Wild animal conservation and welfare in agricultural systems

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Abstract

At least one-third of the land on earth is used for agricultural production and conflicts with the interests of wildlife are inevitable. These conflicts are likely to escalate as the human population expands and as the scale and intensity of agricultural production increases. This paper argues that the same underlying causes frequently affect both wild animal welfare and conservation. Three key threats are discussed: disease transmission from domestic animals and the interventions used to manage wildlife reservoirs of zoonotic diseases; physical operations such as harvesting and the conversion of wildlife habitat to farmland; and the use of agrochemicals, particularly for pest control. While direct effects, such as accidental poisoning, tend to attract the most public attention, it is argued that indirect effects, such as the reduction in food supplies or the disruption of social structures, are likely to be of greater importance. The suffering of pest animals has traditionally been undervalued. There is a need for broader adoption of integrated, ecologically based strategies which minimise suffering and also minimise the numbers of animals involved by preventing population resurgence. New research is urgently required to compare the effects of alternative, economically viable farming strategies on both wildlife conservation and welfare, possibly within the framework of ecosystem services assessments.

Keywords: *animal welfare, culling, disease, habitat fragmentation, pesticides, stress*

Why are we interested in wild animal welfare?

Vertebrates are sentient beings, and as such are capable of suffering. If suffering is a consequence of human actions, then we have a moral responsibility for it. This may be obvious where the impacts are direct as when, for example, neurotoxic symptoms result from a pesticide spill. However, suffering is often overlooked where the impacts are indirect. An example might be the starvation of nestlings when insect supplies are disrupted by the drainage of a marsh to create new farmland.

Many wild animals live in agro-ecosystems, and as a consequence they experience the direct and indirect effects of human activities. We might define the welfare cost of an action by the numbers of individuals affected, the severity or nature of the harm, and by its duration (Kirkwood *et al* 1994). Agricultural systems necessarily involve human activities which may affect the welfare and conservation status of wildlife; and wild animals 'naturally' suffer population instabilities and welfare challenges even in the absence of any human activity. The challenge for agriculture is to evaluate alternative management strategies pragmatically, and to implement those that minimise the additional costs imposed by human activity, and for which we therefore bear responsibility.

General interest in interventions relating to wild animal welfare has increased dramatically over recent years. This may partly reflect the growing urbanisation of human populations and the consequent lack of day-to-day contact with wildlife and nature. For example, many thousands of animals are admitted to rehabilitation centres annually (eg Kirkwood 1993; Mazaris *et al* 2008) and most veterinary degrees now include courses on the care of wildlife. However, the perceived importance of animal welfare issues to humans varies with the context. Outrage is expressed over the suffering of rabbits (*Oryctolagus cuniculus*) in laboratories (particularly if there was a deliberate intent to cause pain); yet different standards are applied to judge the conditions under which children keep pet rabbits; and little concern may be shown for the suffering of rabbits poisoned in an agricultural field. Yet the intention or context of an action is irrelevant to the suffering perceived by the animal. This issue is pertinent in an agricultural context: given that farming is a necessity, the impact on wild animal welfare is often discounted. The suffering of 'pest' species in particular, and the relative humaneness of alternative control options, has been largely ignored until recently (Mason & Littin 2003; Littin *et al* 2004; Sharp & Saunders 2008). Indeed, concern and legislative provision to protect the

welfare of free-living wild animals has lagged considerably behind that for laboratory and farm animals in most countries (see, for example, Russell & Burch 1959; Farm Animal Welfare Council 1992).

The public frequently raise three main areas of animal welfare for discussion (Fraser *et al* 1997). These relate to the feelings of animals, their ability to function, and their opportunity to have a 'natural life'. Charles Elton (1958) commented that most people believe that wild animals have a right to exist and be left alone, or at any rate not to be persecuted and made extinct as a species. Some philosophers also prioritise the autonomy of wild animals (eg Singer 1976) and their 'right' not to be interfered with by humans (Regan 1983). Whether or not they subscribe to the idea of 'rights', most conservation biologists adopt the view that natural processes should be allowed to run their course: natural selection should be free to operate as it would do in the absence of humans. For example, in Kruger National Park, animals injured by direct human interaction, for example by vehicle collisions, will be treated, whereas animals injured by predators will be left. We might usefully draw on the experience of health service researchers who have a long history of using quality of life indices (such as quality-adjusted life-years) to both guide individual patient management and to help formulate policy decisions that maximise the benefit-cost ratio for the entire population (eg Guyatt *et al* 1993). This philosophy does suffer a difficulty in defining where intervention is justified and where it is not: should birds be given winter food to compensate for a loss of natural food reserves; and what of the potential conflict and disease transmission that may occur around the bird feeder?

Except where a species is so rare that the welfare of individuals is seen as directly relevant to conservation efforts — as, for example, in wildlife reintroductions where stress can compromise reproductive output and survival (Teixeira *et al* 2006) — the quality of an animal's life is not typically seen as a conservation issue. In his seminal paper defining conservation biology, Soulé (1985) argued that "conservation and animal welfare are conceptually distinct…. and they should remain politically separate". Some, such as the rights philosopher, Tom Regan, have taken issue with conservation's emphasis on populations or species rather than individuals; so-called 'environmental fascism' (Regan 1983). However, the interests of conservation and individual welfare do not necessarily have to conflict. Populations are composed of individuals and, if we accept that the welfare of an individual can be measured, it follows that approaches can be used that evaluate the welfare status of all animals within these populations. So, for example, utilitarian philosophies allow for costs to all animals in a target group to be compared with the benefits of the action.

It must also be recognised that in the wild, actions affecting one individual will have consequences — potentially relevant to both conservation and welfare — for others in the community, such as dependent young, competitors or predators. Approaches that consider the whole community, rather than just individuals, are therefore not only possible but are necessary. Many of the factors that lead to adverse consequences for conservation, ie those which affect the survival of populations and species, also have consequences for animal welfare. For example, the starvation of fledgling farmland birds following a change in insecticide use or harvesting practice will affect both the stability of the population and the welfare of the individual birds.

How much wildlife is there on farmland and why is it there?

Crop-dominated landscapes or mosaics comprise at least 30% of the total terrestrial area of the earth, another 10–20% is extensively grazed by livestock, and only limited areas are entirely unaffected by agriculture (Wood *et al* 2000). With rising human populations, this proportion can only increase: global demand for agricultural products is projected to rise by more than 50% over the next two decades (UN Millenium Project 2005). More land was converted to cropland in the 30 years after 1950 than in the 150 years between 1700 and 1850. The 'green revolution' has also dramatically increased the intensity of production throughout most of the world: many countries in Asia and Latin America have more than doubled their output of cereals over the last 50 years.

There is a perception that wildlife lives apart from farmland — in woodlands, forest, uncultivated uplands, and (particularly) in specially designated nature reserves. However, this is a misapprehension. Less than 3% of the earth's land surface is designated as protected for wildlife, and much of this is still farmed or used for forestry. More than half of all species live outside protected areas, largely in agricultural landscapes (Blann 2006). Although other areas, such as unprotected copses, scrub and forest, can also act as wildlife refuges, these areas, like many nature reserves, are often fragmented, surrounded by an ever-encroaching sea of agricultural land. The influence of agricultural expansion extends beyond the boundaries of farmland. Not only do animals occupying residual patches on the interface with farmland experience a loss of habitat area, but there are also substantial risks of invasions by alien species (such as cats [*Felis sylvestris catus*] and rats [*Rattus* spp]), disease transmission, and poaching. For example, the establishment of palm oil plantations in Sumatra and Borneo has had devastating consequences for orangutan (*Pongo pygmaeus* and *P. abelii*) populations, not only because of forest loss and fragmentation, but due to disease transmission and wild animal trade (Singleton *et al* 2004).

Wild animals that remain within and around agricultural systems tend to be generalists, and are often those that can exploit sudden gluts of a particular food resource. Agro-ecosystems are frequently dominated by a small number of species that may reach sufficient population densities to be regarded as pests: in contrast, larger, long-lived, slowly reproducing species with specialised diets tend to be lost entirely or much reduced in abundance (Donald 2004; Fitzherbert *et al* 2008). Not only is such loss of species diversity important directly for wildlife conservation, but recent evidence also suggests that increased dominance by

one species can increase the prevalence of pathogens important to human and animal health. This is because contact rates between infected and susceptible hosts is increased as other non-susceptible animals disappear from the community (eg Allan *et al* 2003; Suzán *et al* 2009).

Many animals use farmland only when dispersing, searching for mates, or travelling between patches of more suitable habitat that have been fragmented by agricultural encroachment. Others will be permanent residents. Small mammals use remnants of original habitats, such as the strips of ancient woodland that form some hedgerows in Great Britain, New England and British Columbia, as well as more recently created habitats such as field margins, copses and ditches. Many bird species also spend the majority of their lives within agricultural ecosystems. Indeed, the post-war decline in farmland bird populations in Europe triggered the first serious attempts to alter agricultural practice for the benefit of wildlife. The continued collapse in numbers across a wide range of bird species is strongly linked with the increasing intensification of agriculture, and is a source of considerable concern (Donald *et al* 2001).

The abundance of food resources available in agro-ecosystems undoubtedly provides an incentive for wildlife to be present. Food is often a limiting resource for wild animal productivity — either through direct nutritional constraints, or because of the behaviours required to acquire it. For example, hunting and foraging are costly in terms of energy and time, as are activities such as territorial defence of food supplies. The breakdown of territoriality seen in many rodents as they exploit grain crops allows greater individual investment in reproduction. Elephants (*Elephas maximus*) raiding sugar cane plantations, fruit bats (eg *Pteropus conspicillatus*) eating cultivated fruit crops, and fallow deer (*Dama dama*) browsing new wheat shoots, are all displaying behaviours that have evolved as optimal in their natural environment where high-quality food is patchily distributed in time and space. Whether the behaviour remains optimal in the new agricultural environment varies between species; there are trade-offs with potential adverse effects such as increased disease transmission rates at higher population densities, or the risk of death from poisoning or trapping. The further the advance of agriculture into former wildlife strongholds, the greater the likelihood of this kind of contact between farmland, domestic stock and wildlife: tigers (*Panthera tigris*) in India, for example, are now regularly in conflict with agricultural workers; and between 1983 and 2003 more than 1,150 humans and 370 elephants died as a result of conflict around plantations in northern India (Choudhury 2004).

It is difficult to quantify the numbers of wild animals present within different types of farmland as comprehensive surveys are rarely conducted in these environments. One study in the UK attempted to census systematically small- to medium-sized mammal populations on 12 dairy farms (Mathews *et al* 2006). This showed that mean population density of all small rodents, based on conservative estimates from minimum number alive, was 17 per 100 m of field boundary equating to a mean density of 1,500 animals per 100 hectares (where average field margin density is 9 km per 100 ha and animals are shared equally between fields). In addition, average 100–ha farms were found to have 6 brown rats (*Rattus norvegicus*), 16 grey squirrels (*Sciurus carolinensis*), 17 rabbits, 7 badgers (*Meles meles*), 1 small mustelid, and 1 fox (*Vulpes vulpes*). Note that the estimates for foxes, mustelids and rats are likely to be highly conservative due to the difficulties of trapping these species, and estimates were not made for deer or moles (*Talpa europaea*). The farms studied in this project had relatively low vole populations with few animals living within the pasture. By comparison, populations of 291 individuals per hectare (mainly common voles [*Microtus arvalis*]) were found in pasture grazed at low intensity in Germany (Jacob 2003). Thus, the total wild mammal population of an average British dairy farm of 100 ha is likely to be in excess of 1,600 animals; in lower intensity grassland systems, the population could be very much higher.

Rodents are abundant across all types of farmland system and particularly exploit arable enterprises, where they may become agricultural pests. The precise density appears to vary with crop type and season (Tattershall *et al* 2001) and is positively correlated with the productivity of the ground vegetation (Jędrzejewski & Jędrzejewska 1996). In the UK, for example, peak wood mouse (*Arvicola terrestris*) densities of 33 per ha in carrots (Rogers & Gorman 1995) and 80 per ha in sugar beet (Pelz 1989) have been reported, with long-term densities in cropped fields varying between 0 and 67 animals per hectare. In other parts of the world, much higher densities of wild rodents are reported: long-term studies show very high small-rodent densities in temperate and steppe farmland of the Palearctic (143–490 per ha, average of spring and autumn estimates; Jędrzejewski & Jędrzejewska 1996); and high densities are reported for German wheat and bean crops (90 and 229 per ha, respectively) (Jacob 2003). Systematic population estimates for rats — a key group of agricultural pest — are scarce in the literature, but direct enumeration from fumigating burrows and disturbing straw piles has indicated densities of 120 to 240 rice rats per ha (*Rattus argentiventer*), with similar results being obtained during large-scale eradication campaigns (Leung *et al* 1999).

What are the impacts of agriculture on animal welfare?

Negative impacts on animal welfare can be defined as pain, suffering, distress or lasting harm. Unlike the case for domestic animals, there has been little work examining physiological or behavioural 'stress' responses of wild animals to agricultural variables. Inferences that animals may experience suffering or distress must be drawn from the available data on population dynamics, movement, or mortality: our current picture of the scale and intensity of animal welfare issues associated with farming is therefore likely to be fragmentary.

'Stress' is perhaps the most frequently assessed state. Stress responses have evolved as useful reactions to noxious stimuli, and play an important role in keeping animals alive.

They include physiological, immunological, behavioural and neuroendocrine changes. Broadly, two types of stress responses are measured. These are based on either the cost of dealing with the stressor, for example altered energy budget and diversion of resources from other activities such as reproduction (McEwan 1998); or on measures of defence such as the down-regulation of the immune system and susceptibility to disease (eg Råberg 1998). In most cases, stress is transient and the animal returns to homeostatis. However, if an animal is subjected to a stressor for an extended period, or repeatedly, or if the stressor is very intense, or if many stressors act together, then the animal may develop pathologies. These might include cardiovascular failure or unsuccessful reproduction. Before such extremes are reached, animals can develop pre-pathological states, such as abnormal behaviour, weight loss, immuno-suppression and altered hormonal profiles (Moberg 1987).

The measurement of indices of pre-pathological states, particularly if achieved non-invasively, is extremely useful in assessing welfare. In contrast, indices relating directly to the secretion of adrenal corticosteroids can be difficult to interpret unless there has been validation of their link to negative welfare states in the particular group of animals being studied: they may be elevated as part of an animal's normal stress response, without necessarily indicating a decrease in the animal's well-being (Moberg 1987).

There are three main ways in which an individual wild animal can experience pain, suffering, distress or lasting harm as a result of agriculture. First, it may suffer insults directly, for example, by being run over by a tractor, contracting a disease introduced by domestic animals, or having food supplies removed by harvesting or hedge-trimming. An animal may also be subject to pest-control operations (discussed elsewhere in this issue).

Second, it may suffer indirectly as a consequence of impacts upon other animals on which it depends. For example, an unweaned mammal or unfledged bird will usually starve if its mother is killed, or if it is abandoned as a result of food shortages or disturbance. Similarly, foxes may suffer hunger or starvation as a consequence of the depletion of their prey-base by rabbit and rodent control. One classic example is the deliberate introduction of myxomatosis — a disease with particularly unpleasant symptoms — into Australian rabbit populations in 1950 and European ones in 1952. Not only did this have profound welfare implications for the rabbits, but the disease was so effective in eliminating rabbits (in the 1950s, the disease wiped out 99% of the British rabbit population; Lloyd 1970) that many foxes starved. The consequences of rabbit population crashes from myxomatosis and Rabbit Haemorrhagic Disease are still evident in Iberian lynx (*Lynx pardinus*) and imperial eagle (*Aquila adalberti*) populations in Spain (Delibes-Mateos *et al* 2007).

Thirdly, animals can suffer indirectly through disruption of the biotic environment. For example, increased population density in refuges following the harvesting of a crop field is likely to increase contact rates between individuals.

Particularly in territorial species, sequelae could include increases in bite-wounding, infanticide, immunosuppression, psychological stress, and likelihood of contracting a density-dependent disease.

The impacts of any particular agricultural practice on an individual or population will vary according to other environmental factors. These include the timing of operations relative to the population dynamics of the species in question; landscape ecology; the availability of alternative resources such as food and resting places; as well as other factors that may place the individual or population under stress, such as climatic fluctuations or disease status. Below, I examine direct and indirect effects in three key areas of agricultural practice.

Key conflicts between agriculture and wild animal welfare and conservation

Disease and disease-control measures

Much has been written about wild animals acting as a reservoir of disease for domestic animals. The reverse is rarely considered. Yet, domestic stock, particularly ungulates, have introduced many diseases into wildlife populations, sometimes with catastrophic results for wildlife conservation. These same diseases must also carry welfare implications, causing pain, suffering and distress to infected animals. For instance, rinderpest virus was introduced into wild ruminants in the Horn of Africa at the end of the 19th century. The subsequent epidemic reached the Cape 10 years later, the epidemic having caused massive mortality in wild as well as domestic animals (Plowright 1982). In addition to the direct mortality in ruminants, the disease presumably also caused starvation and subsequent mortality in predators: a vaccine campaign in cattle surrounding the Serengeti was followed by wildebeest (*Connochaetes* spp) and buffalo (*Syncerus caffer*) populations roughly tripling in size over 20 years. Corresponding increases occurred in the numbers of the two main predators of these species, lion (*Panthera leo*) and hyena (*Crocuta crocuta*).

One of the best-studied examples of transmission of disease between wildlife and domestic stock is that of bison (*Bison bison*) and ranched cattle (*Bos primigeneus taurus*). Vast herds of bison once occupied the Great Plains of North America, with more than 50-million animals thought to have been present. They were virtually eliminated by mass-slaughtering in the mid-19th century, with more than 3-million animals being shot within a 3-year period. A remnant population of around 25 animals survived in the Yellowstone National Park. This has been managed for conservation, such that a free-ranging herd of around 5,000 animals now exists. However, brucellosis (*Brucellosis abortus*) was introduced to the Yellowstone bison herd by infected cattle early in the 20th century (Dobson & Meagher 1996). The main symptoms are abortion, weak calves, vaginal discharge and possibly reduced milk yield and retained placentas. Transmission from bison is now seen as a threat to livestock (Baskin 1998) and a variety of bison-culling strategies have been

used as a means of protecting cattle. These have principally focused on animals leaving the park during harsh winters in search of food; and more than 3,400 bison have been killed in this way since the year 2000. However, the risks posed to cattle are extremely low, requiring contamination of the land by aborted products of conception and rapid contact of this land by cattle (Cheville *et al* 1998). Systematic culling of bison is unlikely to eradicate the disease, since transmission within the bison herd is frequency-dependent (Getz & Pickering 1983). Recent analysis suggests that localised hotspots of greatest transmission risk can be identified (based on climate and bison abundance) and that control efforts could focus on these areas (Kilpatrick *et al* 2009). In contrast, there has been little emphasis on the transmission of the disease from cattle to bison, even though infected cattle frequently abort and therefore presumably present an appreciable risk. The endangered chamois (*Rupicapra rupicapra*) in the Western Italian Alps has also been infected with brucellosis (*B. abortus and B. melintensis*) from infected cattle and sheep (*Ovis aries*), and has suffered chronic disease with high levels of mortality (Garin-Bastuji *et al* 1990).

Strategies used to control infectious disease in cattle often have important secondary effects on wild animal welfare. For example, a key element in the control of rinderpest, and more recently Foot and Mouth Disease, in Africa, has been the construction of vast double-electrified 'Veterinary Control Fences' or cordons. The first cordon, the 'Kuke fence', was built in Botswana in 1958, and new fences are still being erected. Their primary purpose is to prevent the movement of infected cattle and game, though some, such as the 240-mile Makgadikgadi fence in Botswana, completed in 2005, also serve to protect people and their animals from attack by lions, and to prevent the grazing of wildlife areas by domestic cattle. Although successful in achieving these aims, the fences have had profound negative implications for wildlife, particularly zebra (*Equus zebra* and *E. grevyi*), hartebeest (*Alcelaphus buselaphus*) and wildebeest, which are prevented from migrating during drought, and consequently die from thirst and starvation. In some areas, animals are effectively trapped in areas with no reliable water sources in the dry season. Animals also become entangled in the fences and are easy prey for predators and poachers. Tens of thousands of wild ungulates have died as a result of the veterinary fencing in Botswana (Child 1970); and in a single week in 2005, local press reported that 253 zebras died at the newly constructed Makgadikgadi fence during their traditional migration.

In the UK, the culling of badgers has formed an integral part of the strategy to control bovine tuberculosis (bTB) in cattle for more than 30 years, and around 30,000 badgers are thought to have been killed. Currently, culling is suspended in England pending the outcome of debates about its effectiveness as a disease-control measure (King 2007), but culls are being reinstated in Wales. Aside from the potential welfare implications of cage trapping, the strategy also appears to cause profound changes in the social organisation of those animals not killed. In undisturbed populations, badger groups in the UK occupy discrete, tesselated territories. Only occasional movements of individuals between these territories occur, for example with mid- or low-ranking males attempting to find a mate in a neighbouring social group. After culling events, the territories of different social groups overlap, there is an increased frequency of extra-territorial excursions by females, and the incidence of bite-wounding increases (Delahay *et al* 2006; Macdonald *et al* 2006; Woodroffe *et al* 2006). It is also postulated that this increased social interaction leads to increased transmission of bTB within badger populations and also to cattle (Donnelly *et al* 2003, 2005). In this case, then, negative impacts on wild animal welfare appear to correspond with considerable negative impacts on agriculture.

Physical impacts

The annual cycles of agricultural production include physically disruptive operations, such as ploughing, rolling, spraying, harvesting (including the cutting of grain crops, cutting of silage and hay, and the harvesting of fruit and vegetables), and the movement of domestic stock between grazing areas. These processes are the cause of death for some individuals. Precise figures are difficult to obtain, but one study in Oxfordshire, UK, reported that one out of 33 wood mice (*Apodemus sylvaticus*) radio-tracked was killed by the combine harvester. Mortalities are particularly high where operations progress from the outside edge of a field, circling inwards. This results in animals being herded towards the centre, with casualties being highly likely. Particularly vulnerable are species that lack underground burrows for escape, such as hares (*Lepus europaeus*), arborial mammals such as harvest mice (*Microtus minutus*), and ground-nesting birds.

Perhaps of more significance than direct mortality due to machinery, is the increased exposure to predators caused by the removal of vegetation (Preston 1990). In the study described above, 28% (9/32) of radio-tracked wood mice were killed by predators within a week of harvest (Tew & Macdonald 1993). No other studies have directly investigated predation in relation to agricultural practice, but there are several reports of sudden drops in population density and survival rates following harvesting or ploughing, at least some of which is likely to be attributable to predation (eg Tew & Macdonald 1993; Macdonald *et al* 2000; Jacob 2003). However, population declines are not inevitable, indeed there may be population increases where long vegetation (eg mown rough grass) remains in the field for long periods to provide cover and food (eg Rogers & Gorman 1995; Jacob 2003). Depending on the process of the particular predation event, the welfare implications for captured animals may be high or low. However, there are likely to be indirect welfare consequences for other members of the population, such as the orphaning of offspring, and the numbers of animals involved is likely to have increased over recent decades. This is because harvest dates in conventional farming systems in temperate regions have moved progressively earlier in the year, particularly for grain, and early

cutting of grass for silage has replaced much traditional, late-summer haymaking. At this time, many animals, for example ground-nesting birds, still have dependent young.

Responses to the perceived threat of predation can also have important animal welfare implications. Increased time spent scanning for predators means less time is available for other activities such as foraging. Animals may also modify their behaviour in other ways that could compromise their own welfare or that of their dependents. For example, radio-tracked wood mice remaining within fields post-harvest were found to almost halve the distance they moved each night, spent 10% less of their time moving, and also moved much more slowly (Tew & Macdonald 1993). Although formal investigations are rare, it would be logical to assume that psychological and physiological responses to the stress of threatened predation, such as increased adrenal activity, would also have a negative long-term impact on an animal's welfare (Ward *et al* 1998).

Field operations also have indirect effects on wild animal welfare. For example, the reproductive output of small mammals has been found to decrease after all mechanical activities (Jacob 2003). The size and organisation of home ranges can also change: this is seen in wood mice in the UK and common voles in Germany. Before harvest, female wood mice have small (approximately 0.6 ha) home ranges which they occupy exclusively, whereas male home ranges are three times larger and overlap those of other individuals (males and females) (Wolton & Flowerdew 1985; Tattershall *et al* 2001). This arrangement changes radically after harvest. In one study, territory size was reduced to just 0.1–0.2 ha in both sexes; female home ranges became non-exclusive; and the position of the home ranges changed so that all centred on the undisturbed habitat at the field boundary (Tattershall *et al* 2001). Similarly, home range size in German common voles was found to decrease by 96% following the harvesting of wheat and by 74% following the mowing of grassland (Jacob & Hempel 2003). The distances travelled by individual animals also fell, suggesting that animals were unwilling to disperse, perhaps due to lack of cover. The magnitude of this response corresponds to the degree of disturbance, with 50% reductions occurring after the harvesting of beans and wheat, whereas mowing and mulching produced smaller changes (Jacob 2003).

Such alterations in the distances travelled by wild animals and their territorial arrangements will influence the frequency of movements between isolated refuges. This can be particularly important in late summer when, in many species, juveniles must migrate out of their natal area. Consequences of failure to disperse include shortages of food and resting sites, and high levels of aggression against juveniles. In conclusion, harvest not only causes direct and indirect mortality, but also influences the availability of food, the spatial arrangement of animals and their social interactions. All of these factors are likely to affect animal welfare.

Use of agrochemicals

A wide range of agrochemicals, including herbicides, insecticides, molluscicides and fungicides, is used in agriculture, and these can have both direct and indirect impacts on wildlife using farmland. The widespread use of organochlorine pesticides in the UK and elsewhere during the 1950s, 1960s and 1970s had profound effects on wildlife populations. Particularly severely affected were the sparrowhawk (*Accipiter nisus*) (Walker & Newton 1998) and the peregrine falcon (*Falco peregrinus*) (Newton & Willey 1992), and contamination of many other animals, including small mammals (Jefferies & French 1976) and bats (Jefferies 1972), was common. Together with polychlorinated biphenols (PCBs), organochlorines have also been implicated as a major cause of declines in otter (*Lutra lutra*) populations (Jefferies 1989; Mason 1989). Voluntary, and later legal bans on the use of organochlorine pesticides, have been effective in reducing residue levels in animals; populations of most affected terrestrial mammals and avian predators have now recovered (Jefferies 1989; Newton & Willey 1992; Ratcliffe 1993).

Although there was public outcry over the conservation implications of organochlorine pesticide use, and a great many scientific papers were written on the topic, the potential implications for animal welfare were not discussed. This trend has continued. More rigorous testing of pesticides is now undertaken before they are licensed for use (with the caveat that there is much extrapolation between species and from the laboratory to the field) and considerable progress is being made in the assessment of long-term risk to population processes and conservation (eg Roelofs *et al* 2005; Shore *et al* 2005; Silby *et al* 2005). However, wild animal welfare remains largely neglected.

Intensively farmed arable land probably receives the most chemical inputs: in Britain alone, over 200 different compounds or mixtures are applied. The majority of these are fungicides and herbicides, but there are also around thirty different formulations that include one or more of the insecticides, including organophosphate, carbamate and pyrethroid compounds (Thomas *et al* 1997). Pastoral systems also use agrochemicals. Although the volumes used are lower, compounds such as rodenticides (and possibly also anthelminthics) can have important conservation implications through effects on non-target organisms (Spratt 1997; McDonald & Birks 2003). Direct and indirect implications for animal welfare from these products are likely.

Rodenticides, particularly anticoagulants as the most widely used group, have profound negative effects on the welfare of target species. When consumed in lethal doses, they cause a protracted and painful death (Mason & Littin 2003). Sublethal doses cause pain associated with haemorrhage. The acute rodenticides, zinc phosphide and calciferol, are also generally inhumane, the former typically causing acute pain for several hours, and the latter pain and illness for several days (Mason & Littin 2003). It would be surprising

if these effects were not seen in non-target organisms, particularly where doses are large, whether due to direct ingestion (for example by non-target rodents) or indirect consumption (as in predators of rodents).

Poisoning of non-target organisms by pesticides and rodenticides is widely viewed as a major concern for wildlife conservation. The experience with organochlorines has certainly highlighted the potential effects. However, the extent of non-target poisoning, and its importance relative to other agricultural operations, such as the use of herbicides or habitat loss, is unclear due to a lack of systematic studies. In the UK (where a large proportion of the work on pesticides originates), the government-run Wildlife Incident Investigation Scheme investigates 'suspicious' deaths of wildlife. Relatively small numbers of animals are studied since the scheme relies on the reporting of wildlife deaths by concerned members of the public. Between 1988 and 1997, 1,156 incidents involving mammals were investigated. The majority (68%) of investigations related to carnivores, primarily badgers and foxes (Shore *et al* 2003). This is likely to reflect the greater probability of their corpses being found and submitted by the public, rather than being a true reflection of the patterns of poisoning in wildlife. Most incidents involved four pesticide groups: organophosphates and carbamates (anticholinesterase compounds that affect the nervous system), organochlorine insecticides (mainly causing deaths in bats and probably due to historical timber treatment rather than agricultural use), rodenticides, and pyrethroids. Some deaths were also due to a range of other compounds, including metaldehyde (a molluscicide used to control slugs), which was often found in dead hedgehogs (*Erinaceus europaeus*), and strychnine and paraquat, both of which are used in the illegal poisoning of badgers.

Non-target poisoning by rodenticides is known to have caused deaths in a range of species including rabbits, hedgehogs, badgers, foxes, stoats (*Mustela erminea*), weasels (*M. nivalis*), barn owls (*Tyto alba*) and buzzards (*Buto buto*) (Berny *et al* 1997; Shore *et al* 1999). Residues of rodenticides have also been found in a range of predatory species, particularly those that feed largely on rodents. The proportion of barn owls containing second-generation rodenticides rose from 5% in 1983 to 35% in 1996, concurrent with increased usage of these compounds (Newton *et al* 1999). Rodenticides have also been identified in 25–30% of small mustelids (stoats, weasels and polecats [*Mustela putorius*]) examined (Shore *et al* 1996; McDonald *et al* 1998). Detectable levels of rodenticide were also found in 46% of a sample of 96 foxes not thought to have died of rodenticide poisoning (Shore *et al* 2003). In New Zealand, where there is widescale use of second-generation anticoagulant rodenticides, residues are commonly found in non-target species (Murphy *et al* 1998; Eason *et al* 2001). Such is concern about the effects of these potent and persistent compounds that one of the most widespread, brodifacoum, is banned from field use in the USA (Stone

1999). The conservation implications of sublethal exposure to rodenticides are unclear. The polecat and barn owl in Britain are currently undergoing population recoveries despite increases in the prevalence of poison consumption (Toms *et al* 2001; Battersby *et al* 2005). It may be that pesticide-induced mortality is limiting, though not preventing, this population expansion. Regardless of the conservation implications at the population level, rodenticide ingestion is an important welfare issue for both target and non-target individuals. More work is required to determine the extent and severity of the problem.

Molluscicides are widely used in agriculture and can be either drilled or broadcast. Concerns have particularly focused on primary or secondary toxicity to hedgehogs from consumption of the molluscicide metaldehyde (commonly used in gardens) (Morris 1993). In agriculture, methiocarb, an anticholinesterase compound, is more commonly used, and is known to be eaten in pellet form by wood mice which are widespread in crop fields (Tarrant & Westlake 1988). The broadcasting of methiocarb pellets was followed by immediate disappearance of a large proportion of wood mice from treated fields in one British study (Shore *et al* 1997), whereas another found lesser effects (Johnson *et al* 1991) and another found no decline (Tarrant *et al* 1990). The differences between the studies are likely to be due to variations in the availability of alternative food, the proximity of source areas for immigration, and the size of the mouse population within and around the field.

The short-term impacts of pesticides on wood mouse population density may not be of conservation concern, since there is rapid recovery by immigration (Johnson *et al* 1991). However, as with rodenticides, there may be important welfare implications: some of the change in population size is likely to be due to direct mortality, and this is unlikely to have occurred without any suffering or distress. Sub-lethal exposure to anti-cholinesterase and carbamide pesticides is known to induce short-term adverse effects that include hypothermia (Grue *et al* 1997) and loss of movement or co-ordination. These pesticides increase vulnerability to predators in mammals (Dell'Omo & Shore 1996a,b) and birds (Buerger *et al* 1991; Hunt *et al* 1992); they also prevent foraging for several hours in bats (Clark 1986; Clark & Rattner 1987), and can cause hypothermia (Grue *et al* 1997). Secondary poisoning of predators including tawny owls (*Strix aluco*), kestrels (*Falco tinnunculus*) and weasels is also considered likely (Shore *et al* 1997).

Pesticide seed-dressings are widely used. Between 1992 and 1997, 90% of all arable seed used in the UK was treated (Thomas *et al* 1997). Seed-dressings present a threat to wildlife that feed on the seed, notably granivorous birds such as woodpigeons (*Columba palumbus*) and geese. Detailed studies have revealed that the risk extends to passerines that take much smaller quantities of seed (and are not generally considered agricultural pests) such as chaffinch (*Fringilla coelebs*) and greenfinch (*Carduelis chloris*). Species that lack the beak structure to de-husk seeds, such as robin (*Erithacus rubecula*) and dunnock (*Prunella modularis*), are

particularly at risk, since the toxins are concentrated in the seed coat. For some of the more toxic dressings, field studies show that many species can obtain a lethal dose in less than one day (Hart 1990; Prosser & Hart 2005). As with other agrochemicals, the extent and severity of the problem is unclear. It is known that some birds have been poisoned by organophosphate dressings (Fletcher *et al* 1992), but a prospective radio-tracking study found that mortality due to poisoning from seed dressings was low (0–5%) in woodpigeons (Prosser *et al* 2006).

Chemical inputs can also reduce the availability of food and habitat resources for wildlife. Wood mice actively avoid areas of arable fields sprayed with herbicides (to control weeds), probably because they have a lower density of preferred plant and invertebrate species (Tew *et al* 1992). This is likely to carry indirect consequences for animal welfare as animals migrate to other habitat areas and compete with resident animals for finite resources there. In addition, it is possible that some animals will suffer as a direct consequence of the removal of a food source. The use of avermectins to control nematodes in livestock is virtually ubiquitous in modern farming. Yet, they often have a secondary consequence of reducing the numbers of invertebrates, particularly dung beetles, that would otherwise feed on the animal dung (Strong 1993). This may not only disrupt nutrient cycling in the ecosystem (Spratt 1997), but can also reduce the availability of prey items key for some bat species, such as the endangered greater horseshoe bat (*Rhinopholus ferrumequinum*) during their breeding season. It is currently unclear whether there are detectable impacts on bat population levels. However, reductions in prey availability may have important effects on animal welfare, particularly if there are other adverse conditions, such as poor weather, operating simultaneously: it is known that mother greater horseshoe bats do not abandon their young when foraging conditions are poor, but will instead continue to feed their offspring until they themselves die of starvation (Ransome 1998).

Options for improving wild animal welfare in agricultural systems

Agriculture is an indispensable part of human civilisation. Processes such as ploughing and harvest are necessities for food production. However, there is room for change in the management of marginal farmland habitat. The incorporation of features such as conservation headlands, beetle banks, and hedgerow buffer strips can not only increase the total amount of habitat available to wildlife, but also offer refuge for animals displaced by in-field operations. The timing of some agricultural activities may also be modifiable. For example, the trimming of hedgerows in late summer removes supplies of berries and nuts upon which many animals depend, and this procedure could equally well be done in late winter. Similarly, altering the timing of cattle treatment to before or after the peak period of activity of dung beetles would help to minimise potential adverse implications for bats (Krüger & Scholtz 1996).

The sympathetic management of non-crop habitat can benefit wildlife in terms of both conservation and welfare. Over the past 50 years, roughly one-third of the hedgerows in Britain have been lost, either by removal to accommodate larger farm machinery, or through neglect (being replaced with wire fences of negligible value to wildlife). Yet these, and other marginal habitats such as walls, ditches and copses, are critical to the maintenance of wildlife populations on farms (Macdonald & Johnson 1995; Gillings & Fuller 1998; Gelling *et al* 2007). The greater the connectivity of wildlife refuges, the more resilient animal populations can be to demographic and environmental fluctuations. Secondary impacts of agriculture on wildlife may similarly be reduced, as animals are more likely to be able to find alternative resources in a well-connected mosaic of suitable habitats, and will also be able to disperse more easily, so reducing the likelihood of overcrowding and social tension. There may also be positive spin-offs for farmers. For example, the risk of bovine tuberculosis in cattle and the availability of natural predators of invertebrate pests can both be improved by sympathetic land management (Landis *et al* 2000; Mathews *et al* 2006).

The extent and severity of damage caused by agrochemicals are unclear and more research is urgently needed. One of the difficulties is that such work needs to be extensive, and conducted over a long time-period: it is therefore also expensive. It is possible, however, that major impacts on animal populations, particularly on welfare, but also on conservation terms, may be being missed. For example, a recent large study found some evidence of benefits to biodiversity from organic versus conventional farming, but the differences for most species were relatively small (Fuller *et al* 2005). But what this, and most similar studies, measured was differences in numbers of birds observed across the farming systems. *In extremis*, it would be possible for both systems to have the same numbers of foraging birds, but a high proportion of those feeding on conventional systems may later die or fail to breed unobserved as a result of toxicity from seed dressings. Simply evaluating the attractiveness of different systems may therefore not be the most appropriate outcome measure. Similarly, very little is known of the impact of rodenticides on wildlife. The high welfare costs of pest control operations are frequently overlooked because of their perceived necessity for economic and health reasons.

Often, modifications to agricultural practice taken to benefit wildlife conservation will also benefit wild animal welfare. But this may not always be the case. For example, hedgerow structure could be improved, providing increased food supplies for resident small mammals. However, these animals may respond with extra reproductive activity, rapidly increasing their population density. This would, in turn, reduce individual food availability, and potentially increase social conflicts, territorial behaviour, and the likelihood of contracting a density-dependent disease. It is therefore not clear, *a priori*, that the welfare of individual animals would necessarily improve.

Some aspects of agriculture will have negative impacts on welfare without carrying any such costs to conservation. For example, secondary rodenticide poisoning may have profound welfare implications for polecats, while having no impact on population viability because of density-dependent mechanisms. Control of alien rats often carries extreme welfare costs to the rats, even if it presents benefits to indigenous wildlife and to agriculture. In this case, it is important to recognise that the welfare interests of all wild animals are due the same consideration — and that interventions must be designed to minimise the duration and intensity of suffering of any sentient animal, regardless of its conservation status. Unfortunately, targeted, effective, ecologically based programmes of rodent control are the exception rather than the rule in agricultural systems (Singleton *et al* 1999; Brown *et al* 2006): instead haphazard application of rodenticides leads to cycles of population reduction and resurgence. Vast numbers of animals therefore suffer protracted and painful deaths. Similarly, it could be argued that crop production elevates rodent populations to 'unnaturally' high densities as harvest approaches. A post-harvest crash may therefore simply be seen as the inevitable consequence, without necessarily having a conservation impact: in some ways agricultural cycles can be thought of as merely exaggerated and annual versions of some rodent cycles seen in 'natural' habitats. However, this does not imply that the death and starvation associated with harvest has no welfare cost. Instead, we must seek ways in which the costs to wildlife can be minimised — for example, by ensuring that alternative food sources are available by preserving interstitial habitats, rather than by operating intensive monocultures.

Animal welfare implications and conclusion

Agro-ecosystems support vast numbers of wild animals. Many, such as rats, mice and sparrows (*Passer domesticus*), have utilised farmland for thousands of years. While the exploitation of unstable habitats can be an evolutionarily successful strategy, the life-history traits that 'fit' them for this environment (such as large litter sizes and early maturity which permit rapid responses to sudden increases in food supply) do not protect individuals from the welfare challenges associated with farming. Death from anticoagulant poisoning or starvation is likely to be a painful process for any species.

Farming also presents challenges to wildlife conservation. The scale and pace of change in modern industrial agriculture has outstripped the ability of many farmland species to adapt: some, such as farmland birds in Europe, are now of explicit conservation concern. In addition, the continued expansion of agriculture, particularly its encroachment into previously forested areas in the tropics, means that animals adapted to other habitats are compelled to use agro-ecosystems. For these animals, the challenges presented by agricultural practice are coupled with other difficulties, such as inability to find mates and insufficient suitable habitat to supply specialised dietary requirements. Their welfare and conservation therefore deserve particular consideration.

While conservation and animal welfare agendas are usually pursued separately, the same underlying factors often result in challenges to both conservation and animal welfare. For example, increases in the extent and rapidity of harvest, brought about by increasing mechanisation and the trend towards monocultures with a lack of traditional refugia, not only threaten population viability, but also bring fear, hunger and increased aggression due to competition for scarce resources. Consideration of conservation and welfare interests simultaneously is likely to improve outcomes for the animals concerned and also offer a more cogent argument for action.

There is an urgent need to increase public awareness of the twin costs of agriculture to wild animal conservation and welfare, and of the potential opportunities for relatively straightforward changes in production systems to yield benefits. Key areas of concern include habitat management, disease and pest-control strategies, and the use of agrochemicals. Although direct mortality, such as the destruction of ground-nesting bird chicks by combine harvesters, attracts the most public attention, it is likely that most costs are indirect, through, for example, habitat destruction. It is important that these costs are acknowledged and accounted for. There is growing recognition of the value of ecosystem services. The maintenance of wildlife biodiversity health and welfare not only provides non-monetary benefits (the inherent value on wildlife) but there are also likely to be benefits in terms of ecosystem function, agricultural productivity and the control of animal disease (Costanza *et al* 1997; Landis *et al* 2000; Buck *et al* 2004; Pearce *et al* 2006; Sherr & McNeely 2008). A coherent strategy of evaluating alternative strategies which provide benefits to wildlife whilst also being economically viable for farmers is required.

References

Allan BF, Keesing F and Ostfeld RA 2003 Effect of forest fragmentation on Lyme disease risk. *Conservation Biology 17*: 267-272

Baskin Y 1998 Home on the range. *BioScience 48*: 245-251

Battersby J 2005 *UK Mammals: Species Status and Population Trends. First Report by the Tracking Mammals Partnership.* JNCC/Tracking Mammals Partnership: Peterborough, UK

Berny PJ, Buronfosse T, Buronfosse F, Lamarque F and Lorgue G 1997 Field evidence of secondary poisoning of foxes (*Vulpes vulpes*) and buzzards (*Buteo buteo*) by bromadiolone, a 4-year survey. *Chemosphere 35*: 1817-1829

Blann K 2006 *Habitat in Agricultural Landscapes: How Much is Enough? A State-of-the-Science Literature Review.* Defenders of Wildlife: West Linn, OR, USA

Brown PR, Tuan NP, Singleton GR, Ha PTT, Hoa PT, Hue DT, Tan TQ, Tuat NV, Jacob J and Müller WJ 2006 Ecologically based management of rodents in the real world: applied to a mixed agroecosystem in Vietnam. *Ecological Applications 16*: 2000-2010

Buck LE, Gavin TA, Lee DR and Uphoff NT 2004 *Ecoagriculture: A Review and Assessement of its Scientific Foundations. Ecoagriculture Discussion Paper Number 1.* Ecoagriculture Partners: Cornell, USA

Buerger TT, Kendall RJ, Mueller BS, DeVos T and Williams BA 1991 Effects of methyl parathion on northern bobwhite survivability. *Environmental Toxicology and Chemistry 10*: 527-532

Choudhury A 2004 Human-elephant conflicts in Northeast India. *Human Dimensions of Wildlife 9:* 261-270

Cheville NF, McCullough DR and Paulson LR 1998 *Brucellosis in the Greater Yellowstone Area.* National Academy of Sciences: Washington DC, USA

Child G 1970 Wildlife utilisation and management in Botswana. *Biological* Conservation 3: 18-22

Clark DJ Jr and Rattner BA 1987 Orthene® toxicity to little brown bats (*Myotis lucifugus*): acetylcholinesterase inhibition, coordination loss and mortality. *Environmental Toxicology and Chemistry 6:* 705-708

Clark DR Jr 1986 Toxicity of methyl parathion to bats: mortality and coordination loss. *Environmental Toxicology and Chemistry 5:* 191-195

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S 1997 The value of the world's ecosystem services and natural capital. *Nature 387:* 253-260

Delahay RJ, Walker NJ, Forrester GJ, Harmsen B, Riordan P, Macdonald DW, Newman C and Cheeseman CL 2006 Demographic correlates of bite-wounding in Eurasian badgers (*Meles meles*) in stable and perturbed populations. *Animal Behaviour 71:* 1047-1055

Delibes-Mateos M, Redpath SM, Angulo E, Ferreras P and Villafuerte R 2007 Rabbits as a keystone species in southern Europe. *Biological Conservation 137:* 149-156

Dell'Omo G and Shore RE 1996a Behavoural effects of sub-lethal exposure to dimethoate on wood mice, *Apodemus sylvaticus:* 1, Laboratory studies. *Archives of Environmental Contamination and Toxicology 31:* 91-97

Dell'Omo G and Shore RE 1996b Behavioural effects of sub-lethal exposure to dimethoate on wood mice, *Apodemus sylvaticus:* II, Field studies on radio-tagged mice in a cereal ecosystem. *Archives of Environmental Contamination and Toxicology 31:* 538-542

Dobson AP and Meagher M 1996 The population dynamics of brucellosis in the Yellowstone National Park. *Ecology 77:* 1026-1036

Donald PF 2004 Biodiversity impacts of some agricultural commodity production systems. *Conservation Biology 18:* 17-37

Donald PF, Green RE and Heath MF 2001 Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society B 268:* 25-29

Donnelly CA, Woodroffe R, Cox DR, Bourne J, Gettinby G, le Fevre AM, McInerney JP and Morrison WI 2003 Impact of localised badger culling on tuberculosis incidence in British cattle. *Nature 426:* 834-837

Donnelly CA, Woodroffe R, Cox DR, Bourne J, Cheeseman DL, Clifton-Hadley R, Wei G, Gettinby G, Gilks P, Jenkins H, Johnston WT, le Fevre AM, McInerney JP and Morrison WI 2005 Positive and negative effects of widespread badger culling on tuberculosis incidence in British cattle. *Nature 439:* 843-846

Eason CA, Murphy EC, Wright GRG and Spurr EB 2001 Assessment of risks of brodifacoum to non-target birds and mammals in New Zealand. *Ecotoxicology 11:* 35-48

Elton CJ 1958 *The Ecology of Invasions by Animals and Plants.* Methuen: London, UK

Farm Animal Welfare Council 1992 FAWC updates the five freedoms. *Veterinary Record 131:* 357

Fitzherbert EB, Struebig MJ, Morel A, Danielsen F, Brühl CA, Donald PF and Phalan B 2008 How will palm oil expansion affect biodiversity? *Trends in Ecology and Evolution 10:* 538-545

Fletcher MR, Hunter K, Quick MP and Grave RC 1992 *Pesticide Poisoning of Animals 1991. Investigation of Suspected Incidents in Great Britain. Report of the Environmental Panel of the Advisory Committee on Pesticides.* MAFF Publications: London, UK

Fraser D, Weary DM, Pajor EA and Milligan BN 1997 A scientific conception of animal welfare that reflects ethical concerns. *Animal Welfare 6:* 187-205

Fuller RJ, Norton LR, Feber RE, Johnson PJ, Chamberlain DE, Joys AC, Mathews F, Stuart RC, Townsend MC, Manley WJ, Wolfe MS, Macdonald DW and Firbank LG 2005 Benefits of organic farming to biodiversity vary among taxa. *Biology Letters 1:* 431-434

Garin-Bastuji B, Oudar J, Richard Y and Gastello J 1990 Isolation of *Brucella melitensis* Biovar 3 from a Chamois (*Rupicapra rupicapra*) in the Southern French Alps. *Journal of Wildlife Diseases 26:* 116-118

Gelling M, Macdonald DW and Mathews F 2007 Are hedgerows the route to increased farmland small mammal density? Use of hedgerows in British pastoral habitats. *Landscape Ecology 22:* 1019-1032

Getz WM and Pickering J 1983 Epidemic models: thresholds and population regulation. *American Naturalist 121:* 892-898

Gillings S and Fuller RJ 1998 Changes in bird populations on sample lowland English farms in relation to loss of hedgerows and other non-crop habitats. *Oecologia 116:* 120-127

Grue CE, Gibert PL and Seeley ME 1997 Neurophysiological and behavioral changes in non-target wildlife exposed to organophosphate and carbamate pesticides: thermoregulation, food consumption and reproduction. *American Zoologist 27:* 369-388

Guyatt GH, Feeny DH and Patrick DL 1993 Measuring health-related quality of life. *Annals of Internal Medicine 118:* 622-629

Hart ADM 1990 The assessment of pesticide hazards to birds: the problem of variable effects. *Ibis 132:* 192-204

Hunt KA, Bird DM, Mineau P and Shutt L 1992 Selective predation of organophosphate-exposed prey by American kestrels. *Animal Behaviour 43:* 971-976

Jacob J 2003 Short-term effects of farming practices on populations of common voles. *Agriculture Ecosystems and Environment 95:* 321-325

Jacob J and Hempel N 2003 Effects of farming practices on spatial behaviour of common voles. *Journal of Ethology 21:* 45-50

Jefferies DJ 1972 Organochlorine insecticide residues in British bats and their significance. *Journal of Zoology London 166:* 245-263

Jefferies DJ 1989 The changing otter population of Britain 1700-1989. *Biological Journal of the Linnean Society 38:* 61-69

Jefferies DJ and French MC 1976 Mercury, cadmium, zinc, copper and organochlorine insecticide levels in small mammals trapped in a wheat field. *Environmental Pollution 10:* 175-182

Jędrzejewski W and Jędrzejewska B 1996 Rodent cycles in relation to biomass and productivity of ground vegetation and predation in the Palearctic. *Acta Theriologia 41:* 1-34

Johnson IP, Flowerdew JR and Hare R 1991 Effects of broadcasting and drilling methiocarb molluscicide pellets on field populations of wood mice, *Apodemus sylvaticus. Bulletin of Environmental Contamination and Toxicology 46:* 84-91

Kilpatrick AM, Cillin CM and Daszak P 2009 Wildlife-livestock conflict: the risk of pathogen transmission from bison to cattle outside Yellowstone National Park. *Journal of Applied Ecology 46:* 476-485

King D 2007 Bovine Tuberculosis in Cattle and Badgers. *A Report by the Chief Scientific Advisor, Sir David King.* DEFRA: London, UK

Kirkwood JK 1993 Interventions for wildlife health, conservation and welfare. *Veterinary Record 132:* 235-238

Kirkwood JK, Sainsbury AW and Bennett PM 1994 The welfare of free-living wild animals: methods of assessment. *Animal Welfare 3:* 257-273

Krüger K and Scholtz CH 1996 Lethal and sublethal effects of ivermectin on the dung-breeding beetles *Euoniticellus intermedius* (Reiche) and *Onitis alexis* Klug (Coleoptera, Scarabaeidae). *Agriculture Ecosystems and Environment 61:* 123-131

Landis DA, Wratten SD and Gurr GM 2000 Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Reviews of Entomology 45*: 175-201

Leung LKP, Singleton FR and Sudarmaji R 1999 Ecologically-based population management of the rice-field rat in Indonesia. In: Singleton G, Hinds L, Leirs H and Zhang H (eds) *Ecologically-based Rodent Management* pp 305-318. Australian Centre for International Agricultural Research: Canberra, Australia

Littin K, Mellor DR, Warburton B and Eason CT 2004 Animal welfare and ethical issues relevant to the humane control of vertebrate pests. *New Zealand Veterinary Journal 52*: 1-10

Lloyd HG 1970 Post-myxomatosis rabbit populations in England and Wales. *European and Mediterranean Plant Protection Organisation Publications Series A. 58*: 197-215

Macdonald DW and Johnson PJ 1995 The relationship between bird diversity and the botanical composition and structure of hedges. *Journal of Applied Ecology 32*: 492-505

Macdonald DW, Riordan R and Mathews F 2006 Biological hurdles to the control of TB in cattle: a test of two hypotheses to explain the failure of control. *Biological Conservation 133*: 268-286

Macdonald DW, Tew TE, Todd AI, Garner JP and Johnson PJ 2000 Arable habitat use by wood mice *Apodemus sylvaticus*. 3: A farm-scale experiment on the effects of crop-rotation. *Journal of Zoology London 250*: 313-320

Mason CF 1989 Water pollution and otter distribution: a review. *Lutra 32*: 97-131

Mason G and Littin KE 2003 The humaneness of rodent pest control. *Animal Welfare 12*: 1-37

Mathews F, Lovett L, Rushton S and Macdonald DW 2006 Bovine tuberculosis in cattle: reduced risk on wildlife-friendly farms. *Biology Letters 2*: 271-274

Mazaris D, Mamakis Y, Kalpakis S, Poulopoulos Y and Matsinos YG 2008 Evaluating potential threats to birds in Greece: an analysis of a 10-year data set from a rehabilitation centre. *Oryx 42:* 408-141

McDonald RA and Birks JDS 2003 Effects of farming practice and wildlife management on small mustelid carnivores. In: Tattershall F and Manley W (eds) *Conservation and Conflict. Farming and Mammals in Britain. Linnean Society Occasional Publications 4* pp 106-119. Westbury Publishing: Otley, UK

McDonald RA, Harris S, Turnbull G, Brown P and Fletcher M 1998 Anticoagulant rodenticides in stoats (*Mustela erminea*) and weasels (*M. nivalis*) in England. *Environmental Pollution 103*: 17-23

McEwan BS 1998 Stress, adaptation and disease: allostasis and allostatic load. *Annals of the New York Academy of Science 840:* 33-44

Millennium Ecosystem Assessment (MA) 2005 *Millennium Ecosystem Assessment Synthesis Reports*. Island Press: Washington DC, USA

Moberg GP 1987 Problems in defining stress and distress in animals. *Journal of the American Veterinary Medical Association 191*: 1207-1211

Morris PA 1993 *A Red Data Book for British Mammals*. The Mammal Society: London, UK

Murphy EC, Clapperton BK, Bradfield PMF and Speed HJ 1998. Brodifacoum residues in target and non-target animals following large-scale poison operations in New Zealand podocarp-hardwood forests. *New Zealand Journal of Zoology 25*: 307-314

Newton I and Willey I 1992 Recovery of a sparrowhawk population in relation to declining pesticide contamination. *Journal of Applied Ecology 29*: 476-484

Newton I, Willey I and Freestone P 1990 Rodenticides in British barn owls. *Environmental Pollution 68*: 101-117

Pearce D, Atkinson G and Mourato S 2006 *Cost-Benefit Analysis and the Environment: Recent Developments*. OECD Publishing: Paris, France

Pelz HJ 1989 Ecological aspects of damage to sugar-beet seeds by *Apodemus sylvaticus*. In: Putman RJ (ed) *Mammals as Pests* pp 34-48. Chapman and Hall: London, UK

Plowright W 1982 The effects of rinderpest and rinderpest control on wildlife in Africa. *Symposium of the Zoological Society London 50*: 1-28

Preston CR 1990 Distribution of raptor foraging in relation to prey biomass and habitat structure. *Condor 92*: 107-112

Prosser PJ and Hart AD 2005 Assessing potential exposure of birds to pesticide-treated seeds. *Ecotoxicology 14*: 679-691

Prosser PJ, Hart ADM, Langton SD, McKay JV and Cooke AS 2006 Estimating the rate of poisoning by insecticide-treated seeds in a bird population. *Ecotoxicology 15*: 657-664

Råberg L, Grahn M, Hasselquist D and Svensson E 1998 On the adaptive significance of stress-induced immunosuppression. *Proceedings of the Royal Society London B 265*: 1637-1641

Ransome RD 1998 *The Impact of Maternity Roost Conditions on Populations of Greater Horseshoe Bats*. English Nature Research Reports 292. English Nature: Peterborough, UK

Ratcliffe DA 1993 *The Peregrine Falcon*. Poyser: London, UK

Regan T 1983 *The Case for Animal Rights*. University of California Press: Berkeley CA, USA

Roelofs W, Crocker DR, Shore RF, Moore DRJ, Smith GC, Akcakaya HR, Bennett RS and Chapman PF 2005 Case study part 2: probabilistic modelling of long-term effects of pesticides on individual breeding success in birds and mammals. *Ecotoxicology 14*: 895-923

Rogers LM and Gorman ML 1995 The population dynamics of small mammals living in set-aside and surrounding semi-natural crop land. *Journal of Zoology 235*: 77-83

Russell WM and Burch R 1959 *The Principles of Humane Experimental Technique*. Methuen & Co: London, UK

Sharp T and Saunders G 2008 *A Model for Assessing the Relative Humaneness of Pest Animal Control Methods*. Australian Government Department of Agriculture, Fisheries and Forestry: Canberra, Australia

Sherr SJ and McNeely JA 2008 Biodiversity conservation and agricultural sustainability: towards a new paradigm of 'ecoagriculture' landscapes. *Philosophical Transactions of the Royal Society London 363*: 477-494

Shore RF, Feber RE, Firbank G, Fishwick SK, Macdonald DW and Norum U 1997 The impacts of molluscicide pellets on spring and autumn populations of wood mice *Apodemus sylvaticus*. *Agriculture, Ecosystems and Environment 64:* 211-217

Shore RF, Birks JDS and Freestone P 1999 Exposure of non-target vertebrates to second-generation rodenticides in Britain, with particular reference to the polecat *Mustela putorius*. *New Zealand Journal of Ecology 23*: 199-206

Shore RF, Fletcher MR and Walker LA 2003 Agricultural pesticides and mammals in Britain. In: Tattershall F and Manley W (eds) *Conservation and Conflict. Mammals and Farming in Britain. Linnean Society Occasional Publications 4* pp 37-50. Westbury Publishing: Otley, UK

Shore RF, Birks JDS, Freestone P and Kitchener AC 1996 Second generation rodenticides and polecats (*Mustela putorius*) in Britain. *Environmental Pollution 91*: 279-282

Shore RF, Crocker DR, Akcakaya HR, Bennett RS, Chapman PF, Clook M, Crane M and Dewhurst IC 2005 Case study part 1: how to calculate appropriate deterministic long-term toxicity to exposure ratio (TERs) for birds and mammals. *Ecotoxicology 14*: 877-893

Sibley RM, Akcakaya HR, Topping CJ and O'Connor RJ 2005 Population-level assessment of risks of pesticides to birds and mammals in the UK. *Ecotoxicology 15*: 863-876

Singer P 1976 *Animal Liberation: Towards an End to Man's Inhumanity to Animals*. Jonathan Cape Ltd: London, UK

Singleton G, Hinds L, Leirs H and Zhang Z 1999 *Ecologically-based Rodent Management*. Australian Centre for International Agricultural Research: Canberra, Australia

Singleton I, Wich SA, Husson S, Atmoko SU, Leighton M, Rosen N, Traylor-Holzer K, Lacy R and Byers O 2004 *Orangutan Population and Habitat Viability Assessment: Final Report*. IUCN/SSC Conservation Breeding Specialist Group: Apple Valley MN, USA

Soulé ME 1985 What is conservation biology? *BioScience 35*: 727-734

Spratt DM 1997 Endoparasite control strategies: implications for biodiversity of native fauna. *International Journal of Parasitology 27*: 173-180

Stone WB, Okoniewski JC and Stedelin JR 1999 Poisoning of wildlife with anticoagulant rodenticides in New York. *Journal of Wildlife Diseases 35*: 187-193

Strong L 1993 Overview: the impact of ivermectin on pasture-land ecology. *Veterinary Parasitology 48*: 3-17

Suzán G, Marcé E, Giermakowski JT, Armién B, Pascale J, Mills J, Ceballos G, Gómez A, Aguirre AA, Salazar-Bravo J, Armién A, Parmenter R and Yates T 2009 The effect of habitat fragmentation and species diversity loss on hantavirus prevalence in Panama. *Annals of the New York Academy of Sciences 1149*: 80-83

Tarrant KA and Westlake GE 1988 Laboratory evaluation of the hazard to wood mice, (*Apodemus sylvaticus*) from the agricultural use of methiocarb molluscicide pellets. *Bulletin of Environmental Contamination and Toxicology 40*: 147-152

Tarrant KA, Johnson IP, Flowerdew JR and Grieg-Smith PW 1990 Effects of pesticide applications on small mammals in arable fields, and the recovery of their populations. In: *Brighton Crop Protection Conference – Pests and Diseases* pp 173-182. The British Crop Protection Council: Farnham, UK

Tattershall FH, Macdonald DW, Feber RE, Hart BJ and Manley WJ 2001 Habitat use by wood mice in a changeable arable landscape. *Journal of Zoology London 255*: 487-494

Teixeira CP, De Azevedo CS, Mendl M, Cipreste CF and Young RJ 2006 Revisiting translocation and reintroduction programmes: the importance of considering stress. *Animal Behaviour 73*: 1-13

Tew TE and Macdonald DW 1993 The effects of harvest on arable wood mice (*Apodemus sylvaticus*). *Biological Conservation 65*: 279-283

Tew TE, Macdonald DW and Rands MRW 1992 Herbicide application affects microhabitat use by arable wood mice (*Apodemus sylvaticus*). *Journal of Applied Ecology 29*: 532-540

Thomas MR, Garthwaite DE and Banham AR 1991 *Arable Farm Crops in Great Britain 1996. Pesticide Usage Survey Report 141*. Ministry of Agriculture, Fisheries and Food Publications: London, UK

Toms MP, Crick HPQ and Shawyer CR 2001 The status of breeding barn owls *Tyto alba* in the United Kingdom 1995-97. *Bird Study 48*: 23-37

Walker CH and Newton I 1998 Effects of cyclodiene insecticides on the sparrowhawk (*Accipiter nisus*) in Britain; a reappraisal of the evidence. *Ecotoxicology 7*: 185-189

Ward JF, Macdonald DW, Doncaster CP and Mauget C 1998 Physiological response of the European hedgehog to predator and nonpredator odour. *Physiology and Behavior 60*: 1469-1472

Wolton RJ and Flowerdew JR 1985 Spatial distribution and movements of wood mice, yellow-necked mice and bank voles. *Symposium of the Zoological Society of London 55*: 249-275

Wood S, Sebastian K and Scherr S 2000 *Pilot Analysis of Global Ecosystems: Agroecosystems*. IFPRI and World Resources Institute: Washington DC, USA

Woodroffe R, Donnelly CA, Cox DR, Bourne JF, Chesseman CL, Delahay RJ, Gettinby G, McInerney JP and Morrison W 2006 Effects of culling on badger (*Meles meles*) spatial organisation: implications for the control of bovine tuberculosis. *Journal of Applied Ecology 43*: 1-10