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FAUNAL EVOLUTION ON ISLANDS: THE IMPACT OF MAN

By

PAUL Y. SONDAAR

SUMMARY

Island environments differ often from the mainland in having an impoverished flora and fauna with endemics.

Only those land vertebrates who are able to swim or to keep themselves floating for a longer period will reach an island.

It could be learned from the Pleistocene islands of the Mediterranean that it are mostly the same land vertebrates which reach the islands a.o. elephant, hippo and deer which are all good swimmers. The lack of large predators (except birds of prey) and the limited available surface area on islands were important factors in determining the evolutionary changes of a colonizing mainland population.

The evolutionary changes these mammals underwent followed parallel patterns on different islands restricted neither to geological age nor geography and can be explained as an adaptation to the island environment.

Some of these changes are dwarfing of large mammals and low gear locomotion in hippo's, elephants and deer. Once such a population is adapted to its island environment, little more changes take place through time.

However, sudden faunal turnovers might occur, which are linked to drastic paleogeographical changes or new successful arrivals of large predators or man.

Presence of man on Pleistocene islands is known from some islands in SE Asia (Philippines, Sulawesi, Timor and Flores). Recent discoveries also demonstrate the presence of man on the island Sardinia in the Pleistocene. A model can be made explaining why some islands were suitable for settlement of Pleistocene man and others not. The arrival of man had an impact on the local endemic island fauna (often with dwarf elephants, hippos and deer). Pleistocene man reached the island by 1) overseas traveling (sweepstake route) or 2) over land after the island became connected with the mainland (corridor filter route).

In the first case there is evidence that the dwarf elephants (Stegodon) and giant tortoises on the islands in SE Asia became extinct. The small Stegodon from Flores is replaced by a large-sized mainland form. On Sardinia the Lower Pleistocene endemic island fauna with a monkey, pig and antelope is replaced in the Middle Pleistocene by a fauna with a small canid, a deer and probably man.

In the second case, a land connection causes migration of the mainland fauna (inclusive man) to the former island. In this case man is an element of a faunal complex which contributed to the final extinction of an endemic island fauna. An example of such

* Πρώιμη ανθρώπινη αποικία και η επιρροή της στο νησιώτικο περιβάλλον.

** Paul Y.Sondaar.Natuur Museum, Rotterdam, Post Office Box 23452, 3001 KL, Rotterdam, The Netherlands.

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is Sicily in the Late Pleistocene. Here the endemic island fauna with dwarf elephants is replaced by a mainland fauna with man. Java is another example. At the end of the Early Pleistocene Java became part of mainland Asia and the arrival of the mainland fauna, together with man, caused the extinction of the Pliocene/Early Pleistocene island fauna (Satir fauna) with a giant tortoise, a deer, a hippo and a Mastodon.

The effect of the arrival of neolithic man on the local endemic island fauna is better documented. In general it can be said that it caused the extinction of the larger mammals (dwarf elephants, deer, etc.). The smaller mammals (rodents, etc.) are replaced gradually by mainland forms. This is the case with the island faunas of the Balearic islands and Cyprus, where the endemic island mammals were rapidly replaced by domestic animals.

I. PALEOGEOGRAPHY AND FAUNAL EVOLUTION

It is evident that the fauna on islands greatly depends on which animals could reach the islands and at what time. For landmammals the most obvious obstacle is water, like channels, straits or wider seas. Simpson (1965) and Dermitzakis & Sondaar (1979) pointed out the dispersal routes of land mammals and their relation to the faunal composition. They distinguish the following routes:

1. A corridor, in which faunal interchange from one region to another is possible;
2. A filter dispersal, spread is probable for some animals but definitely improbable for others;
3. A sweepstake, spread is impossible for the most and very improbable for some, but does occur accidentally;
4. The pendel route, a route which is easily crossed by some mammals, but a insurmountable barrier for others.

The corridor can be a broad land connection. A filter may be a landbridge, while the sweepstake route may be caused by a wider sea.

The faunal evolution of a region depends highly on the possible dispersal route. If there is a corridor to the continent, the fauna will not differ essentially from other parts of the continent, but if an island becomes populated by sweepstake dispersal, only very few taxa will reach the island and when survival is achieved, there will evolve an endemic fauna with very few taxa (unbalanced). In some cases, when the island is large enough and has a diversity in biotopes, radiation can take place, in which various descendant groups from the same ancestor start to occupy different ecological niches.

Examples already mentioned are known from the Pleistocene Mediterranean islands and the Indonesian Archipelago. The various endemic Pleistocene deer from Crete represent a good example for the adaptive radiation that can take place (de Vos and Dermitzakis, 1986).

The other way around it is possible to find such unbalanced endemic faunas with a few taxa on the present mainland. The only conclusion which must be drawn from this fact is that such areas of the mainland must have been an island in the past. An example is the Gargano Peninsula in Italy, which was an island in the Miocene/Pliocene (Freudenthal, 1978).

Java was in the Pleistocene several times connected with the mainland of Asia. The present day fauna of Java is balanced and continental. But the Early Pleistocene Satir fauna (Sondaar, 1984) is clearly unbalanced, endemic and has a low diversity in taxa. Only a giant tortoise, Mastodon, deer and a hippo are known from this fauna. Recent discoveries of a pygmy Stegodon from Sambungmacan in Central Java even suggest that during Early Pleistocene times Java was made up of more than one island, as pygmy stegodonts are not known from the Satir fauna (Aziz & van den Bergh, in press).

If we analyse the fossil faunas, it is possible to draw certain conclusions about the paleogeography:

1. **If we find fossils that indicate a balanced fauna similar to the mainland and we find this fauna on an island, it means that the present island must have been connected by a corridor with mainland in the past. Miocene balanced mainland faunas on the islands Samos, Rhodes, Crete etc. are clear examples of such. These islands were connected to the mainland in the Miocene. The Upper Pleistocene mainland fauna of Sicily indicates a connection of the present island with the mainland in that period**

2. **A somewhat impoverished, balanced fauna can have several explanations, such as restricted environment, a disconnected landmass or a dispersal route which is possible for most animals, but for some an insurmountable obstacle (filterbridge). This is the case for the late Early Pleistocene Trinil H.K. fauna (de Vos et al 1982).**

3. **An unbalanced endemic fauna points to the conclusion that the barrier was a broader sea barrier, crossed only occasionally by some animals (swimming, drifting on natural islets). If we find such a fauna on the present mainland, it indicates that that part of the mainland must have been an island in the past.**

II THE EFFECT OF ISOLATION

The effect of insularity on mammal evolution is approached by considering endemic fossil mammals of islands in the Mediterranean and the Indonesian Archipelago. In general, the same mammals will arrive on the islands by sweepstake dispersal. Among the large mammals this includes the elephants, hippopotamids, deer and pigs: all mammals known for their good swimming and floating capacities.

Dispersal of the mammals

If we look at the way of life of elephants, deer and hippos, then we see that they are all excellent swimmers, especially the elephants, who love bathing. There are plentyof reports of elephants swimming in the open sea near Ceylon; the trunk can be considered as an excellent snorkel device. Deer will flee to the water if they are in danger and there are also plenty of reports of swimming deer. The swimming capability of hippos is sufficiently well-known; there are reports of hippos swimming from the mainland of Africa to the island of Zanzibar, a distance of about 25 miles. In other words, elephants, deer and hippos swim very well even in the open sea and it is not really surprising that those were the very mammals which arrived on the islands.

Another character which enhances their potential to arrive safely on an island, is their digestive system. Bacteria in the intestines of these herbivores produce abundant gases, which give them a high floating capacity. This means that they could manage large sea distances by alternatively drifting and swimming.

If the island happened to be close to the coast they could go back to the mainland. It is well-known that elephants visit islands close to the coast of India and Ceylon in order to gather food and return the same day, thus remaining in contact with the parent population (Johnson, 1978). However, in certain cases, due to strong currents or in stress situations, animals might go further from the coast and if they reached an island from which it was impossible to return they would settle there.

Migration to islands might also have been triggered by behaviour. The animals might have adapted a nomadic way of life, and there might also have been overpopulation in the parental herds of hippos and elephants.

For a successful colonization the founder population must not be too small. In that respect the large carnivores which have a solitary way of life would have had a very slender change to be successful colonizers of an island. Besides, they don't have the floating capacities of deer, elephants and hippos. For these reasons they are not able to cover the same large distances in the sea. Furthermore, most islands are too small to carry a healthy population of carnivores.

The rodents and insectivores could have come to the islands on natural rafts. Probably many of the Pleistocene islands were colonized in this way and the immigrants became isolated from the mainland population and were compelled to live in a completely different environment in which there were no large carnivores.

The fossils we are finding on the islands are showing us what effect this insularity has had on subsequent mammal evolution. To some extent we can compare this sequence of events to what happens in laboratory experiments. In a laboratory we repeat experiments, compare the results and arrive at a conclusion. The island fossils can be regarded as the results of natural experiments. Similar ancestors came to different islands which had the same natural environment. The evolutionary changes, these mammals underwent, follow parallel patterns on different islands restricted within the geological age and geography and can be explained as an additional process to an island environment lacking large carnivores (Sondaar, 1977).

Dwarfism

The most striking change the larger mammals underwent on the islands was diminution in size. The Pleistocene dwarf elephants of Cyprus, Crete and Sicily were the size of a pig (Ambrosetti, 1968; Bate, 1906). On the mainland elephants and hippos did not have natural enemies because of their larger size. On the Pleistocene islands, where there were no large predators in the fauna, size lost its significance. Small size could be advantageous for the following reasons: less food needed daily, greater mobility and reduction of the territorial area.

Low gear locomotion

In smaller mammals one would expect slender limb bones but one finds the opposite. The limbs are heavily built, and the lower part of the leg is shortened. This is especially clear in the endemic island ruminants. This character is just as common in the island mammals as is diminution in size. An extreme example of this is the bovid Myotragus from the Balearic islands. The proportions of this small bovid could be best compared with those of very large bovids such as bison. On the islands speed lost its significance because there were no big carnivores. The extremely short metapodials and phalanges resulted in feet of solid construction, advantageous for low speed locomotion in a variety of mountainous environments.

In the morphology of the isolated reindeer from Spitsbergen clear parallels with the fossil ruminants of the Mediterranean islands were found (Willemsen, 1983). All are small and have relatively short legs. The reindeer on Spitsbergen have no natural enemies. Even the polar bear does not hunt them. The morphology of this reindeer is thought to be an adaptation to the rugged environment of this island. The short legs give better stability in areas where speed is no longer important due to the lack of predators. Spitsbergen has a short summer and its reindeer depend mainly on the food collected in that season. After the summer they are extremely fat and heavy; in other words they store up extra food for the winter. The short legs can be explained as an adaptation to carry the heavy body in a rugged environment. This feeding strategy probably is only possible if there are no large carnivores. A similar explanation probably applies to the heavily built dwarf ruminants on the Mediterranean islands. There must have been a rainy and a dry season, even in the Pleistocene. In the rainy season the animals must have had sufficient food which would be stored as an extra supply for the dry season.

The changes that occurred in the island mammals can be explained as an adaptation to the island environment. They follow parallel patterns not bound to geography or time. The dwarf elephants, hippos and ruminants with low gear locomotion were independent products of evolution occurring in similar environment on different islands.

Allometrical size changes

If we compare the island dwarfs with the mainland ancestors we note that the change in size did not produce scale models. This is not unusual since with a change in the surface/volume ratio the same function could have been achieved by a different shape. A good example of this is the allometrical change in the skull of Elephas falconeri, a dwarf elephant, from Sicily. This elephant was about four times smaller than its ancestor, E. antiquus from the mainland. (Based on morphological (Lister & Bahn 1994) it seems more likely that Mammuthus meridionalis was the ancestor of E. falconeri, in which case this pygmy should be included in the genus Mammuthus as well). The enormous cranial muscles of elephants are attached to an outgrowth of the surface of the cranium formed by pneumatic bone tissue. Most of the skull consists of this tissue which was developed in elephants during their evolutionary trend toward gigantism (Accordi & Palombo, 1971). In E. falconeri this pneumatic bone tissue has been strongly reduced, no matter which of the two mainland ancestors one considers as the right one.

If we multiply the size of a mammal by the factor two, its surface increases by a factor four but its weight becomes eight times as much. Larger mammals need a heavier skeleton. The pillar foot of an elephant is an example of this. The muscles of the neck and lower jaw are attached to the skull of an elephant.

The reduction in size of the island elephant made pneumatic bone tissue superfluous and the general shape of the skull changed drastically. Accordi & Palombo (1971) and Ambrosetti (1968) go further into details of these changes of the brain size. They find that it was relatively bigger in the dwarf which agrees with the pattern that small animals have relatively larger brains. The evolutionary changes that island mammals undergo are allometrical but there are also clear changes which are related to an adaptation to the new environment, such as short and heavy built legs of the dwarf ungulates.

Giants and Birds

When the islands are not too far from the mainland, the small mammals will face the same predators as on the mainland. Birds of prey, small rodents, can hide easily. However, generally the endemic island rodents are larger than their mainland ancestors and in some cases, they show gigantism. An explanation for this gigantism is more complex than the dwarfism in large mammals.

Giant rats are known from the islands of S.E. Asia, like Philippines, Sulawesi and the smaller Sunda islands. Some species are not yet extinct. An interesting case are the giant rodents from the Miocene island Gargano (Italy). In the stratigraphically younger deposits giant murids and hamsters are found (Freudenthal, 1978). On the Miocene island Gargano there were also endemic owls (Ballmann, 1973) and ironically also in the younger deposits there are giant owls. It is supposed that the evolution of giant owls is related to their prey, 'the giant rodents'.

Giant tortoises are an other example of island life. The Galapagos islands are an example of it, but in the past, giant tortoises were living on the Balearic islands and the islands of S.E. Asia, like Sulawesi and the smaller Sunda islands as well. Though it remains uncertain weather this giantism in island tortoises evolved on the islands themselves, or was inherited from giant mainland ancestors, their extinction on island is usually related to the coming of man, and as such they are good indicators for the presence of man. On these islands man arrived in the Middle Pleistocene. Giant tortoises were an easy prey and became extinct, while on the various continents they had become extinct already earlier, probably also due to the arrival of man.

III MAN AND THE FAUNAL EVOLUTION ON ISLANDS

1. Arrival by corridor or filter route

The effect of Pleistocene man on island environments is obscured by the fact that often man came not alone, but together with other mainland mammals.

The first question to solve is how man reached the island; sea or by land? In the last case the island was not anymore an island, but became part of the mainland. Such a land connection between the mainland and the island can easily be detected. In this case we will find a mainland fauna, inclusive man, on the former island. Good examples of such are Sicily in the Upper Pleistocene and Java in the Lower Pleistocene. In both cases the unbalanced (without large carnivores) and endemic faunas became extinct. For Sicily the dwarf elephant and hippos, for Java the Satir fauna with a Mastodon, hippo, deer and a giant tortoise (Sondaar, 1984). It might be clear that the slow moving dwarfs with low gear locomotion had no chance to survive when the mainland predators entered their biotope. It might also be clear that it is difficult to judge which part man played in the final extinction of the island endemics, perhaps with one exception, the Geochelone from Lower Pleistocene Java. Giant tortoises don't have many natural enemies beside man.

2. Arrival by sweepstake dispersal

Only those islands would have been suitable for permanent colonization by Pleistocene man only if the exploitation of the natural resources on the island could support a viable human population over a long period of time, without exhaustion of the resources. On islands with an endemic and unbalanced fauna with a low diversity, the presence of a mammal, large enough in size, with a high rate of reproduction seems to be essential for the permanent settlement of a hunter-gatherer population. The ochotonid (a pika) Prolagus of Pleistocene Sardinia/Corsica fulfilled this requirement and made it the only island in the Mediterranean suitable for permanent colonization by paleolithic man.

Islands with Paleolithic settlements outside the Mediterranean are Flores, Timor, Sulawesi and the Philippines. On those islands giant rats were and are present. Even now, they are eaten by the people on these islands, and they must also have been an important source of food for paleolithic man.

Arrival of man by sweepstake dispersal means arrival of a predator on the island and caused the extinction of the mega island fauna. In Flores we find an endemic island fauna with a dwarf Stegodon and a giant tortoise Geochelone. In a stratigraphic higher level in the same profile a Stegodon of mainland proportions is found. With this same Stegodon trigonocephalus, a giant rat, Hooijeromys and a lithic industry are found (Maringer & Verhoeven 1979). This fauna is Middle Pleistocene in age (Sondaar 1987; Sondaar 1989; Sondaar et al. 1994).

The following scenario might be constructed. In the Middle Pleistocene man arrived on the island Flores. The dwarf Stegodon and the giant tortoise Geochelone were an easy prey and became extinct. The giant rats did survive by their high reproduction rate. These rats were at the same time a major source of protein for Paleolithic man.

The extinction of the dwarf proboscideans and giant tortoises of Sulawesi and Timor might be explained in a similar way. In Timor lack of stratigraphic control of the fossil bearing localities makes it impossible to verify this supposition. However, on Sulawesi we find a similar faunal turnover as on Flores, namely an older, Late Pliocene to early Pleistocene fauna with a giant tortoise and two pygmy proboscideans, E. celebensis and S. sompoensis. This fauna is replaced by a Middle Pleistocene to Upper Pleistocene fauna lacking tortoises and pygmy proboscideans, but instead containing two large-sized proboscideans, Stegodon sp. B and an Elephas species (van den Bergh et al 1992; van den Bergh et al 1994). Though no artefacts have been found so far in association with the younger faunal unit on Sulawesi, the coming of man might have something to do with this pattern analogous to Flores.

The move of man into the insular environment of Sardinia might have taken place in the early part of the Middle Pleistocene. A drastic faunal change can be noted at that age. Many endemics became extinct like the dwarf pig, Nesogoral and probably Maccaca majori.

The younger insular fauna with Cynotherium, Megaceros cazioti, Rhagamys, Tyrrhenicola and probably Homo replaced this fauna.

The lithic industry found in Northern Sardinia (Arca et alii, 1982) is evidence for an early presence of man on the island and the extinction of the many elements of the Nesogoral fauna might be caused by the hunting activities of man. Presence of man gave rise to the development of an unbalanced island fauna with a character different to that from other Mediterranean islands. The question is who was this man. Recently human fossils were found in Corbeddu Cave (Oliena) (Sondaar et alii, 1986): a temporal, maxilla (without teeth) and a proximal part of an ulna. The specimens show archaic and some distinct characters which could set them apart from contemporary mainland populations (Spoor & Sondaar 1986), suggesting a local evolution.

Other arguments for an isolated endemic population of man are the artefacts. The Upper Pleistocene artifacts -bone and lithic- found in Corbeddu Cave, dated ± 16.000-10.000 year BP, are unique.

These characteristics don't suggest that the artefacts were left by sporadic visits as put forward by Cherry (1984), but are the evidence for a permanent colonization of the island by man. It can be argued that these cultures were very well adapted to the Pleistocene island environment of Sardinia with deer and ochotonids. A sporadic visitor of the mainland must have had little chance to survive on the island, which was occupied by a well-adapted man. This changed when Neolithic man settled on the island. He had, as a farmer, a completely different living strategy. Neolithic man caused the downfall of the Paleolithic island man of Sardinia. Together with this man, many Pleistocene island endemics became extinct, because of the same Neolithic man.

3. Survivals and local evolution

It is clear that arrival of man, sometimes together with elements of a contemporary fauna, caused drastic changes in the local endemic fauna. The survivors are mainly the smaller mammals, like rodents and insectivores. On Java it was probably Rattus trinilensis, which also might be a member of the Satir fauna. In the Tyrrhenicola fauna, Rhagamys and Prolagus are represented by different species in the Nesogoral fauna.

On the islands of Flores, Timor and Sulawesi it were the giant rats which did survive.

Within the Tyrrhenicola fauna only small evolutionary changes can be observed. The evolutionary change from one species into the other must have been a fast process and might be considered as an adaptative response to the drastic change in the environment. The mainland mammals, which arrived on the island, changed also; Tyrrhenicola is different from its ancestor Allophaiomys from the mainland. Again the evolutionary change must have been fast. Within the Tyrrhenicola there is little variation in this monospectic genus. The ancestor of Cynotherium must have been a Cuon type of dog and the ancestor of Megaceros cazioti might be a Megaceros verticornis-like deer (Malatesta, 1970; Caloi & Malatesta, 1974).

Human fossils are found together with the Tyrrhenicola fauna. They show differences with contemporary populations from the mainland. The stratigraphic level of those fossils antedates clearly the Neolithic layers in the locality Corbeddu Cave. The difference in morphology between the fossil and the contemporary populations from the mainland might suggest local evolution of man in the island environment. A more detailed study of the human , fossils is presently carried out.

On the island Flores so far no human fossils are found. The Stegodon, which arrived on the island with man, shows some small morphological changes if compared with its ancestor from the mainland.

Presence of man on a Pleistocene island has its impact on the faunal evolution. The fauna will stay impoverished and endemic, but dwarfism and low gear locomotion will not evolve.

CONCLUSIONS

If a corridor or filter route comes into existence between the island and the mainland, man will arrive at the former island together with its accompanying fauna. The local endemic islands fauna will be replaced by the mainland fauna. It might be possible that some endemic, mostly small mammals will survive (Examples are Early Pleistocene Java and Upper Pleistocene Sicily).

If man arrives on the island by sweepstake dispersal, this will cause extinction of the endemic large mammals. The smaller mammals will survive and will show some evolutionary changes just after the arrival of man. When man is settled on the island, an island fauna will evolve different from the islands without man. Dwarfism and low gear locomotion will not evolve (Sardinia, Flores, Timor, Sulawesi and the Philippines).

Islands with unbalanced faunas are only suitable for permanent colonization by Pleistocene Man, if exploitation of the natural resources on the island can support a viable human population over a longer period of time, without exhaustion of the resources. On islands with endemic and unbalanced fauna, with a low diversity, the presence of a mammal, large enough in size, with a high rate of reproduction seems to be essential for the permanent settlement of a hunter-gatherer population (Sardinia, Timor, Sulawesi and the Philippines).

On the islands which were colonized by man, a local economy and probably an endemic industry will develop.

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