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A new look!

Evolution is not restricted to the carbon-based creatures that inhabit this world. The preferences of people evolve, the way we publish our results evolves. Once in a while we discover that the way we did things for years, work no longer. The lay out of Lutra is one of these things. The way information currently comes to us, is very different from when the previous design for Lutra was made. There is more of it and there is more variety in it. This development has changed the way we use and absorb the information that comes to us in printed form. We 'read' differently. This is the reason that the 'look' of Lutra has changed.

Apart from this new look two other changes are worth mentioning. From now on Lutra publishes only in English and Dutch, and English is preferred over Dutch. This was already our policy, but this preference is now more integrated in the design and lay out of the journal. Another change is that Lutra now distinguishes between full articles and short notes. While full articles describe the methods, results and conclusions of comprehensive mammal research, short notes may consist of remarkable observations, simple surveys, methodological aspects or other brief communications. Lutra also publishes book reviews and overviews of recent literature on a regular basis. In the future other categories may be added. These may include anouncements, letters and opinions. The instructions for authors are now available from the internet site of the publisher, the 'Vereniging voor Zoogdierkunde en Zoogdierbescherming' (VZZ): http://www.vzz.nl.

The editorial board has also changed recently. After having served Lutra for several years, Monique Bestman and Sim Broekhuizen resigned. The editorial board thanks them for their valuable contributions over the past years. At the same time we are happy to introduce two new members: Liesbeth Bakker and Ben Verboom.

The contents of this issue of Lutra is varied. It contains articles on the disease and injury in wild hedgehogs brought to a wildlife hospital, the shift in sex ratio of red foxes just before and after birth, how simple measures can benefit mammals in agricultural areas, and the remarkable observation of a beaver in Luxembourg. Finally we bring you up to date with recent publications through literature overviews from Belgium and The Netherlands, and two book reviews. We hope you will enjoy this issue of Lutra.

The incidence of disease and injury in displaced wild hedgehogs (*Erinaceus europaeus*)

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Abstract: The main reasons for the delivery of 168 wild hedgehogs to an animal home in York, England, were investigated between 1998 and 2000. All the animals were subsequently treated at the author's hedgehog sanctuary. Of these 61% were nestlings, 25% juveniles, and 14% adults. Nestlings showed a significantly male-biased sex ratio (m:f = 1.5:1), while juveniles and adults did not. However, there was significant bias (1.4:1) for all age categories combined. The degree of bias did not differ between the age categories, suggesting equal mortality in the two sexes. For all individuals combined, the most common ailments were malnutrition (27% of the animals) and dehydration (15%), while ticks (*Ixodes hexagonus*) (14%), nematodes (*Crenosoma striatum*) (11%), ringworm (4%) and sarcoptic mange (6%) also occurred regularly. Road accidents and other injuries each affected 4%. Nestlings suffered primarily from nest disturbance, bite wounds from domestic animals, prolonged absence of the mother, and accidental entrapment. The overall survival rate was 94% and 84%, 48 hours and 20 days after admission respectively. Most nestlings (74%), juveniles (55%) and adults (58%) survived and were released back to the wild. Anthropogenic factors appear to contribute substantially to the incidence of injury and misfortune in all age groups and emphasise the need for measures directed at maintaining hedgehog populations.

Key words: animal welfare, *Erinaceus europaeus*, conservation, habitat fragmentation, hedgehog, mammals, rehabilitation, wildlife rescue, disease, parasites.

Introduction

Recent population estimates (The Mammal Society 1999) of the British hedgehog (*Erinaceus europaeus*) indicate that the hedgehog is on the decline in England, Scotland and Wales. As the species has so far managed to survive for millions of years, early forms of the spiny hedgehog being distinct 26-38 million years ago (Reeve 1994), signs of its demise are worrying in the extreme.

The hedgehog is susceptible to a range of diseases and can sustain various injuries in suburban areas. It is also host to many intestinal parasites (Boag & Fowler 1968, Smith 1968, Majeed et al. 1989, Keymer et al. 1991). Although it is commonly reported that the most common cause of death of the hedgehog in Britain is road traffic casualties (Stocker 1987), hedgehogs can also die from many other causes (Smith 1968, Stocker 1987, Keymer et al. 1991, Reeve 1994, Sykes & Durrant 1995, Reeve & Huijser 1999, Robinson & Routh 1999).

The removal of hedgerows and small woodland fragments in agricultural areas has caused hedgehog populations to decline locally or regionally (Huijser 1999), while the mere presence of humans, with their garden ponds and strimmers, adds to the death toll each year (Reeve & Huijser 1999). However, there are many benefits to be gained by hedgehogs living in close proximity to humans, such as supplementary food, and shelter in rural and suburban outbuildings. Huijser (1999) considers that traffic mortality is unlikely to be the primary cause of a decline in hedgehog numbers, but that the way humans manage the landscape has far greater effects on the survival probability of hedgehog populations.

This study was conducted in order to shed further light on the reasons for population decline in the British hedgehog and, in so doing, to hopefully help reverse this trend. Specifically, data were collected to determine the number of

hedgehogs that were heavily burdened with parasites, suffered myiasis, leg breaks, eye infections, hypothermia and other ailments, and were hit by cars. The study seeks to determine the impact of these ailments and injuries on the survival rates of hedgehogs presented initially at an animal home in York, England, then taken to the author's sanctuary, over a three year period. The animal home was run under the supervision of the Royal Society for the Prevention of Cruelty to Animals (RSPCA).

The study also attempts to establish whether seasonal variation exists in terms of different age categories arriving for treatment; whether the sex ratio differs significantly from a 1:1 null hypothesis for each category of nestlings, juveniles and adults and for all groups pooled; whether the relative survival of males and females is significantly different across the age classes, and across all categories pooled, and whether there are significant differences in survival (with the sexes combined) for the three age groups.

Material and methods

Sources of data

For the past five years a rehabilitation programme for hedgehogs has been run at a sanctuary in York, solely by the author. The greater majority of the hedgehogs (90%, n=168, 1998-2000) presented at York RSPCA were taken to the sanctuary for the purpose of rehabilitation and eventual return of the survivors back to the wild. Records kept during the study period enabled a detailed analysis of the types of ailments and injuries that afflict displaced animals. Displaced, in this instance, refers to any hedgehog found in an exposed position in daylight hours, such behaviour often bringing it to the attention of the public. With rare exceptions, when a juvenile might appear intermittently during daylight hours due to scarcity of food in the vicinity, it is extremely rare for hedgehogs to be spotted out and about between the hours of dawn and dusk. Increased public awareness has led to a greater number of hedgehogs being taken to the RSPCA.

Coding of ailments and injuries

As the aim of this study was to examine the reasons why hedgehogs had been found out in the open (displaced), and in need of treatment, their detailed assessment on arrival was crucial. All animals were weighed on arrival and assessed for signs of injury or ailment using the following categories: *1. Ringworm* - Flaking or crusting of the skin, with some spine loss, accompanied by microscopic examination of skin scrapings, allowed determination of this disease (Bunnell 2000). *2. Sarcoptic mange* - Often accompanying ringworm, this disease presents as tiny white flakes or dust visible amongst the spines (Sykes & Durrant 1995). The flakes are produced by the Sarcoptes mite (*Sarcoptes spp.*) burrowing beneath the epidermis of the skin. Mites are occasionally visible with the naked eye, and certainly by examination of skin scrapings using a light microscope (Reeve 1994). As mite infestation predisposes the hedgehog to a secondary bacterial infection, mange is often accompanied by an unpleasant smell. *3. Demodectic mange* - As with sarcoptic mange, this type is also caused by a mite, in this case *Demodex erinacei*, which lives in the follicles of the hair or spines, resulting in hair and spine loss. Heavy infestation can lead to massive spine loss and baldness. *4. Puncture wounds* - These are not always visible on initial examination as they can be obscured by the spines. Their presence often becomes evident when the resulting bacterial infection causes an abscess to form which then bursts. The presence of pus then reveals the puncture points. *5. Abscesses* - These are usually present in animals that have received wounds by being attacked by a dog (or, less commonly, a cat). *6. Ticks (Ixodes hexagonus)* - These external parasites are commonly present in animals that have been ill for some time and suggest a poorer prognosis. In very sick animals their removal is dealt with by the application of a safe oil (Bunnell 2001a). *7.*

An orphaned nestling being fed a milk substitute using a syringe. *Photograph: Toni Bunnell.*

Crenosoma striatum - This nematode is a type of lung worm. *8. Capillaria spp.* - This nematode is also a lung worm. *9. Hymenolepis erinacei* - This is a tape worm specific to the hedgehog and is generally detected by the presence of white segments in the faeces. Microscopic examination of faecal smears may reveal the presence of segments and eggs. *10. Isospora spp.* - This internal parasite is a protozoan, infection with which is usually subclinical (Robinson & Routh 1999). However, heavy infestation can result in distinct changes to the faeces (Sykes & Durrant 1995) which appear green, watery or jelly-like, and blood-stained. Clinical signs also include weight loss. *11. Escherichia coli* - This bacterium produces a watery brown diarrhoea which responds rapidly to antibiotic treatment, confirming the initial diagnosis. *12. Malnutrition* - A pointed rear end and prominent ribs were two symptoms used to signify malnutrition. *13. Dehydration* - When the skin was loose, with a noticeable flap where the spines meet the under fur, or when an animal moved in a wobbly, uncoordinated fashion, it was considered to be dehydrated. *14. Hypothermia* - Any animal whose abdomen felt cold to the touch, that is less than 36.9 °C, was considered to be hypothermic. It was provided with an optional heat source from which it could easily remove itself. Animals incapable of movement were placed close to the heat source, but not actually on it, to avoid the possibility of overheating. *15. Breathing difficulties* - These take the form of wheezing, rapid breathing, nasal discharge and often coughing. *16. Myiasis* - Also known as fly strike, myiasis is detectable by the presence of tiny white clumps of blowfly eggs. These are often hidden deep within the fur and require great patience to identify and remove all of them. *17. Hit by car* - Indications that a hedgehog has been hit by a car are scuffed heels (incurred when the animal is dragged or propelled along the ground), and broken spines. In addition, an animal can also sustain broken limbs and internal injuries which require immediate attention. *18. Miscellaneous injuries* - These include hedgehogs becoming covered in engine oil etc. *19. Eye infection* - This is indicated by the presence of discharge from the eye or eye socket, as an eye infection can often cause the eye to burst with the loss of the eye.

The presence of helminths, nematodes and protozoans in the gastrointestinal tract was determined by microscopic examination of simple faecal smear samples. In addition, overburdening by the above parasites and specific bacteria produces characteristic changes in the gross morphology and texture of the faeces (Sykes & Durrant 1995, Bunnell 2001b). Detection of large numbers (accepting that this is a relative term and subject to a margin of error) of specific parasites, accompanied by characteristic changes in gross morphology and texture of the faeces, resulted in administration of the relevant medication. Re-examination of faecal smears, within 24 - 48 hours of the hedgehog receiving medication, showed a fall in number of the relevant parasite(s), a subsequent return to normal gross morphology and texture of the faeces, and the return of normal eating habits.

Age and sex determination

For ease of identification, hedgehogs were categorised according to weight. Hedgehogs weighing under 250 g on arrival were considered to be nestlings as they needed extra care and generally a diet consisting partially of a milk substitute for puppies (in this case Esbilac®), in order to gain weight at a satisfactory rate. Nestlings, ordinarily, would have still been receiving care from their mother. Animals weighing between 250 and 450 g were classed as juveniles, while any over 450 g were classed as adults. Data collected in this study showed that hedgehogs born in spring or summer easily achieve weights of 650-900 g by autumn in the same year. The sex of all animals was also determined on arrival, enabling determination of sex ratios.

Arrival of all age categories of hedgehogs at the RSPCA, and later at the sanctuary, was influenced by factors such as public awareness and localised extensive flooding in York in November 2000.

Results

Seasonal variation

Hedgehogs arrived at the sanctuary for treatment between May and January (figure 1). Adults ar-

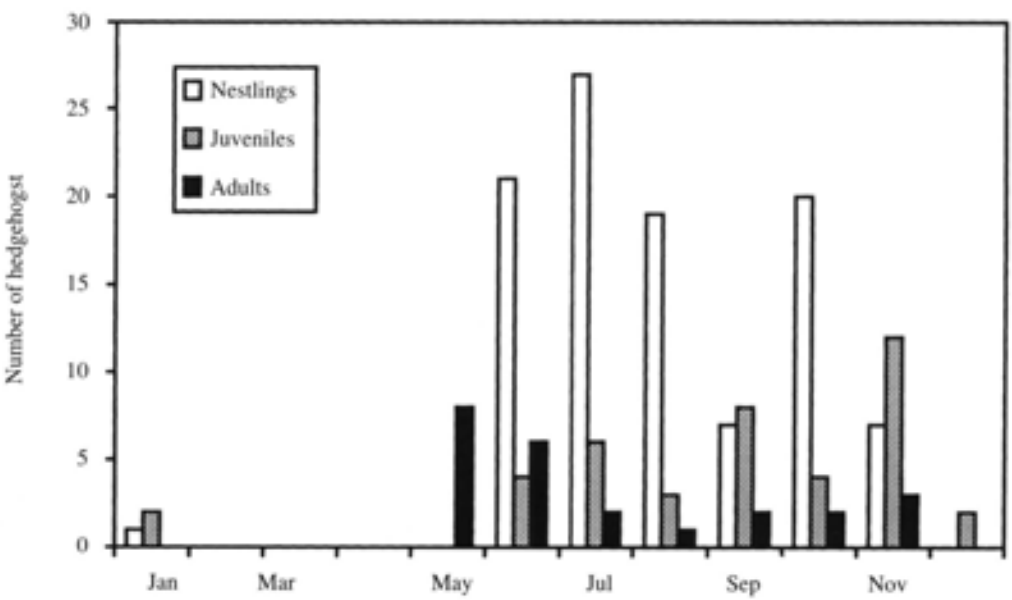

Figure 1. The number of nestling, juvenile and adult hedgehogs arriving for treatment during 1998, 1999 and 2000.

Table 1. Numbers of nestlings (<250 g), juveniles (250-450 g) and adults (>450 g) presenting for treatment 1998-2000.

Age category	Total (*n*)	Females (*n*)	Males (*n*)	Sex ratio (m:f)
Nestlings	102	41	61	1.5:1
Juveniles	42	20	22	1.1:1
Adults	24	9	15	1.7:1

rived mostly in May and June, while the number of juveniles fluctuated between June and January. Nestlings appeared between June and November, peaking twice in July and October.

Age structure and sex ratio

The greatest number of displaced hedgehogs arriving during a three-year period (1998-2000), were nestlings (n=102) which displayed a male-biased sex ratio of 1.5:1 (m:f) (χ^2=3.921, 1 df, P<0.05) (table 1). Examination of 10 individual litters (32 young in total), with a minimum of three siblings in each, showed variable sex ratios between litters, but an overall male-biased sex ratio of 1.5:1 (m:f). Juveniles and adults displayed a sex ratio of 1.1:1 (m:f) (χ^2=0.095, 1 df, ns), and 1.7:1 (m:f) (χ^2=1.50, 1 df, ns), respectively. Therefore, nestlings deviate significantly from a 1:1 ratio, while juveniles and adults do not. However, as there is no heterogeneity in the data (χ^2=0.849, 2 df, ns), pooling across the age categories gives 1.4:1 (m:f). This is significantly different from 1:1 (χ^2=4.667, 1 df, P<0.05).

It can be concluded therefore, that the sex ratio is significantly biased towards males, and that the degree of bias is not significantly different between nestlings, juveniles and adults. This suggests equal mortality rates in the two sexes.

Incidence of disease and injury

Nestlings, juveniles and adults were affected by a variety of ailments or injuries (table 2). Malnutrition was the major ailment, 55% of these being nestlings. Of the 15% affected by dehydration, the majority were again nestlings. Hypothermia was seen mainly in nestlings and juveniles, and breathing difficulties mainly in adults. Puncture wounds were mostly accompanied by abscesses and equally distributed across the age groups.

Myiasis was only observed in three nestlings (2% of the total). Ticks were virtually absent in nestlings, being mainly prevalent in juveniles. The majority of cases of ringworm and sarcoptic mange were found in nestlings (table 2), while demodectic mange only appeared in 1% of all animals. The nematode *Crenosoma striatum* occurred more often than *Capillaria* spp. and the cestode *Hymenolepis erinacei*, with the latter two mainly infesting juveniles. The protozoan *Isospora* spp. also appeared mainly in juveniles. *Escherichia coli* was only detected in 1% of all animals.

Only six animals arrived with road traffic injuries (4%), while two individuals arrived with an eye infection. Two animals (1%) sustained a broken leg, and miscellaneous injuries including contamination with engine oil were seen in 4% of all arrivals.

Survival rate

Of the nestlings, 74% survived to release status, compared with 55% of juveniles, and 58% of adults (table 3). Then the data were further analysed to determine whether mortality is the same in males and females in the three age categories considered separately. There was no significant difference (P>0.05) between survival rate of females and males in nestlings (χ^2=0.925, 1 df, ns), juveniles (χ^2=0.423, 1 df, ns) or adults (Fisher's exact test, ns). It can be concluded that there is no evidence for differential survival be-

Table 2. The incidence of disease and injury in 168 hedgehogs treated during 1998-2000.

Ailment/injury	Nestling (*n*)	Juvenile (*n*)	Adult (*n*)	Total (*n*)	Total (%)
Malnourished	25	10	10	45	27
Dehydrated	13	8	4	25	15
Hypothermia	6	5	1	13	8
Breathing difficulties	2	4	7	13	8
Puncture wounds	3	2	3	8	5
Abscesses	4	1	4	9	5
Myiasis	3	0	0	3	2
Ticks *Ixodes hexagonus*	1	15	8	24	14
Ringworm	6	1	0	7	4
Sarcoptic mange	6	2	2	10	6
Demodectic mange	0	1	1	2	1
Crenosoma striatum	4	7	7	18	11
Capillaria spp.	3	6	0	9	5
Hymenolepsis erinacei	2	5	2	9	5
Isospora spp.	2	5	0	7	4
Escherichia coli	1	1	0	2	1
Hit by car	0	2	4	6	4
Broken leg	1	1	0	2	1
Eye infection	1	1	0	2	1
Miscellaneous injuries	2	2	3	7	4

tween males and females within any of the three age categories. There was no difference in the proportions of males and females surviving in the three age categories (χ^2=1.054, 2 df, ns). Therefore, there is no evidence that the proportions of the sexes surviving differ by age. Pooling across the age categories gives a total of 50 females and 64 males surviving, meaning that 20 females and 34 males died in total. There were, however, no differences in survival rate between the sexes (χ^2=0.702, 1 df, ns). Given that there are no differences in survival rate between the sexes, the male and female data for each age category can be combined in order to compare the proportions of survivors versus deaths. For nestlings, survivors number 77, deaths 25; for juveniles, survivors number 23, deaths 19; and for adults, survivors number 14 and deaths 10. There were significant differences in survival (with the sexes combined) for the three age groups (χ^2=7.025, 2 df, P<0.05). As noted earlier, nestlings had a higher survival rate than either juveniles or adults.

The vast majority (94%) of the animals was still alive 48 hours after admission (total n=168) (figure 2). As all animals were released to the wild as soon as they were fully rehabilitated, the data in the figure includes these animals. Figure 2 also illustrates the time spent at the sanctuary prior to release. During the 20 days following their admission, 15 animals were released and 34 died, giving a survival rate of 84% (n=153). If those animals that were rehabilitated and released after 20 days are considered in the total, the survival rate becomes 80% (168-15=153 total remaining after release). Considering all age categories, 68% of animals arriving for treatment were rehabilitated and successfully returned to the wild (figure 2 and table 3).

Discussion

Sample composition

Nestlings comprised 61%, juveniles 25%, and adults 14% of the hedgehogs arriving over the three-year study period. The number of each age

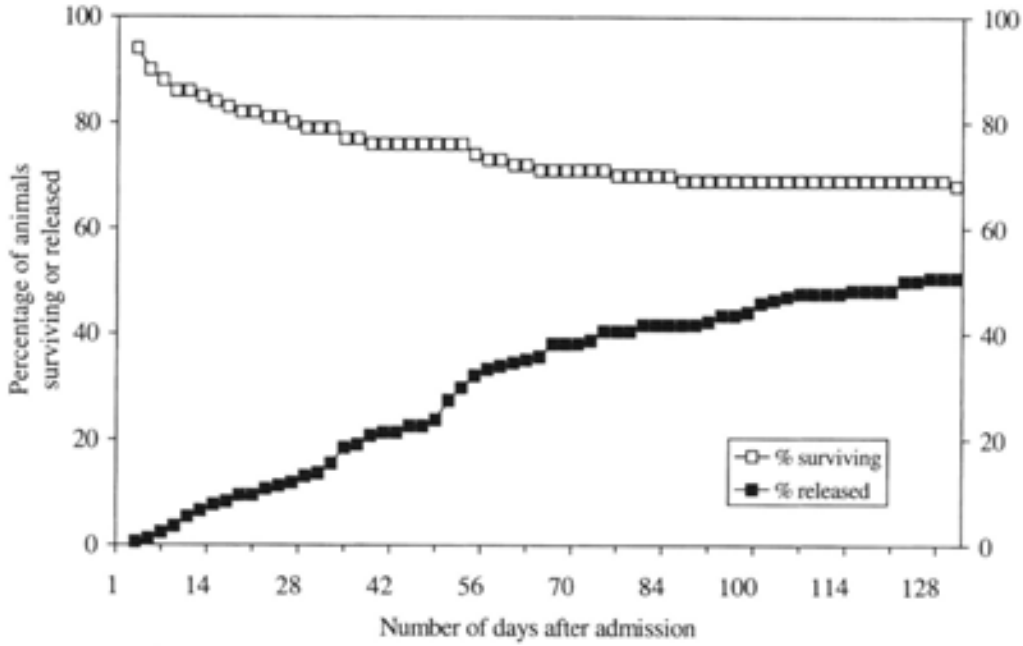

Figure 2. The percentage of hedgehogs (n=168) that survived a certain number of days and the percentage released during the same period.

category arriving throughout the year varied depending on the time of year. With the exception of a solitary animal in January, nestlings arrived between June and November, with two distinct peaks between June and August, and later in October, suggesting two breeding periods. Reeve (1994) comments that in Britain and northern Europe, late litters are common. Such litters may result from the loss of a first litter or a very mild autumn, the latter increasing food availability.

Juveniles arrived between June and January, the maximum number appearing in November, while adults arrived between May and November, the largest number being in May. The appearance of juveniles in larger numbers in the autumn corresponds to the known breeding season (Reeve 1994).

Across the age categories the sex ratio is significantly biased towards males (1.4:1). Reeve and Huijser (1999) also found an overall significant male-biased sex ratio of 1.2:1. In this study, when taking the age groups separately, the nestlings alone showed a significant male-biased sex ratio which suggests that more male hedgehogs are born than females.

Reasons for displacement

Increased awareness by the public has led to greater numbers of displaced hedgehogs being taken to wildlife rescue centres. Despite this some hedgehogs are still reported by some members of the public as appearing to be in good health when they are actually in need of care. The characteristic hyperactive behaviour of juveniles, during the day in late summer or early autumn, is almost certainly due to a heavy burden of intestinal parasites which causes intense discomfort leading to hyperactivity. This fact has been confirmed by the veterinary surgeon consulted during this study, and further verified by the fact that hyperactivity ceased within 24 hours of the animal being dosed with the relevant worming medication. Hyperactivity, in this instance, involves excessive movement during

Table 3. Number of animals and, between parentheses, percentage of total surviving to adulthood.

Age category	Number surviving to adulthood/ released	Females	Males
Nestlings	77 *(74)*	33 *(81)*	44 *(72)*
Juveniles	23 *(55)*	12 *(60)*	11 *(50)*
Adults	14 *(58)*	5 *(56)*	9 *(60)*

daylight hours with a total absence of sleep. The hedgehog moves incessantly, ignoring any food offered. This type of hyperactivity is not to be confused with food-searching behaviour, which inevitably ceases once food has been located and eaten.

The main reasons for displacement of nestlings are removal from the nest by domestic animals, accidental entrapment in farm buildings, and either death of the mother due to road or other accident, or entrapment or incapacitating injury preventing her return to the nest. In any instance when a mother fails to return to the nestlings within an indeterminate period of time, the nestlings tend to move away from the safety of the nest, presumably in search of food. I have observed this on many occasions, and indeed it is the main reason for notification by the public that a litter of hedgehog babies is in need of help. People who become aware that the mother has been absent for several days are reluctant to disturb the nest, tending to wait and see if the mother returns. This is generally followed by the appearance of the young outside the nest this making them vulnerable to predators and unable to survive prior to weaning. The nestlings are then taken into care.

Of the 102 nestlings displaced, 55 were not obviously suffering from any problem other than separation from their mother at too early a stage in their lives. In these cases, rehabilitation was relatively straightforward, requiring hand-feeding at frequent intervals, and the usual care regime used for orphaned mammals (Stocker 1987, Sykes & Durrant 1995).

As most road casualties will die, either immediately or very quickly, from their injuries, they were expected not to feature strongly as a reason for presentation at the RSPCA. This did indeed prove to be the case with only six out of 168 animals (4%) arriving as road casualties.

Combining the data across the age categories, the most common ailments were malnutrition, affecting 27% of animals, and dehydration (15%). Nestlings were particularly affected by malnutrition, forming 55% of those affected, and dehydration (52%). Puncture wounds were evident in 5% of animals, mainly being sustained from dog bites. Indeed, dog bites are a well-known cause of injury to hedgehogs resulting in 2.1% of hedgehog rescue centre deaths (Reeve & Huijser 1999). Myiasis was only seen in 2% of animals, all nestlings. In each instance the animal was also suffering from hypothermia.

Ticks *Ixodes hexagonus* were present in 14% of animals (63% of these being juveniles). This is substantially less than the figure quoted by Smith (1968) who reported that almost every wild hedgehog caught in Europe is infected with one or more ticks. Considering that the 14% of animals infested were all casualties requiring treatment, it might be expected that healthy wild hedgehogs would be less likely to carry ticks. This suggestion is supported by data collected during this study which indicate that the number of ticks infesting a casualty seems to be directly related to its state of health and prognosis for a return to full health. Those animals possessing more than 25 ticks mostly failed to survive. The greatest number of ticks recorded between 1998 and 2000 was 72. However, a hedgehog bearing 199 ticks was treated by the author in 1997, an excessive number for such a small mammal.

Ringworm was found in 4% of all animals, though mainly in nestlings. This figure does not

Hedgehog with grazed heels. These are 'scuff injuries' typically incurred as a result of being kicked, or hit by a car. *Photograph: Toni Bunnell.*

compare with that quoted by Morris and English (1969) where they report an average infection rate of about 20-25% in Britain, with the fungus being cultured from the linings of 23% of 60 nests examined. One possible reason for the discrepancy is that the presence of fungal spores on the spines or fur of a hedgehog, or within the nest material, does not necessarily mean that the animal will actually present symptoms of ringworm. Smith (1968) states that wild hedgehogs harbour a large number of potentially pathogenic organisms without showing visible signs of illness. Those animals that succumb to the disease generally have compromised immune systems due to an underlying illness.

Sarcoptic mange was observed in 6% of animals and was sometimes accompanied by ringworm. This is not surprising as the mites responsible for the mange could also help to spread the ringworm as the fungus has been isolated from their droppings (Reeve 1994). Demodectic mange was only observed in 2% of animals and as Reeve (1994) reports that the mite *Demodex erinacei* commonly inhabits the hair follicles of hedgehogs, this would suggest that it is mainly asymptomatic.

The nematode *Crenosoma striatum* was the parasite most commonly noted to be present in excessive numbers, with an accompanying change in the gross morphology and texture of the faeces (11% of total) (Bunnell 2001b). Infections produced by this lungworm and that of *Capillaria* spp. (5% of total) are commonly fatal in hedgehogs (Reeve 1994) and typically produce consolidation of the lungs as revealed during post mortem. Robinson and Routh (1999) also comment that the morbidity associated with lungworm infection can be very high. Keymer et al. (1991) found nematodes, which they considered to be probably all *Crenosoma striatum,* to be the most important helminth pathogens in 10 casualties, attributing their presence to be largely responsible for the death by pneumonia of six of the animals.

The tapeworm *Hymenolepis erinacei* was present in excessive numbers to the point of producing changes in the faeces, coughing and weight loss, in 5% of all animals. This figure is similar to the 1.2% incidence of tapeworms reported by Reeve and Huijser (1999). Robinson and Routh (1999) state that infection with the tapeworm *Hymenolepis erinacei* is usually asymptomatic. *Escherichia coli* was noted in 1% of animals. The incidence of parasite and pathogen infestation was distributed equally over the sexes.

Broken limbs, thought to have been caused by dogs, were seen in two animals only (1%), while miscellaneous injuries caused by human-related activity were observed in 4% of all animals.

Survival

Considering all age categories, 68% of animals arriving for treatment were rehabilitated and successfully returned to the wild. Out of a total of 168 animals 94% were still alive 48 hours after admission. This compares favourably with survival rates at the Jersey and Den Haag hedgehog rescue centres, where only 45.7% of admissions survived for 48 hours (Reeve & Huijser 1999). Indeed, 80% of animals were still alive 20 days after admission, making the necessary adjustments for the 15 animals released during this time.

Nestlings displayed the highest survival rate at 74%, with juveniles and adults surviving at the almost equal rates of 55% and 58% respectively. Combining male and female data the difference in survival rate between the age groups was significant. Although more females tended to survive than males, this difference was not significant, indicating equal mortality rates for both sexes in all the age categories.

Recommendations

Animals that were successfully restored to good health were returned to selected sites in the wild. Survival of rehabilitated hedgehogs, after release to the wild, has been studied (Morris et al. 1993, Morris & Warwick 1994). These studies concluded that rehabilitated adult hedgehogs probably cope well with release. This is supported by my findings (Bunnell, unpublished data), whereby several marked, rehabilitated animals from my sanctuary have been observed many months after release, mostly close to the release site. Increased awareness by the public, in recognising that hedgehogs found out during the day generally require assistance, is helping to bring more animals to the attention of wildlife rescue centres. This, in turn, increases the number of animals that receive much-needed care and attention, are subsequently rehabilitated and returned to the wild. The action of wildlife centres throughout Britain is undoubtedly ensuring the return to the wild of thousands of hedgehogs that otherwise would have perished. It is hoped that, in some small but significant way, the balance that has been severely disturbed by human habitation and interference in the life of the British hedgehog, is addressed by the care provided by wildlife rescue centres.

It is recommended that public awareness be increased still further, in particular to alert people to check buildings, basement yards, etc. where hedgehogs could accidentally become trapped and subsequently starve. In addition, it would be of great value if all cattle grids, installed prior to the law insisting on a climb-out point for hedgehogs, were to be provided with a means of escape for any hedgehog casualties. The removal of traps altogether from the countryside would prove most beneficial for the hedgehog and eliminate a prolonged death from starvation. Increased diligence by householders, to prevent domestic animals from disturbing hedgehog nests, would also be most useful in attempting to reverse the decline of hedgehog populations.

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Samenvatting

Ziekten en verwondingen bij wilde egels (*Erinaceus europaeus*) in een opvangcentrum

Dit artikel beschrijft wat wilde egels mankeerden die door het publiek naar een egelopvangcentrum werden gebracht van de "Royal Society for the Prevention of Cruelty to Animals" (RSPCA) in York, Engeland. De meeste dieren (90%) werden door de auteur in haar egelopvangcentrum verzorgd. Het gaat om 168 egels over een periode van drie jaar (1998-2000). Van deze dieren was 61% pasgeboren, 25% juveniel en 14% adult.

Bij pasgeboren egels was sprake van een significant scheve geslachtsverhouding met naar verhouding veel mannen. Voor juveniele en adulte dieren kon geen significant verschil in geslachtsverhouding worden aangetoond. Zonder onderscheid naar leeftijdscategorie was de geslachtsverhouding ook significant scheef verdeeld met naar verhouding veel mannen. De mate van scheefheid verschilde niet tussen pasgeborenen, juvenielen en adulten, hetgeen gelijke sterfte voor beide sexen suggereert.

Voor alle leeftijdscategorieën tezamen waren de belangrijkste kwalen ondervoeding (27% van de egels) en uitdroging (15%). Teken *Ixodes hexagonus* werden op 14% van de dieren aangetroffen, ringworm bij 4% en schurft bij 6%. De meest voorkomende parasiet was de nematode *Crenosoma striatum* (11% van het totaal). Verkeersslachtoffers vormden 4% van het totaal, en overige verwondingen, waaronder het in aanraking komen met motorolie, 4%.

Pasgeboren egels werden vooral binnengebracht als gevolg van verstoring van het nest, bijtwonden van huisdieren, langdurige afwezigheid van de moeder, en het per ongeluk opgesloten raken in, of in de buurt van, gebouwen.

De overleving van alle leeftijdscategorieën was 48 uur na opname 94%, en na 20 dagen was dit 84%. Van de pasgeboren dieren overleefde 74%, welke weer in het wild werden uitgezet. Voor de juvenielen en adulten was dit respectievelijk 55 en 58%.

De mens lijkt een belangrijke rol te spelen in het aantal verwondingen binnen alle leeftijdscategorieën en in het voortijdig gescheiden raken van pasgeborenen en hun moeder. Gedurende een periode van drie jaar werden steeds meer hulpbehoevende dieren naar het egelopvangcentrum in York gebracht (RSPCA). Dit benadrukt de noodzaak voor het nemen van maatregelen die het voortbestaan van egelpopulaties ten goede komen en een verdere achteruitgang in aantal voorkomen.

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The sex ratio of the red fox (*Vulpes vulpes*); an adaptive selection?

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Abstract: The data presented here support for the red fox a strictly mendelian determination of sex. The sex ratio of 288 embryos of 50 vixens handed in for rabies diagnosis in Bavaria, Germany, did not differ significantly from unity. However, during many field studies a skewed sex ratio in favour of male cubs has been observed. Hence, the observed shift to a male biased sex ratio occurred not in utero but post partum. Data from captive fox litters (n=162) indicated that the sex-specific cub mortality occurred during the first week after birth. Most probably, because male cubs had a competitive advantage over female litter mates, as a result of a higher body weight at birth. Male embryos were, on average, 4.1% heavier than female embryos. The selective pressure for a male biased sex ratio of fox cubs can be explained by the sex specific dispersal behaviour of foxes. Female foxes often stay in the vicinity of their natal grounds while males leave these areas. Also, dispersal distance of male foxes is, on average, higher than that of females. The higher mortality rate of males, associated with dispersal, would cancel the biased sex ratio, resulting in an operational sex ratio close to unity.

Key words: red fox, *Vulpes vulpes*, embryo, sex ratio.

Introduction

An important aspect of the life history of an animal population is the sex allocation and sex ratio. Fisher (1930) wrote that in a random-mating population, the only evolutionary stable sex ratio would be 1:1. Since this publication, sex ratio is an ongoing subject of interest, especially concerning the evolutionary and behavioural ecological aspects and consequences (e.g. Kolman 1960, Verner 1965, Clutton-Brock & Iason 1986). Several hypotheses of adaptive control of the sex ratio have been put forward, for example the Trivers-Willard hypothesis (Trivers & Willard 1973), the local resource competition model (Clark 1978) and the local resource enhancement model (Gowaty & Lennartz 1985).

The sex ratio of the red fox (*Vulpes vulpes*) has also been discussed by many authors. In most samples a recurrent and significant male bias was observed (Lloyd et al. 1976, Stubbe 1980, Stubbe 1982, Goretzki & Paustian 1982, Lindström 1982, Kappeler 1985, Ansorge 1991). Is this skewed sex ratio of the red fox under selective pressure? For example, Moehlman (1989) predicts a female biased adult sex ratio for foxes. However, there is little empirical evidence to support this or any other hypothesis in foxes. An important limitation is that the obtained sex ratios are mostly based on samples of foxes killed or found dead. These samples do not necessarily represent the sex structure of the living fox population, due to possible differential mortality of both sexes (Kappeler 1985). Even samples of foxes caught alive could be biased through sex-dependent behaviour that facilitate the capture of one sex over the other (Lindström 1982). Data concerning the adult fox sex ratio of the living fox population are unfortunately not available. However, it seems that an adjustment of the sex ratio in red fox cubs occurs at a very early stage. The sex ratio of cubs is biased towards males, although the embryonic sex ratio does not differ from unity (Lloyd et al. 1976, Stubbe 1980). In this paper, the sex ratio of the red fox before and

Table 1. Embryonic sex distribution of 50 fox litters from Bavaria, Germany.

		Number of female embryos				
		1	2	3	4	5
Number of male embryos	**0**	–	1	–	–	–
	1	–	3	2	2	1
	2	1	4	3	4	–
	3	2	4	1	2	2
	4	3	2	2	4	–
	5	–	1	–	1	–
	6	1	2	1	–	–
	7	–	–	–	–	–
	8	–	1	–	–	–

shortly after parturition is discussed. Subsequently, a hypothesis is postulated that explains the sex ratio adjustment in the data sets described.

Material and methods

Data on the embryonic sex ratio were obtained from vixens handed in for rabies diagnosis in Bavaria, Germany, from February till April during the years 1988-1991. Of all vixens handed in during this period the reproductive tract was examined. In case of embryos present, the sex and weight of all embryos was recorded. If weight or sex of an embryo could not be determined, the whole litter was omitted from further analysis. The mean embryonic body weight of the litters was used as indicator of age (Lloyd 1980: figure 17, page 107).

Data on the sex composition of fox litters (n=162) from a protected environment were obtained from the breeding records of captive silver foxes. Due to extreme susceptibility of the vixens to disturbance, which could lead to the complete loss of the litter (Trut 1996), the sex composition of the litters was checked for the first time, approximately, one week post partum.

Results

No significant bias was found for the embryonic sex ratio in the Bavarian sample of 50 complete litters; 151 male and 137 female embryos (Chi²-test, χ^2=0.68, df=1, P>0.05) (table 1). Furthermore, no significant correlation was observed between sex distribution and litter size (r= –0.19). Also, no significant yearly differences in the embryonic sex ratio were found during 1988-1991 (Chi²-test) (table 2). No shift in the embryonic sex ratio in favour of males has been observed during gestation (table 3). The selection of these three weight-groups was done arbitrarily. Male embryos were on average 4.1% heavier than their female embryonic litter mates. In the pooled data set, male embryos were significantly

Table 2. Sex ratio of embryos between 1988 and 1991 (Chi²-test, n.s.: not significantly different from 1:1, P>0.05)

Year	Number of litters	Male (M)	Female (F)	M/F	P
1988	22	77	63	1.22	n.s.
1989	7	17	20	0.85	n.s.
1990	8	23	19	1.21	n.s.
1991	13	34	35	0.97	n.s.
Total	50	151	137	1.10	n.s.

Table 3. Sex ratio of embryos during different stages of gestation (weight: mean body body weight of embryonic litter; Chi²-test, n.s.: not significantly different from 1:1, $P>0.05$).

Weight (g)	Number of embryos	Males (M)	Females (F)	M/F	*P*
≤ 40	127	66	61	1.08	n.s.
41-80	101	51	50	1.02	n.s.
> 80	60	34	26	1.31	n.s.

more often heavier than their female litter mates (n=194) than vice versa (n=148; Chi²-test, χ^2=6.19, df=1, $P<0.05$).

The sex ratio of cubs, approximately one week old and born in captivity, differed significantly from unity (Chi²-test, χ^2=9.72, df=1, $P<0.01$) (table 4). During the following nine weeks almost no mortality was observed; of the 405 male and 321 female cubs only 8 male and 2 female cubs died.

Discussion

The observed embryonic sex ratio in this and other studies indicate that it does not differ from the evolutionary stable sex ratio of 1:1 (table 5). However, in most field studies a (significant) surplus of male cubs is found (table 6). Goretzki et al. (1997) suggested that the sample method used by catching young foxes alive at the den site was probably sex-selective. However, a male surplus was also found when complete litters were considered. Storm et al. (1976) suggested that male cubs probably had a better survival rate than their female litter mates during late gestation or in the first months after birth. The former can be ruled out, because in the data presented here no shift in the embryonic sex ratio in favour of males has been observed during gestation. However, it was observed that male embryos were, on average, heavier than their female embryonic litter mates. Lloyd (1980) also examined 44 embryonic litters in which male embryos were, on average, 11.4% heavier. He suspected, that male cubs had a higher survival rate due to their higher body weight at birth; the heavier male cubs could have an advantage in sibling competition over their female litter mates. However, Bakken (1998) did not find any weight differences between sexes at birth in captive-bred foxes.

One could argue that while male embryos have faster growth rates and, therefore, increased nutritional requirements, they are more susceptible to nutritional stress during gestation than their female litter mates. However, the extraction of nutrients by the offspring is higher during lactation than during gestation (Oftedal & Gittleman 1989). The energy reserves of the vixens are most of the time sufficient for the development of the embryos, but are rapidly depleted during lactation, resulting in intensified sibling compe-

Table 4. Sex distribution of cubs aged approximately one week old from 162 fox litters bred and raised in captivity.

		Number of female cubs						
		0	1	2	3	4	5	6
Number of male cubs	**0**	–	2	4	2	1	–	3
	1	3	7	5	5	2	2	–
	2	6	16	11	9	4	2	1
	3	3	7	11	14	6	–	–
	4	5	9	5	4	–	–	–
	5	3	6	–	–	–	–	–
	6	2	1	–	–	–	–	–

Table 5. The embryonic sex ratio of foxes (Chi^2-test, n.s.: not significantly different from 1:1, $P>0.05$).

Study area	Sex ratio	*n*	*P*	Source
Wales	1.06	222	n.s.	Lloyd et al. 1976
Switzerland	0.96	239	n.s.	Lloyd et al. 1976
Gera, Germany	1.03	177	n.s.	Stubbe 1980
Dresden, Germany	0.95	142	n.s.	Stubbe 1980
Hakel, Germany	1.43	68	n.s.	Stubbe 1980
Illinois, USA	1.04	198	n.s.	Storm et al. 1976

tition and, consequently, in increased female cub mortality. Of course sibling competition is not limited to nutrient intake only, e.g. maternally transferred immunity through the colostrum will take place directly after birth. Hence, the quantity of transferred maternal antibodies depend on the quantity and quality of colostrum ingested by the cubs (Chappuis 1998). Furthermore, lower birth-weight may influence the level of maternally acquired immunity (Wesumperuma et al. 1999), resulting in a higher susceptibility to infectious diseases.

Kappeler (1985) also explained the observed male surplus of fox cubs as a result of sex-specific cub mortality. Unfortunately, no field data are available on the sex composition of fox litters during the first month post partum. However, analysing the data of fox cubs bred and raised in captivity confirms the field data. The sex ratio of these approximately one-week old cubs already differed significantly from the sex ratio 1:1 (table 4). While almost no mortality was observed in the following weeks, the sex specific cub mortality in foxes occurs in the first week after birth. Unfortunately, the mother animal will eat all dead cubs during the early post partum phase, so these losses can not be estimated by observations. Also Trut (1996) found an excess of male cubs in captive-bred foxes.

The sex ratio of this litter is probably already different from the sex ratio at the time of birth. *Photograph: Udo Stubeling.*

Table 6. Sex ratio of fox cubs (Chi^2-test, n.s.: not significantly different from 1:1, $P>0.05$).

Study area	Sex ratio M/F	*n*	*P*	Source
Gera, Germany	0.94	877	n.s.	Stubbe 1980
Hakel, Germany	1.20	249	n.s.	Stubbe 1980
Germany	1.36	248	<0.05	Goretzki et al. 1992
Rügen, Germany	1.13	862*	n.s.	Goretzki et al. 1997
Netherlands	1.28	98*	n.s.	Lloyd et al. 1976
Denmark	1.17	455*	n.s.	Lloyd et al. 1976
Denmark	1.22	841	<0.01	Lloyd et al. 1976
Switzerland	1.28	568	<0.01	Lloyd et al. 1976
Switzerland	1.27	348*	<0.05	Lloyd et al. 1976
Noord-Holland, Netherladns	1.44	132*	<0.05	Mulder 1988
England	1.37	199*	<0.05	Page 1981

*sample of cubs caught alive at den site

The question remains; is there an adaptive selection for the observed sex specific cub mortality, or is it mere a non-adaptive consequence of sexual size dimorphism? So far, no direct evidence of possible parental control of progeny sex ratio of the red fox has been reported. In other animal species, adults may adjust the sex ratio of their offspring to existing social and demographic parameters by means of selective neglect, infanticide or siblicide (Frank 1996). It is also assumed that hormonal levels at conception affects the sex ratio; high levels of estrogens and testosterone correlated with an excess of males (e.g. induced by social rank of mother animal or various other stress factors) (James 1992, Trut 1996).

The adaptive significance of a male biased sex ratio of fox cubs may possibly be found in sex specific dispersal behaviour. The proportion of juvenile males that disperse is higher than that of females. Also the average dispersal distance is higher for males (Storm et al. 1976, Englund 1980, Page 1981, Harris & Trewhella 1988, Mulder 1988, Vos 1993). Daughters settle often within or in the neighbourhood of the home-ranges of their parents (Macdonald 1980). Dispersal in unfamiliar territories bring certain risks along, like competitors and unknown accessibility of food and shelter (Weser 1996). Hence, the mortality rate of dispersers will be higher than that for resident animals. Harris & Trewhella (1988) found that for male foxes, life expectancy was significantly lower in dispersing animals compared to non-dispersing animals. Therefore, the higher mortality rates of the male sub-adults, as a result of the higher dispersal activity, will diminish the skewed sex ratio as observed among the fox cubs. The operational sex ratio, the average ratio of fertile females to sexually active males at any given time, may possibly be close to unity in the adult fox population. As mentioned before, the evolutionary stable sex ratio in a random mating population is 1:1. When the adult sex ratio has moved away from parity, parents could (temporarily) increase their fitness by producing more offspring of the rarer sex. However, to show that the variation in sex ratio is an adaptive response, it is necessary to demonstrate that parents increase their fitness by biasing the sex ratio (Clutton-Brock & Albon 1982). Unfortunately, the data available are not sufficient for such an analysis.

Hence, the here presented explanation of the observed trends in the sex ratio of foxes must be treated with caution, as this biological trait may be subject to different selective pressures. However, it can be concluded from the obtained results, that the sex allocation of the red fox is simply a mechanical consequence of meiosis, but the sex ratio of the living fox population is susceptible for selective pressures at a very early stage of life.

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Male cubs are usually heavier than their female litter mates. *Photograph: Ad Vos.*

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Samenvatting

Geslachtsverhouding van de vos (*Vulpes vulpes*); een mogelijke adaptieve selectie?

De geslachtsverhouding van wildlevende dieren en de mechanismen die deze parameter reguleren is een steeds terugkerend onderwerp. Ook de geslachtsverhouding bij vossen (*Vulpes vulpes*) en de mogelijke adaptieve betekenis is al vele malen besproken. Helaas worden deze theoretische beschouwingen niet door veldgegevens onderbouwd. Steekproeven zijn vaak gebaseerd op gedode en/of dood gevonden dieren. Deze geven echter niet de situatie in de levende vossenpopulatie weer, onder meer als gevolg van geslachtsafhankelijke mortaliteit. In dit artikel worden de geslachtsverhoudingen van vossen en verschuivingen van deze parameter vóór en kort ná de ge-

boorte besproken. Gegevens van 288 embryo's uit 50 worpen zijn gebruikt om de prenatale geslachtsverhouding te bepalen. De drachtige moertjes waren afkomstig uit Beieren, Duitsland, en waren voor rabies onderzoek ingezonden (1988-1991). Verder waren gegevens beschikbaar van 162 worpen van vossen die in gevangenschap waren opgegroeid (1994-1999). De embryonale geslachtsverhouding van vossen week niet significant af van de geslachtsverhouding 1:1. Maar tijdens veldonderzoekingen wordt meestal een overschot aan mannelijke welpen vastgesteld. Vrouwelijke dieren hebben schijnbaar een hoger sterftecijfer dan hun broertjes direct na de geboorte. Waarschijnlijk is dit een gevolg van het hogere geboortegewicht van de mannelijke dieren. Dit verschil in gewicht is al in de embryonale periode aantoonbaar. Hierdoor hebben de mannelijke dieren tijdens lactatie en voedselverstrekking een voordeel (nestconcurrentie) ten opzichte van hun zusjes. Bij welpen (n=726) geboren en opgegroeid in gevangenschap werd na de eerste levensweek al een overschot aan mannelijke welpen vastgesteld. Wat kan nu de biologische betekenis zijn van dit verschijnsel? Of is het niet meer dan een non-adaptieve consequentie van sexueel dimorfisme? Bij vossen is tot nu toe nog geen direct bewijs geleverd dat ouders actief invloed uitoefenen op de geslachtsverhouding van hun nakomelingen. Een mogelijke verklaring is te vinden in het dispersie gedrag van jonge vossen; het zijn voornamelijk de mannelijke dieren die in het najaar wegtrekken, ook de gemiddelde dispersie-afstand van de mannelijke dieren is hoger dan die van de vrouwelijke dieren. Het wegtrekken vanuit de bekende geboortegrond naar onbekende terreinen is niet zonder risico en gaat gepaard met een verhoogde sterftekans. Hierdoor zal het overschot van mannelijke dieren geheel of gedeeltelijk worden opgeheven, zodat de operationele geslachtsverhouding rond het stabiele evenwicht 1:1 ligt.

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Mammals benefit from reduced ditch clearing frequency in an agricultural landscape

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Abstract: We investigated the effect of two types of ditch management on the species richness and abundance of mammals at two sites in an agricultural landscape in Flevoland, The Netherlands. The first management type involved mowing both ditch slopes twice per year with a flailmower and leaving the biomass on the spot (control sections; *n*=3 at Tureluurweg site, *n*=6 at Waiboerhoeve site). Here the vegetation was short throughout winter. The second management type involved mowing the two ditch slopes in alternate years and removing the biomass (reed sections; *n*=3 at Tureluurweg, *n*=6 at Waiboerhoeve). This resulted in reed cover (*Phragmites australis*) at one ditch side in winter. Species richness and abundance of mammals were investigated through sightings and trapping along the ditches and in the adjacent production grasslands. Species richness and overall abundance were highest in the reed sections. Common voles (*Microtus arvalis*), harvest mice (*Micromys minutus*) and common shrews (*Sorex araneus*) occurred mostly in the ditches, especially in the reed sections. Only common voles were also frequently found in the grasslands but here their density was lower than along the ditches. A male-biased sex ratio in the production grasslands also indicated that these were a poor habitat for this species. Although reduced clearing frequency of the ditches benefited the common vole, outbreaks seem unlikely as long as the grasslands continue to be used intensively. Low management costs and possible application of reed biomass on arable land could also ensure a rapid integration of nature-oriented ditch management into existing farming systems.

Keywords: agriculture, cover, ditch, grasslands, management costs, *Microtus arvalis*, nature, *Phragmites australis*, sex ratio, mammals.

Introduction

In western Europe, the scale and intensity of agricultural practice has increased considerably over the past century. Field sizes were enlarged to benefit efficiency (e.g. Dijkstra et al. 1997) and a more intensive management resulted in increased agricultural production. The intensification was particularly strong from the 1950s onwards and was mostly obtained through a high input of nutrients, lowering of the water table, mechanisation and the use of pesticides (e.g. Potter 1997, van der Molen et al. 1998, Jongbloed et al. 1999, Novotny 1999, Tilman 1999, Hooda et al. 2000). Since agriculture is the dominant form of land use in The Netherlands (70% of the land surface, LEI-DLO 1999), the increase in scale and intensity of agricultural practice has had considerable consequences for many wild plant and animal species. Habitat was lost through the removal of hedgerows, ditches and other small landscape elements that separated the fields (e.g.

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Dijkstra et al. 1997, Macdonald & Johnson 2000). Much of the remaining habitat decreased in quality through e.g. eutrophication, use of pesticides, low water tables, and timing and higher frequency of mowing, grazing or harvesting. The decrease in habitat quality applies to certain plant species (e.g. van Strien et al. 1988, van Strien et al. 1989, Freemark & Boutin 1995, Klein & Verbeek 2000) as well as invertebrates (e.g. Davis et al. 1991, Freemark & Boutin 1995), birds (e.g. Kruk 1993, Freemark & Boutin 1995, Fuller et al. 1995, Green & Rayment 1996, Beintema et al. 1997, van Noorden 1999) and mammals (e.g. Tapper & Barnes 1986, Freemark & Boutin 1995, Siriwardena et al. 2000).

As response to the decline of many plant and animal species in The Netherlands environmental policy is now not only focussed on the realisation of a National Ecological Network (LNV 1990) but also on an increase of natural values in agricultural areas (LNV 2000). In The Netherlands a new government program was introduced in 2000 that rewards farmers and other private landowners for the presence and abundance of certain species and landscape elements on their lands (LASER 2000a, LASER 2000b). Unfortunately this system is only valid in designated areas, more farmers have applied than anticipated and funds are insufficient. Thus, to enhance natural values on agricultural lands on a much larger scale and in the short term, inexpensive measures that can be integrated into existing farming systems are required.

In an agricultural landscape the lands that are not used for production are often limited to the premises surrounding farm buildings and the landscape elements that separate parcels (e.g. hedgerows, ditches). These landscape elements can nevertheless contribute considerably to the presence of wild plants and animals in agricultural areas (e.g. Terwan 1992, Fry & Sarlöv-Herlin 1997, Ovenden et al. 1998, Oosterveld & Guldemond 1999). In this study we focus on increasing the ecological value of such linear landscape elements at low cost. We studied the effect of two types of ditch management on the species richness and abundance of mammals. The first management type involved a standard mowing and ditch clearing scheme whereas the second involved a less frequent mowing scheme and, as a consequence, the presence of cover for animals in winter (see methods). We expected the cover to result in a better habitat for mammals in general, including the common vole (*Microtus arvalis*).

Farmers generally associate the common vole with damage to crops and grasslands (e.g. van Wijngaarden 1957a, Lange et al. 1994, Balmelli et al. 1999). In some parts of The Netherlands vole outbreaks occurred regularly until the 1950s (van Wijngaarden 1957a, van Wijngaarden 1957b, Lange et al. 1994) and farmers are reluctant to improve the habitat for this species. To investigate whether this reluctance is justified, we paid special attention to the common vole. In one of our study areas we not only determined their relative population densities along the ditches, but also in the adjacent production grasslands.

Agriculture has changed much since vole outbreaks were common and current grassland management does not seem very favourable to the common vole. Most grasslands now have a monoculture of perennial rye-grass (*Lolium perenne*), an intensive mowing and grazing regime that keeps the vegetation short across the whole parcel, a high input of nutrients including manure injection, re-seeding, rolling and harrowing. We expect these conditions and activities to have a negative influence on common vole populations and keep them from reaching high densities in production grasslands, regardless of the type of ditch management (see Van Wijngaarden 1957b, Ogilvie & Furman 1959, Birney et al. 1976, Cornelissen et al. 1997, review in La Haye 1999, Beemster & Vulink 2001). Apart from their relative population densities we were also interested in the sex ratio and weight of the common voles as additional indicators of habitat quality. We expected the ditches, particularly reed ditches, to be high quality habitat compared to the adjacent production grasslands. In contrast to males, female common voles may share the same home range (e.g. Boyce & Boyce 1988, van Apeldoorn 1989) and high vole densities are associated with a female-

biased sex ratio (see review in Van Wijngaarden 1960). Therefore we expected relatively high numbers of females along the ditches. We also expected relatively high body weights of both females and males along the ditches compared to the adjacent grasslands, as weight is an indicator of condition.

Our hypotheses are that a less frequent mowing scheme of the ditch vegetation results in an increase of the species richness and abundance of mammals along the ditches and that common vole density does not increase in the intensively used grasslands adjacent to these ditches. If this is confirmed it may remove one of the objections a farmer may have to using a less frequent mowing scheme.

Methods

Study sites

The study was conducted on two locations in Flevoland, The Netherlands. The first part took

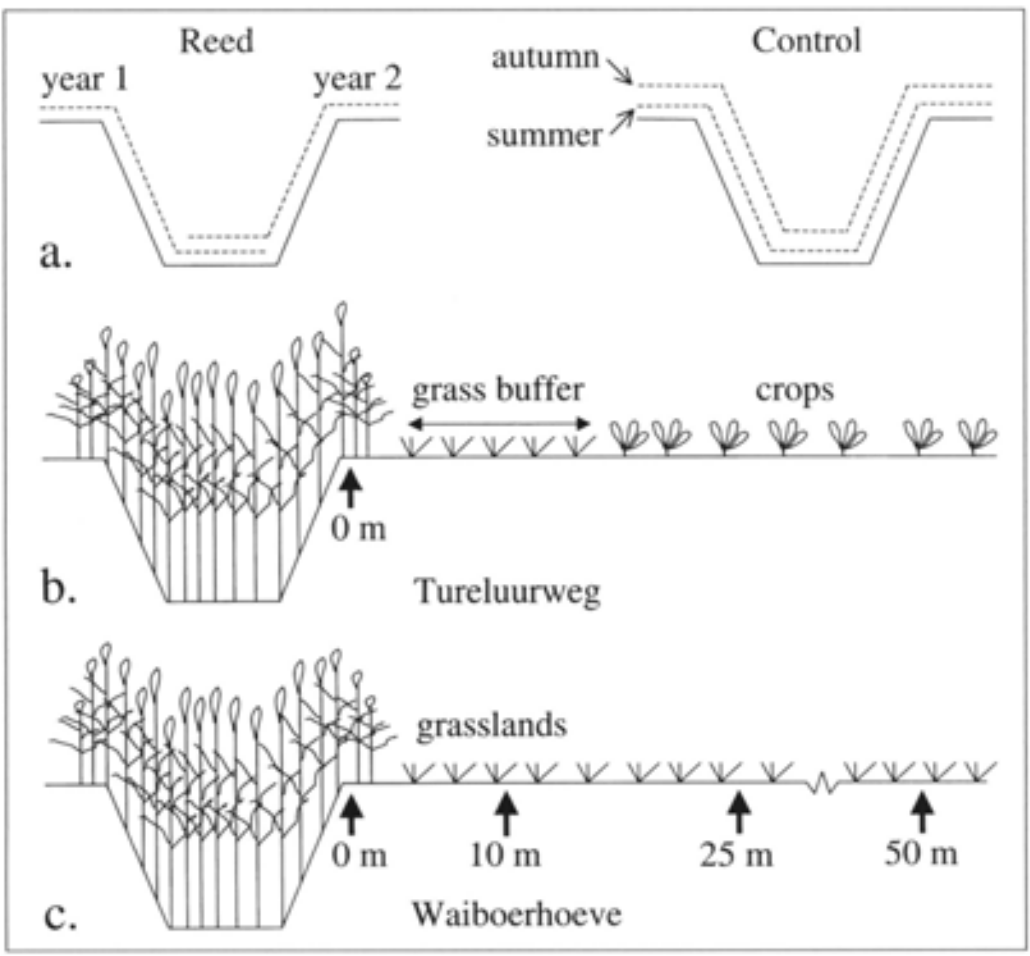

Figure 1. Mowing scheme (-----) of the reed and control sections (a), and the location of the trapping lines at the Tureluurweg (b; 0 m only) and Waiboerhoeve sites (c; 0, 10, 25 and 50 m). Note: the grass buffer zone at the Tureluurweg site was 3 m wide and was only present along the reed sections, the crops grew right up to the ditches along the control sections.

Photo 1. The appearance of a reed section after autumn clearing at the Waiboerhoeve site in Flevoland, The Netherlands. *Photograph: Marcel Huijser.*

Photo 2. The appearance of a control section after autumn clearing at the Waiboerhoeve site in Flevoland, The Netherlands. *Photograph: Marcel Huijser.*

place between 1993 and 1995 along the road 'Tureluurweg' in Zuidelijk Flevoland (area surrounding 5°20´, 52°20´). The second part took place in 2000 on the experimental farm 'De Waiboerhoeve' in Oostelijk Flevoland (area surrounding 5°35´, 52°31´). For the exact boundaries of the study areas see Remmelzwaal & Voslamber (1996) and Meerburg (2001).

Tureluurweg site

At the time of the study, the Tureluurweg site (250 ha) was characterised by a large scale agricultural landscape. The clay soil (30% clay particles) was used to grow wheat, potatoes, sugar beets and peas. The fields (approximately 50 ha each) were separated by ditches that lay parallel at 450 m distance from each other. The ditches did not carry water year-round.

In the winter of 1992-1993, three ditches were divided into six sections of about 500 m length (two sections per ditch). In autumn, the vegetation in three sections (one per ditch) was cut and removed. However, only one slope and a 1 m wide zone adjacent to the slope were mowed at the same time. The opposite slope and a 1 m wide zone adjacent to that slope were mowed in the autumn of the following year (figure 1a). The bottom of a ditch was cleared each autumn to ensure sufficient drainage in winter. Thus uncut vegetation, mainly reed (*Phragmites australis*), was present on one side in winter. These sections are from now on referred to as 'reed sections' (see photo 1).

The reed sections had 3 m wide buffer zones adjacent to the 1 m strips (figure 1b). These 3 m wide zones were sown with red fescue (*Festuca rubra*), perennial rye-grass, smooth meadow-grass (*Poa pratensis*) and white clover (*Trifolium repens*) to allow for weed control through frequent mowing (5 times per year). Thus the edge of the crops next to the reed sections was 4 m from the ditch slope. The other three ditch sections ('control sections') were cut twice per year (summer and autumn) using a flailmower (figure 1a). Here the biomass was left on the spot, and the crops grew right up to the slope of the ditches. The vegetation on the slopes was short throughout winter (see photo 2).

In December 1992 a 0.5 ha woodland (72x72 m) was planted adjacent to each of the three reed sections. There was no grass buffer strip between the woodlands and the ditches. Furthermore a pond was dug in the centre of each of these woodlands. The ponds measured about 380 m^2 and had a minimum water depth of 1.5–2.0 m at the deepest point.

Waiboerhoeve site

The approximately 260 ha study area was also characterised by large scale agricultural lands on heavy clay soil (38% clay particles). The area

consisted mostly of grasslands, but some parcels were used to grow maize or potatoes. The parcels (each about 30 ha) were separated by parallel ditches roughly 300 m apart. The ditches did not carry water year-round and the vegetation in these ditches was dominated by reed.

In autumn 1999 six ditches were split into two sections (12 sections in total). Each section was about 500 m in length. One section per ditch continued to be mown with a flailmower twice a year (summer and autumn) and the biomass was left on the spot ('control sections') (figure 1a). This type of ditch management was typical for the region and similar to that of the control sections at the Tureluurweg site. The other sections were managed in the same way as the 'reed sections' at the Tureluurweg site (figure 1a). However, at the Waiboerhoeve site there was no additional buffer zone adjacent to the ditches (figure 1c), nor were there any wood-

Photo 3. The agricultural landscape surrounding the Waiboerhoeve site. The ditches that separate the parcels run from left to right. *Photograph: Research Institute for Animal Husbandry.*

lands or ponds. The six ditches that were used in this study lay adjacent to production grassland. The grasslands ran up to 1 m from the slope of a ditch and were mown or grazed by cattle or sheep.

Trapping and sampling schemes

Tureluurweg site

Between 1993 and 1995 small mammals were caught in snap traps along transect lines directly adjacent to the ditches (0 m distance, figure 1b). We placed 50 traps at 5 m intervals per section, which resulted in 245 m long trapping lines. We stayed about 200 m away from the small woodlands and ponds. We trapped in 1993 through 1995, three times per year (March, July and October). Each trapping session lasted three nights with one check per day. The traps were baited with carrot. We determined the species, and for common voles we also recorded the sex and weight of the captured individuals. Other observations of mammals were recorded while walking monitoring routes for insects (afternoon) or birds (early morning and afternoon) one time per month (November through February, afternoons only) or four times per month (March through October) (see Remmelzwaal & Voslamber 1996). These observations were added to those from the trapping lines to investigate species richness. We also recorded observations of mammals when not sampling a monitoring route, but these were ignored when we calculated species richness.

Waiboerhoeve site

In October 2000 we determined small mammal abundance directly along the ditches and in the adjacent grasslands. We placed Longworth live traps along 180 m trapping lines for each section. Each trapping line had 10 capture points (two traps per point) at 20 m intervals. Placing two traps at one capture point prevented territorial and easily captured species from occupying most of the traps (see Bergers 1997, Bergers & La Haye 2000).

Many studies use 10 m spacing between capture points. This distance is based on the average home range size of small mammal species that are relatively common, the estimation of absolute population densities in trapping grids, and tradition. We used greater distances between capture points since we sampled linear habitats that were about 500 m in length (ditch sections). Furthermore, we were only interested in relative population densities. Our 180 m long trapping lines also enabled us to have 160 m wide buffer zones at the end of each section which decreased the chance of possible edge effects. When we assume the home range of common voles to be circular in shape, the buffer zone was much wider than the average radius of their home range (males r=19.5-21.9 m; females r=9.8-11.3 m) (Lange et al. 1994). The buffer zone was also wider than recorded dispersal distances (100 m) for common voles (review in La Haye 1999).

The traps were baited with carrot and apple. To minimise shrew mortality we also put dried cat food in the traps. Hay was put in the traps to prevent the animals from cooling off. The traps were pre-baited for two or three days directly before the actual trapping which lasted two consecutive nights. The traps were checked twice a day, just after sunset and just after sunrise. We determined the species, and for common voles we also recorded sex and weight. We clipped the fur to distinguish between newly captured individuals and recaptures. This study was found to be in accordance with Dutch law and regulations on animal experiments.

The trapping lines were set at four different distances from the ditches: at 0, 10, 25 and 50 m (figure 1c). These distances were based on the size of the home range of common voles (see earlier). If the animals have the centre of their home range in the vegetation of the ditches the males may venture up to 22 m into the grassland. Common voles captured at greater distances are likely to have the centre of their home range in the grasslands rather than in the ditches. Captures at the 10 m trapping lines may include males and females that have the centre of their home range in the ditches and may therefore be influenced by the ditch management.

Table 1. Mammal species observed along the monitoring routes and trapping lines along the reed and control sections of ditches at the Tureluurweg and Waiboerhoeve site. [1] = only indirect evidence through e.g. tracks, faeces, nest or burrow. x = observed, – = not observed.

Species	Reed sections	Control sections
Tureluurweg (1993-1995)		
Common mole (*Talpa europaea*)	x	–
Common shrew (*Sorex araneus*)	x	x
Pygmy shrew (*Sorex minutus*)	x	–
Serotine bat (*Eptesicus serotinus*)	x	–
Noctule (*Nyctalus noctula*)	x	x
European hare (*Lepus europaeus*)	x	x
Rabbit (*Oryctolagus cuniculus*)	x	x
Common vole (*Microtus arvalis*)	x	x
Harvest mouse (*Micromys minutus*)	x	x
Wood mouse (*Apodemus sylvaticus*)	x	x
Norway rat (*Rattus norvegicus*)	x	x[1]
Weasel (*Mustela nivalis*)	x	x[1]
Stoat (*Mustela erminea*)	x	x[1]
Western polecat (*Mustela putorius*)	x	–
Red fox (*Vulpes vulpes*)	x[1]	x[1]
Roe deer (*Capreolus capreolus*)	x	x
Waiboerhoeve (2000)		
Common shrew (*Sorex araneus*)	x	x
Greater white-toothed shrew (*Crocidura russula*)	x	x
Bank vole (*Clethrionomys glareolus*)	x	–
Common vole (*Microtus arvalis*)	x	x
Harvest mouse (*Micromys minutus*)	x	x
Wood mouse (*Apodemus sylvaticus*)	x	–

The 0, 10, 25, and 50 m trapping lines were not sampled simultaneously, but in random order for each ditch (combination of a reed and control section). If we had sampled different distances at the same time, voles with the centre of their home range in the ditches may have been captured at the 0 m line before they would have had a chance of entering the traps at the 10 m line. However, while trapping on a certain line, we did pre-bait another line for efficiency purposes. Therefore only half of the traps (480 in total) were in operation at the same time.

When clipping the fur of the animals, the location of the mark was unique for each distance (0, 10, 25 and 50 m). This enabled us to determine at which distance to the ditch an individual was caught before.

Some of the ditches had a paved path that ran parallel to it. We did not sample at the path side of a ditch since a path may be a barrier to small mammals that avoid open areas.

The grasslands were divided into management units with different grazing and mowing regimes with no consistent differences between reed and control sections. To prevent cattle from disturbing the traps and its immediate surroundings, metal frames were placed over the capture points (see also La Haye 1999).

Sward height is an important habitat quality feature for common voles. Short grassland offers little cover for predators and is typically associated with relatively low vole densities (van Wijngaarden 1957b, Cornelissen et al. 1997, review in La Haye 1999, Beemster & Vulink 2001, E.S. Bakker, unpublished data). To check for consistent differences in sward height in the grasslands adjacent to reed and control sections we measured the height at 10 locations (capture points)

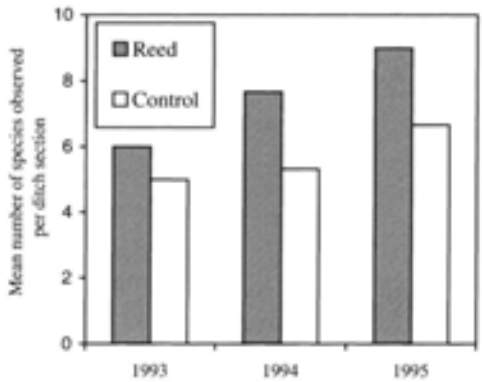

Figure 2. Species richness of mammals in the control (n=3) and reed sections (n=3) at the Tureluurweg site in 1993, 1994 and 1995. The species richness was expressed as the average number of mammal species recorded per ditch section.

per section. Sward height was measured by lowering a circular foam disk onto the sward and its height was read from a measuring stick in the centre of the disk. The sward height of the grasslands adjacent to reed sections was similar to that of the ones adjacent to control sections (ANOVA with block structure to correct for variation caused by differences between the ditches, 2-tailed, P=0.988). The average height along reed sections was 8.27 cm whereas it was 8.28 cm for those adjacent to control sections.

Apart from the captures on the trapping lines we also recorded incidental observations of mammals in the area.

Analyses

Tureluurweg site

We calculated the total number of species observed in and along the six ditch sections (3 reed sections, 3 control sections) between 1993 and 1995. We used an ANOVA with block structure for the ditches to test whether species richness of the reed and control sections differed. However, the data were first transformed to a logarithmic scale (ln (number)). The block structure of the ANOVA corrected for variation caused by differences between the ditches.

We also determined the effect of ditch management on the abundance of the four most frequently observed mammal species. First we calculated the average number of individuals for each of the six ditch sections (all trapping periods and years combined). Then we transformed the data into a logarithmic scale: ln (number). For the common shrew a small value was added to be able to transform a 0-value: ln (number + 0.1). The effect of ditch management on abundance was determined through an ANOVA with a block structure (ditches).

For common voles possible differences in sex ratio between the reed and control sections were

Table 2. Incidental observations of mammal species species at the Tureluurweg and Waiboerhoeve site. [1] = species already observed along trapping line or monitoring route (see table 1), [2] = only indirect evidence through e.g. tracks, faeces, nest or burrow. x = observed, – = not observed.

	Tureluurweg (1993-1995)	Waiboerhoeve (2000)
Hedgehog (*Erinaceus europaeus*)	x	x
Common mole (*Talpa europaea*)	–[1]	x
Common pipistrelle (*Pipistrellus pipistrellus*)	x	–
Pond bat (*Myotis dasycneme*)	x	–
Bats, unknown species	–	x
European hare (*Lepus europaeus*)	–[1]	x
Rabbit (*Oryctolagus cuniculus*)	–[1]	x
Northern water vole (*Arvicola terrestris*)	x[2]	–
Muskrat (*Ondatra zibethicus*)	–	x
House mouse (*Mus musculus*)	–	x
Norway rat (*Rattus norvegicus*)	–[1]	x
Red fox (*Vulpes vulpes*)	–[1]	x

analysed with a log odds ratio, and differences were tested for significance with a subsequent Z-test. We also tested for the effects of ditch management on the weight of male and female common voles (ANOVA).

Waiboerhoeve site

We calculated the total number of species caught in and along the 12 ditch sections (6 reed sections, 6 control sections) in 2000. We used an ANOVA with block structure for the ditches to test whether species richness of the reed and control sections differed. However, the data were first transformed to a logarithmic scale (ln (number)). The block structure of the ANOVA corrected for variation caused by differences between the ditches.

For the three most frequently recorded species and all species combined, we analysed the effect of ditch management on the number of individuals. For these analyses we excluded recaptures on the same trapping line. The analyses were similar to those described above, involving a transformation (ln (number + 0.1)) and an ANOVA with block structure (ditches).

For the common vole and all species combined we also determined possible differences in numbers between the ditch sections (0 m) and the grasslands (average of 10, 25 and 50 m) (ln (number + 0.01), ANOVAs with block structure for the ditches).

To detect possible differences in the sex ratio of common voles between the two ditch management types and ditches (0 m) versus grassland (average of 10, 25 and 50 m) a log odds ratio was calculated and differences were tested for significance with a subsequent Z-test. When no significant differences were found for ditches versus grassland an additional analysis was done. This involved a comparison of the sex ratio along the ditches (0 m) with the average of the two trapping lines that were beyond the radius of the home range of common voles (25 and 50 m). We also tested for effects of ditch management and distance (0 m versus the average of 25 and 50 m) on the weight of male and female common voles (ANOVA).

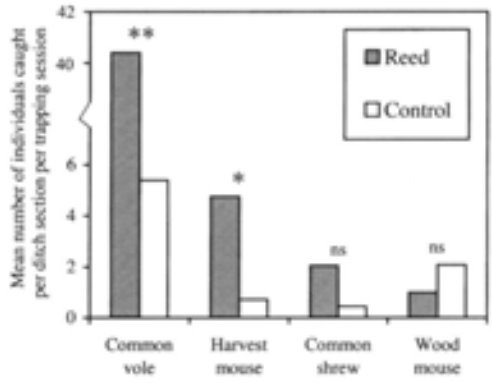

Figure 3. The abundance of the four most frequently caught mammal species at the Tureluurweg site (ANOVAs, 2-tailed, *=$P \leq 0.05$, **=$P \leq 0.01$, ns = not significant). The total number of captures was 1099 for the common vole, 131 for the harvest mouse, 45 for the common shrewand 74 for the wood mouse.

Results

Species richness

In total 16 mammal species were observed at the Tureluurweg site during various trapping sessions and sampling of monitoring routes (table 1). Reed sections had higher species richness than control sections (figure 2; ANOVA, 1-tailed, $P<0.05$).

At the Waiboerhoeve site six mammal species were captured in the traps (table 1). We found higher species richness in the reed sections (3.0 species on average at 0 m) than in the control sections (2.2 species), but the difference was not significant (ANOVA, 1-tailed, $P=0.143$). The large scale agricultural landscape of Flevoland is also home to other mammal species (table 2), but these incidental observations could not be included in our analysis for species richness of the reed and control sections.

Mammal abundance

At the Tureluurweg site almost eight times more common voles were present in the reed sections than in the control sections (ANOVA, 1-tailed, $P<0.01$) (figure 3). Harvest mice (*Micromys*

Table 3. Weight of male and female common voles in the control and reed sections at the Tureluurweg (0 m) and Waiboerhoeve site (0, 25 and 50 m combined) (ANOVAs, 2-tailed *P*-values).

	Reed		Control		
	Weight (g)	(*n*)	Weight (g)	(*n*)	*P*
Tureluurweg					
June					
Males	21.03	138	24.56	31	0.037
Females	20.08	175	22.41	38	0.061
October					
Males	16.52	308	16.76	33	0.722
Females	16.67	363	16.82	26	0.846
Waiboerhoeve					
October					
Males	19.78	16	16.46	13	0.054
Females	17.62	17	18.80	5	0.610

minutus) ($P<0.05$) and common shrews (*Sorex araneus*) ($P=0.077$) were also more abundant in the reed sections, but this was marginally insignificant for the second species. Catches of wood mice (*Apodemus sylvaticus*) were higher in the control sections than in the reed sections, but the difference was not significant (ANOVA, 2-tailed, $P=0.537$). Here a 2-tailed ANOVA was appropriate since the direction of the effect contradicted our original hypothesis.

At the Waiboerhoeve, the number of individuals for all species combined was higher along the ditches (0 m) than in the adjacent grasslands (10, 25 and 50 m combined) (ANOVAs, 1-tailed, reed $P<0.05$; control $P<0.05$) (figure 4). The reed sections also had more individuals at 0 m than the control sections ($P<0.05$). Differences between the reed and control sections in the adjacent grasslands were not significant (ANOVAs, 1-tailed, 10 m: $P=0.182$; 25 m: $P=0.363$). For 50 m a 2-tailed ANOVA was appropriate ($P=0.178$) since there were more individuals in the control sections than in the reed sections.

The common vole was the most frequently caught species at the Waiboerhoeve site ($n=54$ excluding recaptures, 46% of total). The mean number of common voles caught per section was also higher along the ditches (3.1 on average for reed and control sections combined) than in the adjacent grasslands (0.47 on average for 10, 25 and 50 m), but this difference was marginally insignificant (ANOVA, 1-tailed, $P=0.065$). When this analysis was conducted separately for reed (4.3 at 0 m; $P=0.174$) and control sections (1.8 at 0 m; $P=0.179$) the difference between the ditches and the grasslands was also not significant. An analysis that excluded the data from the 10 m trapping line was not useful since there were fewer common voles there than at 25 or 50 m distance. Differences between reed and control sections in the adjacent grasslands at 10 m ($P=0.443$) and 25 m ($P=0.134$) were also not significant (ANOVAs, 1-tailed). At 50 m there were more common voles adjacent to control sections (0.7) than adjacent to the reed sections (0) (ANOVA, 2-tailed, $P=0.078$). Harvest mice (23 individuals in total) and common shrews (21 individuals) occurred mostly or only along the ditches. At 0 m the mean number of harvest mice was higher in the reed sections (2.7) than in the control sections (1.0), but this difference was not significant (ANOVA, 1-tailed, $P=0.143$). Harvest mice were recorded on the grasslands only once (at 10 m). Common shrews occurred only at 0 m and were more abundant in reed sections (2.3) than in control sections (1.2) (ANOVA, 1-tailed, $P<0.05$).

On the Waiboerhoeve site all recaptures were on the same trapping line as the individuals were first caught on. However, there was one exception for a greater white-toothed shrew (*Crocidura russula*). The individual was first caught along a ditch (0 m) and later recaptured at 25 m distance from that same ditch.

Sex ratio of common voles

At the Tureluurweg site there was no difference in sex ratio for common voles between the reed and control sections in June (overall m:f = 1:1.29; 1-tailed Z-test, P=0.473). In October we found relatively more females in the reed sections (1:1.16) than in the control sections (1:0.85), but this difference in sex ratio was marginally insignificant (P=0.059). For March there were insufficient numbers to calculate a sex ratio. The difference in sex ratio between reed and control sections for June and October combined was also not significant (overall 1:1.19; 1-tailed Z-test, P=0.272).

At the Waiboerhoeve site the sex ratio along the ditches (0 m) was nearly equal (1:1.06). Although not significant (1-tailed Z-test, P=0.121), there were relatively more females in the reed sections (1:1.36) than in the control sections at 0 m (1:0.57). In the grasslands (10, 25 and 50 m combined) there were relatively more males than females (1:0.42), but the number of individuals was too low to allow for a test between reed and control sections. There were relatively more females along the ditches (overall 1:1.06) than in the grasslands (overall 1:0.42) (10, 25 and 50 m combined), but the difference was marginally insignificant (1-tailed Z-test, P=0.057). However, when the captures at the 10 m trapping line were excluded, the P-value dropped to 0.016 (1-tailed Z-test) and the sex ratio in the grasslands was even more strongly male-biased (overall 1:0.27).

Weight of common voles

For the Tureluurweg site we investigated the main effect of ditch management (1993, 1994 and 1995 combined) (table 3). Data from March were excluded because of low capture numbers. In June, male common voles weighed less in the reed sections than in the control sections. This was also true for females, but here the difference was marginally insignificant. Both results contradict our initial hypotheses. In October there were no apparent differences in weight between the reed and control sections.

For the Waiboerhoeve site there was no significant interaction between ditch management and distance (0 m versus a combination of 25 and 50 m) (ANOVAs, 2-tailed, males P=0.211, females P=0.444). The main effect of distance was also not significant (males P=0.533, females P= 0.895). We did however find that males in the reed sections and the adjacent grasslands (0, 25 and 50 m combined) were heavier than those in and adjacent to the control sections (ANOVA, 1-tailed, P=0.027) (table 3). For females there was no indication of differences in weight related to ditch management.

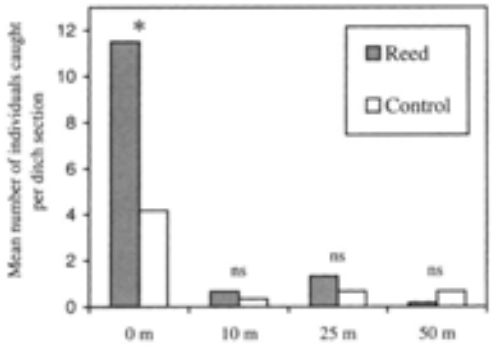

Figure 4. The abundance of small mammals (all species combined) in the reed (n=6) and control sections (n=6) and on the adjacent production grasslands at the Waiboerhoeve site (ANOVAs, 2-tailed, * = $P \leq 0.05$, ns = not significant). The total number of individuals caught was 117.

Discussion

Species richness and abundance

The reduced clearing frequency of the ditches was beneficial for the species richness and over-

all abundance of mammals. For common voles, common shrews and harvest mice we could also show an increase in abundance on the species level on at least one of the two study sites. This seems to be related to vegetation structure. The vegetation in the reed sections was taller and covered more of the soil and litter layer than in he control sections (Remmelzwaal & Voslamber 1996). However, different mammal species may have responded to different factors. We discuss these for the common vole, harvest mouse, common shrew and wood mouse.

The common vole benefited strongly from the reduced clearing frequency of the ditches at the Tureluurweg site, whereas the response was less strong and very variable at the Waiboerhoeve site. The grassland buffer zones that lay adjacent to the ditches at the Tureluurweg site could explain this difference. On these buffer zones no fertiliser or manure was applied and domesticated herbivores were absent. Thus the grassland buffer zones did not have the high in- and output levels of the production grasslands at the Waiboerhoeve site. Since non-intensively managed grasslands and high-intermediate sward heights are associated with high vole densities (van Wijngaarden 1957b, Cornelissen et al. 1997, review by La Haye 1999, Beemster & Vulink 2001, E.S. Bakker, unpublished data), the presence of grassland buffer zones could explain the abundance of common voles caught in the reed sections at the Tureluurweg site and the relatively weak response along the ditches at the Waiboerhoeve site.

Although the grasslands of the Waiboerhoeve site were divided into management units with different mowing and grazing regimes, the average sward height of the grasslands adjacent to the reed and control sections was almost identical (see methods). Thus sward height is unlikely to have confounded our study design. Apparently the intensively used grasslands and short sward height (about 8 cm) did not permit high population densities of the common vole. We were also unable to demonstrate an effect of ditch management on relative population density in the grasslands.

The harvest mouse also benefited from the reduced clearing frequency of the ditches. Harvest mice were almost totally restricted to the ditches and reed sections had the highest numbers. Harvest mice have a strong preference for relatively high vegetation dominated by reed or other high grasses and herbs (e.g. Ylönen 1990, Lange et al. 1994, Churchfield et al. 1997, Cornelissen et al. 1997). Harvest mice spend much of their life off the ground and attach their nests to tall reed stems or other vegetation (Lange et al. 1994). The reed sections had tall reed stems available year round which explains the positive effect of the reduced clearing frequency of the ditches on harvest mice.

The common shrew occurred only along the ditches. Other studies also indicated that this species has low population densities in crops or grasslands (Loman 1991, Reeve & Jones 1996). Furthermore, the presence of water in the ditches may have had a positive effect on the abundance of common shrews (see Kotzageorgis & Mason 1997). Common shrew population density is related to the availability of food (Ivanter & Makarov 1994), and since invertebrates were most abundant in the reed sections (Remmelzwaal & Voslamber 1996), this could explain why more individuals were captured there.

The wood mouse is a common species in agricultural areas with crops, but hedgerows and other wooded vegetation serve as refugia in winter (Alcántara & Tellería 1991, Loman 1991, Ylönen et al. 1991, Montgomery & Dowie 1993, Tew & Macdonald 1993, Kotzageorgis & Mason 1997, Macdonald et al. 2000, Ouin et al. 2000). The relatively high number of captures at the Tureluurweg site and low numbers at the Waiboerhoeve site are probably related to the vegetation on the parcels themselves. Crops can provide the wood mouse with enough cover and food, while grassland is a much poorer habitat (Montgomery & Dowie 1993). If enough cover is available, wood mice can survive on the fields year round (Loman 1991), but if the crops are harvested the habitat surrounding the fields becomes important to their survival. In our study

areas wooded vegetation was either very young or absent, and the only cover available was provided by the reed sections. Although wood mice do less well in reed vegetation than in woodland (Canova et al. 1994) the reed sections may have served as winter refugia. Subsequent migration to the fields and control sections in spring could explain why we did not find an effect of ditch management for this species.

Common voles and possible outbreaks

Although the reduced clearing frequency of the ditches led to an increase of common voles along the ditches, there was no indication of a population increase in the adjacent grasslands. Van Wijngaarden (1957b) argued that three conditions have to be met for a vole outbreak to occur: 1. the presence of ditches, field margins, road side verges or other refugia dominated by non-intensively managed grasses and herbs (see e.g. Van der Reest 1992, Meunier et al. 1999) in which the species concentrates when numbers are low, 2. the presence of non-intensively used grassland with tussocks which the animals use as a base to further colonise the grasslands, and 3. a cluster of non-intensively used grasslands to build up a sizeable population in an area. Van Wijngaarden (1957b) stated that intensive grassland management and low sward height would prevent the common voles from reaching extremely high densities in agricultural areas. This does not mean that population densities no longer vary (see e.g. Buker 1984), but densities are less likely to reach outbreak proportions. It has also been suggested there is relatively little chance of cyclic population fluctuations and associated outbreaks in heterogeneous landscapes in temperate climate zones. These landscapes have more generalist predators compared to the homogeneous landscapes in the boreal and arctic zones which have relatively simple food chains (Hanski 1987, Delattre et al. 1992, Jędrzejewski & Jędrzejewska 1996, Delattre et al. 1999). A reduced clearing frequency of the ditches in agricultural areas in Flevoland would increase the habitat quality of refugia, but since the management of the grasslands remains intensive, chances of outbreaks seem small. If the theory concerning heterogeneous landscapes holds, the chance of outbreaks could be reduced even further by making the landscape more heterogeneous through increasing woody habitats (e.g. hedges, small woodlots, including those surrounding farm buildings) and more attractive to generalist predators such as red fox (*Vulpes vulpes*), badger (*Meles meles*), western polecat (*Mustela putorius*), pine marten (*Martes martes*), and possibly stone marten (*Martes foina*). The red fox and western polecat are common in most parts of Flevoland, but badgers and pine martens are colonising or dispersing into the area too (Dekker 2001, Müskens et al. 2001).

In addition to the low number of common voles in the production grasslands at the Waiboerhoeve site, we found a male-biased sex ratio of the captured animals whereas the sex ratio was almost equal along the ditches. In contrast to males, females can have overlapping home ranges and can live in groups (e.g. Boyce & Boyce 1988). This is associated with high population densities (see review by Van Wijngaarden 1960) and is likely to be related to habitat quality. The male-biased sex ratio of the captures in the grasslands of the Waiboerhoeve site indicates that common voles probably found them to be poor quality habitat. We also lacked recaptures of individuals in the grasslands that were previously caught along the ditches. The above supports the hypothesis that the chance of outbreaks remains small when applying a reduced clearing frequency of ditches. A further indication of a difference in habitat quality can be derived from the body weights. At the Waiboerhoeve site male common voles were heavier in or adjacent to the reed sections than in or adjacent to the control sections. This could indicate that reed ditches are a better habitat for common voles than control ditches and matches with the relatively high number of females in the reed sections at both study sites. However, this seems to conflict with the pattern of body weights found at the Tureluurweg site. Here males and females in the control sections were or tended to be heavier than those in the reed sections, at least in

summer. A possible explanation is that young or relatively low weight individuals had little opportunity of migrating at the Tureluurweg site since the grassland buffer zone was only a few metres wide and bordered less favoured arable land.

Management costs

The management costs of reed sections were higher than those of the control sections at both the Tureluurweg (+17%, total costs 1.22 Euro per m ditch per year) and Waiboerhoeve site (+5%, 0.58 Euro per m ditch per year). However, the costs of the management of the reed sections at the Tureluurweg site included the mowing of the 3 m wide grass buffer zones. When these costs were subtracted, the management was considerably cheaper than that of the control sections (-42%). The costs for the management of the reed sections included the removal and on-farm storage of the biomass. Possible costs or income deriving from further treatment, transport or use were not taken into account. The same applied for the loss of production area through the 3 m wide grass buffer zone at the Tureluurweg site. However, these non-productive grass buffer zones are not relevant in grassland areas.

Since the management of the reed sections was either cheaper (Tureluurweg site) or only slightly more expensive (Waiboerhoeve site) than that of the control sections, it seems to be an inexpensive way to increase natural values in agricultural areas. On-farm composting or the direct spreading over arable land seem to be the cheapest applications for the biomass (see Meerburg 2001). On the long term agricultural production could benefit through a possible increase of the percentage of organic matter in the soil (now ±4%). Such on-farm applications would enhance the integration of nature and agriculture at the level of individual farms.

Conclusion

The species richness and abundance of mammals increased when the clearing frequency of the ditches was reduced and cover remained on one ditch side in winter. Small mammals, mainly common voles, harvest mice and common shrews, were largely restricted to the ditches. Only common voles were also found in reasonable numbers in the grasslands. Although the differences were not significant, common voles occurred in lower densities in the grasslands than along the ditches. The male-biased sex ratio of common voles also indicated that the intensively used production grasslands are a poor habitat. Although the number of common voles increases with a less frequent mowing scheme of the ditches, their population density is unlikely to reach outbreak proportions in an area as long as the grasslands continue to be managed intensively. Furthermore, the reduced clearing frequency of the ditches proved to be inexpensive, and a rapid integration into existing farming systems seems possible.

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Samenvatting

Zoogdieren hebben voordeel bij het minder vaak maaien van slootkanten in een agrarisch landschap

Het effect van slootbeheer op het aantal soorten zoogdieren en hun relatieve populatiegrootte is onderzocht op twee locaties in een grootschalig agrarisch landschap in Flevoland, Nederland. We vergeleken twee typen slootbeheer. Het eerste type slootbeheer bestond uit het twee keer per jaar maaien van beide slootkanten met een klepelmaaier, de biomassa bleef vervolgens liggen (controle secties; n=3 voor Tureluurweg locatie, n=6 voor Waiboerhoeve locatie). Dit resulteerde in een korte slootkantvegetatie in de winterperiode. Het tweede type slootbeheer bestond uit het afwisselend maaien van beide slootkanten in opeenvolgende jaren, de biomassa werd afgevoerd (riet secties; n=3 voor Tureluurweg locatie, n=6 voor Waiboerhoeve locatie). Hierbij bleef dekking van vooral riet (*Phragmites australis*) aan één slootzijde aanwezig gedurende de winter.

We bepaalden het aantal soorten zoogdieren en hun relatieve populatiegrootte door zichtwaarnemingen op monitoringroutes (Tureluurweg) en vangsten direct naast de sloten (Tureluurweg en Waiboerhoeve). In het Waiboerhoeve gebied vingen we bovendien kleine zoogdieren op de intensief gebruikte productiegraslanden die naast de sloten lagen (extra vanglijnen op 10, 25 en 50 m van de sloten). Het aantal soorten zoogdieren en hun relatieve populatiegrootte was het grootst in riet secties. Kleine zoogdieren, vooral veldmuizen (*Microtus arvalis*), dwergmuizen (*Micromys minutus*) en bospitsmuizen (*Sorex araneus*), waren grotendeels beperkt tot de vegetatie in de sloten en namen op tenminste één van de locaties toe door het extensiever maaibeheer. Alleen veldmuizen werden ook in redelijke aantallen op de graslanden zelf aangetroffen. Hoewel het verschil niet significant was, was hun gemiddelde dichtheid op de graslanden lager dan in de sloten. Een ongelijke geslachtsverhouding van de veldmuizen op de intensief gebruikte productiegraslanden, met

naar verhouding veel mannen, vormt ook een aanwijzing dat deze een marginaal habitat zijn voor veldmuizen.

Hoewel veldmuizen toenemen bij het minder vaak maaien van slootkanten lijkt de kans op plagen niet groot zolang de graslanden intensief gebruikt worden. Het minder vaak maaien van slootkanten was iets duurder (+5%) in het Waiboerhoeve gebied, maar goedkoper (-42%) in het Tureluurweg gebied. Lage beheerkosten, een geringe kans op veldmuisplagen, en mogelijk positieve effecten van riet biomassa op het percentage organische stof in de bodem (door compost of het direct verspreiden over akkers) kunnen zorgdragen voor een snelle integratie van een natuurvriendelijk slootbeheer in bestaande bedrijfssystemen.

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Short Note

First record of the beaver *Castor fiber* in Luxembourg since at least the 19th century

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On January 25th 2000, the second author discovered an animal path in a strip of grassland next to the river Clerve in the north of Luxembourg. The path ended in the river in one direction, and in a strip of forest in the other direction. In the forest strip, he discovered an aspen tree (*Populus tremula*) of 29 cm in diameter, which had been felled (figure 1). Tooth marks were clearly visible on the tree. Until December 2000, the river Clerve was inspected closely several times by the first and third authors; at nearly every visit, freshly felled trees were found, varying in diameter from 1 to 43 cm. On December 16th 2000, a photograph of a large animal was taken near one of the felled trees (figure 2). The conclusion was that there was a beaver (*Castor fiber* L., 1758) present on the river Clerve (figure 3).

It is not clear when the beaver became extinct in Luxembourg, but according to maps presented by Véron (1992), the species existed in our regions until the 17th century. However, the last record of a beaver in neighbouring Belgium dated from 1848 (Lange et al. 1986), so the species may also have survived in Luxembourg until the 19th century. Therefore, to our knowledge, the individual on the Clerve is the first free-living beaver in Luxembourg since at least the 19th, but probably since the 18th or even the 17th century. The question then arising is where this animal came from. One possibility is that it has migrated from a small population from the river Rur close to the border between Germany and Belgium (Huijser & Nolet 1991). However, it seems more likely that the beaver originates from a reintroduction project undertaken in Belgium, where around 120 beavers have been reintroduced since 1998 without authorisation from the Belgian authorities; all those beavers seem to originate from the population in Bavaria, Germany (J. Stein, personal communication). The population closest to the Belgium-Luxembourg

Figure 1. Aspen tree (*Populus tremula)* felled by beaver (*Castor fiber)* on the river Clerve (Luxembourg). *Photograph: Laurent Schley.*

Figure 2. Beaver (*Castor fiber*) next to the river Clerve (Luxembourg). *Photograph: Laurent Schley & Claude Schanck.*

border, just north of Houffalize, which currently holds an estimated 30 individuals (B. Manet, personal communication), is around 22 km from the site on the river Clerve. This is thus well within the maximum migration distance of 170 km observed in beavers (Heidecke 1984), and much closer than the population in the German-Belgian border region on the river Rur. Also, the timing of the appearance of the beaver in Luxembourg supports the idea that it came from the recent unofficial reintroduction into Belgium. Even though the habitat does not seem optimal for beavers on the river Clerve, the beaver was still present there a year after observation of the first signs.

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Figure 3. Geographic location of the beaver site within Luxembourg. Thin line, border of Luxembourg; thick lines, main rivers (numbers 2-10); 1 star, beaver site (50°0'10"N, 6°1'46"E); 2, Clerve; 3, Wiltz; 4, Our; 5, Sûre; 6, Attert; 7, Eisch; 8, Mamer; 9, Alzette; 10, Moselle; 11 black dot, Luxembourg City.

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Samenvatting

Eerste waarneming van een bever (*Castor fiber* L., 1758) in Luxemburg sinds de 19e eeuw

Op 16 december 2000 is een bever (*Castor fiber* L., 1758) gezien in rivier de Clerve in het noorden van Luxemburg. Al aan het begin van datzelfde jaar werden rond de rivier vraatsporen van bevers aangetroffen. Voor zover bekend is dit de eerste bever in Luxemburg sinds de 19e eeuw, en wellicht zelfs sinds de 18e of 17e eeuw. Het lijkt waarschijnlijk dat de bever afkomstig is van een populatie bevers net ten noorden van Houffalize in België, waar sinds 1998 illegaal bevers uit Beieren (Duitsland) zijn geïntroduceerd.

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Publicaties over recente zoogdieren van België verschenen in de jaren 1998-2000

Met aantekeningen betreffende genera en onderwerpen

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Introductie: Elke referentie wordt gevolgd door codes die de behandelde onderwerpen en genera weergeven (zie Appendix, tabel 1, 2 en 3). Wanneer een publicatie niet is gezien, of slechts een samenvatting is ingezien, is dit eveneens met codes aangegeven.

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Appendix

Tabel 1. Algemene codes.

*	Niet verkrijgbaar, maar ter inzage in de bibliotheek van de betreffende instelling
$	Hierover verschenen, in dezelfde periode, artikelen in de meeste Belgische kranten en tijdschriften
NG	Publicatie niet gezien
SG	Van deze publicatie werd enkel een samenvatting gezien

Tabel 2. Codes onderwerpen.

AL:	Algemeen	FY:	Fysiologie-Biochemie
AN:	Anatomie	HE:	Hervestiging-Introductie
BB:	Bibliografie-Literatuuroverzicht	MO:	Morfologie
BE:	Natuurbescherming-Soortbescherming	PA:	Parasieten-Ziekten
BI:	Biometrie	SC:	Schade-Bestrijding
CH:	Chromosomen	SY:	Systematiek-Taxonomie
EC:	Ecologie	TE:	Aantallen-Tellingen-Dichtheden
ET:	Ethologie	VE:	Verspreiding-Voorkomen
EV:	Evolutie	WE:	Wetgeving

Tabel 3. Codes genera.

apo:	Apodemus	ept:	Eptesicus	mir:	Microtus	phy:	Physeter
arv:	Arvicola	eri:	Erinaceus	min:	Miniopterus	pip:	Pipistrellus
bal:	Balaenoptera	eub:	Eubalaena	mus:	Mus	ple:	Plecotus
bar:	Barbastella	equ:	Equus	muc:	Muscardinus	pro:	Procyon
bos:	Bos	fel:	Felis	mut:	Mustela	rat:	Rattus
can:	Canis	gen:	Genetta	myo:	Myocastor	rhi:	Rhinolophus
cap:	Capreolus	glo:	Globicephala	myt:	Myotis	sci:	Sciurus
cas:	Castor	hal:	Halichoerus	myx:	Myoxus	sor:	Sorex
cer:	Cervus	hyp:	Hyperoodon	neo:	Neomys	ste:	Stenella
chi:	Chiroptera spec.	lag:	Lagenorhynchus	nyc:	Nyctalus	sus:	Sus
cle:	Clethrionomys	lep:	Lepus	nyt:	Nyctereutes	syl:	Sylvilagus
cri:	Cricetus	lut:	Lutra	odo:	Odobenus	tal:	Talpa
cro:	Crocidura	lur:	Lutreola	ond:	Ondatra	tam:	Tamias
cys:	Cystophora	lyn:	Lynx	orc:	Orcinus	(incl. Eutamias)	
dam:	Dama	mar:	Martes	ory:	Oryctolagus	tur:	Tursiops
del:	Delphinus	mel:	Meles	ovi:	Ovis	ves:	Vespertilio
dep:	Delphinapterus	mes:	Mesoplodon	pho:	Phoca (incl. Pusa)	vul:	Vulpes
eli:	Eliomys	mic:	Micromys	phc:	Phocoena	zip:	Ziphius

Publicaties over recente zoogdieren van België verschenen in de jaren 1994-1997 (aanvulling)

Met aantekeningen betreffende genera en onderwerpen

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Introductie: In Lutra 38 (2) en Lutra 40 (2) verschenen voor de periode 1991-1994 respectievelijk 1995-1997 publicatielijsten over recente zoogdieren van België. Deze lijst bevat een aantal aanvullingen op genoemde publicatielijsten. Elke referentie wordt gevolgd door codes die de behandelde onderwerpen en genera weergeven (zie Appendix, tabel 1, 2 en 3). Wanneer een publicatie niet is gezien, of slechts een samenvatting is ingezien, is dit eveneens met codes aangegeven.

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Appendix

Tabel 1. Algemene codes.

*	Niet verkrijgbaar, maar ter inzage in de bibliotheek van de betreffende instelling
$	Hierover verschenen, in dezelfde periode, artikelen in de meeste Belgische kranten en tijdschriften
NG	Publicatie niet gezien
SG	Van deze publicatie werd enkel een samenvatting gezien

Tabel 2. Codes onderwerpen.

AL:	Algemeen	FY:	Fysiologie-Biochemie
AN:	Anatomie	HE:	Hervestiging-Introductie
BB:	Bibliografie-Literatuuroverzicht	MO:	Morfologie
BE:	Natuurbescherming-Soortbescherming	PA:	Parasieten-Ziekten
BI:	Biometrie	SC:	Schade-Bestrijding
CH:	Chromosomen	SY:	Systematiek-Taxonomie
EC:	Ecologie	TE:	Aantallen-Tellingen-Dichtheden
ET:	Ethologie	VE:	Verspreiding-Voorkomen
EV:	Evolutie	WE:	Wetgeving

Tabel 3. Codes genera.

apo:	Apodemus	ept:	Eptesicus	mir:	Microtus	phy:	Physeter
arv:	Arvicola	eri:	Erinaceus	min:	Miniopterus	pip:	Pipistrellus
bal:	Balaenoptera	eub:	Eubalaena	mus:	Mus	ple:	Plecotus
bar:	Barbastella	equ:	Equus	muc:	Muscardinus	pro:	Procyon
bos:	Bos	fel:	Felis	mut:	Mustela	rat:	Rattus
can:	Canis	gen:	Genetta	myo:	Myocastor	rhi:	Rhinolophus
cap:	Capreolus	glo:	Globicephala	myt:	Myotis	sci:	Sciurus
cas:	Castor	hal:	Halichoerus	myx:	Myoxus	sor:	Sorex
cer:	Cervus	hyp:	Hyperoodon	neo:	Neomys	ste:	Stenella
chi:	Chiroptera spec.	lag:	Lagenorhynchus	nyc:	Nyctalus	sus:	Sus
cle:	Clethrionomys	lep:	Lepus	nyt:	Nyctereutes	syl:	Sylvilagus
cri:	Cricetus	lut:	Lutra	odo:	Odobenus	tal:	Talpa
cro:	Crocidura	lur:	Lutreola	ond:	Ondatra	tam:	Tamias
cys:	Cystophora	lyn:	Lynx	orc:	Orcinus	(incl. Eutamias)	
dam:	Dama	mar:	Martes	ory:	Oryctolagus	tur:	Tursiops
del:	Delphinus	mel:	Meles	ovi:	Ovis	ves:	Vespertilio
dep:	Delphinapterus	mes:	Mesoplodon	pho:	Phoca (incl. Pusa)	vul:	Vulpes
eli:	Eliomys	mic:	Micromys	phc:	Phocoena	zip:	Ziphius

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Heck cattle graze within the Oostvaardersplassen area year-round since 1983. *Photograph: Edgar van der Grift.*

Book Reviews

Lowland wetlands grazed by hungry herds

Hungry Herds. Management of temperate lowland wetlands by grazing. J.T. Vulink 2001. Van Zee tot Land 66. Rijkswaterstaat, Directie IJsselmeergebied, Lelystad. PhD thesis. Rijksuniversiteit Groningen, Groningen, The Netherlands. 394 pp. ISBN 90-369-1258-x

Wetlands are very important areas from a conservation point of view because of their characteristic plant communities and very species-rich birdlife. Under natural conditions many wetlands contain a significant proportion of short, open vegetation brought about by processes such as regular flooding and the working of ice which tend to reverse successional development. These extensive early successional short grassland vegetations provide suitable habitat for herbivorous water birds, breeding waders and vole-feeding raptors. Furthermore, Dutch wetlands function as stepping stones between the vast breeding areas in the Arctic and the wintering areas in Africa. The short vegetations, however, have become very scarce because of man's impact on the disturbance forces through drainage, embankment and cultivation. Therefore natural functioning wetlands have become very scarce. Luckily several thousands of hectares of new wetlands have been created in the Netherlands as a spin-off from major reclamation projects, mainly in new polders. The management of these wetlands is predominantly aimed at developing and maintaining an array of vegetation types ranging from short open grassland vegetation to shrub and forest. Since the natural disturbance factors are frequently absent from these new areas, active management is applied to partly maintain early successional stages and an important management tool in this respect is grazing by cattle and horses.

Sixteen years ago, the now Dr. J.T. Vulink took the opportunity to set out and study the question 'to what extent grazing by large herbivores, i.e. cattle and horses, can retard vegetation development in reclaimed wetlands in the Netherlands and thus favour plant and bird species whose preferred habitat is short, open vegetation'. On 27 April 2001 he defended the resulting doctoral thesis titled 'Hungry herds - Management of temperate lowland wetlands by grazing' at the University of Groningen. It is a beautiful book: glossy paper, clear figures and tables, and containing a wealth of information in its 394 pages! Sixteen years of work condensed in sixteen chapters. A thesis this size has become a rare bird indeed. The work is the last in a series, called 'Van Land tot Zee' (From Land to Sea), that started in 1951 and had as purpose to document the various aspects and effects of the reclamation of the Flevopolder. Most of these studies have been carried out under the auspices of the scientific department of the IJsselmeerpolders Development Authorities (RIJP) and the Institute for Inland Water Management and Waste Water Management (RIZA). The actual research focuses on three subquestions: (1) What are the ecological differences between cattle and horses? (2) What is the effect of ungulates on the vegetation? (3) Can grazing facilitate birds that are confined to different stages of the wetland habitat?

Although the work was carried out in three study sites, the Lauwersmeerpolder, the Grevelingen and the Oostvaardersplassen, most of the work was done in the last mentioned area. The Oostvaardersplassen (5600 ha) is a recent developed wetland in Zuidelijk Flevoland, drained in 1968, and reclaimed from the freshwater lake IJsselmeer. The reserve consists of a central reed marsh (3600 ha) and a well-drained border zone of 2000 ha, where the ungulates concentrate. Parts of the reserve used to be grazed during summer by domestic cattle and horses. In 1983 Heck cattle and Konik horses were introduced while red deer were introduced in 1992.

The first subquestion was if cattle and horses differ in feeding ecology. The botanical diet composition and the quality of the diets selected turned out to be very similar in the two species. Nevertheless a few differences were found that can be attributed to differences in digestive physiology. As typical ruminants cattle are better able to cope with secondary plant compounds, because they can detoxify toxic compounds in the rumen, while horses are able to consume more coarse grasses because their dry matter intake is not constrained by a rumen bottleneck. As a consequence, cattle can consume more *Sambucus nigra* (which contains a toxic component as a defense mechanisms against herbivory) while horses have more of the coarse grasses *Phragmites australis* and *Calamagrostis epigejos* in their diet. These differences imply different effects on vegetation development. Other differences are related to behaviour and social organization. On average, horses spent 4.5 hours a day more on grazing than cattle and this resulted in a higher dry matter intake for horses. Therefore horses lost less body mass during winter than cattle and they also required less fat reserves to survive the winter period. Important social differences are that, while the Konik horses mainly operate in one big herd, the social units of the Heck cattle (solitary bulls, mixed groups and bull groups) are spatially separated. The grazing pressure of the Heck cattle is therefore more evenly distributed over the whole area, while the horses have a heavy impact on the short grasslands where they congregate.

The second subquestion dealt with the effects of herbivory on the vegetation. Different grazing regimes were compared in the two former estuaries, Lauwersmeerpolder and Grevelingen, and the one inland area, Oostvaardersplassen: year-round grazing at low densities (0.1-0.2 animals ha^{-1}), summer grazing at intermediate densities (0.3-0.5 animals ha^{-1}) and summer grazing at high densities (0.9-1.2 animals ha^{-1}). Year-round grazing at low stocking densities in reclaimed temperate wetlands was not suitable for retaining the open vegetation stages. For such an effect, a high grazing pressure in the summer is required. At the studied summer densities, it appeared possible to maintain a short vegetation and to prevent the expansion of tall grasses, herbs and shrubs. According to the author these densities cannot be reached by a year-round grazing regime unless supplementary feeding is applied because the maximum animal densities for herbivores grazing year-round are set by the probability of cattle and horses to build up fat reserves and by feeding conditions in winter. In spring and summer, when vegetation starts growing and plant biomass peaks, the overwintering herbivores are thus faced with a food abundance that surpasses their foraging needs. As a consequence, unpalatable plant species will escape from grazing while plant biomass will accumulate at the expense of the area of short vegetation. One of the options to overcome this problem is to connect nature reserves in lowland wetlands with large-scale nature reserves in highland areas, characterized by coversand soils. During summer large herds will concentrate in the lowland wetlands but migration to higher grounds will take place in winter when food becomes scarce in the summer habitat or conditions worsen otherwise (flooding).

The final subquestion was if grazing can facilitate birds that are confined to different stages of the wetland habitat. In ungrazed areas with spontaneous vegetation development the total number of breeding bird species remained constant over the years, although a continuous turnover of species took place. The turnover in composition of the breeding bird community was delayed but not halted by summer grazing at moderate levels.

The indirect effects of reed cover proved to be an important factor in habitat selection of most bird species studied. Variation in reed cover strongly influenced habitat selection of marsh birds. Visits of several foraging species like Eurasian spoonbill, herons, waders, dabbling ducks and some passerines correlated negatively with reed cover. Other species such as foraging little grebes and some marshland passerines increased in numbers in relation to reed cover. Wintering geese also reacted strongly to reed

cover. The area of short reed (also low reed cover) was most intensively grazed by geese and had a shorter sward than the area of moderate reed height. A reduction of the open grassy areas, as a result of natural vegetation succession, resulted in a sharp decline of the preferred habitat of wintering geese, vole-feeding raptors and breeding waders and thus in a decline in bird numbers. Summer grazing strongly facilitated greylag geese.

In the last part of the final chapter 'Evaluation and Synthesis' the author makes a plea for an integrated system approach for the management of wetlands. The most important management activities are the reinstating of abiotic and biotic key processes to let the system run. Abiotic key processes are salinisation and flooding to restore fertility and estuary gradients. Superimposed on the restoration of the abiotic processes would be the implementation of herbivory by ungulate herbivore assemblages, including species representing the major feeding styles such as grazers (cattle, horses, European bison), intermediate feeders (red deer, fallow deer) and browsers (roe deer, moose). It will be clear that for a complete assemblage sufficient space is required (while also species-specific requirements have to be met). Therefore the only way forward is to create large areas (10 000 - 50 000 ha) by connecting nature reserves according to the Ecological Network concept. To be able to implement this concept, it is necessary to understand the ecology of the systems involved and of their reference systems, which can act as a model for a particular area. For this understanding to develop, Vulink feels that we need more fully explore the options of critical field experiments and we can only wholeheartedly underline this statement.

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Life on the edge

Life on the edge. Hedgehog traffic victims and mitigation strategies in an anthropogenic landscape. M.P. Huijser 2000. PhD thesis. Wageningen University, Wageningen, The Netherlands. 165 pp. ISBN 90-5808-301-2.

Life on the edge. Hedgehog traffic victims and mitigation strategies in an anthropogenic landscape forms the PhD thesis of the author. The book is made up of eight chapters including one that forms a wrap-up discussion of research results at the end. Three of the chapters are published journal articles, the remaining were submitted for publication at the time of printing.

Chapter 1 sets the stage for the thesis and provides a review of hedgehog habitat, ecology, biogeography, the implications of human activities (past and present) and urban environments on hedgehog populations and fragmenting of them. Given the increasing number of roads and vehicles traveling on them in the Netherlands, road mortality and its demographic consequences is of increasing concern. The author and Nigel Reeve ask how important is traffic-related mortality of hedgehogs compared to other mortality sources in developed landscapes? In Chapter 2, they review the causes of mortality of more than 12 000 hedgehogs logged at wildlife rescue centres between 1992-98. On average, every other mammal casualty was a hedgehog and 41% of all hedgehog deaths were from unnatural causes. Although there were inherent biases using rescue centre data, the authors emphasize the extent of unnatural mortality among hedgehogs should be a cause for concern and may seriously debilitate some populations locally.

Chapter 3 reports on a mark-recapture study looking at sex differences among traffic-related mortalities of hedgehogs and their body condition. Not surprisingly males traveled greater distances, crossed more roads, lost more weight during breeding season, were killed on roads more often, and had lower survival probabilities than females. Interestingly, the author and others estimated 12% of their study population was

killed on roads including 6% to 9% of their study animals.

Numerous studies have shown that roads can have a significant effect on population densities of large mammals, birds and amphibians. In Chapter 4, using baited foot-print tunnels the author and Piet Bergers investigated the effect of roads on hedgehog population density. Although a power analysis prior to starting the work indicated that only an effect greater than 35% could be detected, 30% fewer tracks were found in road plots compared to controls. Confounding factors between control and road plots may have explained their result. Nonetheless, the authors underscore that roads may reduce hedgehog density by 30% or more and can affect the persistence of local populations.

There is little doubt that vehicles are efficient at killing or maiming any living thing that they encounter in their path. Tires, bumpers and windshields are the agents of bodily destruction we most readily think of, however, we tend to forget that low undercarriages and even airflow beneath vehicles can be potential means of killing small fauna such as hedgehogs. In a highly unique experiment (Chapter 5) we learn that airflow underneath a car is not strong enough to lift a hedgehog (although it can be for common toads *Bufo bufo*). Because the height of different-aged hedgehogs varies between a crouching and walking position, the author painstakingly obtained those measures and contrasted them with the average minimum clearance of 100 used cars at a lot in Hoevelaken. Vehicle clearance astonishingly was only 14 cm, however, this was high enough 75% of the time to avoid making contact with a hedgehog. Probably more important than pure morphological traits are behavioural ones that might make a hedgehog more or less susceptible to collisions when caught between the headlights.

Chapters 6 and 7 concentrate on how habitat, landscape, road, and traffic features influence hedgehog movement in small-scale agricultural landscapes and their mortality on roads. Radiotagged hedgehogs provided information on habitat selection at different scales. Hedgerows were by far the most important habitat, for feeding as well as resting, and most of their nighttime locations were less than 5 m from hedgerows. An important result of this work suggests that hedgerows can be used in mitigation strategies to reduce traffic victims and maintain habitat connectivity. Chapter 7 is a continuation of the previous chapter and evaluates by a rigorous statistical approach the many other variables related to roads, traffic on them, and the landscape they are imbedded. Linear elements such as hedgerows, forest edges or grass verges, when positioned parallel to roads resulted in fewer traffic victims than when placed perpendicular to roads. These findings have important implications for planning mitigation passages and enhancing their use by hedgehogs and other fauna. Finally, Chapter 8 summarizes the research results and provides suggestions for mitigating road infrastructures for hedgehogs and integrating hedgehog mitigation schemes within the context of larger, regional scale plans to defragmentize the Dutch landscape.

The book provides an in-depth look at the relationship between hedgehog populations and roads and vehicles traveling on them. Overall, the book is well written and organized and reflects the same care and penchant for details the author shows for field data collection and analysis. The chapters fit well together, scarcely overlap and provide an excellent account of the cumulative effects of road networks on one small but very mobile species. I particularly liked the applied aspect of the research, always present in the author's mind, providing options and alternatives for reducing road effects on hedgehogs. The Dutch Ministry of Transport and entire transportation community will benefit from the results of Chapters 6 and 7, knowing that modifying landscape elements such as hedgerows can be an effective means of improving habitat connectivity for a variety of wildlife.

Being unfamiliar with the Dutch fauna and ecological networks, I was left wondering, what is the importance of this research other than knowing how one species of insectivore is af-

fected by roads? So what if hedgehogs disappear from the Dutch landscape or other roaded landscapes? What are the implications of this at an ecosystem scale? I would have liked to learn from the author where hedgehogs fit into the larger scheme of things? What ecosystem function or service do they provide that merits such an exhaustive investigation?

The book is exceptional in that the scope of investigation is broad covering species demographics, behaviour, landscape ecology and mitigation planning. This superb collection of articles will be required reading for anyone interested in the budding field of road ecology, the growing pains of transportation networks, and "charismatic microfauna" which hedgehogs portray so well.

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Living on the edge has its disadvantages: several hundreds of thousands of hedgehogs fall victim to traffic in The Netherlands each year.
Photographs: Niels Kooyman (above), Marcel Huijser (left).

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