumption is valid when the number of sffspring is of the order of 25. The error introduced in this case is less than 5%. The equations for the evolution of the frequencies of the other types of sites are derived in a similar manner. These along with equation (A4) specify the dynamics of the model which forms the basis of the simulations carried out.

APPENDIX B

The Malthusian parameter of a genotype i is

$$m_i = b_i - \mu_{di} - \mu_{ci}$$

where b_i = number of offspring per individual of type i, μ_{di} = number of deaths of type i during dispersal per individual of genotype i, μ_{ci} = number of deaths of type i during competition for sites per individual of genotype i.

From Appendix A,

$$b_i = \frac{n_i}{2p_i}; \qquad \mu_{di} = \frac{(1-\alpha)n_i d_i}{2p_i}.$$

The risk of mortality due to competition for genotype 1 at sites of types $i-j$ is given in terms of D_{ij} (equation (A2)) as

$$R_{ij} = 1 - \frac{1}{D_{ij}}. \tag{B1}$$

The competition mortality per individual of genotype 1 is then

$$\mu_{c1} = (R_{11}z_{11}f_{11} + R_{12}z_{12}f_{12} + R_{22}z_{22}f_{22})/2p_1$$

where z_{ij} is the number of individuals of type 1 at a site of type ij, that is

$$\begin{aligned} z_{11} &= 2 + 2X_{11}(1-d_1) + \alpha d_1 n_1; \\ z_{12} &= 1 + X_{12}(1-d_1) + \alpha d_1 n_1; \\ z_{22} &= \alpha d_1 n_1. \end{aligned} \tag{B2}$$

A similar expression can be derived for μ_{c2}. Hence

$$m_1 - m_2 = \frac{n_1}{2p_1}(1 - d_1 + \alpha d_1) - \mu_{c1} - \frac{n_2}{2p_2}(1 - d_2 + \alpha d_2) + \mu_{c2}. \tag{B3}$$

Note that equation (B3) measuring the difference in the fitnesses depends upon the site frequencies, fertilities and dispersal rates.

APPENDIX C

1. Equifitness Curves

Here we consider the results for the special case when all elements of the fertility matrix X_{ij} are equal (say X). In other words, the genotypes differ only in their dispersal strategies. Then the total number of offspring of each genotype are

$$n_i = 2p_iX. \tag{C1}$$

The numbers competing at each site type are proportional to

$$D_{ij} = [1-(d_i+d_j/2)+\alpha(d_1p_1+d_2p_2)]X+1. \tag{C2}$$

Since X is large, the last term in equation (C2), corresponding to the presence of the parents in competition at the sites, becomes negligible, and to zeroth order in $1/X$, the expression for m_1-m_2 (equation (B3) reduces to

$$\begin{aligned} m_1-m_2 = {} & \frac{f_{11}(1-d_1)}{p_1D_{11}} - \frac{f_{22}(1-d_2)}{p_2D_{22}} + \left[\frac{1-d_1}{2p_1} - \frac{1-d_2}{2p_2}\right]\frac{f_{12}}{D_{12}} \\ & + \alpha(d_1-d_2)\left[\frac{f_{11}}{D_{11}} + \frac{f_{12}}{D_{12}} + \frac{f_{22}}{D_{22}}\right]. \end{aligned} \tag{C3}$$

If we also assume that the selection is slow enough for a quasi-steady site frequency distribution to be achieved i.e.

$$f_{11}-p_1^2 = f_{22}-p_2^2 = \beta p_1p_2. \tag{C4}$$

The expression for m_1-m_2 can be further simplified to

$$\begin{aligned} m_1-m_2 = {} & (1-d_1)\left[\frac{p_1+\beta p_2}{D_{11}} + \frac{p_2(1-\beta)}{D_{12}}\right] \\ & -(1-d_2)\left[\frac{p_2+\beta p_1}{D_{22}} + \frac{p_1(1-\beta)}{D_{12}}\right] \\ & +\alpha(d_1-d_2)\left[\frac{p_1^2}{D_{11}} + \frac{p_2^2}{D_{22}} + \frac{2p_1p_2}{D_{12}} \right. \\ & \left. +\beta p_1p_2\left(\frac{1}{D_{11}} + \frac{1}{D_{22}} - \frac{1}{D_{12}}\right)\right]. \end{aligned} \tag{C5}$$

Equations determining the set of curves delineating the different regions in d_1-d_2 plane are given by setting expression (C5) equal to zero.

The limiting curves of this set can be obtained by taking the limits $p_1 \to 1$; $p_1 \to 0$. This yields the equations of these curves as

$$\frac{1-d_1+\alpha(d_1-d_2)}{1-d_1+\alpha d_1}-\frac{(1-d_2)\beta}{1-d_2+\alpha d_1}-\frac{2(1-\beta)(1-d_2)}{2-(d_1+d_2)+2\alpha d_1}=0 \qquad \text{(C6)}$$

$$\frac{1-d_2+\alpha(d_2-d_1)}{1-d_2+\alpha d_2}-\frac{(1-d_1)\beta}{1-d_1+\alpha d_2}-\frac{2(1-\beta)(1-d_1)}{2-(d_1+d_2)+2\alpha d_2}=0. \qquad \text{(C7)}$$

Note that both the equations (C6) and (C7) are satisfied along the line

$$d_1 = d_2. \qquad \text{(C8)}$$

The set of curves satisfying equations (C6) and (C7) which does not contain the line (C8) intersects it at a single point d^+. Our calculations show that for this set of curves the value of β is nearly constant, say β^+. Equations (C6) and (C7) with β set equal to β^+ then specify the curves delineating the region C in Fig. 5. To determine d^+ and β^+, we first determine the relation of β to the dispersal rates and the probability of survival α, in the vicinity of the line (C8).

2. Population Viscosity

Once a quasi-steady frequency distribution has been attained, i.e.

$$f_{11}(t)-p_1^2(t)=f_{22}(t)-p_2^2(t)=\beta p_1(t)p_2(t) \qquad \text{(C9)}$$

then the relation holds for all subsequent generations. Hence

$$f_{11}(t+1)-p_1^2(t+1)=\beta p_1(t+1)p_2(t+1). \qquad \text{(C10)}$$

These equations are used in the derivation of the expression for β. The relations between $f_{11}(t+1)$, $p_1(t+1)$ and the genotypic and site frequencies at t is given by equations (A1)–(A5). We consider the limiting forms of these as the dispersal rates d_2 and d_1 become equal. Then in terms of

$$D = 1-d+\alpha d \qquad \text{(C11)}$$

the transition probabilities η_{11} etc. become

$$\eta_{11}=\frac{1-d+\alpha d p_1}{D}; \qquad \eta_{12}=\frac{1-d+2\alpha d p_1}{2D}; \qquad \eta_{22}=\frac{\alpha d p_1}{D}.$$

Use of equations (C9) and (A4) and simplification yields the frequency of the 1-1 type of site at the next generation as

$$f_{11}(t+1)=\frac{(1-d)^2}{2D^2}(1+\beta)p_1p_2+p_1^2.$$

In the limit of equal dispersal rates, the genotypic frequency remains the same

$$p_1(t+1)=p_1(t).$$

Hence the equation determining β becomes

$$\beta=\frac{(1-d)^2}{2D^2}[1+\beta]$$

i.e.

$$\beta=\frac{(1-d)^2}{2D^2-(1-d)^2}$$

$$\beta=\frac{(1-d)^2}{2(1-d+\alpha d)^2-(1-d)^2}. \tag{C12}$$

Note that as d changes from zero to unity β changes from unity to zero. The above derivation can also be interpreted as follows: Even when the genotypes are identical in all respects, the site frequencies change with time until quasi-steady distribution (C9) with β given by (C12) is attained.

3. Unbeatable Strategy

In the limit of equal dispersal rates, the expression (C5) can be approximated by

$$m_1-m_2\approx\frac{(d_1-d_2)}{2(1-d+\alpha d)^2}\varphi(d,\alpha) \tag{C13}$$

where

$$\varphi(d,\alpha)=(1-d)[\beta-1+2\alpha]-2\alpha d(1-\alpha) \tag{C14}$$

with d referring to the average of the two dispersal rates. In the approximation of equations (C13) and (C14) higher order terms beginning with those of order $(d_1-d_2)^2$ have been neglected. The parameter β in this limit is given by equations (C12).

The set of curves along which m_1 equals m_2 but $d_1\neq d_2$, is represented in the vicinity of the line $d_1=d_2$ by the equation

$$\varphi=0.$$

Thus the intersection of this set of curves and the line $d_1=d_2$ occurs at the point $d=d^+$ which satisfies

$$(1-d^+)[\beta(d^+,\alpha)-1+2\alpha]-2\alpha d^+(1-\alpha)=0$$

or combining with equation (C12) we get

$$(1-d^+)\left[\frac{(1-d^+)^2}{2(1-d^+ + \alpha d^+)^2-(1-d^+)^2} - 1 + 2\alpha\right] - 2\alpha d^+(1-\alpha) = 0. \qquad \text{(C15)}$$

Note that φ is a monotonically decreasing function of d. Hence in the neighbourhood of d^+

$$\varphi(d) > 0 \quad \text{if } d < d^+$$

$$\varphi(d) < 0 \quad \text{if } d > d^+.$$

Hence if $d_1 = d^+$, and $d_2 < d_1$, then since $\varphi(d)$ is positive

$$m_1 > m_2.$$

Again if $d_2 > d_1$ then since $\varphi(d)$ is negative

$$m_1 > m_2.$$

Hence the dispersal strategy

$$d = d^+$$

which is a root of the equation (C15) is the unbeatable strategy.

APPENDIX D

The dynamics of the distribution of the site frequencies f_{11}, f_{12} and f_{22}, for a given set of d_1, d_2 and α, has been described in Appendix A. The time evolution of the site frequencies can be expressed as

$$\begin{pmatrix} f_{11}(t+1) \\ f_{22}(t+1) \end{pmatrix} = \mathbf{A}\begin{pmatrix} f_{11}(t) \\ f_{22}(t) \end{pmatrix} + \mathbf{B}. \qquad \text{(D1)}$$

Where **A** is a 2×2 matrix and **B** a column vector, and the elements of **A** and **B** are functions of d_1, d_2, α_1, $f_{11}(t)$ and $f_{22}(t)$. For equilibrium

$$\begin{pmatrix} f_{11}(t+1) \\ f_{22}(t+1) \end{pmatrix} = \begin{pmatrix} f_{11}(t) \\ f_{22}(t) \end{pmatrix}. \qquad \text{(D2)}$$

Clearly, a population consisting of only one genotype, corresponds to an equilibrium point. It is of interest to determine whether such equilibria are stable with respect to invasions by the other genotype. If the initial perturbation in the site frequencies induced by the invasion decays (increases) with time, i.e. if the equilibrium is stable (unstable), the population will be considered uninvadable (invadable). The initial growth of the perturbation is governed by the equation

$$\begin{pmatrix} f_{11}^0(t+1)+\delta f_{11}(t+1) \\ f_{22}^0(t+1)+\delta f_{22}(t+1) \end{pmatrix} = (\mathbf{A}^0+\mathbf{A}')\begin{pmatrix} f_{11}(t)+\delta f_{11}(t) \\ f_{22}(t)+\delta f_{22}(t) \end{pmatrix} + \mathbf{B}^0+\mathbf{B}'. \qquad \text{(D3)}$$

Where the superscript zero denotes equilibrium values and the prime, differentiation with respect to f_{11} and f_{22}. The above equations reduce to

$$\begin{pmatrix} \delta f_{11}(t+1) \\ \delta f_{22}(t+1) \end{pmatrix} = \mathbf{T}\begin{pmatrix} \delta f_{11}(t) \\ \delta f_{22}(t) \end{pmatrix}. \qquad \text{(D4)}$$

Where the elements of the 2×2 matrix $\mathbf{T}$, obtained from the elements of $\mathbf{A}^0$, $\mathbf{A}'$ and $\mathbf{B}'$, are functions of f_{11}^0, f_{22}^0, α, d_1 and d_2.

The equilibrium (f_{11}^0, f_{22}^0) is *unstable* if λ_{max}, the largest eigenvalue of $\mathbf{T}$ is greater than unity, and is stable otherwise. (Beddington, 1974).

To obtain the fate maps for a given payoff matrix and for a given value of α, the above analysis was carried out for various pairs of (d_1, d_2), for the two equilibrium points $(f_{11}^0 = 1{\cdot}0, f_{22}^0 = 0{\cdot}0)$ and $(f_{11}^0 = 0{\cdot}0, f_{22}^0 = 1{\cdot}0)$. Any genotype which is uninvadable by the other and is able to invade the other, is selected for. When both the populations are uninvadable, the final state is determined by the initial composition. In the case in which both the populations are invadable, both genotypes co-exist.

The contours of $\lambda_{\text{max}} = 1$ form the boundaries of the various regions in the fate maps. In fact, the value of $(\lambda_{\text{max}} - 1)$ is equal to the difference between the fitnesses, $m_1 - m_2$. This fact was used for the calculations carried out to obtain Figs 9 and 10.

It may be mentioned here that this analysis was carried out separately for the case of non-overlapping generations as well as for overlapping generations, and within the assumptions of our model (number of offspring $\gtrsim 25$), the results were identical.

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Workshop on Frontiers of Evolutionary Biology

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The last two decades have witnessed major advances in our understanding of evolution. On one hand, the spectacular progress of molecular biology has made it possible to look at molecular events which lead to evolutionary changes in organisms. On the other hand, beginning with the concept of inclusive fitness developed by William Hamilton, a theoretical framework is being established which promises to give insights into the evolution of complex social and cultural behaviour.

To review these experimental and theoretical findings in a coherent manner and to take a critical look at the impact these have had on evolutionary theory, a workshop on 'Frontiers of Evolutionary Biology', organized by the Center for Theoretical Studies and the Centre for Ecological Sciences of the Indian Institute of Science, Bangalore, was held at Rishi Valley School, Madanapalli, Andhra Pradesh, India during 26 June - 2 July 1983. The speakers were Madhav Gadgil, M.S. Shaila, Raghavendra Gadagkar, N.V. Joshi and Sulochana Gadgil from Indian Institute of Science, Bangalore and Vidyanand Nanjundiah and L.C. Padhy from Tata Institute of Fundamental Research, Bombay.

The serene surroundings of the Rishi Valley School, the lively interest and curiosity of the students and the enthusiastic hospitality of the staff of Krishnamurthy Foundation contributed greatly towards making the workshop a very enjoyable and successful one.

Historical Perspective

The inaugural lecture by Madhav Gadgil was on the history of evolutionary ideas. Discussing the riddle of the origin of the tremendous variety of living forms, he pointed out that any history explaining this should also account for the fitness of design observed in living organisms, and for the presence in them of only a small number of basic structural plans. Beginning with the views of Hindu and Christian mythologies on these matters, he traced the development of the subject through the catastrophist ideas of Baron Cuvier, the uniformist approach of Charles Lyell and the organic evolution hypothesis of Lamark up to Charles Darwin. The rigorousness of the scientific method as practised by Darwin when putting forward his principle of natural selection was discussed, and the heuristic value of theory in making testable predictions was emphasized. A description of the advances in evolutionary theory by Fischer, Haldane and Wright, who brought together Mendelism and Darwinism, was followed by a discussion on Seawall Wright's studies on evolutionary processes in small subdivided populations. While commenting on the current focus of the theory on the interplay between the levels of selection—individual, kin, group, communities, etc.—Madhav Gadgil also briefly indicated the topics to be discussed in the workshop.

Tempo and Mode of Evolution

Vidyanand Nanjundiah, in a series of four talks, discussed the tempo and mode of evolution, especially in view of the recent advances in the knowledge about the structure and function of genes, and the recent surge of interest in paleontology, bringing the concept of punctuated equilibrium to the forefront.

Describing 'What has happened during evolution', he pointed out that though the diversity of biological forms was enormous (an estimated 200 million species having existed so far, with 2 million currently existing), the distribution was very uneven. Thus, arthropods account for more than 80% of the animal forms, and insects, more than 90% of the arthropods. Tracing the course of evolution from prebiotic times, he indicated that the basic structural body plans of today were already present around 500 Myr BP, shortly after the emergence of multicellular organisms. The 'trends' observed in evolution, including increase in complexity, reduction in the number of identical body parts, increase in the number of specialised cell types, increase in DNA content, etc., were discussed with a cautionary note that many of these sequences could be simulated by random walk models. Evolutionary changes in the genome were reviewed next, with the observation that perhaps 90% of the enzymes were common between procaryots and mammals. This suggested that changes in the regulatory genes might have been important in evolution. The possible role of gene duplication and of whole genome duplication in evolution was described, together with the supportive data on distribution of DNA contents in related organisms. The recent laboratory studies which showed that recently evolved genes tended to be positioned 180° away from functionally similar genes on the circular DNA of bacteria highlight the importance of genome duplication in evolution.

Reviewing the rates of evolution, Vidyanand Nanjundiah described the two rates — the morphological rate dealing with changes in quantitative characters, and the taxonomic rate dealing with diversification. These two are correlated, but show a wide range of variation. Moreover, this variation seems to be such that short periods of rapid evolution are interspaced with relatively long periods of slow changes. This was strikingly illustrated with the examples of Molluscan lineages from lake Turkana in East Africa, where periods of slow changes in morphology stretching over 5×10^5 years are interspaced with two episodes of 5×10^3 years' duration, when rapid modification and speciation occurred. The possible role of environmental changes on evolutionary rates was also discussed.

Looking at biochemical evolution, he pointed out that the rates seemed constant for any given protein, but differed widely from one protein to another. Moreover, these do not seem to correlate with morphological or taxonomic rates. On the other hand, rates of gene rearrangement, as reflected in changes in chromosome numbers, correlated well with taxonomic rates. This suggested two modes of evolution — the slow microevolution, confined to changes within a lineage and the rapid macroevolution, leading to taxonomic diversity.

The two current viewpoints on macroevolution were described. The orthodox or neo-Darwinist view takes it to be due to speeded up rates of evolution. Most cases of speciation are said to be allopatric. The scenario is that of a small population on the periphery of a large one, exposed to a somewhat different environment. If isolated from the parent population due to some reason, inbreeding and environmental stress would lead to the occurrence and rapid selection of new phenotypes. The geographical isolation is thus likely to be succeeded by reproductive isolation, giving rise to speciation. The unorthodox school emphasizes macromutations — large scale changes such as gene duplication or genome duplication as well as developmental mutation, which cause drastic changes in the phenotype (homeotic mutations). This point of view holds that there are saltatory jumps in evolution and the unit of selection for macroevolution is the species, this being qualitatively different from microevolution.

Changes at the Genome Level

Vidyanand Nanjundiah concluded his series of talks by describing the transposable elements. These are segments of DNA which can transpose from one location to the other within a genome. A functional gene is transcribed into a messenger RNA, which in turn acts as a template for the synthesis of complementary DNA segment, which is then reintegrated into the genome. The evolutionary potential of this phenomenon is obvious. He also described hybrid dysgenesis in drosophila, wherein hybrid sterility (reproductive barriers) seems to be present for certain inter-strain mating. This could serve as a model for the beginning of speciation, and the possible role of transposable elements in hybrid dysgenesis was discussed in detail.

A historical overview of the processes which bring about changes in the genetic material was presented by L.C. Padhy. Emphasizing the fact that the pairing of the complementary strands was the fundamental feature for self-perpetuation, he discussed chemical evolution from the point of view of natural selection. The specificities of polymerization for the nucleic acids were described, and the importance of nearly faithful (as opposed to totally faithful) replication was brought out. The possibility that RNA might have been the first genetic material was indicated and was followed up with a fascinating account of experiments which simulated RNA evolution in a test tube. A brief summary of the processes involved in macroevolution — inversion, recombination, reverse transcription, gene amplification, etc. — was also given by Padhy.

M.S. Shaila discussed genetic variation in the natural populations, and the methods of estimating it. The two indices of genetic variation in a population are: (i) the proportion of polymorphic loci in the genome, and (ii) the average proportion of heterozygous loci in an individual. The electrophoresis techniques of measuring these indices were discussed, along with the problems associated with the measurement. Shaila also discussed the relationship between fitness and heterozygosity in natural populations, and described various factors responsible for the maintenance of heterozygosity in natural populations.

Levels of Natural Selection

The concept of kin selection was discussed by Madhav Gadgil. Casting individual selection in the formalism of population genetics, he pointed out that only those traits would be selected which benefit an individual, even if they are detrimental to the species as a whole. With this background, it was difficult to account for the evolution of altruistic traits, till W.D. Hamilton looked at the problem in terms of interactions between close relatives. It was formally shown that the gene giving rise to an altruistic trait would spread in a population if the recipient of such an act was a blood relative of the donor, and the product of the benefit to the recipient and the coefficient of relationship was greater than the cost to the donor. Gadgil demonstrated how this concept of kin selection led to several predictions, especially for social insects, and illustrated the case of sex ratio control of reproductives by sterile workers in social hymenoptera. He also emphasized the importance of the ability of recognising conspecifics (kin recognition) and suggested that developing behavioral strategies appropriate for specific individual interactions would have played a significant role in the evolution of the capacity for learning.

Raghavendra Gadagkar presented an indepth analysis of the evidences put forward to account for the evolution of altruistic traits in social insects. Discussing the three hypotheses about the evolution of sterile castes in social hymenoptera — kin selection, mutualism and parental manipulation — he indicated the kind of data necessary to test these. A critical analysis of the available field data showed that it was indeed difficult to unambiguously accept any one of them. The various factors making the phenomenon more complex — local mate competition, multiple mating, etc. — were also discussed. Gadagkar then emphasized the importance of kin recognition for kin selection to be operative and described the experiments aimed at elucidating these. Thus, a guard bee is more likely to let a worker bee enter the nest, if they are genetically more closely related. Describing evidences from the study of honey bees, wasps, sweat bees, ground squirrels, vervet monkey, etc., he pointed out that genetic relatedness as well as environment was important for kin recognition, and suggested that learning is also likely to play a major role. He also emphasized the necessity of distinguishing between the evolutionary factors responsible for the origin of sociality, and those responsible for its maintenance.

Selection acting at the level of groups of individuals (group selection), dealing particularly with conditions where traits beneficial to the group as a whole at some cost to the individual are selected for, was discussed by N.V. Joshi. Early mathematical models of group selection had indicated that the conditions required to favour group selection were too stringent to make it a significant evolutionary force. However, the recent work of D.S. Wilson has shown that if the population consists of well-separated groups of individuals, with occasional episodes of mixing, group productivity assumes an important role. This concept of structured demes was discussed in detail along with a number of biological examples illustrating it. The approach together with more recent mathematical models, suggests that group selection is likely to have played a major role, especially in the evolution of communities.

Evolution of Sex

Sulochana Gadgil discussed the theories dealing with the origin and maintenance of sex. The basic difference between parthenogenetic and sexual reproduction is the existence of genetical dissimilarity between offspring and parent in the latter. Theoretical models had pointed out the two-fold advantage of parthenogeny over sexual reproduction. Arguments for evolution of sex based on group selection and group extinction mechanisms were not very conclusive. Sulochana Gadgil discussed the ecological correlates of parthenogenetic species and pointed out that these enjoyed relatively stable and non-responsive environment. Simple models incorporating fluctuating environment were formulated, and were shown to be rather inadequate to account for evolution of sex. Only when population genetic models with multiple loci were considered, it was seen that sexual reproduction did have an advantage over parthenogeny. Based on this analysis, mainly due to Hamilton, Gadgil suggested that evolution under complex biotic environment (hostile co-evolution) would favour the evolution of sex. She also pointed out the similarities in the conditions favouring evolution and maintenance of sex, and those favouring preponderance of polymorphism.

Cultural Evolution

Evolution and spread of cultural traits was discussed by Madhav Gadgil in the last three lectures of the workshop. Though much of the animal behaviour is genetically programmed, it is both necessary and advantageous 'to learn' certain aspects of behaviour — use of landmarks by digger wasps to identify their nests, for example. Especially in higher animals, many aspects of behaviour dealing with food choice, predator avoidance and conspecific recognition are not completely genetically programmed and have to be learned. Discussing teaching and learning in animals, Gadgil defined culture to be the transmission of behavioral information through non-genetic means, and pointed out that the genetic make-up may introduce biases and impose constraints on the ability and capacity to learn. A mathematical model describing such a co-evolution of genetic and behavioral traits was discussed. Gadgil described how natural selection could operate on cultural traits as well, and suggested that an approach incorporating the hierarchy of habitat — economy — social structure and cultural behaviour would be needed to understand the evolution and spread of cultural traits in complex human societies. Tracing the history of the social systems in India through the last several thousand years, he indicated how one can look at the caste system in India from an ecological perspective. Illustrating this point with his study of the hunting habits of some of the castes in Maharashtra, he indicated that the application of notions of evolutionary biology to the whole field of human social behaviour would be an exciting endeavour in the years to come.