

## CHAPTER 9

# *Wildlife Conservation and the Invasion of Nature Reserves by Introduced Species: a Global Perspective*

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### 9.1 INTRODUCTION

In this chapter we address some of the ways in which introduced species can affect nature conservation, the current extent of invasions of nature reserves by these species and some of the observed effects of these invasions. We then give examples of successes and failures in past efforts at controlling these invasions. Finally we draw some conclusions related to the prospects of controlling them in the future.

The World Conservation Strategy gives three main objectives for nature conservation; the maintenance of essential life support systems, the maintenance of natural diversity and the sustained utilization of species and ecosystems. In terms of conventional ecological terminology the first two objectives can be paraphrased as maintaining ecosystem function and ecosystem structure (Watt, 1947).

This chapter is restricted to wildlife conservation (i.e. the *in situ* conservation of natural communities) as implemented within a framework of proclaimed nature reserves. For the purposes of this chapter a 'nature reserve' is any area set aside primarily for the conservation of its native biota and these can range from urban reserves of a few hectares to national parks thousands of square kilometres in extent.

Whenever possible, reserves have been classified according to the biome and realm system of Udvardy (1975) and the names used throughout the chapter follow this system. The area of natural vegetation in each of these biomes has not yet been surveyed. Rough approximations of these areas derived from two surveys using different 'biome' classification systems, (Whittaker and Likens, 1975; World Resources Institute, 1986) together with the number and area of national parks and equivalent reserves that had been proclaimed up to 1982 (after Harrison *et al.*, 1984) are given in Table 9.1.

The percentage of the world's non-marine area currently included in nature reserves (*Sensu* Harrison *et al.*, 1984) lies somewhere between 2.7 and 3.4%,

Table 9.1. The area of natural ecosystems estimated as remaining in the continental and insular biomes of the world and the total number and area of reserves in these biomes

Biome (after Udvardy, 1975)	Area of Natural Resources (after World Resources Institute, 1980)	Area of Natural Vegetation (million of km <sup>2</sup> ) (after Whittaker and Likens, 1975)	No. of Reserves	Area of Reserves (from Darrison <i>et al.</i> , 1984) (thousand of km <sup>2</sup> )
Tropical humid forests	15.6	17.0	355	475.2
Subtropical and temperate rainforests or woodlands	1.5	8.5	201	113.3
Temperate broadleaf forests or woodlands	12.5	12.0	270	144.1
Temperate needleleaf forests or woodlands	11.8	12.0	114	278.3
Evergreen sclerophyllous forests, scrub or woodlands	42	Included in temperate forest	426	82.7
Tropical dry or deciduous forests or woodlands	10.2	7.5	481	703.7
Tropical grasslands and savanna	27.4	15.0	31	87.7
Temperate grasslands	?	9.0	05	32.8
Warm deserts and semi deserts	24.5	42.0	67	603.3
Cold winter deserts		42.0	48	76.1
Tundra communities and barren arctic communities	7.4	8.0	31	1012.4
Mixed mountain and highland systems with complex zonation	Included above under constituent biome	Included above under constituent biome	318	283.7
Mixed island systems	Not included	2.0	74	15.8
River and lake systems	Not included	2.0	10	4.3
Swamp and marsh	[17.5]	[14.0]	Included above under constituent biome [not normally present within reserves.]	
[Cultivated lands]	132.5	149.0	2511	3973.2
Total land area				

depending on which estimate of the total area one accepts (Table 9.1). By 1983 some 13% of the total ice-free land area had been transformed by cultivation (Table 9.1; World Resources Institute, 1986). Eight of the 30 global vegetation types had already been reduced by between 25% and 45% of their original areas (World Resources Institute, 1986). As the human population increases the conversion of natural vegetation through cultivation will intensify. The remaining areas of natural vegetation outside nature reserves will become progressively more modified. Increasingly, the conservation of the world's wild genetic resources will come to depend on that small percentage of its area included in nature reserves.

This chapter concentrates on invasive introduced species which affect the maintenance of ecosystem structure (i.e. species composition, genetic diversity) and ecosystem function (e.g. nutrient cycling, hydrology, soil erosion, decomposition) within nature reserves. An introduced species is defined as one which only occurs in the reserve as a result of the intentional or accidental movement of the species by humans from its natural distribution range. To be classified as 'invasive' the introduced species must be capable of establishing self-sustaining populations in areas of natural or semi-natural vegetation (i.e. untransformed ecosystems) within the reserve.

Any significant alteration of ecosystem function by an introduced species is considered deleterious. This is not simply a subjective value judgement as it is a fundamental goal of nature reserves that they should serve as unaltered natural baselines against which can be measured the effects of anthropogenic changes in adjacent unprotected areas.

If an invasion alters the relative abundances of a reserve's native species this cannot always be taken to be deleterious. Thus, although introduced species most probably have important effects on nature reserves through changing their native species composition, such cases do not form the main subject matter of this chapter. There are, however, two categories of structural change to ecosystems that can be relatively easily quantified and which are universally held to be in conflict with the goals of nature conservation. The first category is the reduction in species richness of a community through local extinction. The second is the adulteration of gene pools through the hybridization of introduced and native species. However, before examining these effects, the extent of the invasion of nature reserves by introduced species in some of the world's biomes is first described.

## **9.2 THE EXTENT OF THE INVASION OF NATURE RESERVES BY INTRODUCED SPECIES**

The measurement of the actual extent of invasions of nature reserves has been carried out only for a handful of introduced species in a few of the world's reserves. In almost all cases the measures of extent differ between reserves and

between different types of introduced organisms. In the absence of a large, standardized data base, three simpler measures have been used: the proportion of reserves in a biome reporting problems with introduced species (e.g. Machlis and Tichnell, 1985), the number of such species recorded from the reserve (Loope, in press; Macdonald, in press; Macdonald *et al.*, 1986) and the extent of resource allocation to control operations within a reserve (Macdonald, in press). Data on the number of invasive introduced species known to be present, expressed both as an absolute number and as a percentage of the total number of species (native and invasive), are given in Table 9.2.

The number of invasive introduced plant species present in a reserve is an order of magnitude greater than the number of such species in any vertebrate class. Introduced invertebrates are however known to reach numbers similar to those of vascular plants in the national parks of Hawaii (Loope, in press). If the number of introduced species is expressed as a percentage of the total species present, the differences between plants and vertebrate classes are not so great, with fish often showing the highest percentage. The major difference between biomes is that the reserves in mixed island systems have higher mean absolute and proportional numbers of introduced species than do reserves in any of the continental biomes.

If there is any trend between continental biomes it is for the more xeric environments to have smaller absolute numbers of introduced species, in particular of introduced vascular plant species. This is most obvious in the warm deserts and semi deserts but is also apparent in the tropical dry forests or woodlands. There are no invasive introduced plants and vertebrates in the Barren Arctic Deserts of Antarctica (Usher, unpublished). The trend then is for biomes with extreme abiotic conditions i.e. very hot, cold or dry, to have fewer invasive introduced species.

In their analyses of the numbers of introduced species in 41 southern African nature reserves, Macdonald *et al.* (1986) found that the only reserve characteristic which gave rise to significantly different numbers of introduced vascular plants was the annual number of visitors to the reserve. This relationship was explored more fully in both the southern African data set (slightly modified to include more recent data) and one for 21 continental reserves in the USA (Loope, in press) with annual visitor numbers for 1985 (Statistical Office, Denver Service Center, 1986). The relationships between the numbers of introduced and native species per reserve were also investigated by regression analyses of untransformed and logarithmically transformed variables.

The significant results obtained in these regression analyses are presented in Table 9.3. Some of the bivariate scatter plots showing the linear regressions are presented in Figures 9.1 and 9.2.

The correlation between the number of introduced species and visitor numbers was significant for 11 of the 13 reserve groupings tested here. There were also positive correlations between numbers of introduced and native species in nine of the 13 groupings of reserves.



Table 9.2. Data on the extent of invasions of nature reserves in different biomes. The number of reserves for which data were available is given in brackets; the three numbers represent the minimum, mean and maximum for that sample respectively. No information was available for biomes listed in Table 9.1 but omitted from this table

Biome	No. of Invasive Spp. per Reserve				Invasive Introduced Spp. as Percentage of Total Species			
	Vascular plants	Freshwater fish	Birds	Mammals	Vascular plants	Freshwater fish	Birds	Mammals
Subtropical and temperate rainforests or woodlands	20-139-260 (3)				3-15-22 (3)			
Temperate broadleaf forests or woodlands	23-157-249 (5)				7-13-17 (5)			
Temperate needleleaf forests or woodlands	27-115-222 (3)				4-13-21 (3)			
Evergreen sclerophyllous forests, scrub or woodlands	69-88-113 (5)	1-3-6 (4)	1-3-5 (6)	2-4-8 (5)	6-11-28 (5)	37-56-86 (4)	1-3-6 (6)	5-13-26 (5)
Tropical dry or deciduous forests or woodlands	12-60-113 (5)	0-1-1 (3)	0-1-3 (3)	1-2-4 (3)	3-5-7 (5)	0-17-50 (3)	0-0-1 (3)	1-2-5 (3)
Warm deserts and semi-deserts	7-20-33 (3)	0-2-6 (5)	1-3-6 (5)	0-1-3 (5)	4-5-6 (3)	0-30-100 (5)	1-1-2 (5)	0-3-6 (5)
Mixed mountain and highland systems with complex zonation	67-98-120 (4)				7-10-12 (4)			
Mixed island systems	240-358-520 (3)		1-9-17 (2)	9-9-10 (2)	31-47-64 (3)		3-20-53 (2)	71-81-90 (2)

Table 9.3. Significant results in the regression analyses of the number of alien plant species in continental nature reserves of North America and southern Africa. ( $P$  = significance of the regression. Where  $P > 0.05$  the regression was considered not to be significant (N.S.) % = percentage of variance accounted for by regression)

Group of reserves	No. of reserves in sample	No. of alien species on log visitors/year	% = 43	$P < 0.001$	Log no. of alien spp. on log visitors/year	$P < 0.001$	% = 45	No. of alien species on no. of native spp.	N.S.	Log no. of alien spp. on log no. native spp.	$P < 0.002$	% = 41
All American reserves	21											
Temperate broadleaf forests or woodlands	6	$P < 0.004$	% = 90		$P < 0.004$	% = 70		$P < 0.04$	% = 72		$P < 0.006$	% = 88
Warm deserts and semideserts	4	$P < 0.002$	% = 60		N.S.			N.S.			N.S.	
Mixed mountain systems	5			N.S.				N.S.			N.S.	
All Southern African reserves	41	$P < 0.001$	% = 40		$P < 0.001$	% = 26		$P < 0.001$	% = 59		$P < 0.001$	% = 44
Tropical dry forest or woodlands	15	$P < 0.015$	% = 38		N.S.			$P < 0.001$	% = 77		$P < 0.001$	% = 71

Evergreen sclerophyllous forests, scrub or woodland	15	$P < 0.001$	% = 71	$P < 0.001$	% = 64	$P < 0.01$	% = 41	N.S.
Warm deserts and semideserts	8	N.S.		N.S.		N.S.		N.S.
All reserves	62	$P < 0.001$	% = 53	$P < 0.001$	% = 56	$P < 0.01$	% = 38	$P < 0.001$
Tropical dry forest or woodlands	16	$P < 0.002$	% = 52	$P < 0.02$	% = 37	$P < 0.002$	% = 51	$P < 0.001$
Evergreen sclerophyll vegetation	16	$P < 0.001$	% = 74	$P < 0.001$	% = 67	$P < 0.04$	% = 29	N.S.
Warm deserts and semideserts	12	$P < 0.003$	% = 60	$P < 0.02$	% = 43	$P < 0.001$	% = 86	$P < 0.001$
Mixed mountain systems	8	$P < 0.002$	% = 81	$P < 0.001$	% = 87	$P < 0.04$	% = 65	$P < 0.008$

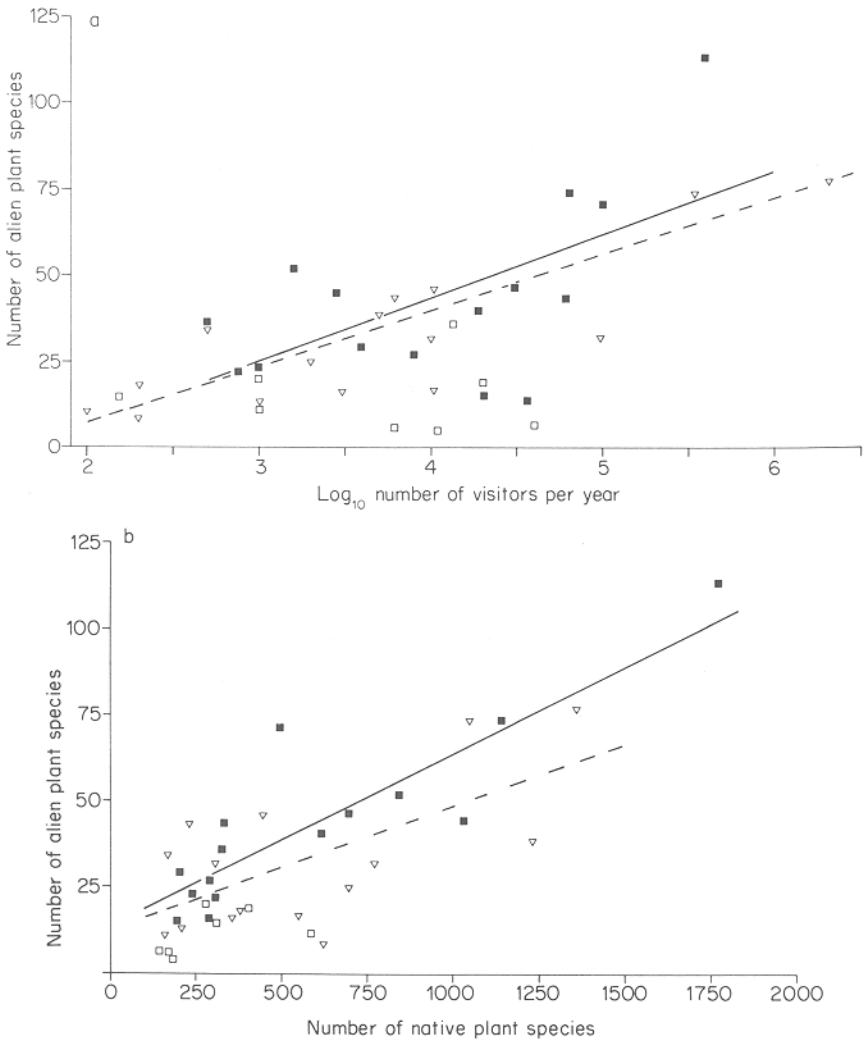


Figure 9.1. The number of introduced vascular plant species (y) recorded from southern African nature reserves, plotted against (A) the log of the number of visitors per annum to the reserve (x) and (B) the number of native vascular plant species recorded from the reserve (z).

Key: Reserves in Tropical Dry Forest or Woodland biome

(■; ——— = regressions  $y = 18,41x - 30,93$

$y = 0,05z + 13,52$ )

Reserves in Evergreen Sclerophyllous Forest, Scrub or Woodland biome

(▽; - - - - = regressions  $y = 14,55x - 21,55$

$y = 0,035z + 12,57$ )

Reserves in Warm Desert or Semidesert biome

(□)

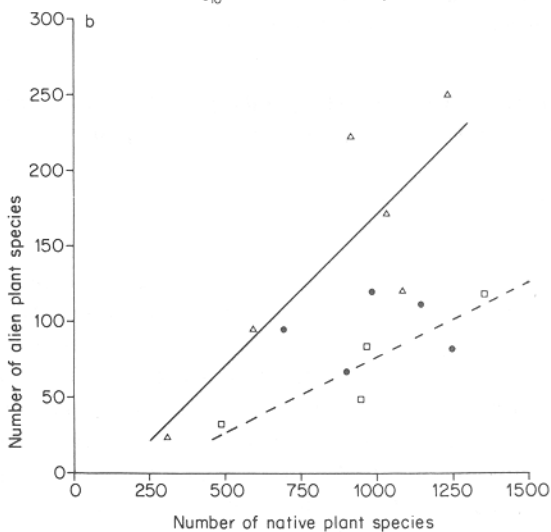
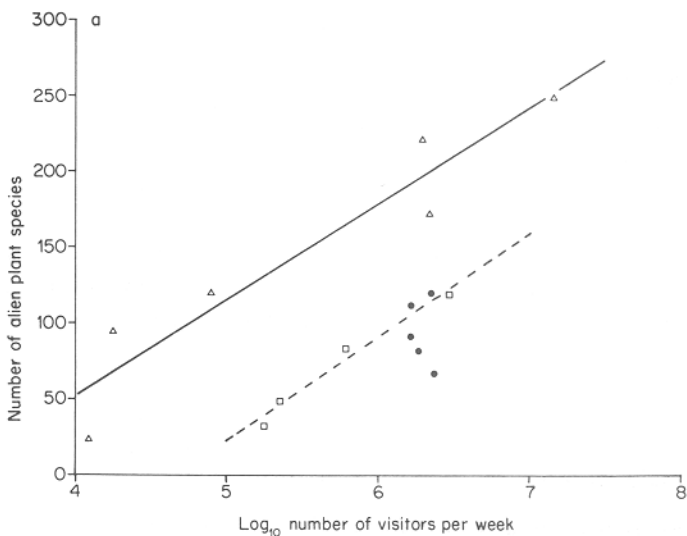


Figure 9.2. The number of introduced vascular plant species ( $y$ ) recorded from North American nature reserves, plotted against (A) the log of the number of visitors per annum to the reserve ( $x$ ) and (B) the number of native vascular plant species recorded from the reserve ( $z$ ).

Key: Reserves in Temperate Broadleaf Forest or Woodland biome

( $\Delta$ ; — = regressions  $y = 63,17x - 200,86$

$y = 0,20z - 29,32$ )

Reserves in Warm Desert or Semidesert biome

( $\square$ ; - - - = regressions  $y = 67,66x - 315,74$

$y = 0,098z - 21,60$ )

Reserves in Mixed Mountain or Highland Systems with Complex Zonation biome

( $\bullet$ )

These relationships suggest the following hypotheses:

1. An increase in the number of visitors to a reserve leads to an increase in the number of introduced plant species present in the reserve.
2. This increase in species is a direct result of the importance of introduced plant propagules either by visitors or their vehicles.
3. This increase in species results from habitat modification brought about in the reserve either through the provision of visitor facilities (e.g. roads, campgrounds) or by the visitors themselves (e.g. trampling, incidence of accidental fires).
4. Environments and parks with more native species tend also to have more introduced species, possibly as a result of increased habitat diversity [reserve size has not been found to be a significant factor in southern Africa (Macdonald, in press; Macdonald *et al.*, 1986)].

It is not possible from the data presented here to make any statements as to the relative contributions of the above factors to the observed relationships.

### 9.3 SOME EFFECTS OF INTRODUCED SPECIES ON ECOSYSTEM FUNCTION IN NATURE RESERVES

#### 9.3.1. Acceleration of soil erosion rates

Grazing, browsing and trampling by feral mammals have accelerated soil erosion rates in many parts of the world, especially on islands (Coblentz, 1978), though rigorous documentation seems to be lacking. In Channel Islands National Park, California, USA, for example, irreversible loss of topsoil through gully and sheet erosion is thought to have been initiated by destruction of vegetation cover by feral mammals, e.g. European rabbits *Oryctolagus cuniculus* (Halvorson, in press).

A relatively well-studied example is provided by Himalayan tahr *Hemitragus jemlahicus* in the Table Mountain Nature Reserve, South Africa (Lloyd, 1975). The progeny of a single pair that escaped into the reserve in 1938 numbered approximately 330 animals by 1972, when they were concentrated in some 300 hectares of optimal habitat. Using exclosures situated in the main concentration areas, the tahr were estimated to be removing through browsing or reducing by trampling the annual above-ground net plant production by 5300 kg dry matter (DM) ha<sup>-1</sup> (73% of that recorded inside the exclosures). All the concentration areas showed accelerated soil erosion, with a loss of 8 mm of soil being measured over an 11 month period in one area (Lloyd, 1975).

#### 9.3.2 Alteration of other geomorphological processes

Any changes in the geomorphological processes which shape the landscapes and habitats of nature reserves will affect the long-term conservation of their

constituent ecosystems. Introduced species have already been demonstrated to have affected some of the more dynamic of these processes, namely soil erosion, sand dune formation and changes in riverbank configuration.

The European grass *Ammophila arenaria* has been planted world-wide for sand-fixation. It has become an aggressive invader along the coast of western North America, in northern California and Oregon, and is believed to have changed the topography of dunes in this area. Before its introduction, foredunes were low, rose gradually, and were accompanied by an inland dune system parallel to the prevailing on-shore winds (perpendicular to the coast). Most dune systems now have steep foredunes dominated by *A. arenaria* with an inland system of dunes and swales oriented parallel to the coast (Barbour and Johnson, 1977). Introduced plants have been implicated in similar alterations of dune configurations in Africa and Australia (Macdonald and Richardson, 1986).

Stands of invasive *Casuarina equisetifolia* on the west coast of Everglades National Park, Florida, have been found to result in sand accumulation, leading to development of steeper shorelines that can not be surmounted by sea turtles *Caretta caretta* searching for nesting sites (Klukas and Truesdell, 1969).

A study by Graf (1978) on the Green River in Canyonlands National Park, Utah, documented the effects of the invasive tree *Tamarix ramosissima* on the fluvial geomorphology of the area. Before the introduction of tamarisk, the native plants (primarily *Distichlis stricta* and *Salix exigua*) occupying the river floodplain were repeatedly swept away by floods, but once introduced and established, tamarisk was able to withstand inundation, continue to grow, stabilize the underlying surface, and induce sedimentation. Dense tamarisk thickets along the Green River have trapped and stabilized sediment, causing a reduction in channel width of 13–57%, increasing overbank flooding, and stabilizing and altering dimensions of islands and bars.

An interesting example of how an introduced species has caused a range of geomorphological effects is provided by *Spartina* species in the estuaries of England. *Spartina alterniflora* appears to have been introduced to Southampton Water, southern England, accidentally, probably in shipping ballast, from the east coast of North America. Prior to 1870 it hybridized with the native species, *Spartina maritima*, to produce the sterile hybrid, *Spartina* × *townsendii*. *S. alterniflora* has not been invasive and, although it has persisted, it is now considered to be 'very rare' (Hubbard, 1968). To some extent the sterile hybrid has been invasive, spreading throughout the southern coastal areas of England. However, a highly invasive fertile amphidiploid, *Spartina anglica*, has been derived from the sterile hybrid by a doubling of the chromosomes, and it is the new species which has invaded many coastal mud-flats around the shores of Great Britain.

The effects of *s* × *townsendii* and *S. anglica* on geomorphological processes are documented in Doody (1984). Hubbard (1968) recorded that these species, especially the latter, stabilized the soft coastal mud of tidal mud-flats by means of their extensive system of roots and rhizomes. The filtering action of the culms and

leaves collect silt and debris, thus raising the level of the mud-flats. Due to this, *S. anglica* has been widely planted to protect foreshores from erosion and to reclaim previously useless land. Such accretion had occurred, for example, in the North Solent National Nature Reserve, but the *S. anglica* stands are now experiencing an unexplained dieback. Degeneration within the reserve is so severe that it is accompanied by destruction of the terminal cliffs of the marsh along an exposed face and the Nature Conservancy Council is having to devise means of encouraging longshore drift to build a protective shingle barrier (C.R. Tubbs, personal communication). The *Spartina* species have, during the first half century or so of their invasion, been associated with a geomorphological process of accelerated accretion; subsequently their degeneration is threatening the plant and animal communities that have previously been protected from marine erosion in many areas.

### 9.3.3 Alteration of biogeochemical cycling

Singer *et al.* (1984) found that feral pigs *Sus scrofa* rooting in deciduous forests of the Great Smoky Mountains USA accelerated leaching of Ca, P, Zn, Cu, and Mg from leaf litter and soil. Nitrate concentrations were higher in soil, soil water, and stream water from rooted areas suggesting alterations in nitrogen mineralization processes. Rooting was not found to increase sediment yield in this study, however.

The invasive introduced plants *Myrica faya* and *Leucaena leucocephala* in Hawaii Volcanoes National Park actively fix nitrogen in association with symbiotic bacteria, resulting in much elevated nitrogen levels on otherwise nitrogen-poor sites on young lava flows. Since most introduced plant invaders in Hawaii are most successful on more fertile sites, the invasion of these nitrogen-fixers may facilitate further invasions (Vitousek, 1986).

At Channel Islands National Park, California, the introduced annual iceplant *Mesembryanthemum crystallinum* accumulates salt which enters the soil profile during decomposition. The species excludes other vegetation by shading and by increasing the salt content in the soil above the osmotic tolerance of potential competitors in former grassland ecosystems (Halvorson, in press). [The mechanism was documented for mainland California by Vivrette and Muller (1977)].

### 9.3.4 Alteration of hydrological cycles

Invasive introduced plants can primarily affect hydrological cycles by utilizing more or less of the annual precipitation than was used by the native vegetation they replace. Several examples of these changes are known to have occurred in nature reserves.

The invasion of nature reserves in the jarrah *Eucalyptus marginata* forests of southwestern Australia by the introduced soil-borne fungus *Phytophthora*



*cinnamomi* (see Von Broembsen, this volume) has given rise to major hydrological changes. The extent of the invasion is considerable, with 10% of the total area of  $1.5 \times 10^6$  hectares covered by this forest type being severely diseased by 1972 (Shea, 1981). Once it has invaded the forest the fungus causes the death of all the individuals of the deep-rooted dominant tree species, *E marginata*. The majority of the other species in the shrub and understorey layer of the forest are also killed (Shea, 1981). Following dieback, transpiration losses are severely reduced, the soil water table rises and catchment discharge increases. In areas where soil salinity levels are high this change in soil hydrology results in salination of the runoff water (Shea *et al.*, 1975).

Another example of introduced species giving rise to hydrological changes in a mediterranean-type climate region comes from the fynbos biome of South Africa. Numerous nature reserves in the mountain catchments are being invaded by introduced trees and shrubs, such as *Hakea sericea*, *Pinus pinaster*, *Acacia longifolia* and *Acacia mearnsii* (Macdonald *et al.*, 1985), which reduce stream flow from the affected mountain catchments (Macdonald and Richardson, 1986; Versfeld and van Wilgen, 1986).

In parks and reserves of southwestern USA (including Death Valley National Monument and Big Bend National Park), evapotranspiration of invasive *Tamarix* spp. lowers water tables and dries up springs (Vitousek, 1986). One of the indirect consequences of this is habitat degradation for, and population decline of, desert bighorn sheep *Ovis canadensis* (US National Park Service, 1981). In the Namib Naukluft and Skeleton Coast Parks of South West Africa/Namibia, invasions of the rivercourses by introduced plants such as *Datura innoxia*, *Nicotiana glauca* and *Prosopis* spp. are considered to be having an analogous effect on the subsurface hydrology of these desert rivers (Brown *et al.*, 1985; Macdonald and Nott, 1987).

Another example of the potential of an invasive species to alter hydrological cycles is provided by a mammal, the coypu *Myocastor coypus*. In moving towards a policy for the total eradication of this species in Great Britain, the case for Drainage Authorities was summarized by Morton *et al.*, (1978) as 'The damage caused... was not quantifiable but involved boring into the bank of watercourses, railway embankments, culverts and foundations of pumping stations'. Although many of these effects were not observed on nature reserves the potential of this introduced species to upset the hydrological balance in a countryside of relatively small nature reserves interspersed in an agricultural environment is considerable.

### 9.3.5 Alteration of fire regimes

The fire regime is a critical component of the environment in all except the wettest (e.g. tropical humid forests and tundra) and driest terrestrial biomes (e.g. deserts). Where introduced species alter the fire regime this can have profound implications for ecosystem structure and function.

In both the New World and Australia the invasion of introduced grasses has affected fire regimes (Clark, 1956; Parsons, 1972; Christensen and Burrows, 1986). In all cases the change is thought to have been to a regime of more frequent fires. Invasion by *Andropogon* species and other introduced grasses has greatly increased the quantity and continuity of fine fuels and consequently the extent and intensity of wildfires in Hawaii Volcanoes National Park (Smith, 1985). The introduced annual cheatgrass *Bromus tectorum* has a similar effect over wide areas of the western USA. Unlike most perennial grasses of western North America, which reach maturity slowly and often do not readily burn until the major fire season is past, *B. tectorum* matures in early June and dries 1 to 2 weeks after maturing. At maturity, it has an exceptionally low moisture content (Klemmedson and Smith, 1964). Following fire, stands typically return quickly to domination by cheatgrass. The invasion has radically altered fire regimes in several reserves, e.g. in Capital Reef, Zion, Canyonlands, and Arches National Parks, in Utah. Similarly, in three reserves in the mediterranean-type climate region of California the almost total replacement of the indigenous ground layer by introduced European grasses is thought to have made spring and early summer fires more frequent (Macdonald *et al.*, 1988).

In African savanna reserves fire is generally considered to have limited the invasion of introduced plants rather than to have been affected by their invasion. (Macdonald and Frame, 1988). An exception to this is the composite climber *Chromolaena (Eupatorium) odorata*. This species has extensively invaded reserves, such as the Hluhluwe-Umfolozi Game Reserve, in the moister eastern savannas of South Africa (Macdonald, in press). The plant is extremely flammable and it invades savanna-forest ecotones which normally act as natural fire breaks. Following invasion by *C. odorata*, fires burn from the savanna into the forest margins killing the fire-sensitive forest tree species and thus reducing the size of forest patches (Macdonald, 1983).

In the fynbos reserves of South Africa the replacement of the indigenous sclerophyll vegetation by dense thickets of introduced trees such as *Hakea sericea* and *Acacia saligna* is thought to have decreased the frequency and mean intensity of fire by altering fuel characteristics (Van Wilgen and Richardson, 1985). However, when dense stands of these species are felled and then burned, high intensity fires result. These fires reduce both the diversity of plant species, particularly those which have underground structures which normally survive fires, and the density of termites (Breytenbach, 1986b).

These altered fire regimes often lead to recruitment failures of native species. However, invasions can have more direct effects on the recruitment of native species.

### 9.3.6 Prevention of recruitment of native species

The prevention of recruitment is often the causal process in long-term changes in the gross structural, and hence the functional, aspects of a reserve's ecosystems.

An example of an introduced plant preventing the recruitment of indigenous plant species is provided by one of the most serious plant invasions in the British Isles. In the mixed oak *Quercus petraea* and holly *Ilex aquifolium* woodland reserves in southwest Ireland, the introduced species, *Rhododendron ponticum*, is thought to inhibit woodland regeneration both by casting a dense shade and by forming an impenetrable litter layer (Usher, 1987). Cross (1982) quoted data for a mixed oak and holly stand, with 9% of incident daylight beneath the canopy, having seedlings of four tree species as well as a ground flora of seven fern and herbaceous plant species and thirteen bryophyte species. In an equivalent stand invaded by rhododendron, the light intensity was only 2% of daylight; there were no tree seedlings and only two species of fern and herbaceous plant and four species of bryophytes.

In one of the few quantitative studies ever made of the impacts of introduced plants in a nature reserve, Thomas (1980) showed that two species of vines were, in combination, preventing the recruitment of native forest species on Theodore Roosevelt Island, Washington DC. Japanese honeysuckle *Lonicera japonica* inhibited the reproduction of dominant forest trees such as *Ulmus americana*, *Prunus serotina* and *Liriodendron tulipifera*. English ivy *Hedera helix*, by contrast, primarily inhibited the recruitment of herbaceous species. Both species suppress and eventually kill established forest trees through shading. By inhibiting the subsequent recruitment of native species they were literally 'destroying the forests of this low lying island' (Thomas, 1980).

On Juan Fernandez Island the introduced plant *Aristotelia chilensis* is gradually replacing the endemic species *Myrceugenia fernandeziana* and *Drimys confertifolia*. Similarly, the native *Ugni selkirkii* is being replaced by the invasive *U. molinae*. Sanders, *et al.* (1982) conclude that these and other native plant species, 'especially many of the rosette Compositae, are disappearing, seemingly because seedlings are not becoming established to replace the senescing plants. Most of these oddities appear to be adapted to specific habitats and do not compete well for growing space as the vegetation around them changes.'

Alien animals can have equally significant impacts on the recruitment of native plants. In the Pinnacles National Monument, California, feral pigs are considered to be preventing the recruitment of oak, *Quercus* species (Macdonald *et al.*, 1988). Similarly European rabbits are thought to be inhibiting the recruitment of perennial herbs and shrubs in La Campana National Park, Chile (Macdonald *et al.*, 1988).

In the fynbos reserves of South Africa wherever the introduced Argentine ant *Iridomyrmex humilis* invades, it displaces the native ant community (Macdonald and Richardson, 1986). Many of the native plant species are myrmecochorous and the Argentine ant fails to carry out the seed removal and seed burial function of the native ant species. This leads to an almost complete recruitment failure in myrmecochorous plant species (Bond and Slingsby, 1984; Bond and Breytenbach, 1985).

In island reserves the introduction of animals has often given rise to

recruitment failures. An example of an introduced animal apparently preventing the recruitment of an island plant is provided by the house mouse *Mus musculus* on the south Atlantic Gough Island. Seed predation by the mouse is thought to be preventing the recruitment of the locally important tree *Phylica arborea* (Breytenbach, 1986a). Feral goats *Capra hircus* are probably the single most important introduced herbivore in terms of their effect on the recruitment of native plants on island nature reserves (Holdgate, 1967; Coblenz, 1978). In the Galapagos Islands the recruitment of trees such as *Scalesia pedunculata*, *Zanthoxylum fagara* and *Acnistus ellipticus* has been totally prevented by goat browsing (Hoeck, 1984).

Island nature reserves also provide examples where introduced animals have prevented the recruitment of native animal species. In the Galapagos Islands, the introduced black rat *Rattus rattus* has had a devastating effect on the Pinzon Island race of the giant tortoise *Geochelone elephantopus ephippium*. According to Hoeck (1984) black rats were established on this island around 1880 and each year since then they have killed almost every tortoise hatchling that emerges from its nest. MacFarland *et al.* (1974) calculated that in a period of 10 years between 7000 and 19 000 hatchlings were produced, but only a single one-year-old tortoise was found on the entire island. On other islands in the Galapagos (Santa Cruz, San Cristobal, Isabela and Santiago), feral pigs effectively reduce the recruitment of tortoises, and of land and marine iguanas, by regularly digging up and eating the eggs. Furthermore, on a number of sandy beaches feral pigs dig up every nest of the green turtle *Chelonia mydas* and eat the eggs.

An example of an introduced plant having the potential to prevent the recruitment of a native animal species is provided by *Lantana camara* on the Galapagos island of Floreana. The dense thickets formed by this species are spreading towards the largest remaining colony of the threatened dark-rumped petrel *Pterodroma phaeopygia*. If this invasion is not halted, it is considered likely (Cruz *et al.*, 1986) that the thickets will prevent the petrels from flying in and out of their nest burrows.

On the island of Mauritius a wide range of introduced species in combination prevent the recruitment of native plant species. Introduced monkeys *Macaca fascicularis* cause extensive damage to native trees such as *Erythrospermum monticolum* and *Mimusops petiolaris* by selectively pulling off branches, flowers and unripe fruits. The few seeds of these native trees that survive to germinate are subjected to heavy browsing at the seedling stage by deer *Cervus timorensis* and feral pigs and intense competition from introduced plants such as *Ligustrum robustum* and *Psidium cattleianum* which form dense thickets. In addition, the established individuals of 26 native tree species are being ringbacked by the deer (Strahm, 1986).

### 9.3.7 Concluding comment on effects on ecosystem function

This is by no means an exhaustive listing of the perturbations in ecosystem function

that can be brought about by introduced species in nature reserves. If one looks at any one of the myriad different ecosystem functions already known, one can normally find an example of how an introduced species is affecting this function. However, few of these ecological impacts have been studied and the listing simply documents some of those which have. These examples serve merely to indicate the wide range and, often, the insidious nature of such effects.

## 9.4 SOME EFFECTS OF ALIEN SPECIES ON ECOSYSTEM STRUCTURE IN NATURE RESERVES

### 9.4.1 Acceleration of local and global extinction rates

Although it would be desirable to use data from recent extinctions to investigate the role that introduced species play in extinction, this is generally not possible for two reasons. Firstly, it is very difficult to 'prove' that a species has in fact become extinct, e.g. the case of the Australian noisy scrub-bird *Atrichornis clamosus* which was incorrectly thought to have been extinct for 70 years (Whittell, 1943; Webster, 1982). Secondly, very few of the species that have become extinct were studied prior to their extinction, so that the factors responsible for their demise are almost invariably unknown or have been inferred from incomplete information. Thus, in the case of *A. clamosus*, it was originally deduced that its 'extinction' had been brought about by deforestation by humans and predation by feral cats *Felis catus* (Whittell, 1943). It was only after detailed investigations of the remnant population that it was possible to ascribe the decline to alterations in fire regime (Smith and Robinson, 1976) and, more specifically, to reductions in invertebrate prey following too frequent burning (Blakers *et al.*, 1984). Currently *A. clamosus* is not considered threatened by any introduced species (Conservation Monitoring Centre, personal communication). Thus, although recent extinctions will be covered they will not be analysed quantitatively.

Instead, data on the species currently considered to be threatened with extinction have been analysed to indicate the potential role introduced invasions might play in future extinctions. These data have been extracted from the computerized Red Data Book data bases of the International Union for the Conservation of Nature's Conservation Monitoring Centre in Cambridge, UK. Only data on vertebrates have been used (Table 9.4) as these are the only taxonomic groups for which global coverage is considered to be adequate to show real trends as distinct from artefacts of incomplete knowledge (N. Phillips, personal communication).

The proportion of threatened species, all species with any Red Data Book status other than 'O' (out of danger), that are known to be threatened in any way by introduced species is shown to vary markedly between taxonomic groups, between biogeographic realms and between island and mainland species. Islands were defined as all landmasses smaller than New Guinea.

Using chi-squared tests with Yates' correction with 1 d.f., the number of

Table 9.4. The percentage of threatened terrestrial vertebrate species affected by introductions in the continental landmasses of the different biogeographic realms and on the world's islands. The total number of threatened species in the realm is given in brackets

Taxonomic Group	Percentage of threatened species affected by introductions											
	Continental areas within biogeographic realms						All mainland areas		All insular areas			
	Eurasia % (n)	N. America % (n)	Africa % (n)	Indo-Malaya % (n)	Oceania % (n)	Australia % (n)	Antarctica % (n)	S. America % (n)	% (n)	% (n)	% (n)	% (n)
Mammals	16.7 (42)	3.4 (29)	8.0 (100)	12.7 (55)	0.0 (8)	64.4 (45)	0.0 (0)	10.0 (60)	19.4 (283)	11.5 (61)		
Birds	4.2 (24)	13.3 (15)	2.5 (118)	0.0 (30)	0.0 (1)	27.3 (11)	0.0 (0)	4.2 (71)	5.2 (250)	38.2 (144)		
Reptiles	5.9 (17)	16.7 (24)	25.0 (16)	4.3 (23)	14.3 (7)	22.2 (9)	0.0 (0)	14.3 (28)	15.5 (84)	32.9 (76)		
Amphibians	0.0 (8)	6.3 (16)	0.0 (3)	0.0 (0)	0.0 (0)	0.0 (2)	0.0 (0)	0.0 (1)	3.3 (30)	30.8 (13)		
Total for all groups considered	9.9 (91)	9.5 (84)	6.3 (237)	7.4 (108)	6.3 (16)	50.7 (67)	0.0 (0)	8.1 (160)	12.7 (647)	31.0 (294)		

threatened species having introductions as a threat as compared to those having only other threats were compared for all islands and mainlands. The frequency of introduction-threatened species was significantly higher on islands for birds ( $\chi^2 = 67.4$ ;  $P < 0.001$ ), reptiles ( $\chi^2 = 5.76$ ;  $P < 0.03$ ) and amphibians ( $\chi^2 = 4.24$ ;  $P < 0.05$ ) but not for mammals ( $\chi^2 = 1.65$ ;  $P > 0.1$ ). The percentage of threatened mammals threatened by introductions was actually lower on islands than on mainlands (Table 9.4) but this was almost entirely due to 29 of Australia's threatened mammal species having introduced species as a major factor in their ecology. When this Australian frequency was compared with that of the sum of all other continental areas it was found to be significantly higher ( $\chi^2 = 78.2$ ;  $P < 0.001$ ). Over all groups, the Australian fauna tends to be more severely affected by introduced invasions than the fauna of the other continents (Table 9.4).

Of the 941 vertebrate species currently thought to be in danger of extinction 18,4% are known to be threatened in some way by introduced species. This figure is probably an underestimate as many of the threatened species have not been intensively studied, and the effects of introduced species are not always obvious.

It is not possible from these data to show how significant introductions are to the fauna as a whole, as distinct from that component of the fauna that is known to be threatened. Collar and Stuart's (1985) study of the threatened birds of Africa and related islands allowed Stuart and Collar (in press) to estimate the threat introductions are posing to the fauna as a whole. For the Africotropical portion of Africa they estimate the total avifauna to comprise 1481 species. Of these 96 (6.5%) are considered threatened and 91 (6.1%) 'near-threatened'. Only two of the 'near-threatened' species are known to be affected by introduced animals and one of the threatened species is believed to be so affected, constituting less than 0.2% of the Africotropical continental avifauna. By contrast, on the oceanic islands 35 of the 49 threatened species and three of the 13 'near-threatened' are known or believed to be affected by introduced animals. Although the native breeding avifauna of these islands is not given by Stuart and Collar (in press) a total of 285 species was obtained from published lists of the individual island faunas (Macdonald and Jones, unpublished). This means that approximately 13% of the insular avifauna is considered threatened by introductions.

Analysing the total avifauna of Australia, the continent showing the highest proportion of introduction-threatened species, there are 656 regularly occurring species (Blakers *et al.*, 1984) of which only three are considered threatened by introduced species (Table 9.4). This is less than 0.5% of the total avifauna. By contrast, 12.9% of Australia's mammalian fauna of 224 species (Pianka and Schall, 1984) are considered threatened by introductions.

It therefore appears that, with the exception of Australian mammals, it is only on islands that introductions are currently playing a significant role in the extinction of vertebrate faunas.

#### 9.4.1.1 Extinction of oceanic island birds

Although only a small percentage of the world's land and freshwater avifauna occurs on oceanic islands '93% of the 93 species and 83 subspecies of birds that have become extinct since 1600 A. D. have been island forms' (King, 1985). After habitat destruction, predation by introduced predators ranks as the second most important cause of these extinctions; rats (*Rattus* spp.) are implicated in 54% of these (King, 1985).

This is hardly surprising as rats have been introduced to 82% of the world's major islands and island groups (Atkinson, 1985). Of 53 island bird species known to have been preyed on by the brown rat *R. norvegicus* four are known to have been locally eliminated by this predation. The comparable statistics for *R. rattus* are 39 species of which 12 have become extinct either as a species or as a subspecies. The Pacific rat *R. exulans* was generally introduced prior to the period of scientific observation and only 15 species are known to have been preyed on by it and none of these have become extinct as a result (Atkinson, 1985). However, *R. exulans* had been introduced to islands such as those of the Hawaiian Archipelago in the prehistoric period during which most of the endemic avifauna became extinct (Olson and James, 1984). The contribution of *R. exulans* predation to these extinctions has not yet been assessed although it is considered likely to have played a role (Olson and James, 1982).

Two examples of the extinction of oceanic island birds by introduced mammalian predators will be given. The endemic Socorro dove *Zenaida graysoni* has apparently become extinct since the introduction of cats to Isla Socorro in about 1958, with two other ground-foraging endemic bird species becoming less common during the same period. Although data are not available to test whether it was predation by feral cats that caused these declines, this is considered likely by the researchers involved (Jehl and Parkes, 1982). Similarly, Curry (1986) argues that the local extinction of the Floreana mockingbird *Nesomimus trifasciatus* from Floreana Island in the Galapagos was the result of nest predation by introduced *R. rattus*. The principle that island species that have evolved in the absence of predators are more likely to become extinct when predators are introduced (e.g. Clark, 1981) is born out by both the above studies: On Isla Socorro a mainland dove of the genus *Zenaida* became common during the period when the island species became extinct (Jehl and Parkes, 1982). Similarly, in the Galapagos, mockingbirds of the genus *Nesomimus* have been less severely affected by introduced rats on islands which originally held native rat species, than on islands, such as Floreana, which had never had any rats present (Curry, 1986). Atkinson (1985) has argued that rats have had most impact on temperate islands because the avifaunas of tropical islands had evolved predator defence mechanisms in response to the presence of land crabs.

It is not only rats and cats that have brought about extinctions of birds on islands. On the island of Guam the brown tree snake *Boiga irregularis*, which was introduced in 1947, suddenly expanded its population in the late 1970s and by



early 1985 had severely reduced several of the island's endemic bird species and subspecies. The Guam broadbill *Myiagra freycineti*, and rufous-fronted fantail *Rhipidura rufifrons uraniae* had been reduced to a few individuals while the Guam bridled white-eye *Zosterops conspicillata conspicillata* was already extinct. It was reported that experimental work carried out on the island 'just about fixes the entire blame upon the snake' (Marshall, 1985). However, there is a chance that introduced diseases might also have played a role in these declines.

In the Hawaiian Islands introduced diseases are considered to be important: Hawaiian honeycreepers evolved without exposure to avian malaria. The mosquito *Culex quinquefasciatus* was introduced into the islands in the 1800s. The avian malaria protozoan parasite *Plasmodium relictum* arrived in the early 1900s. The result is thought to have been extinction of some honeycreeper populations and reduction of others (van Riper *et al.*, 1982).

#### 9.4.1.2 Other island extinctions

Although avian extinctions on islands are relatively well studied this does not mean that they are the faunal group most threatened by extinctions. For example, of 11 native rodent species, or island populations of species, known from the Galapagos Islands, eight are now extinct. *Rattus rattus* is implicated in five or six of these extinctions. Native rodents only persist on the two islands from which *R. rattus* is absent (Clark, 1984). Predation by mongooses in the Virgin Islands has caused, in addition to the near extinction of the ground-nesting quail dove *Geotrygon mystacea*, the local extirpation of a ground lizard *Ameiva polops*, and the destruction of many eggs and hatchlings of hawksbill turtles *Eretmochelys imbricata* on beaches (Nellis and Everard, 1983; Philobosin and Ruibal, 1971; Small, 1982).

Mauritius provides a classic example of the acceleration in extinction rates in a tropical insular fauna following human colonization and the associated introduction of plant and animal species. Prior to colonization in the 17th century there were at least 23 taxa of endemic landbirds, 12 reptiles (including giant land tortoises, skinks, geckos and snakes) and two fruit bats. Currently only nine endemic landbirds, four geckos, one skink and one fruit bat survive on the mainland of Mauritius (Cheke, in press). Most of the island's surface (95%) has been transformed and the remnants of the natural ecosystems have been highly modified by a wide range of plant and animal introductions (Strahm, 1986; Cheke, in press).

Honegger (1981) lists two amphibian and 28 reptile taxa known to have become extinct since 1600 AD. The reptiles were all island forms and introduced species are implicated in the extinction of at least eight of them and one of the two amphibians. For most of the other taxa no information is available on their extinction, or they were extirpated by humans.

Invertebrate groups have also been severely affected by introductions. On the island of Moorea, French Polynesia, the carnivorous snail *Euglandina rosea* was

introduced in 1977 and by 1982 had already caused the endemic snail *Partula aurantia* to become extinct. On the basis of its rate of spread and its observed ability to eliminate native snails, Clarke *et al.*, (1984) predicted the extinction of all but one of the remaining six species of *Partula* on Moorea by 1987. *E. rosea* has also brought about the extinction of the Hawaiian endemic snail *Achatinella mustelina* (Hadfield and Mountain, 1980).

A similar example is the ant *Wasmannia auropunctata* which now occurs on four of the islands comprising the Galapagos Islands National Park (Santa Cruz, Floreana, San Cristobal, and Isabela). It is believed to have been introduced in the early 1900s to Santa Cruz Island, where at least 17 of 28 ant taxa present, including four probably endemic species, are negatively affected. *Wasmannia* was found to reduce population densities of, or eliminate altogether, three species of arachnids as well as reducing abundance and species diversity of flying and arboreal insects (Lubin, 1984).

It should be emphasized that it is not only the native fauna of islands that has been depleted by introductions. The flora has also been affected. For example, feral goats have damaged the native flora of Hawaii Volcanoes and Haleakala National Parks for many years (Stone and Loope, 1987). At Haleakala, browsing of feral mammals (goats and cattle *Bos taurus*) has been directly responsible for extinction of at least three flowering plant species and local elimination and depletion of many others (Medeiros *et al.*, 1986). At Hawaii Volcanoes Park, construction of a goat-proof enclosure in 1971 resulted in the appearance of a previously undescribed leguminous plant species, *Canavalia kauensis*, which is believed to have survived nearly two centuries of goat browsing only as stored seeds in the soil (Mueller-Dombois, 1981).

#### 9.4.1.3 Extinctions in continental ecosystems

Although no example is known of the global extinction of a continental species purely as a result of the invasion of introduced organisms, there are several cases where a species has either been locally eliminated or brought to the brink of global extinction by introductions. Not surprisingly several of these come from the 'island' continent, Australia (see Table 9.4). At least 19 introduced mammal species have successfully invaded large areas within Australia (Myers, 1986). By contrast only three introduced rodents and the feral cat can be considered to have widespread populations in southern Africa and these are generally at low densities away from transformed areas (Brooke *et al.*, 1986; Macdonald *et al.*, 1986).

Foxes *Vulpes vulpes* were introduced to Australia about 1870 for hunting; feral populations of domestic cats have probably existed there for longer. Kinnear *et al.* (1984) posed the question 'Has the cat and the fox affected our [Australian] native fauna?' Despite an element of controversy in interpreting a mass of observational data, their studies of the rock wallaby *Petrogale lateralis* indicate

that these invasive introduced predators have a marked impact on these native marsupials (see Usher, this volume).

Further circumstantial evidence for the importance of introduced predators comes from the moister southwest of Western Australia. There the fox is now the major predator of medium-sized indigenous mammals (Christensen, 1980). The introduction of the fox in about 1915 was followed by the disappearance from much of its former distribution of the woylie *Bettongia penicillata*. Also, recent declines in abundance and distribution of medium-sized indigenous mammals in the jarrah forests have been correlated with an increase in fox abundance following the reduction of poison baiting programmes for rabbits in the mid-1970s (King *et al.*, 1981; Christensen, 1983). Ironically this adverse effect on indigenous mammal species was apparently brought about by the improvement in myxomatosis biocontrol of rabbits following the successful release of this disease's vector, the European rabbit flea *Spilopsyllus cuniculi* (Christensen, 1983; King and Wheeler, 1984). The subsequent increases of some of the affected mammal species in localized areas has thrown doubts on Christensen's (1980) initial interpretation of the fox's central role in the decline. However, as Christensen (1980, 1983) makes abundantly clear, the population dynamics of these native species are controlled by a complex interaction of fire, habitat and predation. There seems little doubt that introduced predation pressure is now one of the more important factors, and one which in time could lead to local and, possibly, to global extinction of some of these species. Already two species of rat-kangaroos, *Bettongia gaimardi* and *B. lesueur*, have become locally extinct on the Australian mainland: *B. gaimardi* is now only found on the fox-free island of Tasmania and *B. lesueur* became extinct in mainland Western Australia in the 1930s after the area's colonization by foxes (King *et al.*, 1981).

It is not only mammals that have been affected by fox predation. On the Murray River in South Australia the fox has been found to destroy 93% of nests of two species of aquatic tortoise *Chelodina longicollis* and *Emydura macquarii* (Thompson, 1983). This predation is thought likely to lead to a significant decline in the populations of both species unless fox predation is decreased.

From Australia too comes one of the few observations of an introduced invasive herbivore giving rise to local extinctions of plant species in a continental situation. The intense grazing pressure exerted by feral buffalo *Bubalis bubalis* in the Northern Territory is considered likely to eliminate certain native plant species from the swamp vegetation, e.g. the grasses *Hymenachne acutigluma* and *Phragmites karka* (Williams and Ridpath, 1982).

There is only one well-documented case where invasions by introduced plants pose a major threat to native plant species diversity in a continental situation. In the fynbos and karoo biomes of South Africa there are 1808 threatened plant species. Analyses of the threatened species from two fynbos areas show that just over 50% are threatened by the spread of introduced trees and shrubs, mainly species of *Acacia*, *Hakea* and *Pinus* (Hall and Ashton, 1983; Hall and Veldhuis,

1985). This threat is present in nature reserves, as has been documented for the Cape of Good Hope Nature Reserve by Taylor (1977).

#### 9.4.1.4 Continental nature reserves—the significance of introduced plant pathogens

One group of invasions that has brought about extinctions on continents is plant pathogens. The invasion of southwestern Australia by the fungus *Phytophthora cinnamomi* is likely to have such an effect given the large number of localized endemic plant species found in the affected area (Rye, 1982). But it is from North America that there are definite examples.

Chestnut blight, caused by a fungal pathogen *Cryphonectria parasitica*, within 50 years eliminated the American chestnut *Castanea dentata* as a dominant tree species over much of the eastern USA (see Von Broembsen, this volume), including Great Smoky Mountains and Shenandoah National Parks. One apparent side-effect of the demise of the American chestnut is the loss of at least five native microlepidopterans, including the chestnut borer *Synanthedon castaneae* (Pyle *et al.* 1981). In addition to this, Quimby (1982) has postulated that the increase in oak wilt disease *Ceratocystis fagacearum* affecting native oaks in the northeastern USA resulted from changes in the density and distribution of the susceptible red oak *Quercus rubra* following the removal of *C. dentata* by chestnut blight. These 'ripple effects' of introduced species generally go unnoticed.

Dutch elm disease, caused by the fungal pathogen *Ophiostoma ulmi* (see Von Broembsen, this volume), primarily affected the native American elm *Ulmus americana*, an important successional tree species throughout eastern North America (Braun, 1950). American elm has been reduced but not eliminated in native stands; but the disease continues to run its course. Some indication of the extent of the dieback in a nature reserve comes from Theodore Roosevelt Island, where in 1972 there were 187 healthy *U. americana* canopy trees, 32 classed as dying, 105 standing dead individuals, 46 trees which had died and fallen and 94 which had been cut as part of a Dutch elm disease control programme in 1963 (Thomas, 1980). Although it is not possible to attribute all the deaths to *O. ulmi*, it is apparent that the proportion of the recent population known to have been infected (94 out of 464) is high. In addition it is inferred by Thomas (1980) that the individuals classified as dying were mainly doing so as a result of *O. ulmi* infestations.

#### 9.4.1.5 Continental nature reserves—the significance of introduced insect herbivores

Introduced insect predators of temperate forest trees have also had major impacts on nature reserves, in some cases leading to the near extinction of affected species. *Lymantria dispar*, the gypsy moth, introduced to the northeastern USA

(Massachusetts) from Europe in 1869, has a very broad host tolerance (it prefers *Quercus* spp., but attacks most broad-leaved tree species and even conifers) and has been spreading rapidly during the past decade. It has recently caused heavy defoliation in Shenandoah National Park, Virginia, and is expected to spread throughout much of the USA. Mortality mostly affects less robust, subdominant trees (Campbell and Sloan, 1977; Marshall, 1981).

Balsam woolly aphid *Adelges piceae*, native to Europe, was introduced into Maine, USA, about 1900 and has now spread throughout *Abies* forests of eastern North America. It was first detected in the mountains near Great Smoky Mountains National Park in the 1950s. It currently threatens nearly to eliminate Fraser fir *Abies fraseri*, a dominant in the high-elevation spruce/fir zone of Great Smoky Mountains National Park and elsewhere in the southern Appalachian mountains. Interactive effects between pollutant-induced stress of Fraser fir and aphid-caused mortality are suspected but untested. Total mortality of fir overstorey and partial mortality of understorey fir is expected within the next few years. In addition, the understorey flora adapted to cool, moist, low-light environments will lose much of its habitat (Eager, 1984). In high-elevation stands that have been invaded in the last three to seven years, fuel loading has been found to be two to four times that in stands not yet attacked by aphids, creating a short-term fire hazard. Afterwards, decomposition results in fuel loads similar to those in uninvaded stands (Nicholas and White, 1985).

#### 9.4.1.6 Future risks, arising through 'trophic cascades'

One of the important points that emerges from several of the above examples is that an introduced species might indirectly bring about the extinction of a species which is itself unaffected by the introduced organism. This arises through the interrelationships that exist between organisms at different trophic levels in an ecosystem, and the sequence of such extinctions has been termed a 'trophic cascade'.

A possible example of this phenomenon is the extinction of insectivorous Hawaiian bird species as a result of reductions in native lepidopteran populations following the introduction of insect parasites. These lepidopterans formed a critical food resource for the birds involved and it has been convincingly argued that their reduction could have been an important contributory factor in several avian extinctions (Howarth, 1983).

Two further examples come from recent studies of the effects of the Argentine ant *Iridomyrmex humilis*. The first of these is the possible future extinction of fynbos plant species as a result of the displacement of native ants formerly responsible for these plants' seed dispersal (Bond and Slingsby, 1984). The second is the ant's possible future role in the extinction of endemic Hawaiian plant species. The Hawaiian biota lacks endemic ants and introduced ants have proved to be devastating to the low elevation insect fauna of these islands. Argentine ants

have recently become established within a limited area (184 hectares) at high elevations in Haleakala National Park. Comparisons of areas with and without *I. humilis* have shown that these ants severely deplete the native ground-dwelling arthropod faunas of high-elevation shrubland, including major pollinators of native shrubs and herbaceous plants (Medeiros *et al.*, 1986). The Haleakala silversword *Argyroxiphium macrocephalum* and some of its near relatives, *Dubautia* spp., have been shown to be self-incompatible, requiring pollinators for seed set. These locally endemic species reproduce only by seed and would decline rapidly if pollination failed.

#### 9.4.2 Genetic effects of introduced species

Another deleterious impact of introduced species on ecosystem structure is that of hybridization. The following examples serve to illustrate the threat posed by invasions in this regard.

The mallard duck *Anas platyrhynchos* is a highly successful species, has substantial invasive capacity, and has expanded its range into many areas with habitats modified by human activities. It has a remarkable degree of reproductive and genetic compatibility with congeners with which it has only recently come into contact—including *Anas poecilorhyncha superciliosa* of New Zealand and Australia, *Anas rubripes* of eastern North America, and *Anas diazi* in southwestern North America. Nevertheless, the maximum recorded frequencies of hybrids (12.9% for *A. rubripes* × *A. platyrhynchos* in Massachusetts, USA) suggest that hybrids have lower fitness than parent forms. A high embryonic death rate has been noted for hybrids in New Zealand, reducing genetic swamping, but probably leading to depression of population size of the native taxon (Cade, 1983).

Another widespread and successful introduction, *Felis catus*, has also been responsible for hybridization with native congeners. In southern Africa there is concern for the long-term survival of the African wild cat *F. lybica* due to its observed ability to hybridize with *F. catus* (Brown *et al.*, 1985; Brooke *et al.*, in press). Similarly, there is increasing evidence from many areas in Scotland, including nature reserves especially in the Grampian Region, for the presence of *F. catus* genes in populations of the Scottish wild cat *F. silvestris grampia* (D. French, personal communication).

The hybridization of native and introduced fish species has been pinpointed as potentially being the most important impact of fish introductions in southern Africa (Bruton and van As, 1986). This mostly arises from interbasin transfers of formerly allopatric southern African species. This problem has already arisen in North America and is currently affecting several taxa within nature reserves. For example, in Rocky Mountain National Park, Colorado the greenback cutthroat trout *Salmo clarki stomias* narrowly escaped extinction in the recent past due to overharvesting, competition, and interbreeding with introduced trout. A restor-

ation programme is underway, involving removal of non-native fish (using a toxicant) above barriers to upstream movement and restocking with pure genetic stocks of *S. c. stomias* (Stevens and Rosenlund, 1986).

An invertebrate example is provided by the introduction of African honeybees *Apis mellifera adansonii* into the fynbos biome where the Cape honeybee *A. m. capensis* occurs. Fortunately, although hybridization occurs, the native subspecies is able to withstand this human-aided invasion with only minimal genetic pollution (Tribe, 1983).

An example of how an introduced species can indirectly result in the hybridization of a taxonomically unrelated native species is provided by the introduction of herbivorous fish to Madagascan freshwaters and the subsequent threat to the genetic integrity of the Alaotra grebe *Tachybaptus rufolavatus*. The little grebe *T. ruficollis*, although native, has recently increased in abundance throughout Madagascar, apparently as a consequence of the widespread introduction of introduced *Tilapia* species to lakes and pools. The cosmopolitan little grebe has invaded the waters, mainly Lake Alaotra, formerly occupied by this localized island species and is now hybridizing freely with it. As a direct result of this hybridization Collar and Stuart (1985) conclude that 'nothing can be done to prevent the extermination of the Alaotra grebe in the wild'.

The hybridization of the introduced marsh grass *Spartina arterniflora* with the native *S. maritima* in England, as detailed previously, provides, a classic example of this phenomenon in plants. Another less well-known example is the hybridization of the introduced *Tamarix ramosissima* with the native *T. usneoides* on the Swakop River in South West Africa/Namibia (Palgrave, 1977). The hybridization between introduced and native *Rubus* species in South Africa provides a further example (Spies and du Plessis, 1985).

The irreversible nature of these genetic effects makes them of particular significance to nature conservation. Another aspect which is possibly significant is that several hybrids have exhibited a high invasive capacity (see Dean *et al.*, 1986). Plant examples of this are *Spartina anglica*, *Lantana camara* (Spies, 1984) and the *Psidium guajava* complex (Macdonald and Jarman, 1985). The Africanized honeybee, an *Apis mellifera* subspecific hybrid, has invaded vast areas in the neotropics (Michener, 1975). These 'new' genetic combinations have often proved difficult to control, particularly in respect to the application of classical biocontrol measures (Kluge *et al.*, 1986). This aspect has considerable relevance to the possible conservation implications of genetic engineering (Colwell *et al.*, 1985).

The widespread occurrence of hybridization following introductions in certain groups, e.g. the genus *Anas* and some freshwater fishes, must inevitably bring up the taxonomic question of species limits. Although taxonomic identity is not a prime concern of conservationists, genetic variability is. Perhaps the primary aim of conserving ecosystem structure is the retention of the maximum genetic variation in the ecosystem. Hence the loss of species and subspecies are both

detrimental. In addition population 'bottlenecks', which often result from the effects of introductions (see Usher, this volume), are undesirable since, in general, genetic variation is lost during these events.

## 9.5 CONTROL OF ALIENS IN NATURE RESERVES

The preceding sections have attempted to outline some of the problems introduced organisms pose to wildlife conservation. In this section the possible solutions to these problems are investigated. Where information is available these solutions are illustrated using actual examples of past control programmes. Once again the emphasis is on programmes carried out within nature reserves.

### 9.5.1 Controlling introduced plant invasions

In a questionnaire survey of 299 southern African reserves it was found that, on average, only 0.4 invasive introduced plant species were known to have been eradicated from each reserve. This statistic should be compared with the average of 8.2 species recorded as having invaded each reserve and the average of 2.1 species for which control operations were known to have been initiated. The proportion of invasive introduced plants eliminated is considered to be even lower than these statistics indicate as the total number of introduced plants reported per reserve is considered to be a gross underestimate (possibly by a factor of 2 or 3) since herbaceous introduced plants tend to be ignored by reserve managers (Macdonald, in press).

In the Cape of Good Hope Nature Reserve monitoring of fixed plots has shown that two decades of control operations have eliminated only two of the 19 introduced tree and shrub species present in the reserve. Both species were initially rare and only marginally invasive within the reserve. The frequency of occurrence of the really invasive species such as *Acacia cyclops* and *Acacia saligna* has not declined significantly over the period despite intensive control operations. However, the density of all species has been reduced and species such as *Pinus pinaster*, in which the plants are easily killed and which do not accumulate large soil-stored seed banks, have been substantially reduced in frequency of occurrence. Relatively rare species, such as *Eucalyptus lehmannii*, for which cost-effective techniques for killing established plants have not been developed, have not been reduced in frequency (Taylor *et al.*, 1985; Macdonald *et al.*, in press).

Usher (1987) investigated the control of *Rhododendron ponticum* in nature reserves in Great Britain. Data from 19 National Nature Reserves indicated that no mechanical or chemical means of control—cutting, hand-pulling of regrowth, spraying—was successful. These examples from nature reserves confirm Robinson's (1980) conclusion that rhododendron invasions of forestry plantations could only be contained, not controlled or eradicated. *Rhododendron* has an extremely small and widely distributed seed that germinates prolifically in



disturbed sites (Cross, 1981). Indeed, control operations disturb the litter and fermentation layers of forest soils and, paradoxically, make the environment even more suitable for regeneration of rhododendron seedlings (Usher, 1987).

*Myrica faya* in Hawaii Volcanoes National Park provides an example of a particularly discouraging failure to control a highly invasive and damaging introduced plant. One individual was noted in the park in 1961. By 1978, 609 hectares were mapped as supporting *M. faya* infestations of varying densities. In 1985, 12 000 hectares were infested—indicating a 20-fold increase in 8 years in spite of attempted control by park managers (Whiteaker and Gardner, 1986). In this case success was thwarted by the biology of the plant (abundant seed production, dispersal by birds, rapid growth to maturity), occurrence of seed sources adjacent to park boundaries and probably by periodic lapses in control efforts.

Another major failure at Hawaii Volcanoes National Park involved fountain grass *Pennisetum setaceum*. Over a 5-year period, US \$250 000 were spent in efforts to control this invader through hand-pulling. Tunison (in press) determined that long-term control using this method would require at least US \$100 000 per year and the project had to be abandoned. Success was here thwarted by the biology of the plant (abundant seed production, dispersal by wind, inconspicuousness of young non-flowering individuals, huge area of potential habitat), occurrence of seed sources adjacent to park boundaries, and probably by hesitance in control efforts in the early stages of the invasion.

In the Galapagos National Park repeated attempts to control guava *Psidium guajava* have all failed. A proportion of the plants treated, using a variety of herbicides, has always managed to survive, often suckering from the roots after extensive time periods [An analogous situation has been reported for this species in the Hluhluwe-Umfolozi Game Reserve, South Africa (Macdonald, 1983).] Until an effective control technique has been developed this species will continue to spread; already it occupies extensive areas on four of the islands and on Santa Cruz it has been suggested to be the main reason for the decrease of the endemic *Miconia robinsonia*. Recent control efforts have centred on a 14 hectare area on Santa Cruz Island and this is being kept clear of both *P. guajava* and the shrub *Cinchona succirubra*. However, the long-term solution to the Park's problems lies in controlling these species in adjacent farming areas; the seeds of *P. guajava* are dispersed into the park from these areas by cattle and birds while *C. succirubra* has light wind-dispersed seeds (Hamann, 1984).

Success in controlling or eradicating introduced plants in nature reserves is not common, but it should also be documented (see Macdonald, in press). The giant hogweed *Heracleum mantegazzianum* has been successfully controlled in the Aberlady Bay Local Nature Reserve in the east of Scotland. As individuals established within the reserve they were killed by cutting and spraying with herbicides as pinpoint applications (Usher, 1973). On the 40 hectare Masthead Island Reserve off Queensland, Australia, the prickly pear *Opuntia stricta* has been

effectively controlled using herbicides (Messersmith, 1986). In Organ Pipe Cactus National Monument, Arizona, two species of *Tamarix* and *Nicotiana glauca* have been recorded and removed wherever found and have so far not become a problem (Loope *et al.*, 1988). At Haleakala National Park, *Ulex europaeus*, *Pinus radiata*, *Pinus pinaster*, and *Pinus patula* have been kept in check along the northwest park boundary through periodic removal (Loope *et al.*, in press). *Melaleuca quinquenervia*, a tree invading marshes of southern Florida, has been successfully kept out of Everglades National Park for 15 years (in spite of established stands nearby) by periodically searching for and removing all individuals established within the park (La Rosa, in press). Managers at Hawaii Volcanoes National Park have been and continue to be successful in controlling 37 invasive plant species that are confined to small areas within park boundaries, forestalling their range expansion and attainment of levels at which they are uncontrollable (Taylor, in press). It is not possible to say how much they would have spread without this control.

### 9.5.2 Controlling introduced animals in nature reserves

Although control of certain introduced animal species has proved to be impossible, control of animal invaders appears to have been more successful than control of plant invaders in nature reserves. The following examples indicate the type of programmes that have been carried out and which of these have proved successful.

Between 1920 and 1970 approximately 70 000 goats were removed from Hawaii Volcanoes National Park, yet the population had not been noticeably reduced. A long term plan was developed that included the construction and maintenance of a goat-proof boundary fence and internal drift fences, frequent organized goat hunts and drives, long term monitoring of vegetation recovery and goat population levels, and measures to gain public support. Between 1971 and 1975 13 000 goats were eliminated; from 1976 to 1979, 1600 goats were eliminated. By 1980 most goat habitat had been fenced and less than 100 goats remained in managed areas (Stone and Loope, 1987).

Feral burros *Equus asinus*, originally released by prospectors and miners in the southwestern USA in the 19th century, have caused extensive damage to vegetation of numerous parks and reserves in that area. Serious efforts at removal, begun in the 1960s and early 1970s were thwarted by organizations and individuals who opposed any killing of burros on 'humanitarian' grounds. This obstacle was finally overcome in such reserves as Grand Canyon National Park and Death Valley National Monument, after 10 years of assessment, study and public participation. In Death Valley, the project included boundary fencing; 5724 burros were removed by live-trapping during 1983–1986, leaving only about 230 burros as of March 1986 (Loope *et al.*, 1988).

Rabbits were eradicated from the 260 hectare Santa Barbara Island in Channel

Islands National Park through intensive shooting during 1979–1981. By 1985, native shrubs were conspicuously recovering (Halvorson, in press). At Haleakala National Park, live trapping is being used successfully to control mongooses and feral cats near burrows of dark-rumped petrels *Pterodroma phaeopghia*. Petrel reproductive success rose from 35% in 1979 to 66% in 1980 and 1981 when predation was eliminated, apparently due to trapping (Simons, 1983). Coblentz and Coblentz (1985) have reported success in dramatically reducing mongoose populations in Virgin Islands National Park by repeated intensive trapping.

The importance of limiting reinvasion during the control programme was highlighted on Marcus Island, which forms part of the Langebaan Lagoon National Park in South Africa. This 11 hectare offshore island was joined to the mainland by a causeway in 1976 and within two years had been invaded by at least eight mammal species, including three viverrids and three canids. Control operations failed to reduce the frequency of sightings of introduced predators or the associated mortality rate in island birds until a predator-proof wall across the causeway was completed in April 1982. After this date trapping and shooting operations finally led to the elimination of introduced mammalian predators (Cooper *et al.*, 1985). However, even where reinvasion is not possible, as on the subantarctic Marion Island, where the island is big and cover for the introduced mammal abundant, the elimination of a species such as *Felis catus* has, to date, proven to be impossible (Cooper and Brooke, 1986).

When reserve managers are faced with introduced animals which prove difficult to control, e.g. the cats on Marion Island, they often consider the introduction of some form of biological control agent (see Usher, this volume). Although these measures are often relatively inexpensive, the possibilities for deleterious side effects need to be very carefully evaluated prior to their introduction (Howarth, 1983).

## 9.6 SUMMARY AND CONCLUSIONS

There are several principles affecting management which emerge from this study. Firstly, it must be emphasized that in most cases what we are observing is simply the short-term effects of a few hundred years or a few decades of rapid species movement into nature reserves. There is no *a priori* reason for assuming that invasions will not continue to occur. In fact, the indications are that plant introductions are likely to occur with increasing frequency unless improved preventative measures are implemented; i.e. all reserves can look forward to receiving propagules of all the world's worst weeds. The prospects for faunal invasions, excluding invertebrates, are not quite so bleak. Most of these have tended to be deliberate introductions and a heightened awareness of the problem should limit further such introductions in the future. The current situation where reserve managers are more aware of introduced animals as a problem than of introduced plants (e.g. Machlis and Tichnell, 1985) will need to be reversed in the

future. Also, reserve managers are often unaware of plant and animal pathogens, and the impact of introduced pathogens in reserves remains largely unknown.

Given the fragmentation of the world's major biomes into relatively small 'quasi-insular' reserves with all the attendant changes in faunal composition, altered microclimates, altered fire regimes, and increased proximity to transformed areas, we can actually predict that the circumstances conducive to the invasion of introduced species will become more widespread in the future, not less widespread. It is, however, unlikely that 'island' continental reserves will rapidly come to resemble oceanic islands in their extreme vulnerability to introduction-induced extinctions. This vulnerability apparently stems from a history of evolution in isolation, something which to a large extent cannot manifest itself in continental situations.

There is a need for reserve managers to identify and subsequently eliminate or ameliorate changes in disturbance regimes which are beyond the evolutionary experience of the native biota. These anthropogenic changes in disturbance regimes have often been implicated in the invasion of nature reserves by introduced species. An example is the invasion of Kosciusko National Park, Australia, by a number of introduced species as a result of an artificial fire regime (Medhurst and Good, 1984). In some cases these changes in disturbance regimes within the park arise from land use practices outside the park's boundaries; e.g. the altered flooding regime in Everglades National Park, Florida, USA which favours the establishment of introduced plant species (Morehead, 1984). In these cases the conservation agency has to work in cooperation with external agencies in an attempt to ameliorate the changes.

Where more than one serious invasion is occurring within a reserve, and where resource limitations prevent all invasions being combated simultaneously, it is important that reserve managers establish their priorities correctly. In particular there is a need to identify keystone introduced species which themselves give rise to ecosystem-level impacts (see Sections 9.3 and 9.4.1.6). An example of this comes from the well-studied Haleakala and Hawaii Volcanoes National Parks. In both parks the feral pig is recognized as constituting a keystone introduced species, since pigs are the single major factor contributing to the spread of many introduced plants, not only by creating open habitats through digging, but also by transporting propagules in their hair and faeces. They also create depressions that collect standing water in which the bird malaria vector *Culex quinquefasciatus* breeds (Stone and Loope, 1987).

In almost all cases the successful elimination or control of invasive introduced species has only been possible where management has been initiated during the early stages of the invasion. Wherever the populations of the invading plant or animal have been allowed to build up within the reserve's boundaries prior to the initiation of a control programme, control has subsequently proven to be either extremely costly or ineffective. Accordingly the creation of an 'early warning' monitoring system to detect invasions in their earliest stages is essential for all

reserves. Similarly, the critical importance of follow-up control operations must be recognized and budgeted for from the outset. It is during follow-up operations that the last few remaining individuals are killed or kept under control. Lapses in vigilance at this stage have often undermined all that has been achieved in initially successful large-scale campaigns, e.g. the gypsy moth campaign in Massachusetts (Marshall, 1981).

In controlling both introduced plants and animals the critical factor is in all cases the balance between the rate of removal of established individuals from within the reserve and their recruitment within the reserve. In highly mobile species, for instance plants with windblown seeds and many animals, it is often necessary to create impermeable barriers along the reserve boundaries or to initiate control in areas adjacent to the reserve in order to limit this recruitment. Where introduced organisms are dispersed into the reserve by riverflow it is important to conduct control on a 'whole catchment' basis (Macdonald, in press). Where introduced plant species are recruiting from buried seed banks it is important that the dynamics of this seedbank are understood at the outset of the control programme (Milton and Hall, 1981; Holmes *et al.*, 1987).

Finally, in all control campaigns the possible deleterious side effects of alternative control techniques should be predicted, assessed and included in the cost/benefit analysis of the techniques. However, short-term deleterious effects should not be allowed to preclude the adoption of techniques which will in the long-term give rise to benefits through the effective eradication of the introduced species. Thus the killing of large numbers of non-target animals during the successful eradication of muskrat in Scotland was a short-term disadvantage which was outweighed by the long-term advantage of eradicating this species (Matthews, 1952; Usher, 1987). Conservation agencies will have to counter the public's emotional arguments against campaigns if they are to discharge their conservation duties effectively.

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