

The exploitation of spatially structured populations

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Introduction

In order to predict the behaviour of ecological systems, it is helpful to characterise them using a model. For example, if we wish to predict the effects of a given level of exploitation on a population, we first need to develop a model of the dynamics of that population and its density dependent response. Very simple models of population dynamics, such as the logistic equation, are sometimes adequate representations of how a population behaves, but generally more realism is needed before a model becomes a useful tool for prediction (Milner-Gulland and Mace 1998). Realism is often introduced by explicitly modelling the structure of the population, perhaps by breaking the population into different age or size classes, which might be differentially targetted by harvesters, or might have different roles in population dynamics. The spatial location of individuals or of sub-groups of the population is often an important component of a population's ecology. Few populations exist for which it is valid to assume that there is no spatial structuring, and the degree of population sub-division affects both evolutionary and ecological processes.

In order to be useful, a predictive model must be as simple as possible, while still capturing the essentials of the dynamics of the system. Whether a model to predict the effects of exploitation requires spatial structure depends on the importance of spatial structure to the ecology of the species, or to the behaviour of hunters, in the real world. It is increasingly being realised that spatial location is a key determinant of both the ecology and the susceptibility to exploitation of many species. The large conservation literature on the effects of habitat fragmentation, and the long-running debates on issues such as reserve size and shape, the effectiveness of corridors, and the problems of small isolated populations demonstrate the importance of the spatial structure of populations for conservation (Primack 1993, Soulé 1987).

In this chapter I will first outline the main approaches to modelling spatial structure in ecology, and I will then give an overview of some of the ways in which spatial structure is important for the conservation of exploited species. Two case studies will be used to illustrate the different ways in which spatial structure can influence the relationship between the ecology of exploited species and the incentives faced by those who exploit them. Finally, I will summarise the important issues that need to be borne in mind when considering the influence of spatial structure on the conservation of exploited species, and how these issues can be addressed.

Modelling spatial structure in ecology.

The modelling of spatial structure in ecology is a rapidly developing field, excellently reviewed by Keeling (1999). Models that do not include the spatial structure of the population are making the mean field assumption, that the average density over the whole area is the same as the density in the area where any individual is. In this case, the local environment in which an individual exists is ignored, and only the global behaviour of the system is considered. This can work well in some cases where there is a lot of mixing, such as many aquatic systems, but in cases where local interactions are important, adding spatial structure can make the behaviour of a modelled system much more realistic. There is also a thriving literature on the analysis of spatial data in ecology and the search for underlying mechanisms (e.g. Bjørnstad et al. 1999), but here I will concentrate on the theoretical modelling aspects.

Much of the early work on modelling spatial structure in biology involved the use of partial differential equations. These have been used to explain structures as diverse as the patterns of animal markings (Murray 1981) and fish dispersal between harvested and unharvested areas

(Clark 1990). Although these equations can be solved analytically, they soon get too complex for analytical solution as the degree of ecological realism increases. They also make the assumption that space, time and population size are all continuous; in many ecological systems this is not a tenable assumption. Conservation, in particular, often deals with small populations; when the total population size is small and subject to stochastic variation, results obtained from models of populations containing fractions of individuals are misleading.

Meta-population models are also extremely popular among ecologists and conservation biologists. They divide the population into a number of identical patches, connected by dispersal between the patches. The amount of dispersal between patches must be quite low, or the spatial structure of the system is lost. The original meta-population model, developed by Levins (1969) and discussed by Gilpin & Hanski (1991), makes quite restrictive assumptions about the relative time-scales of inter-patch and intra-patch dynamics; patches are assumed to be either at carrying capacity or empty, so that intra-patch population dynamics are not relevant to the dynamics of the system as a whole. This assumption fits the original system of insect patch dynamics well, but is not suitable for more slow-growing species such as mammals. Nonetheless, there have been applications of this model even to species such as badgers (which fitted the model rather well, Verboom et al. 1991). These models have been widely used in ecology, because of their flexibility and relative simplicity. The models can be made more realistic by allowing the population size in each patch to be below carrying capacity, or by allowing the patches to be different rather than identical (Keeling 1999); these more complex models are often referred to as patch models.

With the advent of increasingly high-powered computers, there has been a huge increase in the modelling of spatial population dynamics through numerical simulation rather than

analytical solution. This allows more complicated, and so more realistic, systems to be modelled. A current major research area is in the use of discrete lattice models; these are models in which space is divided up into a lattice of cells, each of which may contain a single individual or a sub-population. The cells interact with each other, usually through dispersal between neighbouring cells. Discrete lattice models are simple to visualise, but are nonetheless very powerful tools, which open up a lot of interesting theoretical questions, particularly concerning the scales at which processes happen, and so the size of the lattice that is needed correctly to capture the dynamics of the system (Keeling et al 1997). Two main kinds of lattice model are used; coupled map lattices, in which the population size in a cell is assumed to be a continuous variable, connected to other cells through a set of coupled equations, and cellular automata models, where the population size is a discrete variable, and there are probabilistic rules connecting the cells. Coupled map lattice models have been used in applications such as insect population dynamics (Hassell et al 1991), plant growth (Hendry et al 1996) and crown of thorn outbreaks on coral reefs (Green 1990). However, for conservation applications where small population sizes are important, cellular automata models may be more appropriate, though they are also more computer-intensive (Bascombe & Solé, 1996).

Approaches to spatial structure in harvesting theory and conservation.

There are two components to exploitation; the ecology of the species being exploited and the decision-making of the people that exploit them. Both of these components need to be taken into account when modelling exploitation; only when both are included can answers be found to questions such as: what will the size of the exploited population be in the long term, how many hunters will there be, and how many individuals will they harvest every year? When the two components are combined in a model of the system, it is called a bio-economic model.

The biological component of the bio-economic model describes how the population grows, both naturally and under exploitation. The economic component describes how much effort will be put into harvesting the population. This depends both on the biological characteristics of the species and on the the costs of harvesting and the price received for the products of harvesting. Thus the decision-making of harvesters is usually expressed in monetary terms - they are aiming to maximise their profits. Other influences on decision-making can also be included in the model, such as the user's attitude to uncertainty or their wish to retain the population above a certain size for conservation reasons. More details on bio-economic modelling can be found in Milner-Gulland and Mace (1998).

Both the ecological and the economic components of a bio-economic model can be affected by spatial structure. For example, the economic component can be affected by the costs involved in travelling to a location to harvest; the longer it takes to reach a particular area, the costlier this area is to harvest. The ecological component could include the dispersal ability of the species, and so the degree of isolation of a particular sub-population. Exploiting a species in which dispersal is minimal may lead to localised extinctions as particular areas are harvested, while harvesting a species that mixes at a high rate may cause the whole population to decline. Wherever the spatial structure is expressed, either in the ecological or economic components, the effect is to alter the predicted levels of harvesting effort, yield and long-term population size of the harvested species. Later I discuss two case studies, one of which has the spatial structuring on the economic side, the other on the ecological side. First, I will discuss three of the main areas in which spatial considerations have been included in harvesting models; harvesting source-sink populations, marine reserves and spatial behaviour of hunters.

Harvesting source-sink populations

The first people to address the issue of the effects of exploitation on a meta-population were Tuck & Possingham (1994). Their definition of a meta-population is two local populations connected by dispersal of juveniles; the internal dynamics of the local populations are modelled, so this is a patch model rather than a Levins meta-population. They assume that the per-capita larval production in one population (the source population) is higher than in the other (the sink population). The model shows that the source population should be exploited at a lower rate than if the population was homogeneously mixed, and the sink population at a higher rate. This is because part of the value of the source population to harvesters is its ability to produce recruits for future exploitation. In the extreme case where all the recruits to the population are produced by the source population and none by the sink, the sink should be harvested completely each year (assuming harvesting is costless). Lundberg & Jonzén (in press, a) have also addressed this issue, using a similar model. They show that source and sink populations vary in their optimal harvest rates, yields and equilibrium population sizes under harvesting, so that it is important to harvest differently in the two types of area. However, population densities are not necessarily higher in source populations, and so it can be difficult to tell whether a given population is a source or a sink.

Marine reserves

The main area of current research interest in the conservation of spatially structured harvested populations is marine reserves. Although the theory of reserve design for the conservation of terrestrial species is well-developed, it has virtually ignored the potential of reserves as tools for sustainable harvesting (except for suggestions that buffer zones allowing limited traditional harvesting may be useful; but these have yet to be explored theoretically). On the

other hand, the discussion of marine reserves usually has the explicit aim of maintaining or increasing sustainable yields of harvested species.

A large number of papers have been published recently addressing the effects of setting aside no-take areas on the yield and sustainability of fishing, the biology of fish populations and the socio-economic status of fishers (e.g. Roberts 1997, Valdes-Pizzini 1995, Malleret-King 1998). Although early discussions of the benefits of marine reserves tended to be quite speculative, recent discussions have been based on more theoretical analysis. However, there has still been little theoretical work done on the spatial dynamics of the fish populations protected by marine reserves, and on the consequences of spatial structure for the effectiveness of reserves. Generally, the emphasis has instead been on their role as a buffer against uncertainty in the management of fish resources. Uncertainty can be approached by actively aiming to learn more about the system while managing it (adaptive management, Parma et al. 1998, Walters 1986, MacNab 1983), by testing management strategies exhaustively in simulation models to ensure that the chosen strategy is robust to uncertainty (Kirkwood & Smith 1996, Hilborn and Walters 1992), or by setting aside an unharvested area in recognition that our abilities to predict the effects of harvesting and to manage these resources are limited in the face of uncertainty. Lauck et al. (1998) show, using a simple non-spatial logistic population model, that if actual harvest rates follow a probability distribution around the target harvest rate, and if the variability in harvest rate is high, then over-harvesting can occur even when the target harvest rate is low. This is also shown by Milner-Gulland et al. (in review). Although in a deterministic situation, not harvesting a proportion of the population is identical to harvesting the entire population at a lower rate, Lauck et al. (1998) show that when there is a high level of uncertainty in harvest rates, not harvesting a proportion of the population is an effective buffer against over-exploitation.

Other authors have emphasised the issues of spatial structure raised by marine reserves (Hatcher 1995, Guénette & Pitcher 1999, Lundberg & Jonzén in press, b). The reason why marine reserves involve issues of spatial structure is that in order for them to work, the reserve must act as a refuge for individuals that would otherwise suffer fishing mortality. This implies that there is not full random mixing in the fish population; otherwise fishing effort could simply move from the closed area to the remainder of the area and have exactly the same effect on the population as before (assuming there is enough space for the vessels to fish unhindered by others and that there is no uncertainty in the level of harvest). Guénette and Pitcher (1999) use a non-equilibrium age-structured population model with random movement of fish between the reserve and the fished area. They show that at low transfer rates between the reserve and fished area, yield is lower with the reserve than without it, but that as transfer rates increase, yield increases with a reserve and surpasses yield in the no-reserve scenario. By using an age-structured model they are able to capture the improvements in recruitment caused by the reserve, because larger fish produce more recruits than smaller ones. They suggest that future work should include more realistic representations of spatial structure and seasonal changes in fish movement patterns (for example fish movement into spawning areas or to deeper water in particular seasons). Lundberg & Jonzén's (in press, b) model includes habitat heterogeneity; they use a very simple model in which there are two different qualities of habitat, one of which is fully protected by a marine reserve, the other of which is fished. They also assume an ideal free distribution of individuals, so that the individuals are distributed such that the fitness in each habitat is equal; thus the poorer quality habitat contains fewer individuals. Their results suggest that the catch and optimal harvest rate are affected only by the quality of the unprotected area, not by the quality of the reserve. When an export of recruits from the reserve to the fished area is included, the quality of the

reserve habitat does affect catch rates. Although this is an unrealistically simple model, it does emphasise the requirement to think in more depth about how populations distribute themselves in the environment when considering whether marine reserves are effective tools for the conservation of exploited species.

Spatial behaviour of hunters

The previous topics concentrated on the ecological effects of harvesting on population dynamics and so on yield when populations are spatially structured. Marine reserves can also be seen as a way in which the spatial behaviour of fishers can be controlled; the management authority decides where harvesting should take place, and puts regulations in place to enforce this. A more general approach to the problem of the spatial behaviour of harvesters would look at how they choose where to harvest, how this choice can be influenced by managers and how this decision-making process interacts with the spatial ecology of the harvested species. This requires consideration of the incentives that harvesters face; the costs and benefits of harvesting in one area rather than another. The problem has obvious similarities to patch selection in behavioural ecology. There has been much research done on search effort by fishers, assuming that fish are found in identifiable schools and the search process is random (Mangel 1982, Mangel & Beder 1985). Extensions could include incorporating learning by fishermen, and modelling clumped distributions of fish aggregations so that the fish population is explicitly spatially structured (Mangel & Beder 1985), as well as considering the costs and benefits of different searching strategies. Hart (1997) has addressed the costs and benefits of fishing in one area rather than another, with particular reference to the incentives to fish illegally in a closed zone; he shows, for example, that as the end of a fishing trip gets closer, there is more incentive to risk entering the closed zone. Although this model is not

explicitly spatial, it could easily be extended to include the costs and benefits of travelling to a particular location.

A few authors have looked at the spatial aspects of game hunter behaviour. For example, Hofer et al. (1996) explore the spatial distribution of poachers within the Serengeti National Park, and show that poaching rates in an area are related to the distance from the boundary of the Park, the suitability of the area for hunting (the density of resident wildlife), and the demand for meat at the periphery of the Park (human population density). Marks (1994) collected data on the frequency of encounters between hunters and wildlife in Zambia, and noted that there has been a marked decrease over time in the frequency of wildlife sightings near settlements, with hunters having to go further to find game. He suggests that this is a result of game avoidance of inhabited areas and an increase in the use of snaring as a hunting technique. Although there has been some work done on the spatial behaviour of hunters, this remains a relatively under-researched area, and one that is as important for understanding the spatial dynamics of exploitation as studying the spatial behaviour of prey populations.

Case study: Red deer hinds on Rum

This case study is based on a paper by Milner-Gulland et al (in press). Red deer (*Cervus elaphus*) on Rum have been studied in detail since 1971, and so there are detailed individual-based data available on which to base a spatially-structured model (Clutton-Brock et al 1982, Clutton-Brock et al 1997). An important consideration in modelling spatially structured populations is the scale at which spatial variation occurs. In the case of red deer on Rum, the scale is rather small; Milner-Gulland et al (in press) show that there are differences in fecundity and mortality rates, especially among juveniles, between neighbouring hind groups. This has implications for the management of deer harvesting, because decisions about harvest

rates tend to be made at the Estate level; if neighbouring groups of hinds are significantly different in their population dynamics, they will also require different harvesting strategies if harvesting is to be optimal.

Red deer population dynamics

Adult male and female red deer have very different behaviour patterns in their use of space (Clutton-Brock et al. 1982); females are typically loyal to their maternal home range throughout their lives, while males disperse. Males occupy different areas to females throughout most of the year. Because of these differences, only females are considered in this case study. Two neighbouring hind groups are modelled, occupying home ranges of 2km² and 3km² respectively, a few hundred metres apart. The sizes of the two Rum groups are significantly positively correlated over time, because they are exposed to similar climatic conditions (Grenfell et al. 1998). Juvenile mortality, in particular, is strongly correlated between the groups, because it is strongly affected by the climate. However, although group sizes are correlated, this correlation only explains 31% of the variance, suggesting that the rates of dispersal between sub-populations are not sufficient to allow close entrainment of the dynamics. There are various reasons why two geographically proximate sub-populations of individuals of the same species might show different dynamics. In this case, the differences are likely to be linked to differences in the quality of the forage available to each group; the group with the more variable dynamics has a lower proportion of herb-rich *Agrostis-Festuca* grassland, which is favoured by the females (Clutton-Brock et al. 1987).

There is little migration between the two groups, despite their geographical proximity. Red deer females do not move readily between groups, because of the cohesive nature of group social structure. Over the 22 years during which the deer have been studied, only 32

individuals have been observed moving between the groups, with an average dispersal rate from one sub-population to the other of 0.73 females/year (Milner-Gulland et al, in press). Most studies of dispersal among vertebrates, both theoretical and empirical, suggest that density-dependent dispersal is likely to be the norm (Doncaster et al. 1997; McPeck & Holt 1992). However, in red deer, dispersal rate is not density-dependent and does not vary significantly between the two sub-populations. The number of individuals dispersing from a group each year is well described by a Poisson distribution (Fig. 1).

A model for red deer harvesting

The model used to describe the dynamics of the two red deer groups is age-structured (Getz & Haight 1989). Juvenile and adult mortality rates are linearly dependent on group size, but fecundity is independent of group size. Fecundity varies from year to year according to a Normal distribution, with the mean and variance observed in the Rum groups. Mortality rates are also assumed to be Normally distributed, but are correlated between the two groups. Dispersal is density-independent and follows a Poisson distribution. Deer managers are assumed to aim to maximise their profits from culling females. They are assumed to have a strategy of culling a certain proportion of each group each year, and to be able to cull different proportions of the two female groups. In calculating the monetary yield from a particular culling strategy, only the variable costs of deer culling are considered, ignoring the fixed costs of management. These fixed costs are not relevant to the decision-making of a manager when deciding how many of each group to cull, rather than whether to cull at all. The variable costs of culling are assumed to be predominately related to search time, with the costs of searching inversely proportional to group size.

Figure 2 shows how the monetary yield from harvesting varies with different harvest rates. The maximum profit can be made by harvesting 10% of one group (the Kilmory Glen group) each year and 14% of the other group (Shamhnan Insir) each year. The Shamhnan Insir group is more variable in its fecundity and mortality rates than Kilmory Glen, and also has stronger density dependence; this is why it is able to sustain a higher hunting mortality rate. Variability in vital rates serves to reduce the optimal hunting mortality rates; if the model was deterministic, the optimal harvest mortality rates would be 12% and 16% respectively. The fact that the maximum monetary yield from the Shamhnan Insir group is obtained at a harvest rate 40% higher than that producing the maximum yield in Kilmory might suggest that the harvesters could be losing a substantial proportion of their potential profits by harvesting the two groups at the same rate, rather than considering them separately. However, because the yields are relatively similar over the range of harvesting mortalities in question (10-14%), the actual losses incurred are small; in this case managers harvesting the groups at the same rate still receive 96% of the yield obtainable under differential harvesting.

Lessons from the case study

This case study uses long-run data on the population dynamics of a particular red deer population, so that its detailed predictions are specific to that population. However, they do give some more general lessons for harvesting structured populations:

- Two sub-populations can react very differently to harvesting and have very different vital rates, however close they are geographically. This means that a detailed understanding of the dynamics of harvested populations is needed, to discern whether there are sub-populations within an area which have sufficiently different dynamics for this to have a significant effect on optimal harvest rates. An added complication is that the dynamics of neighbouring groups

may be correlated through exposure to similar climatic variation, and/or may be linked through migration. These two processes need to be disentangled, as they have different implications for the effects of harvesting pressure on the population: Harvesting a group that is not linked to others, but has correlated dynamics due to exposure to the same climatic conditions, has no effect on the rest of the population, while harvesting a group that is linked by dispersal to another will affect the rest of the population.

- Dispersal is the key factor determining how closely coupled the sub-populations are; it is particularly important to know whether it is density-dependent or density-independent. The model discussed here can be used to show that at low hunting mortalities, density-independent dispersal is very similar in effect to no dispersal, and so the linkage between the groups is not likely to be significant in determining optimal hunting strategies. However, if the groups were linked by density-dependent migration, as is thought to be more usual among vertebrates, the model shows that the effect would be to even out the density-related differences between the groups, and make the optimal harvest rate in one group much more dependent on the size of the other group.

- The complex social and age structure of this species means that the predictions of simple theoretical models are not upheld. McPeck and Holt (1992) showed theoretically that when ecological conditions in patches fluctuate in time and space, but with broadly similar ranges in each patch, selection should favour generalist adaptations to this range of ecological conditions, and a high dispersal propensity. Thus sub-population differentiation is not likely in these conditions. In the area inhabited by the two hind groups discussed here, ecological conditions fluctuate in space and time over a broadly similar range. However, this population has a rather complex, sex-differentiated social structure, in which life-history parameters are

strongly age-determined. Female dispersal is rare and density-independent, and the dynamics of the two sub-populations are not as closely coupled as might have been expected from their geographical proximity. This case study thus provides an empirical example suggesting that further theoretical work is required on the spatial dynamics of populations in cases where population structure is complex.

Case study: Wild pigs in North Sulawesi

This case study is based on papers by Clayton et al. (1997) and Keeling et al. (1999). The previous case study emphasised the importance of a detailed knowledge of the ecology of harvested species, to ensure that the spatial structure of harvested populations is taken into account by managers. In this case study, by contrast, the emphasis is on how the spatial distribution of harvested species acts as a cost to harvesters, and how hunter behaviour is determined by the costs of travel to areas where they can hunt. This difference in emphasis is determined by the major processes driving the interaction between harvesters and their prey in each case.

Wild pig population dynamics

Sulawesi contains two endemic wild pig species, the babirusa (*Babyrousa babyrussa*) and Sulawesi Wild Pig (*Sus celebensis*). The babirusa is found at low densities in primary forest only, and is classified as endangered by IUCN and protected by Indonesian law. The total babirusa population size is estimated at only around 5000 individuals. The Sulawesi Wild Pig is found at much higher densities, in both primary and disturbed forest, and is not protected by law or classified as threatened by IUCN. Details of the biology of the babirusa can be found in Clayton (1996), and of the Sulawesi Wild Pig in Macdonald (1993). The two wild pig species are consumed in the market towns of the eastern tip of North Sulawesi, where the

people are predominately Christian, and are rarely consumed elsewhere in the island, where the population is predominately Muslim. There is a single road running through North Sulawesi along which dealers travel to the forests to buy wild pigs (Fig. 3). The dealers also buy other species, such as bats and domestic dogs, but these are less important goods. Hunters snare pigs in the forests, and carry them to the forest edge to sell to the dealers. The dealers are competitive, and the resource is treated as open access. The trade is described in more detail in Clayton & Milner-Gulland (in press). The road was fully tarmacked only in 1992, and there has recently been a massive expansion of the number of hunters and dealers operating in the province, suggesting that the trade is still in disequilibrium. Wild pigs in Sulawesi make an interesting case study for two reasons:

- 1) Hunting costs vary in a directional manner, increasing as dealers drive further along a single road to collect pigs. The distance that a location is from the market has a major effect on the travel costs of the dealer, and so on the profitability of pig harvesting. The distance that a hunter has to walk from the road into the forest to snare pigs, and the topography of the area he has to walk in, are also major components of the cost of harvesting pigs. This is why it is essential to include a spatial component into any model of wild pig harvesting in North Sulawesi.

- 2) There are two species of pig hunted together, which are not discriminated between by hunters, but which have very different population dynamics. One is endangered, the other is not. The fact that hunters and consumers do not distinguish between these two species mean that a two-species model is needed to characterise the system properly.

A model of wild pig harvesting

Spatial models can be used to predict the equilibrium distribution of pigs under open access harvesting, and the effect of various management actions on the equilibrium distribution of wild pigs. Clayton et al. (1997) used a coupled map lattice model to calculate the equilibrium sizes of the Sulawesi wild pig and babirusa populations under open access harvesting (see a previous section for a description of coupled map lattice models). The unusual features of the model include the use of the underlying structure of vegetation type and road location as the base for the model, rather than assuming a homogeneous environment - another example of this approach is Green (1990). Also, global spatial distributions drive the dynamics, not a localised neighbourhood of sites, because spatial structure enters the model through the dealers' travel costs. The implementation of the coupled map lattice involves the discretisation of space into a lattice of square cells, each with an area of 4km^2 . Five variables are assigned to each cell: the type of habitat to be found at the site (i.e. sea, major road, minor road, forest, logged area etc.); the average cost of snaring and transporting a single pig to market from that site; the number of pigs to be harvested from the site and the population of babirusas and Sulawesi Wild Pigs at the site. The population dynamics of the two species are represented by coupled differential equations assuming simple logistic growth of the populations. The two species experience identical hunting effort, but have different population dynamics and different catchabilities (babirusas are generally slower-growing, found at lower densities and are easier to catch than Sulawesi Wild Pigs).

Harvest costs depend on the cost of transporting a pig along the road divided by the number of pigs being transported. They also depend on the density of pigs in an area; the lower the density, the more effort it takes to catch one, and so the higher the harvest cost. Unlike in the previous case study, here it is assumed that there is no dispersal of pigs between neighbouring

sites. The omission of dispersal is justifiable because harvesting varies slowly over space so that each wild pig would experience little or no variation over its usual home range. Also, this model is concerned with the final equilibrium state while dispersal has a definite temporal scale which would greatly complicate the model. The effect of including dispersal would be a slight reduction in population sizes as wild pigs disperse out of the less hunted areas into the more heavily hunted areas.

Results of the model

The model predicts that under the current physical and economic circumstances the snaring of wild pigs will increase to such a rate that the Babirusa will become extinct over the vast majority of the northern arm of Sulawesi (Fig. 4). Only a relatively small amount of harvesting is necessary for the babirusa to be wiped out in any one area, whereas this amount of harvesting leaves the Sulawesi Wild Pig population virtually intact, causing a decline of less than 5%. In order to see whether the range contraction of the babirusa is an inevitable outcome of hunting or whether it is driven by the recent expansion of the road network, making it easier to reach all areas of the island quickly and easily, the model was re-run using the approximate road network from the 1950's; most of today's roads were in place then but their condition was far worse, little better than dirt tracks. As can be seen from Figure 5, when the road network is less developed the transportation times are greatly increased with it taking almost four days to reach some areas, the consequence of this being that in many regions babirusas survive. The areas in which babirusas remain extant correspond fairly well to the regions where the population can be found today, thus supporting the results from the model if it is assumed that the real system is slow to equilibrate.

Table 1 shows the effect of the major features of the model on its results. Firstly, it is clear that it is the Sulawesi Wild Pig driving the dynamics of the harvesting, and that although babirusas suffer the heaviest losses, their presence or absence in an area is virtually irrelevant to hunters' decision-making. If the two species are not hunted together, but separately, then hunting babirusas alone is not economically viable, as the costs outweigh the profits from hunting. Thus the fact that babirusas are hunted along with Sulawesi Wild Pigs is the reason why it is worth hunting them at all - a similar result to that found for rhino and elephant hunting in the Luangwa Valley, Zambia (Milner-Gulland & Leader-Williams 1992). If, however, Sulawesi Wild Pigs are hunted alone, without babirusas, the increase in harvesting costs is small, leading to only a small increase in the Sulawesi Wild Pig population over its size under two-species harvesting.

Secondly, one of the most interesting features of this system is the effect of religious taboo on the hunting of wild pigs - in effect it is religious taboos which introduce the spatial element of the system through the need to transport wild pigs to market in the Christian tip of the province. It is clear from the sensitivity analyses that this imposes a substantial cost on the harvesters, allowing the equilibrium population of both species to remain much higher than it would be under the more usual circumstances of meat being hunted principally for local consumption.

Several points emerge from this case study:

- Travel costs have a key influence on the outcome of harvesting. Keeling et al (1999) found that the results are even more sensitive to the time taken for a hunter to walk through the forest to find pigs from the road, than to the costs of driving along the road from the forest edge to the market.

- This case study used a digitised map of the province, showing the different vegetation types and topographies of each area, to provide the base for the coupled map lattice model. This use of a heterogeneous underlying physical environment for the model is not common in coupled map lattice models, but it is useful because it enables us to make predictions for the real system. It also opens the way for future modelling work in which changes in habitat availability (through logging and forest clearance) can be included in the model as well as changes in the economic situation.

- If harvesting costs vary spatially, then the least accessible areas can act as refuges for endangered species, by being too costly to harvest. By showing where harvesting costs are highest, the model can predict which areas are likely to hold out longest as refuges for the babirusa. This allows conservation actions to be targetted at areas where babirusas might still survive.

Conclusions

There are two angles from which spatial population structure can be approached in the conservation of exploited species - the ecological and the economic angles. Both are equally important. The two case studies have shown how including a spatial element on either of these sides can improve our understanding of the effects of harvesting on exploited species, and help in the formulation of conservation policy. In the case of the red deer, including the ecological differences between hind groups allowed us to explore the yield improvements that could be obtained by harvesting the groups as separate entities. In the case of the wild pigs, the explicit consideration of spatial heterogeneity and its effect on the economics of harvesting led to predictions about where refuges might exist for the endangered babirusa.

Spatial structure has not had enough attention in the conservation and harvesting literature as yet, either from the ecological or the economic angles. This is true of research into spatial structure in ecology in general, but in mainstream ecology, modelling spatial structure is currently an exciting and expanding field. It is to be hoped that it is only a matter of time before these ideas spill over into the more applied disciplines of conservation and harvesting theory, and there are hopeful signs that this is already happening. The huge amount of recent interest in the theory and practice of marine reserves is one such example. The increasing use of Geographical Information Systems will help to make spatial data much more accessible to conservationists and researchers, although a theoretical basis is also needed if GIS work is to move from being merely descriptive to being usefully predictive. The approaches described in this chapter could form part of the foundation of this spatial theory of the conservation of exploited species.

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Table 1. The effects of the assumptions made in the wild pig harvesting model on its results. The figures given are the equilibrium population sizes of the two species as a percentage of carrying capacity (thus 100 implies that the population is not harvested, while a low number implies that the population is heavily overharvested). The results under the baseline assumptions are shown spatially in Figure 4, the results under the 1950s road network are shown in Figure 5. Data from Clayton et al (1997). SWP = Sulawesi Wild Pig.

Situation	SWP	Babirusa
Baseline assumptions	37	4
Only babirusa hunted	100	100
Only SWP hunted	43	100
1950s road network	66	31
Meat consumed locally	13	0.2

Figures

Figure 1. The observed number of individuals moving from one group of red deer hinds on Rum to the other in a year, plotted against a Poisson distribution, with the mean number moving taken from the data as 0.727 per year. There is no significant difference between the observed frequency of migrations and the expected frequency under a Poisson distribution ($\chi^2=1.52$, NS). Data are aggregated for both sub-populations, and for the years 1974-1995. Figure from Milner-Gulland et al (in press).

Figure 2. The effects of using different harvesting mortality rates on each hind group, shown as the mean monetary yield per year (in pounds) from harvesting the two groups. Means are calculated over 20 years (after transitional effects have finished) for 100 simulations. There are two hind groups: KG = Kilmory Glen, SI = Shamhnan Insir. SI is the more variable population, with stronger density dependence operating. The strategy that maximises monetary yield involves harvesting 10% of the KG population and 14% of the SI population each year. Figure from Milner-Gulland et al (in press).

Figure 3. A map of North Sulawesi. Wild pigs are mainly sold at Langowan, Tomohon and Kawangkoan markets in Minahasa, a predominately Christian area, but are caught in the forests of Bolong Mongondow and Gorontalo. The trans-Sulawesi highway links Manado and Gorontalo, and continues to Central Sulawesi. All dealers must drive down this road to buy wild pigs and other meats. Figure from Clayton et al (1997).

Figure 4. Output of the wild pig harvesting model under 1995 parameter values. In the figures white represents a complete absence, and the sites are then scaled from light grey to black,

black corresponding to the maximum sustainable harvest rate or the population being at carrying capacity. a) The amount of harvesting at each site. b) The number of Sulawesi Wild Pigs that can be supported at each site under this harvesting rate. c) The number of babirusas that can be supported at each site under this harvesting rate. Figure from Clayton et al (1997).

Figure 5. Output of the wild pig harvesting model under 1950s road conditions. In the figures white represents a complete absence, and the sites are then scaled from light grey to black, black corresponding to the maximum sustainable harvest rate or the population being at carrying capacity. a) The amount of harvesting at each site. b) The number of Sulawesi Wild Pigs that can be supported at each site under this harvesting rate. c) The number of babirusas that can be supported at each site under this harvesting rate. Figure from Clayton et al (1997).





