Insect Distribution Patterns in the Solomon Islands

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LAND FAUNA

Insect distribution patterns in the Solomon Islands

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Among insects in the Solomon Islands some endemic taxa show restricted island distributions. An account of these is given and they are related to a continuous process of expansion of new taxa from the West and replacement of older ones. This is accompanied by speciation and subspeciation and shifts in habitat. The results of ecological studies are summarized which illustrate the types of selection operating at different stages of the cycle. The importance of island area and distance from other islands is emphasized.

Introduction

A striking feature of animal distributions in the Solomon Islands, as in other Pacific archipelagoes, is the presence of endemic taxa restricted to one or a few islands. Zoogeographical problems presented by the Solomons' fauna are to establish what are the most important types of restricted pattern, their probable origin and the relation they bear to other distribution patterns on a larger scale in the South-West Pacific. Analyses of these local distributions have already been made for birds and for certain insects in the Solomons (Greenslade 1968*a*, *b*). The conclusions are summarized here with a discussion of assumptions which were necessary. In addition, the results of some ecological studies are briefly described to support the zoogeographical approach which is adopted. Although the main concern is with insects reference is made also to birds since much better distribution data are available in this group.

Distance and area in the South-West Pacific

The dominant distribution patterns in the region of the Solomon Islands result from the expansion of species' areas eastwards into the Pacific out of New Guinea and the wet, tropical land mass of continental Asia to the west. With successive sea gaps between islands and archipelagoes and increasing distance from these sources the diversity of island faunas declines in terms of the number and range of taxa represented, as one species or group after another fails to cross water barriers. This sets up what have been referred to as immigrant patterns by Darlington (1957) and these have been demonstrated for a variety of vertebrates and invertebrates by Darlington (1957), Zimmerman (1949), Gressitt (1961) and others. As land masses are much smaller in the Pacific than to the west, land area is also involved in determining the size of faunas on islands. A positive relation between land area and the number of species present has been found in the great majority of cases examined in the tropical Pacific. Even so there remains much work to be done on the area–fauna size relation. In many animal groups there are obstacles to obtaining complete species lists in the form of taxonomic and collecting difficulties. An alternative approach which to some extent circumvents these is through studying the numbers of species in local faunas since Wilson (1961) was able to show a correlation between total fauna size and the number of species in typical localities for Melanesian ants. A possible extension of this would be to use the diversity of species in many small samples (Williams 1964) in those cases where it is measurable. This method might allow investigation of the area relationship itself and provide a tool for studying its ecological implications. Although large area will in practice often include a habitat diversity factor this does not seem essential to the fauna size–area relation. A small island would be expected in theory to support fewer species than a larger one even if the habitats were identical on each, simply because the average population density of species would be lower and the chances of extinction correspondingly high.

The most important large-scale pattern in the tropical western Pacific then is one of diminishing size of faunas with distance from sources lying to the west. Included are an observable area effect and assumed eastwards expansion. This assumption is the only one to provide a satisfactory general explanation for the majority of distribution patterns in the area of the Solomon Islands and should present no difficulties given Darlington's (1957) distinction between immigrant and relict patterns. On this basis it is often possible to identify source areas as those with large numbers of species and to recognize as expanding species those with continuous distributions extending from sources. Supporting evidence comes from the taxonomic affinity of species. It is also possible to distinguish cases of peripheral radiation or of central replacement.

MacArthur & Wilson (1963, 1967) put forward an equilibrium model which incorporates both distance and area. According to this, immigration rates vary with the distance of islands from sources so that the greater the intervening sea gaps the smaller the chances of propagules of a species crossing them. At the same time extinction rates on islands vary with their area and the number of species present. In the case of a large fauna on an island the extinction rate is higher than if the fauna were small since there are many species available to become extinct and average population densities must be relatively low. Mayr (1965) independently suggested from a study of endemism among island birds that extinction is a surprisingly frequent event on islands. The actual number of species on an island will be that at which the rate of extinction balances the rate of immigration. A distant island for example, will reach equilibrium with a smaller number of species than one of the same size nearer a large source island or continent; its fauna will in effect be limited by distance acting through a low rate of immigration.

If it is accepted that organisms continually disperse and that new species appear while others become extinct, the principles of the equilibrium model seem inescapable so long as there is some relation between area and number of species. A series of arguments follow from the model, but they need not be discussed here. Although MacArthur & Wilson state that some of them may prove to require modification the model itself is important for several reasons: it allows quantitative prediction of various properties of island faunas and emphasizes that they are the result of continuing immigration and extinction. The theory also provides a starting-point for the integration of ecological and zoogeographical observations. It is mainly in connexion with this last aspect that the writer's work in the Solomon Islands is relevant.

Distance and area in the Solomon Islands

In dealing with distribution patterns within the Solomon Islands the following assumptions can be made:

(1) That movement in expanding taxa will tend to be in the direction from large to smaller islands. This assumption can be derived either from the equilibrium model which suggests a dominating effect for larger islands or from a consideration of the chance exchange of colonists when numbers of species available and the number and percentage of endemics of originating on islands vary with island area; alternatively Darlington's (1957) concept of general adaptation can be introduced to suggest that endemic taxa originating on large islands are likely to be more effective competitors than those from smaller islands. The actual ratios of exchange between pairs of islands are not yet clear but they are immaterial now when the only requirement is that more expansion should occur out of large islands than small ones. This does not exclude the possibility of some movement in the reverse direction.

(2) That there is an over-all west to east movement of taxa. This is the larger pattern of expansion from the New Guinea area out into the Pacific operating within the Solomons archipelago. Again it is unnecessary to demand that there can be no east–west movement. In fact a case of local expansion in this general direction has been described in the Protectorate (Greenslade 1965). A hispine chrysomelid beetle, *Promecotheca opacicollis* Gestro, reached large numbers on the island of Tikopia in the Santa Cruz group where it was not previously known. It could be shown that this was most probably due to colonization from outlying islands of the New Hebrides.

(3) That narrow water gaps between islands are crossed more readily than broader ones.

With these assumptions the most important routes of faunal movement in the main islands will be those indicated by arrows in figure 16.

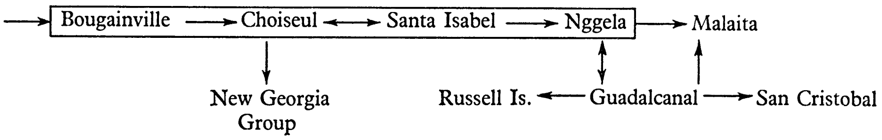

Figure 16. Main routes and directions of faunal movement in the Solomon Islands (see text for explanation).

This shows how San Cristobal, as well as being the most distant island from New Giunea, is furthest from Bougainville which occupies a critical position being both the largest island in the Solomons and relatively close to New Guinea and the Bismarck Archipelago. San Cristobal is also an extra sea gap away from the Bougainville–Nggela chain compared with any other large island. The diagram demonstrates, further, that the origin of any species on Malaita is more likely to be Guadalcanal or Nggela than Santa Isabel. Similarly, there is a higher probability of members of the New Georgia group and Russell Is. faunas being derived from Choiseul, Santa Isabel and Guadalcanal respectively, than from Bougainville, or in the case of the Russell Is., Santa Isabel or the New Georgia group.

This depends on the present distribution of land areas, but past changes in their size and distribution also need to be considered. In fact the main Bougainville–Nggela route into the Solomons coincides with a possible Pleistocene land mass which would have been exposed by a fall in sea level of 200 ft. if there were no differences in the elevation of the land. Such a sea level fall would also unite certain islands in the New Georgia group. However, restricted distribution patterns here are not dealt with in the present series of papers since much more extensive collections are needed from the area. But it can be noted that endemics occur here including some on Kolombangara which this Symposium has shown is probably of Pleistocene age. This implies that animal distribution patterns at the same taxonomic level elsewhere in the Solomons are equally recent.

Apart from these changes in sea level the land masses of the Solomons are themselves unstable with recent faulting (Coleman, Grover, Stanton & Thompson 1965) and volcanic activity. In some areas coastal relief, probable submerged valleys (for example the Boli and Maramasike passages) and extensive reef systems indicate subsidence, while in other parts of the archipelago the absence of reefs, poorly developed coastal structure and raised reef limestones and associated sediments (at 1400 ft. above sea level on Mt Austen, Guadalcanal) suggest uplift. Therefore estimates can be made for earlier maximum and minimum island areas making allowance for subsidence or uplift. However, no further important land connexions are obtained and the relative areas of major islands remain very similar.

Reference must also be made to the possibility of relatively recent climatic changes although they can be largely discounted. Equatorial islands such as the Solomon Islands are distant and insulated by sea from Pleistocene climatic fluctuation in other regions. If there were any changes, trends toward a wetter climate are most likely and these could be expected to extend montane zones to lower altitudes. This might allow inter-island dispersal of mountain species some of which are geographically widespread. Examples from the ants and Collembola are discussed in this Symposium by Penelope Greenslade.

ISLAND DISTRIBUTIONS AND THE EXPANSION CYCLE

The preceding section shows that the problem of restricted island distributions within the Solomons can be analysed simply in terms of the existing islands, their areas and distances from each other and from major sources. Only if these factors fail to account for observed animal distributions is it necessary to introduce any others. Details of actual island patterns in birds and selected insects and the sources of this information are recorded elsewhere (Greenslade 1968 *a*, *b*). The insects concerned are all those whose island distributions in the Solomons were adequately known. They include relatively well-collected Lepidoptera, species of *Amblypelta*, an important pest genus and common, conspicuous Lygaeidae among the Hemiptera and, in the Coleoptera, some Hispine Chrysomelidae which have been the subject of special study by the Bishop Museum.

All but the smallest islands support endemic taxa in these groups and shared taxa of restricted distribution can be found for virtually any pair of adjacent islands. However, a coefficient of faunal similarity was calculated for all pairs of major islands in the earlier papers. It demonstrated that in birds and in these selected insects there are two patterns of major importance. The first is a high incidence of endemics on San Cristobal, while the other is shown by taxa restricted to two or more of the islands extending from Bougainville to Nggela. It is apparent from literature records and collecting in the Solomons that these patterns occur in other animal groups. Recent collections may fill distribution gaps so that their distributions can be analysed quantitatively as well. It can also be suggested that taxonomists working with this material should look for these dominant patterns in order to determine the range of groups in which they are present.

In the remainder of this paper it is argued that these two distributions are best explained as the result of expansion of taxa through the Solomon Islands from the west and it is considered unnecessary to postulate any movement of islands or sea levels to account for them.

In both the birds and insects the number of taxa on islands varies directly with their area. In the birds there is a further, inverse correlation between fauna size and degree of isolation measured by the distance an island lies from another, large island. Mayr (1965) showed that among birds the proportion of endemics varies with island area and isolation, being high on larger and more distant islands. Similarly, in the Solomons the incidence of endemics increases with area on the distant islands and is in general lower in the main archipelago, hence the comparatively high proportion of endemic taxa on the large, distant island of Rennell (Bradley & Wolff 1956). As MacArthur & Wilson (1967) point out for Mayr's observation this agrees with their argument that a high percentage of endemics is associated with a low rate of turnover of species; this in turn results from large area or isolation.

The effect of isolation cannot be examined in this way for insects because faunas are not sufficiently well known on enough distant islands. But it is significant that on San Cristobal in the main archipelago there are fewer taxa than would be expected from the fauna size–area relation when all the islands are taken together. As noted already San Cristobal also carries a high percentage of endemic forms. An explanation is available for this in that the fauna is limited in size by its relatively great distance from New Guinea and Bougainville. There is consequently a low rate of species replacement and as it is one of the larger islands the incidence of endemism is high.

In neither the birds nor the insects is it possible to consider the area–endemism relationship in detail for the rest of the main islands since the percentage of endemics falls off for the larger ones. This is interpreted as being caused by the expansion of species, each initially restricted to a large island, to adjacent smaller ones (the first assumption) so that they lose their endemic status. The topic of range extension introduces the second major distribution pattern in the Solomon Islands, the Bougainville–Nggela faunal affinity which coincides with the chief route of expansion through the archipelago from the west. Assuming that eastward movement predominates, three stages can be distinguished in a cycle of expansion, divergence on islands with some further local expansion, and finally replacements and extinction. Stage I species are those with continuous distributions covering the whole of the Solomon Islands and an early phase in which ranges extend varying distances eastward from Bougainville. Stage I therefore includes the Bougainville–Nggela pattern while Stage II is represented by species in which taxa occur on individual islands with local extinction and perhaps evidence of secondary expansion to small islands. In Stage III, distributions are further fragmented and species' total areas appear to be contracting with more or less closely allied forms occurring on only a few islands.

Actual distributions are often more complicated or less clear-cut than this. A common situation is the presence of one taxon throughout the main archipelago as far as San Cristobal where an allied one occurs. This may represent early Stage II with differentiation first on San Cristobal or Stage I, an expanding taxon having replaced an earlier arrival except on this island. Alternatively a Stage I taxon may extend only as far as one of the islands between Bougainville and Nggela penetrating Stage II or Stage III patterns and replacing island endemics. A number of examples of bird distributions belonging to simple and more complex variants of these basic stages of expansion are given by Greenslade (1968*a*). Island patterns shown by species of three hemipteran genera are repeated here as they provide a good illustration of replacement leading to a series of Stage I and Stage II distributions. The genera are *Amblypelta* (Coreidae) and *Astacops* and *Scopiastes* (Lygaeidae) and the island distributions of the species (1–3) are shown diagrammatically in figure 17. It can be added that these genera are ecologically very similar; individuals of all the species are of the same order of size and build, are mainly diurnal, occur naturally in and on the edge of forest, are phytophagous, feeding on a variety of plants and are moderately gregarious and able to fly.

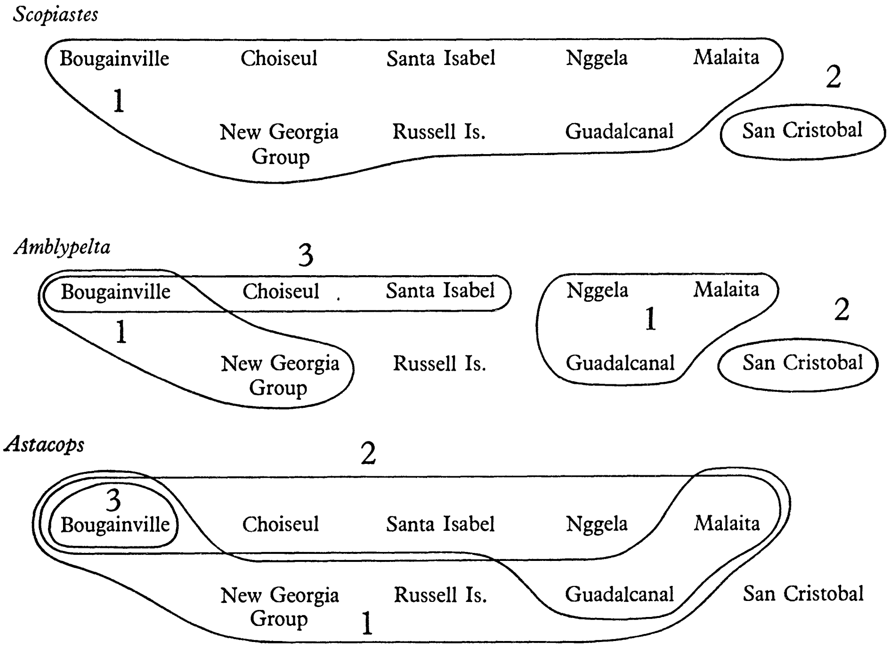

FIGURE 17. Island distribution of species (1–3) in three genera of Hemiptera.

Their distribution patterns can be explained as follows: *Scopiastes* represents Stages I (sp. 1) and Stage II (sp. 2) or early Stage II with differentiation of San Cristobal. In *Amblypelta* a population of a late Stage II species (sp. 1) has diverged to separate specific status on San Cristobal (sp. 2) while there has been replacement of sp. 1 by a Stage I species (sp. 3) expanding from Bougainville. This island is large enough to contain both this species and sp. 1, but the genus is not represented on the rather small area of the

Russell Is. group which is also isolated from the Bougainville–Nggela axis if its fauna is derived mainly from Guadalcanal. A later stage is shown by *Astacops* in which a Stage I representative (sp. 2) has reached Malaita and Guadalcanal replacing sp. 1 on the small area of Nggela, but co-existing with it on the larger islands of Guadalcanal, Malaita and Bougainville. On the last another species (sp. 3) is present. This genus does occur in the Russell Is. but not on San Cristobal; there relative isolation may have prevented colonization or re-colonization as in the case of *Amblypelta* on the Russell Is.

Even taking these three genera with a total of only eight species the numbers on each main island can be related, perhaps fortuitously, to area and distance. Bougainville, the largest island carries five species, Guadalcanal and Malaita four each and the other major islands which are rather smaller have three species on each. San Cristobal, isolated, and the Russell Is., small and isolated, have only two species while Nggela, small but close to three large islands supports three species.

The Bougainville–Santa Isabel *Amblypelta* species (sp. 3 on the diagram), *A. gallegonis* Lever, should in theory displace the earlier species *A. cocophaga* China (sp. 1) if introduced to Nggela. This is being tested by an introduction since *A. gallegonis* is not a coconut pest while *A. cocophaga* is and its replacement by *A. gallegonis* offers a chance of control. However, the results of the introduction are not known as yet.

Although *Amblypelta* species fit satisfactorily into this sequence of expansion and replacement *A. gallegonis* is atypical in two respects. First, it occupies a taxonomically isolated position in the genus without allies in New Guinea (Brown 1958) so the range extension eastwards out of Bougainville is best regarded as a secondary one. In addition to this the species occurs as a form on Bougainville and Choiseul different from that on Santa Isabel. This indicates divergence and expansion within the Stage I species' area; as the taxonomy of economically less important genera becomes better known this kind of minor pattern within a major one may prove to be common.

Habitat distributions

The members of these successive stages in the cycle of expansion and replacement tend to differ in their habitat distributions. Three broad habitat divisions can be recognized in the Solomon Islands. First there are 'coastal' habitats such as the shoreline itself, river beds and young second growth and also a variety of man-made habitats such as gardens and plantations. All these situations are temporary in that they lack the forest cover. Next there is lowland forest including any well-grown forest even if the tree species present suggest past disturbance. Finally there is a mountain zone,the lower and upper montane forest. Although 'coastal' habitats are commonly interspersed with lowland forest there is rough correspondence between low elevation or proximity to the coast and the frequency of open habitats.

Among birds those species which are classed in Stage I from their island distribution patterns either show a wide habitat range or occur at low elevations in coastal habitats. The habitat distribution of Stage II species is centred on the lowland rain forest, while those in Stage III are most frequently associated with the montane zone. In the temporary coastal habitats of Stage I species there is likely to be selection for migratory ability; this is the case in arthropods (Southwood 1962) and probably applies to birds as well. If so the inhabitants of coastal habitats will be preadapted for inter-island dispersal. Having dispersed they are also well adapted to colonize the coastal habitats in which they are likely to arrive. In these situations faunas are generally less diverse than in the forest so immigrant species will face least competition here. Therefore expansion seems to take place between coastal habitats. In the next stage, in which there is divergence on individual islands, this accompanies a shift in habitat to the lowland forest with its larger fauna and probably higher incidence of competition. There is a strong suggestion here of adaptation to the local environment, especially if the habitat shift is associated with any loss of dispersal ability and consequent break up of the population on an island into smaller units. Finally in Stage III extinction appears frequent in that island distributions become fragmented and discontinuous; many of the taxa at this stage occur on mountains where competition may be reduced (Braestrup 1956) indicating exclusion from habitats with larger faunas at lower elevations.

The insect species whose island distributions were studied are relatively few and little is known of their altitude or habitat range. Therefore the relation between island and habitat distribution cannot be examined for them as in the birds. However, studies on the ecology and taxonomy of the log-inhabiting, staphylinid genus *Priochirus* (Coleoptera) support conclusions reached from bird distributions. In this genus there is a correlation between endemism and altitude with the most geographically widespread species occurring in open sites or disturbed vegetation near the coast. Habitat segregation among the relatively large number of lowland forest species suggests competition and ecological specialization. On the other hand, in the montane species there is a trend towards a morphology which renders them poorly adapted to re-enter lowland habitats while records of the coexistence of more than one species in the same log or other niche is evidence of reduced competition compared with lowland forest (Greenslade 1967, and in preparation).

Turning to the birds again, it was noted that some Stage I species have a wide habitat distribution in the Solomons and a similar situation is found among insects. MacArthur & Wilson (1967) record that certain ant species which occupy coastal habitats in New Guinea occur also in forest on islands in the Pacific. The present writer has made the same observation while collecting in the Solomon Islands and the New Hebrides. Some ant species which are mainly coastal in the Solomons are found in forest to a much greater extent in the noticeably poorer ant fauna of the New Hebrides. Another case is the introduced ant *Pheidole megacephala* (F.) which is only found in coastal habitats in the Solomons but occurs up to 3000 ft. in Polynesia where there are no native ants (Wilson & Taylor 1967). It can be concluded from this that an expanding species moving eastwards and generally passing from rich to smaller faunas, is in a favourable position to expand its habitat range on colonization. This provides an explanation for the wide range of habitat in some Stage I birds.

It can be noted that the cycle of expansion and replacement in the Solomons becomes almost identical with Wilson's (1959, 1961) taxon cycle, described for Melanesian ants, once habitat and geographical distributions are related to each other. In the Solomon Islands a reasonable case for continuous cycles of expansion can be made on the basis of geographical distributions alone, but it might be objected that there are alternative explanations for the major island patterns in terms of Pleistocene land connexions or possibly the earlier history of individual islands. Similarly, the relation between habitat and geographical range is not in itself dependent on the cycle. For example, montane distributions are inevitably restricted and discontinuous and the wide occurrence of coastal species need only reflect the relation between migratory ability and the permanence of habitats. However, taking geographical and habitat distributions together the expansion cycle seems to be the only explanation to fit both sets of data. In addition, there is a theoretical foundation on which to base it.

POPULATION ECOLOGY OF COLONIZING SPECIES

MacArthur & Wilson (1967) contrast the types of selection acting on populations at early and later stages in the colonization establishment sequence. A colonizing population will be subject to what these authors term *r* selection. If the habitat is uncrowded there will be selective advantage in productivity, especially for high rates of increase in numbers. Subsequently, there will be a change to *K* selection, favouring efficiency, during adaptation to an environment which is more crowded and in which, consequently, a greater range of resources are already utilized. MacArthur & Wilson also suggest that *r* selection will operate to a greater extent in unfavourable or seasonal environments and *K* selection in less rigorous ones. Therefore *r* selection would be expected to act on colonizing, expanding species in their lowland habitats outside rain forest on account of the relatively small faunas present in these habitats, their temporary nature and, so far as tropical invertebrates are concerned, the unfavourable physical environment of open habitats with no tree cover, in which there is a considerable desiccation risk. Properties of what can be called *r* and *K* species are illustrated by four ant species which are dominant in Solomon Islands coconut plantations.

Two of these control the coconut pest *Amblypelta cocophaga* and changes in the frequency of the four species have been recorded in coconut plantations on Guadalcanal by successive entomologists in the Protectorate Department of Agriculture (including, most recently, the present writer) since 1948. Two of the species, *Oecophylla smaragdina* F. and *Iridomyrmex cordatus* Fr. Smith, are native to Melanesia, while the other two have been inadvertently introduced by man over wide areas of the tropics, including the Solomon Islands. Of these *Pheidole megacephala* probably arrived in the 1920s and the fourth species, *Anoplolepis longipes* (Jerdon), at some time before this. These two species pairs, the one immigrant and the other established, should show differences between the effects of *r* and *K* selection. Contrasting attributes of the two sets of species are shown particularly clearly since they compete in the unusually uniform environment of coconut plantations.

An account of population structure and of fluctuations in frequency of the species for most of the first decade of records since 1948 are given by Brown (1959*a*, *b*). Records of changes since then and a detailed account of ecological studies by the present author are in preparation. It is appropriate to summarize some of the results here as they contribute to this zoogeographical discussion.

Since 1948 *Pheidole megacephala*, the dominant ant in plantations from the 1930s, has declined. It was followed by an increase in *Anoplolepis longipes* whose numbers in turn fell.

Throughout the 1960s there have been few changes, these two species maintaining a low but steady frequency on palms. In contrast the two native ants show stable populations. Although *Oecophylla* is susceptible to being displaced by the other three species it is almost invariably dominant in areas not occupied by them.

The '*r*' and '*K*' species differ in several respects. Both the introduced ants have demonstrated a capacity for high rates of numerical increase and extension of population area. *I. cordatus*, in contrast, expands its territories very slowly while those of *O. smaragdina* appear to be limited in size by the presence of only one queen per colony. The *Pheidole* and *A. longipes* are able to occur in a wide range of habitats, while the native species nest only in trees and so are restricted by nest site availability. As mentioned previously *P. megacephala* is probably limited to the coast in the Solomons by the diversity of the lowland forest ant fauna but is able to penetrate mountains elsewhere in the Pacific. Neither *I. cordatus* nor *O. smaragdina* have been found above 2000 ft. in the Solomon Islands and at least in the former there is evidence of altitudinal limitation by climate. In these properties the introduced species seem to have an advantage. Both *A. longipes* and *P. megacephala* populations can cover very extensive areas, larger even than those of *I. cordatus*, and they also have a wide food range. All four species are to some extent predacious and also obtain food as honeydew from Homoptera but there are indications that introduced populations of *P. megacephala* and *A. longipes* feed on honeydew less and on prey to a greater extent than in their source area, Africa. This results in a degree of independence of appropriate honeydew producing Homoptera but combined with large population area the predatory habit can lead to exhaustion of food resources. In contrast, the small individual populations of *O. smaragdina* have a relatively large, accessible, peripheral zone for foraging. In addition in this species and in *I. cordatus* feeding on honeydew contributes to population stability since ant density and the food supply can be mutually regulated (Way 1963). However, this may reduce the rate of population growth, as perhaps in *I. cordatus*. The native species are also well adapted to the lowland climate of the Solomon Islands while the introduced species are not. However, this is largely overcome by plasticity in their daily rhythms of foraging activity. In these two species, and in *I. cordatus* the level of activity depends on temperature and humidity; only in the native *O. smaragdina* is there a rhythm tied to light and darkness.

These features of the introduced ants in combination make them successful colonizing species in coconut plantations and other temporary and disturbed habitats. Especially to be noticed are the lack of population organization which permits large areas to be occupied rapidly, and plasticity in their responses to different environments. On the other hand, they hardly occur among the numerous ant species of lowland forest and populations fluctuate violently. In the case of *P. megacephala* a possible explanation is that post-war clearing of plantations made the microclimate at ground level less suitable. In *A. longipes* overpopulation may have led to shortage of prey. As foraging activity in this species is limited in the day by high saturation deficits and at night by low temperature a climatically unfavourable period could restrict foraging activity. If this coincided with prey shortage demanding more time spent in searching to obtain a given quantity of food a population decline might ensue.

This account of plantation ants raises several points. First, it has been noticed already that for a species to persist in temporary, coastal habitats migratory ability is necessary. Another factor in the tropics is the ability to withstand high saturation deficits; adaptations may be physiological or behavioural.

MacArthur & Wilson discuss *K* and *r* selections in terms of capacity for increase, and habitat and food range. The daily activity rhythm can be added to these as another aspect of species' bionomics liable to be affected by these two selection types. In uncrowded habitats there will be an advantage in plasticity; variable rhythms will be favoured as they allow extended feeding and avoidance of unsuitable periods in the daily cycle. On the other hand, in the diverse fauna and climatically less rigorous environment of the lowland forest *K* selection would be expected to restrict activity to periods when energy is most productively expended. Williams (1962) suggested as a general rule that in a species occurring over a wide range of habitats the daily periodicity is more sharply circumscribed in the habitat which is most favourable. This was qualified by excluding populations at the limits of the species' geographical range where physical restraints are limiting. If several ecologically comparable species were distributed over a number of habitats each species would show the most circumscribed rhythm in the habitat which was most favourable to it, or in this context, the habitat to which it was best adapted. The rule can be restated that when a number of species occur together in a habitat the daily periodicity will be most sharply circumscribed in the species best adapted to it. Again a qualification is necessary so that circumscribed applies to a strict endogenous rhythm or one regulated by light and darkness rather than a periodicity directly limited by other physical factors. The daily rhythms of the ants discussed here agree with this extension of William's rule. *O. smaragdina*, which is almost independent of daily humidity and temperature changes, is the only one to possess a consistent colonial rhythm regulated by light intensity. In the other species, which are less well adapted to the Solomons' climate, activity rhythms are irregular. This is especially the case in *P. megacephala* and *A. longipes* which are the most poorly adapted.

The differences between adaptations to *r* and *K* selection illustrated by these ants would normally occur as a temporal sequence in a single species. There would be replacement of *r* by *K* selection on a scale of evolutionary time during the change from Stages I to II for example in the expansion pattern suggested here for the Solomon Islands. However, MacArthur & Wilson (1967) observe that there may also be a switch from one type of selection to another on an immigrant population over a few generations in the habitat in which it initially becomes established. If population growth is logistic the period of the ascending curve would represent *r* selection and that beyond the asymptote, *K* selection. The introduced plantation ants may also provide examples of this short term change. Neither *P. megacephala* nor *A. longipes* has shown any major increase after declining from their maxima. In the former this may be due to a change in plantation conditions, or perhaps competition from a further, yet more recently introduced ant, *Solenopsis geminata* (F). But in *A. longipes* no complete explanation in terms of external agencies is available; if the decline was caused by absolute or relative food shortage oscillation rather than the present persistence at a low level of abundance would be expected. Goscline (1968) gives similar examples of an introduced mollusc and a spider in Hawaii in which there was a population overshoot followed by a decline to a fluctuating equilibrium. Here, and in these ants, the reasons for apparent stability following a period of high density may lie within the population, the result of the change from r to K selection. Ford (1964) has stressed differences in selection between times of population increase and decline and that genetic changes may be correlated with fluctuation in numbers; he was able to give a few examples of genetic change following colonization and expansion in which there was evidence of adaptation to a new habitat. This introduces the question of qualitative changes in populations in relation to variation in density, a subject on which there is a considerable literature (Uvarov 1961; Klomp 1966; Wellington 1960; Chitty 1965; and others). Although it can be denied that genetic change is important in population control (Milne 1962) the concern here is with the effect of changes in numbers on the genetic constitution of populations for which there is some evidence (Ford 1964; Baltensweiler 1968).

Discussion

The Solomon Islands provide an almost ideal situation for the type of analysis described here. The distance from Bougainville at one end of the archipelago to San Cristobal at the other is considerable in relation to the distance from the major source island, New Guinea. Therefore the expansion and replacement cycle is strongly directional, occurring along a rather simple linear axis. In addition, it can be presumed that there are only minor ecological or habitat differences between islands. There are differences of course so to some extent this is an over-simplification. For instance, the mountain climate on Kolombangara differs from that on Mt Popomanaseu in central Guadalcanal and this is reflected in their montane faunas. Similarly, the degree of isolation of any island is also an over-simplification as measured here by the distance to the nearest large island. Probably a more accurate estimate of this distance factor would be obtained from an index incorporating the distances, suitably weighted, for direction and area, from all possible source islands. Again no allowance is made for island to island differences in the range and importance of the various habitats which are present. For example, there is a rough correlation between island area and altitude but no simple relationship exists between area or altitude and extent of montane vegetation. However, the question of habitat diversity need not be considered further at present. In most taxa montane forests and grasslands contain few species compared with the lowland forest, by far the most extensive vegetation type, so that among the birds the area fauna-size relation is much the same whether the species of habitats other than lowland forest are included or not. At this stage then it is reasonable to simplify the problem and emphasize area and distance. The proof of this is the extent to which the distribution patterns in the archipelago can be related to these factors. However, it still remains very desirable that more refined analyses are carried out to assess the importance of other variables.

The premises of MacArthur & Wilson's equilibrium model seem to work well in the Solomon Islands for the groups which are dealt with in this paper. The object has not been to test or employ the quantitative predictive power of the model, but to concentrate on ecological aspects. The cases which have been described, the staphylinid genus *Priochirus*, briefly, and coconut plantation ants, in more detail, in fact agree very well with MacArthur & Wilson's more theoretical approach. They also show how zoogeographical investigations extend into the field of population ecology.

There is, however, a bias in the groups which have been studied, birds and higher insects. They have in common an ability to disperse, which is found in only a few groups, in that they are able to fly. Their distributions incidentally support the assumption that restricted patterns in the Solomons can be treated on the basis of the islands as they are now and a continuous process of expansion and replacement. These groups show local patterns which might be attributed to Pleistocene sea-level changes in the case of the Bougainville–Nggela faunal affinity or to a special regional geological history for San Cristobal endemics. Although in the former case any land connexion would undoubtedly be important it is significant that the appropriate distribution patterns are well developed in the groups least likely to be affected by such past geographical changes. The Mollusca can also be included since they show restricted island patterns and have effective dispersal mechanisms judging by their wide Pacific distribution. On the other hand, these patterns are less well developed in taxa which seem to have less dispersal ability, for example earthworms and Collembola (Lee, Lawrence & Penelope Greenslade, in this Symposium). In these groups there is no indication from material examined so far of restricted distributions within the archipelago. At the same time some species show wide habitat, altitude and geographical ranges. In these cases though there are likely to be other factors involved as well as dispersal ability, in particular the time factor, but genetic variability and length of generations can also be mentioned. It will be of interest to determine the range of taxa in which the patterns described here are found and the extent to which the present approach, based on area and distance, is useful. This will require more collections from the Solomon Islands and, equally important, thorough taxonomic study of material resulting from recent field work. The theory which is available now allows hypothesis, prediction and test of hypothesis for many properties of island faunas, removing much of zoogeography from the realm of mere opinion. However, any account of geographical distributions deals with abstractions in that, inevitably, very complex spatial patterns must be simplified. Therefore the ecological aspect has been stressed here since it is concerned with measurable attributes of populations.

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