



LUTRA

Journal of the Dutch Mammal Society
Volume 55 - Number 1 - June 2012



Do right and fear no one

For some years now, the European Community has faced very serious financial and economic problems. In this context, there is a drive to cut back on what is seen as unnecessary expenditure. Nature conservation and scientific research on conservation biology do not figure highly in the priority lists of many policy makers and have been greatly affected by these cutbacks. More than before, publicly funded research has to provide clear evidence of its probable (economic) benefits to humans and society, or show that it can deliver straight-forward answers to questions about the effectiveness of European regulations and policy measures. At the same time, scientific research programmes are also being forced to fit in with increasingly rigid time-management, and provide ever-more detailed budget estimates.

In contrast to these actual trends in how research is organised and funded, much biological investigation depends greatly on the personal interest or passion of the researchers involved. Professional biologists are sometimes – pejoratively – considered to be the most ‘emotional’ of scientists. Not everybody realises the surplus value that stems from biologists being highly involved in and engaged with their research topics. The dedication of research workers goes some way to explaining their willingness to undertake bizarre activities, such as analysing animal faeces, doing autopsies of half-rotten bodies, controlling live traps or making observations

in the middle of the night at -20°C. If one had to pay someone who doesn’t really want to do such things, prefers a nine to five job and has no empathy with the aim and the context of the investigation, the quality of the findings and results might be questionable. Moreover, only a dedicated researcher will be paying attention to possible unexpected phenomena, or be able to postulate new hypotheses while out in the field (or in the lab) performing the planned research activities. One usually needs a lot of expert knowledge to postulate the right new questions. The development of scientific knowledge rests to a great extent on the passion and involvement of those engaged in it. There is a price attached to this progress but it can’t be calculated in purely monetary terms.

On top of all this, mammals are not the easiest biological subjects to study: most species lead very hidden lives. Studying them often requires lots of time and patience – again requiring the researcher’s involvement, passion, and sense of precision. Bekker’s description (2011) of the mammalogist’s material toolkit might be extended by other non-material characteristics: passion, patience and sense of precision. By working for a long term in a specific research field it becomes possible to penetrate the inner world of the subject, and really become an expert – even at risk of being considered by outsiders as a kind of a bizarre hobbyist. One needs to question whether the existing trend towards economically man-

aged 'science-to-order' can ever generate the same deep expertise and the effect that this has as a driving force for science.

In this context, professional researchers are often very grateful for the support they receive from many dedicated volunteer workers. This relationship is often symbiotic. Amateur naturalists learn much and feel a sense of value when participating in formally structured scientific surveys. The volume of work (often at unsocial hours) and expertise that volunteers contribute is very impressive and would hardly be affordable through the wage economy. One only needs to look at the wealth of articles that have appeared in *Lutra* that have been dependent on this volunteer labour pool to realise what a valuable resource it is. Volunteers deserve some 'pay back' for this. One way we try to do this is by ensuring that *Lutra* remains an open access science journal, giving volunteers the same access to publications as professional researchers.

In this volume of *Lutra* we present a diverse mix of papers, originating from different contexts. Hardly any of them could have been the product of ordinary nine-to-five-jobs. Wijzman's paper on the relation between the reproduction of pine martens (*Martes martes*) and food availability brings together data from different origins, much of it gathered by many passionate volunteers over several years – representing a priceless amount of work. Chanin and Gubert perform some clear tests and highlight the impact of fragmentation on common dormice (*Muscardinus avellanarius*), a species that is strictly protected by the European Habitat Directive. Kuipers et al. report their findings on the food ecology of the garden dormouse (*Eliomys quercinus*), another member of the dormouse family. In contrast to the former species and analogous to the pine marten, the garden dormouse is not protected at

the European level although being of prime conservation interest in the Netherlands and Flanders. The analyses of dormouse faeces (mostly collected by volunteers) is a striking illustration of the need for lots of patience and enthusiasm. Economic managers might find it hard to believe that this is part of a real job, but from this painstaking work they have developed clear recommendations on habitat management that might help conserve this Red List species. Haigh et al.'s paper on western hedgehogs (*Erinaceus europaeus*) illustrates how science works: a continuous bringing together of carefully made observations on a species that helps to complete our knowledge of its – elementary – biology. The study by de Vooy et al. on the harbour seal (*Phoca vitulina*) population in the estuarine area in the south-western Netherlands is a long term study that provides critical information about the evolving relationship between man and nature over the centuries. Curiosity and the passion to increase our biological knowledge can often drive the development and application of new techniques. Camphuysen and Siemensma brought together a large amount of knowledge in their conservation plan for the harbour porpoise (*Phocoena phocoena*) in Dutch waters, here thoroughly reviewed by Smeenk.

So, mammalogists should not hesitate to continue to pursue their job or hobby: there are plenty of interesting cases to investigate and many questions still to answer. And, even in an age of crisis, we should never abandon our most powerful strengths: our passion, patience and sense of precision.

Bekker, J.P. 2011. The mammalogist's toolkit. *Lutra* 54 (2): 65-68.

Koen Van Den Berge

Common dormouse (*Muscardinus avellanarius*) movements in a landscape fragmented by roads

Paul Chanin¹ & Leonardo Gubert²

¹ North View Cottage, Union Road, Crediton, Devon, EX17 3AL, United Kingdom,
e-mail: mammals@chaninweb.co.uk

² EnterpriseMouchel Ltd, Ash House, Falcon Road, Exeter, Devon, EX2 7LB, United Kingdom

Abstract: The common dormouse (*Muscardinus avellanarius*) is widespread in Europe but populations have declined in some countries as a result of habitat loss and fragmentation. A population of common dormice living beside a dual carriageway road in southwest England was studied in 2007-2010 in order to investigate the impacts of roads on habitat fragmentation at the local scale (tens of metres), i.e. the possible isolating effects of roads for a population. Each carriageway was eight metres wide with verges of two metres. Nest boxes and nest tubes were installed on each side of the road, and on the central reservation where areas of woodland or scrub existed. Animals were individually marked using implanted microchips (PIT tags). Common dormice were found in fragments of woodland or scrub as small as 0.2 ha and breeding was regularly recorded in fragments of 0.5 ha or larger. Common dormice were not present in all fragments in all years. Two individuals moved between the central reservation and the side of the road and there was indirect evidence of additional road crossings. This has implications for the conservation of dormice at the landscape scale where it is important to understand the extent to which roads are barriers to movement and the extent to which dormice will use fragmented habitats. It is also important to understand the extent to which dormice use habitats which are fragmented by roads when carrying out surveys for common dormice in connection with development and in mitigating the impacts of this development.

Keywords: *Muscardinus avellanarius*, dormouse, habitat fragmentation, metapopulation, road.

Introduction

The common dormouse (*Muscardinus avellanarius*) is a small arboreal rodent which is found throughout Europe, from southwest England and Brittany to northern Turkey and parts of central Russia and from southern Sweden to Sicily and central Greece (Juškaitis 2008). In many parts of its range (including the UK) it has declined in numbers in recent years (Verbeylen 2006) and is protected throughout the European Union as a consequence (Bright et al. 2006).

It has been suggested that the main reasons

for its decline in the UK are loss and fragmentation of habitat combined with changes in woodland management practices which have led to a massive reduction in the practice of coppicing (Anonymous 2010). Juškaitis (2008) reviewed reports from several European countries citing similar impacts.

Common dormice are considered to be woodland specialists and it has been suggested that semi-natural ancient woodland where hazel is managed on a long rotation coppice cycle provides the best conditions for them (Bright et al. 1996). However, Eden & Eden (1999) have pointed out the importance of both hedgerows and scrub as habitats for common dormice in southern England and the Dormouse Conservation Handbook

© 2012 Zoogdierveniging. Lutra articles also on the internet: <http://www.zoogdierveniging.nl>

(Bright et al. 2006) advises that all woody areas should be regarded as potential habitats for this species. Elsewhere in Europe common dormice are able to exploit a wide range of woodland habitats, including those dominated by spruce (*Picea abies*) and birch (*Betula pendula* and *Betula pubescens*) in Lithuania (Juškaitis 2008) and, as reviewed by Juškaitis (l.c.) dwarf pine (*Pinus mugo*) in the Tatra mountains (Miklós & Buchamerová 2004), former Czechoslovakia (Andera 1987) and former Yugoslavia (Kryštufek & Tvrkovič 1988, Kryštufek & Petkovski 1990). In several countries, common dormice have been recorded in non-wooded habitats including Culm grassland (poorly drained, acid pasture dominated by *Molinia caerulea* and *Juncus* spp.) in the UK (Chanin & Woods 2003), and, again following Juškaitis (l.c.), wet meadow in Poland (Białas et al. 1989) and reedbeds in Germany (Berthold & Querner 1986).

Studies by Bright et al. (1994) in the UK and Mortelliti et al. (2010) in Italy have examined the effects of habitat fragmentation and isolation on common dormice at the landscape scale. Bright et al. (l.c.) reported that both isolation and woodland size affected distribution and also noted the effects of hedgerow prevalence on common dormouse incidence. They suggested that for isolated woodlands, 20 ha might represent the minimum size which could ensure the long term survival of a common dormouse population. Mortelliti et al. (l.c.), working in a very different landscape, demonstrated the independent importance of habitat loss and of habitat fragmentation in determining the distribution of common dormice and red squirrels (*Sciurus vulgaris*), showing that habitat loss has the greater effect. They also showed that hedgerows were a factor in determining the distribution of dormice but not of squirrels.

Bright & Morris (1991, 1992) reported that radio-tracked common dormice were reluctant to descend to the ground to cross quite small gaps (a few metres) between blocks of continuous habitat. They noted that on



Figure 1. Location of the site in southwest England. The inset detail shows the route of the A30 (thick line) heading west from Exeter, past Bodmin (filled squares).

some occasions dormice made quite substantial detours to avoid doing so. However, P.A. Morris (personal communication) has also found dormice on the central reservation of a dual carriageway in southeast England (the A21). Wouters et al. (2010) reported finding dormouse nests in a dense patch of bramble scrub, less than 100 m² in area which was isolated from other habitat by 15 m of tarmac. In central Germany dormice were found to inhabit a high proportion of traffic island at interchanges between a motorway and side roads (Schulz et al., in press). All 20 islands larger than 0.2 ha had signs of dormice whereas signs were only found at two of the four islands smaller than this. Moreover, Juškaitis (2008) reported several examples of common dormice crossing distances of 5 m to 50 m across the ground and Büchner (2008) reported six common dormice crossing 250-500 m across a treeless landscape between patches of woodland. These greater distances were probably made during dispersal but Juškaitis (l.c.) found one common dormouse using an isolated nest box which it had to cross 50 m on the ground to reach, suggesting that such distances may be covered in the

course of day to day activities.

Radio tracked common dormice in woodland rarely moved more than 70 m from their nest (Bright et al. 1991), while Naim (2010) observed movements up to 600 m within continuous woodland. In these cases dormice did not need to cross the ground.

We have detected common dormice crossing the ground over small distances (10-20 m) to use small fragments of habitat (<100 m²) in the course of survey work in the UK (personal observations), but were unable to determine whether or not this was frequent behaviour.

Dormice are frequently present at sites where developments are planned in southern England (personal observation of the first author) and it is important to take their behaviour into account when planning mitigation for this (Bright et al. 2006). There is a clear need to understand the extent to which roads are a barrier to movement and to which dormice can exploit fragmented habitats. The discovery that dormice occurred on the central reservation of a major road in southwest

England in 2003 (M. Pickard, personal communication) encouraged us to investigate this further. During 2006, a preliminary survey using nest tubes showed that dormice were still present and a larger scale study was initiated in 2007. The aim of the work described here is to determine the extent to which such movements might enable common dormice to exploit habitats which are fragmented by roads at the scale of tens of metres, creating fragments of habitat which are less than one hectare in size.

Methods

Our study site in southwest England, UK stretched along two kilometres of the A30 in Cornwall, and is five kilometres to the northwest of Bodmin (figure 1). The road is dual carriageway with narrow strips of woodland and scrub less than 20 m wide on the central reservation and adjacent road sides. The estimated Average Annual Daily Flow of vehicles

Table 1. Habitat description, area and number of nest boxes for each section.

Sections	Approximate area (ha)	No. of boxes	Habitat description
S1	0.5	11	Small young woodland plot. Mostly birch, pine and sycamore surrounded by gorse and bramble.
S2	0.4	9	Scattered scrub comprising gorse, bramble and pockets of hawthorn.
S3*	0.2	5	Dense scrub comprising tall gorse, hazel and hawthorn. This section is connected to a large area of gorse and blackthorn scrub over ten hectares.
S4*	10	3	This section is connected to S3 via habitat outside the highway boundary. Mostly young blackthorn thicket close to the road.
C1	0.3	6	Tree plot with ash and hazel predominantly, surrounded by gorse and bramble.
C2	0.9	20	Linear tree plot in central reservation with ash and sycamore being the main species and occasional oak, hazel and hawthorn. Gorse and bramble is found at localised areas throughout this plot.
C3	0.7	20	Long plot of linear willow, hazel and hawthorn with occasional gorse and pockets of bramble.
N1	0.3	13	A fairly open area at the eastern end of the plot with localised areas of gorse and scattered oak, willow, hawthorn and bracken changing to dense gorse and blackthorn/hawthorn thicket to the west.
N2*	0.7	13	Mature hazel, willow and stunted oak from a remnant hedgerow dominate this section together with occasional gorse, blackthorn, bramble and honeysuckle.

*connected with suitable habitat outside the study site.



Figure 2. View from section C1 looking west with C2 to the left, N1 and N2 to the right. *Photograph: Paul Chanin.*



Figure 3. Semi-natural woodland at N2 in early spring with oak and hazel predominating. *Photograph: Paul Chanin.*



Figure 4. C1 during the summer with ash, hazel and gorse in view. *Photograph: Paul Chanin.*



Figure 5. C2 in winter with ash and hawthorn visible. *Photograph: Paul Chanin.*

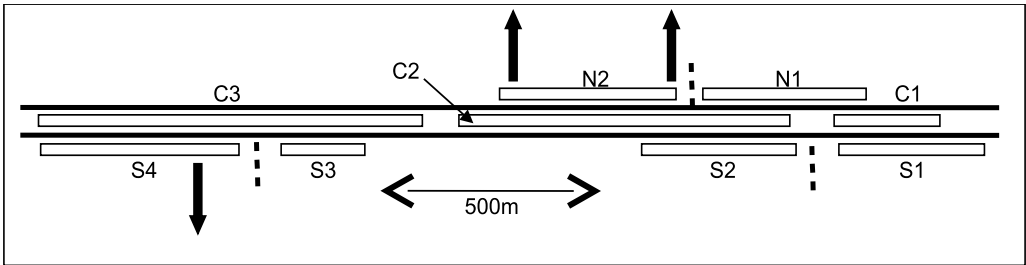


Figure 6. Schematic layout of sections with width not to scale. The study site is two km long and up to 75 m wide. Solid lines are carriageways, dashed lines are side roads, arrows indicate connections to off-site habitat.

was 23,143 between 2007 and 2010 (Department for Transport 2012). However this road is a major holiday route and traffic flows peak at summer weekends. The highest recorded flow on a single day in 2011 was 36,039 vehicles in August (O. Dash, personal communication). The study site was limited to land designated as highway, which was all within 20 m of the road edge. The maximum width across the site was 70 m.

The habitats in which common dormice were found consisted of semi-natural woodland, plantation (including broadleaved as well as coniferous species) and scrub, beside the road and on the central reservation (table 1 and figures 2-5). Some of this was close, or connected, to off-site vegetation which was suitable for dormice but there were several isolated fragments of potential common dormouse habitat which could not be reached without crossing the ground, including three separate sections on the central reservation. The fragments on the central reservation were separated from previously connected habitat when the road was upgraded from single to dual carriageway. They have been isolated for a minimum of 25 years. All isolated habitat fragments were less than 1 ha in size and all could be reached by crossing gaps no greater than twelve metres (of which eight metres was road surface and four metres grass verge). Gaps between some adjacent fragments along the length of the road were greater than this (maximum of 100 m on central reservation, 500 m on south side of the road) and some

were less, across minor roads or tracks. Eight of the fragments were narrow (<20 m wide) and connections to nearby habitat were via hedges or trees and shrubs of a similar width. One, S4, was connected throughout its length to off-site habitat which was not surveyed.

Nine fragments of common dormouse habitat, referred to as 'sections', were numbered sequentially from east to west with a prefix letter referring to their location on the north side of the road, south side, or central reservation (N, S, C respectively) (figure 6). Nest boxes were distributed amongst them, approximately in proportion to the length of road along which they stretched, due to the linear nature of the habitat which did not permit a grid to be used. Within these, nest box density was fairly uniform (approximating to 20 ha⁻¹). In S4, where only a small proportion of the habitat was at the roadside, approximately 100 m of road was monitored but the density of boxes was very low (0.3 ha⁻¹).

We used 100 dormouse nest boxes (Heavy Duty Dormouse Boxes supplied by Alana Ecology Ltd, Totnes, UK) as our principle means of sampling the population, since we wished to monitor all aspects of common dormouse behaviour, including breeding (figure 7). These were spaced at intervals of 30 m and at heights up to two metres, attached by wire to trees or shrubs. In the hope that it would increase the probability of finding dormice we also installed 200 nest tubes, interspersed with the boxes at a spacing of ten metres and wired to horizontal branches (Chanin &



Figure 7. A nest box attached to a small tree by wire. *Photograph: Paul Chanin.*

Gubert 2011) (figure 8).

Boxes and tubes were installed in March 2007 and checked monthly from April to October in 2007 and 2008. In 2009 and 2010 checking ended in September as no dormice had been recorded in October in the previous years. Most boxes were only checked once per month but on a few occasions, checks were spread over two days when a large number of animals had to be handled. When this occurred, small numbers of nest boxes and nest tubes which had been occupied on the first day were rechecked on the second to determine whether occupancy had changed overnight.

Dormice over 12 g in weight were marked on first capture with radio-frequency identification tags, also known as PIT (passive integrated transponder) tags (FDXB – 8 mm tags manufactured by pet-iD UK Ltd, Hassocks, UK) under the terms of annual licences from Natural England. Dormice which did not have an adult pelage (i.e. they had greyer fur) were classified as juveniles. One adult female dor-



Figure 8. A nest tube wired to a small sycamore. *Photograph: Paul Chanin.*

mouse was not tagged because she was heavily pregnant. Captured dormice were scanned with an 'iDentifier' (manufactured by pet-iD UK Ltd) weighed, sexed and their reproductive condition assessed.

Results

Captures and movements

Sixty-two common dormice were marked during the course of the study, and a few individuals escaped before marking. Nine juveniles were tagged (three females, six males) and of the 53 tagged adults, 37 (70%) were female. Animals which were not tagged (including the pregnant female referred to above) were discounted from analyses as we were unable to record their movements and they could have been subsequently recaptured and included in the marked population. 88% of all captures were in nest boxes. More detailed information, such as the number of

Table 2. Evidence for dormice crossing a carriageway.

	Common dormice	Between sections
Proven: <i>n</i> =3		
	Dm 02	S3 to C3
	Dm39	C1 to N1 N1 to C1
Strong evidence: <i>n</i> =5		
	Dm39 before first capture Dm03, Dm09, Dm45, Dm60	N1 to C1

males, females and juveniles (re)captured per patch and year, has been published elsewhere (Chanin & Gubert 2011).

Only four adult dormice were first 'caught' (i.e. found in a nest box or tube) on the south side of the road, 25 on the central reservation and 24 on the north side. Two animals were caught on the side of the road as well as on the central reservation. Twenty-two of the marked animals were caught more than once (including one juvenile), with the total number of captures reaching 103.

We observed three movements between sections. One adult female (Dm02) was caught first on the south side of the road (S3) in April 2007 and again 12 months later on the central reservation (C3) approximately 80 m away in a direct line. An adult male (Dm39), first caught in C1 in April 2009 was found a month later in N1, almost directly opposite - ca. 30 m away. The following day it was back in the original nest box on the central reservation. No evidence of breeding was recorded in C1 (no juveniles were found, no females showing signs of pregnancy, lactation or recent lactation). We therefore conclude that Dm39 must have crossed one additional time from the edge of the road (probably N1) to get to the central reservation before we first caught it.

We have no other direct evidence of movements between sections but noted that in addition to Dm39, four dormice were caught in C1 (two males, two females), despite the fact that we never recorded breeding in this small (0.2 ha) section. The only source of the dormice in C1 is that they crossed the road to get there

and we consider this to be strong indirect evidence of further crossings. We therefore have strong or direct evidence for 8 crossings of the road during the four years of our study (table 2). We know that at least two male and four female dormice were involved.

We know that Dm39 crossed the carriageway twice between 28 April and 28 May, 2009. Captures of Dm02 were a year apart but she was first recorded on the central reservation in May 2008. Three of the other four dormice caught in C1 were first captured in either April or May, one in July.

Use of sections

Dormice were never recorded in sections S2 and S4 but were present in the other sections for one to four years of the study (table 3). Breeding occurred in three out of four years in C2 and N2, less frequently elsewhere. The highest numbers of captures were also recorded in these two sections.

Although section S4 was considerably larger than others, much of this was away from the road side and outside the study site. Only three nest boxes (and four tubes) were installed along the carriageway here and the density of boxes much lower than in others. The absence of dormouse captures from this large block may be influenced by this. Excluding S4, breeding was more likely to occur in sections of 0.5 ha or greater (eight times out of a possible 16 opportunities - four sections for four years) than those smaller than 0.5 ha

Table 3. Pattern of use of each section by dormice during the four years of the study.

	2007	2008	2009	2010
N1	-	Present	Present	Present
N2	Breeding	Breeding	Breeding	-
C1	Present	Present	Present	Present
C2	Breeding	Breeding	Present	Breeding
C3	Breeding	Present	Present	Present
S1	-	-	Present	Breeding
S2	-	-	-	-
S3	Present	-	Breeding	Present
S4	-	-	-	-

(two out of 16 opportunities). Nevertheless one female dormouse produced a litter in the smallest section, i.e. 0.2 ha in extent (table 3). Excluding S4 there is a significant difference in the frequency that breeding was recorded in blocks less than 0.5 ha compared to those of 0.5 ha or greater ($\chi^2 = 5.24$, $df=1$, $P<0.05$)

Discussion

Our results do not contradict those of Bright et al. (1994) and Bright (1998) who stated that common dormice were 'reluctant' to cross gaps and populations were 'less likely to persist' in woods smaller than 20 ha. However, the results presented here do demonstrate that common dormice are more flexible in their use of habitats than may be implied by these authors. While dormice might be reluctant to cross gaps, they are clearly capable of crossing at least one carriageway of a major road which, during the summer, can be very busy. In addition, while isolated populations in small woods may be vulnerable to extinction, aggregations of very small fragments of habitat (<1 ha) might enable populations to persist over considerable periods of time, where they are sufficiently close to one another to permit recolonisation.

It is difficult to compare our results with those of Mortelliti et al. (2010) who worked in a very different landscape where arable

land and land cultivated for vines, fruit and olive trees dominated the landscape. Much of southwest England is farmed as pasture with very small fields and a dense network of hedges. Their conclusion, that the distribution of common dormice is affected by habitat fragmentation, is likely to be dependent on the scale at which fragmentation is measured. We have shown that dormice were breeding in fragments of habitat isolated by roads at least 25 years after the road was constructed.

The area studied by Büchner (2008) in East Germany is more similar to ours, in that his habitat fragments were relatively small (0.66 ha to 4.25 ha), though more widely separated than ours. Capturing common dormice in both nest boxes and live traps, he marked 204 animals in a two year period. Of the 164 recaptures of dormice, six were of dormice which had moved between woodlands over distances ranging from 350-840 m. All these movements involved travelling on the ground through crops including clover, wheat and maize. The minimum distances crossed on the ground ranged between 250 m and 500 m.

Schulz et al. (in press), found considerable numbers of dormouse nests in some areas of roadside habitat. At one complex interchange they recorded 153 nests over a period of three years in 8.8 ha of woodland. Seventy-five percent of these were in fragments of habitat isolated by roads from the surrounding countryside. They concluded that dormice do not avoid the proximity of roads and suggested that roadside habitat might function as a good habitat for dormice, including as dispersal routes. However they also pointed out that as well as offering potential benefits to dormice, roads might have negative impacts resulting from noise, pollution and road deaths.

They observed the presence of dormice in fragments smaller than any of ours (<0.2 ha) noting that in their sample, fragments large than this all had dormice present whereas not all of those smaller than this did. They did not catch or mark individual dormice and had no indication as to whether or not breeding

occurred but pointed out that they recorded more than 20 instances where dormice had crossed a road at least once to colonise habitat which had been planted following road construction.

Bright et al. (1994) stated that their data imply a possible metapopulation model and our results, together with those of Büchner (2008) and Schulz et al. (l.c.) support that hypothesis. Bright et al. emphasised the importance of connecting hedges in this context but we have shown that dormice are willing to cross very open, exposed ground for short distances as have Schulz et al. while Büchner's data indicate that they may cross a few hundred metres over ground which has no trees or shrubs but does offer concealment in the form of agricultural crops.

A study by Macpherson et al. (2010) showed that both wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*) crossed small, single carriageway roads. In the absence of intervention, 7% of wood mice and 12% of bank voles crossed a six metre wide road, with 28% and 22% respectively crossing a road of 2.5 metres in width. Both species frequently travelled distances greater than these road widths in the course of their normal travels, suggesting that home ranges were normally confined to one side of the road or the other. Forty nine animals were translocated from one side of a road to the other and 16 (33%) of these crossed back again. In our study there is strong evidence that six (11%) of 53 adults crossed the road with no intervention. Given that common dormice are arboreal whereas wood mice and bank voles spend a considerable amount of time on the ground, this seems high, but may reflect the fragmented nature of the habitat in our study site such that dispersal movements of any dormice were likely to include a road crossing.

We were unable to determine whether or not the presence of the road has an impact on the mortality of common dormice. Of the 62 dormice marked, 10 were caught in two consecutive years and none in three or more years.

However, our sample is very small and apart from the few juveniles that were marked we did not know the ages of the animals we captured. Therefore comparisons with the life tables presented by Juškaitis (2008) are very difficult to make. He showed that spring-born young had mortality rates of 60-70% in the first two years of life so the probability of finding dormice of three years or greater was small in our area with the sample size that was achieved.

Reasons for crossing

We only know the actual timing of crossing for one animal (Dm39), which crossed twice in April/May but there is a preponderance of first captures of dormice in S1 and C1 during these two months, not long after dormice have left hibernation and just before the onset of the breeding season. However we do not know whether these dormice had crossed the carriageway immediately before they were captured or in the previous autumn prior to hibernation. Crossing of the road might therefore be a dispersal movement or in connection with breeding.

A further possibility is that dormice crossed the road to gain access to food. Comparisons of the species present in the sections between which movements occurred or were inferred, show that ash (*Fraxinus excelsior*) is the main species present in C1 but not N1. One would expect ash to be particularly favoured when it is fruiting, later in the year than these movements. Bright and Morris (1993) found that common dormice did not favour ash trees and that fruit-bearing species, such as way-faring tree (*Viburnum lantana*) and bramble (*Rubus fruticosus*), were taken in preference. Ash trees were visited most frequently during August and October in their study. The main difference between S3 and C3 (one movement recorded) is that willow (*Salix sp.*) is present in the latter. The timing of crossing is unknown but the animal was present in C3 in the spring not the fruiting season.

Juškaitis (2008) observed that 90% of first year common dormice were found in the same area in the spring as they had been the previous autumn suggesting that most dispersal on his study site occurred before hibernation although dispersal movements also occurred at the beginning of the year following birth, where young male dormice were found sharing nest boxes with adult males and subsequently moved away. The high proportion of females crossing the road in our study suggests that breeding may not be the primary motivation since there is good evidence that it is the males which move the greatest distances during the breeding season (Juškaitis 2008, Naim 2010). Our data therefore provide greater (though weak) support for movements across the road being related to dispersal rather than breeding.

One factor which may promote dispersal across roads in our study site is the fact that habitat fragments are small.

Conclusions

We have shown that common dormice are able to exploit small fragments of habitat (<1 ha) separated by roads where the distances to be crossed are no greater than twelve metres. These results have implications for the conservation of this rare species and in the practical implementation of legislation which affects it.

A recent review of national conservation efforts in the UK pointed out the need to “Enhance connections between, or join up, sites, either through physical corridors, or through ‘stepping stones’.” (Lawton et al. 2010). Local efforts to achieve this have been initiated, with common dormice considered a significant beneficiary (Nelson 2010, Al Fulajj 2010). Small fragments of habitat, which are partially isolated but not remote from each other may have an important role to play as such ‘stepping stones’, and medium sized roads (up to 12 m including verge) should not be seen as barriers to the movements of common dormice.

These factors may also be important in planning mitigation for common dormice where development might otherwise lead to fragmentation and loss of habitat. Consideration could be given to incorporating roadside planting in an effort to minimise the distances that dormice have to cross over open ground as an alternative to promising, although somewhat more complex, approaches using bridges over roads (Stride 2009, Morris & Minato 2012). Planting of even quite small areas of scrub or woodland may increase breeding opportunities for dormice provided the level of isolation is low and the areas are greater than 0.5 ha. Extensive planting of suitable habitat along roads will also promote dispersal and has the potential to link patches of habitat which would otherwise be otherwise isolated. Further studies to assess the risk of these patches creating a sink would be valuable.

We also believe that guidelines for ecological consultants who are considering whether or not habitat is suitable for common dormice, may need to be revised to take into account the fact that small fragments of habitat are readily used by them. For example, the Dormouse Conservation Handbook (Bright et al. 2006) states that “Dormice have been found in small woods (even down to two hectares where other suitable habitat is adjacent)”. Clearly this value can be reduced by an order of magnitude.

In addition, the fact that dormice do not permanently inhabit some fragments means that surveys done in a single season and limited to one fragment may fail to reveal the fact that an area is used by dormice, though not on a permanent basis. Under such circumstances, where dormice are not found during surveys but are known to be present nearby, it would be prudent to act on the assumption that dormice could be present in subsequent years.

Acknowledgements: This research was supported by the Highways Agency and EnterpriseMouchel. English Nature provided grants covering equipment and Paul Chanin’s time in the second year. We are grateful to

Ursula Digby for supporting a pilot project in 2006 and to Matt Pickard for drawing our attention to the existence of dormice on the central reservation of the A30. Pat Morris, Johnny Birks and Sven Büchner very kindly read a draft and suggested several improvements. We are grateful to two referees whose comments enabled us to substantially improve the manuscript.

References

- Al Fulajj, N. 2010. Reconnecting the Countryside 2010. People's Trust for Endangered Species (PTES), Dormouse Monitor, Autumn 2010: 13. URL: http://www.ptes.org/files/1330_2010_autumn_dormouse_monitor.pdf; viewed May 2012.
- Andera, M. 1987. Dormice (Gliridae) in Czechoslovakia. Part II. *Muscardinus avellanarius*, *Dryomys nitedula* (Rodentia: Mammalia). Folia Musei Rerum Naturalium Bohemiae Occidentalis, Plzen, Zoologica 26: 1-78.
- Anonymous 2010. Species Action Plan: Dormouse. In: Anonymous. Biodiversity: The UK Steering Group Report - Volume II: Action Plans. Joint Nature Conservation Committee, Peterborough, UK. URL: <http://webarchive.nationalarchives.gov.uk/20110303145213/http://ukbap.org.uk/UKPlans.aspx?ID=462>; viewed May 2012.
- Berthold, P. & U. Querner 1986. Die Haselmaus (*Muscardinus avellanarius*) in Nestern freibrütender Singvögel. Zeitschrift für Säugetierkunde 51: 255-256.
- Białas, I., W. Chętnicki & T. Kupryjanowicz 1989. A biometric description of common dormice from Gorce (Beskid Wysoki Mts), Southern Poland. Acta Theriologica 34: 648-651.
- Bright, P. 1998. Behaviour of specialist species in habitat corridors: arboreal dormice avoid corridor gaps. Animal Behaviour 56: 1485-1490.
- Bright, P.W., P. Mitchel & P.A. Morris 1994. Dormouse distribution: survey techniques, insular ecology and selection of sites for conservation. Journal of Applied Ecology 31: 329-339.
- Bright, P.W. & P.A. Morris 1991. Ranging and nesting behaviour of the dormouse, *Muscardinus avellanarius*, in diverse low-growing woodland. Journal of Zoology (London) 224: 177-190.
- Bright, P.W. & P.A. Morris 1992. Ranging and nesting behaviour of the dormouse, *Muscardinus avellanarius*, in coppice-with-standards woodland. Journal of Zoology (London) 226: 589-600.
- Bright, P.W. & P.A. Morris 1993. Foraging behaviour of dormice *Muscardinus avellanarius* in two contrasting habitats. Journal of Zoology (London) 230: 69-85.
- Bright, P., P. Morris & T. Mitchell-Jones 1996. The dormouse conservation handbook. First edition. English Nature, Peterborough, UK.
- Bright, P., P. Morris & T. Mitchell-Jones 2006. The dormouse conservation handbook. Second edition. English Nature, Peterborough, UK.
- Büchner, S. 2008. Dispersal of common dormice *Muscardinus avellanarius* in a habitat mosaic. Acta Theriologica 53: 259-262.
- Chanin, P. & L. Gubert 2011. Surveying hazel dormice (*Muscardinus avellanarius*) with tubes and boxes: a comparison. Mammal Notes 4: 1-6.
- Chanin, P. & M.J. Woods 2003. Surveying Dormice using Nest Tubes. Results and Experience from the South West Dormouse Project. Research report 524. English Nature, Peterborough, UK.
- Department for Transport 2012. Transport statistics. URL: <http://www.dft.gov.uk/traffic-counts>; viewed May 2012.
- Eden, S.M. & R.M.G. Eden 1999. Dormice in Dorset - the importance of hedges and scrub. British Wildlife 10: 185-189.
- Juškaitis, R. 2008. The Common Dormouse *Muscardinus avellanarius*: Ecology, Population Structure and Dynamics. Institute of Ecology of Vilnius University, Vilnius, Lithuania.
- Kryštufek, B. & S. Petkovski 1990. New records of Mammals from Macedonia (Mammalia). Fragmenta balcanica 14: 117-129.
- Kryštufek, B. & N. Tvrtković 1988. Insectivores and rodents of the Central Dinaric Karst of Yugoslavia. Scopolia 15: 1-59.
- Lawton, J.H., P.N.M. Brotherton, V.K. Brown, C. Elphick, A.H. Fitter, J. Forshaw, R.W. Haddow, S. Hilborne, R.N. Leafé, G.M. Mace, M.P. Southgate, W.J. Sutherland, T.E. Tew, J. Varley & G.R. Wynne 2010. Making Space for Nature: a review of England's wildlife sites and ecological network. Report to Department for Environment, Food and

Rural Affairs. Defra, London, UK. URL: <http://archive.defra.gov.uk/environment/biodiversity/documents/201009space-for-nature.pdf>; viewed May 2012.

Macpherson, D., J.L. Macpherson & P. Morris 2011. Rural roads as barriers to the movements of small mammals. *Applied Ecology and Environmental Research* 9 (2): 167-180.

Mikloš, P. & V. Buchamerová 2004. Spatial activity of common dormouse (*Muscardinus avellanarius* L.) in dwarf pine habitat. In: M. Adamec & P. Urban (eds.). *Vyskum a Ochrana Cicavcov na Slovensku VI. Zborník referatov z konferencie (Zvolen 10-11 102003)*: 93-100. *Statná ochrana prírody SR, Centrum ochrany prírody a krajiny, Banská Bystrica, Slovakia* (with English summary).

Morris, P. & S. Minato 2012. Wildlife Bridges for small mammals. *British Wildlife* 23: 153-157.

Mortelliti, A., G. Amori, D. Capizzi, C. Cervone, S. Fagiani, B. Pollini & L. Boitani 2011. Independent effects of habitat loss, habitat fragmentation and structural connectivity on the distribution of two arboreal rodents. *Journal of Applied Ecology* 48: 153-162.

Naim, D. Md. 2010. Conservation genetics of the common dormouse *Muscardinus avellanarius* in the UK. PhD Thesis. University of Liverpool, UK.

Nelson, J. 2010. Restoring hedgerow havens. People's Trust for Endangered Species (PTES), Dormouse Monitor, Autumn 2010: 8-9. URL: http://www.ptes.org/files/1330_2010_autumn_dormouse_monitor.pdf; viewed May 2012.

Schulz, B., S. Ehlers, J. Lang & S. Büchner, in press. What role do roadside habitats play for hazel dormice?

Stride, I. 2009. Dormouse Bridge Design and Use. Unpublished report to the People's Trust for Endangered Species. URL: http://www.ptes.org/files/1262_dormice_bridges_final_report_1.pdf; viewed May 2012.

Verbeylen, G. 2006. Status and conservation of the common dormouse (*Muscardinus avellanarius*) in the Province of Limburg (Flanders, Belgium). *Lutra* 49: 75-88.

Wouters, A., W. Cresswell, D. Wells, N. Downs & M. Dean 2010. Dormouse mitigation and translocation. People's Trust for Endangered Species (PTES), Dormouse Monitor, Autumn 2010: 3. URL: http://www.ptes.org/files/1330_2010_autumn_dormouse_monitor.pdf; viewed May 2012.

www.ptes.org/files/1330_2010_autumn_dormouse_monitor.pdf; viewed May 2012.

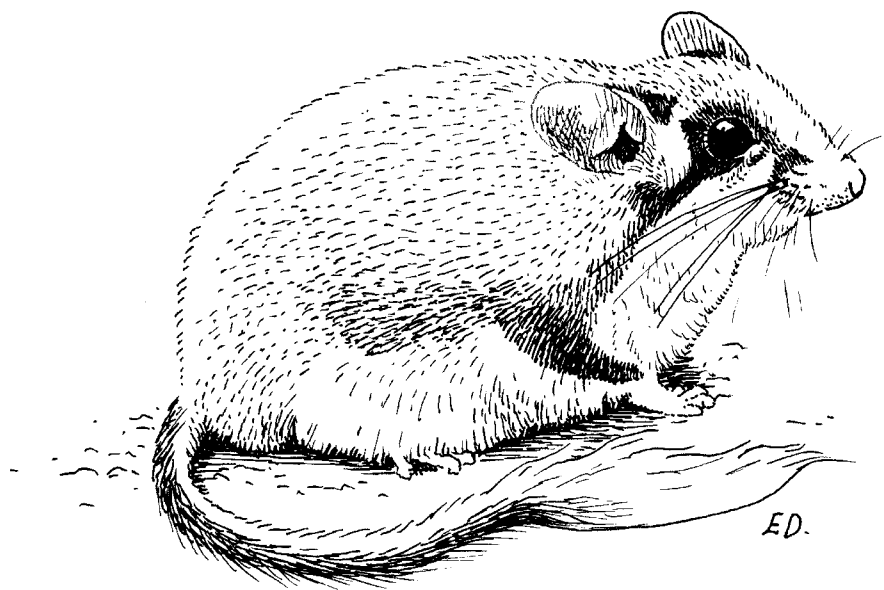
Samenvatting

Verplaatsingen van hazelmuizen (*Muscardinus avellanarius*) in een door een weg verdeeld landschap

De hazelmuis komt in Europa op veel plaatsen voor. In sommige landen zijn de populaties afgenomen als gevolg van het verlies en versnippering van habitat. Wij bestudeerden een populatie hazelmuizen die leeft langs een autosnelweg in zuidwestelijk Engeland met als doel om op plaatselijk niveau na te gaan wat de invloed van die weg is in de vorm van versnippering van het habitat van de hazelmuis. Beide wegstroken zijn acht meter breed en hebben bermen van twee meter breed. Op plaatsen met wat bomen en struikgewas installeerden we nestkasten en nestbuizen, aan beide kanten van de weg en in de middenberm. Gevangen dieren werden met een microchip individueel herkenbaar gemerkt. We troffen hazelmuizen aan in bosjes met een omvang van minimaal 0,2 ha, in bosjes van minimaal 0,5 ha vonden we regelmatig nesten. Op de onderzochte locaties waren niet in alle onderzoeksjaren hazelmuizen aanwezig. Twee individuen verplaatsten zich van de middenberm naar de zijbermen van de weg en we verkregen indirect bewijs voor meer van dergelijke verplaatsingen. Deze waarnemingen hebben implicaties voor de bescherming van de hazelmuis op landschapsniveau, aangezien het daarbij van belang is om te weten of en in welke mate wegen barrières vormen voor verplaatsingen tussen dit soort snippers en daarmee voor de mate waarin deze snippers geïsoleerd zijn. Kennis van de versnipperende werking van wegen is ook van belang in verband met de ontwikkeling en het vaststellen van de effectiviteit van mitigerende maatregelen.

Received: 29 October 2011

Accepted: 28 March 2012



The diet of the garden dormouse (*Eliomys quercinus*) in the Netherlands in summer and autumn

Laura Kuipers¹, Janneke Scholten¹, Johan B.M. Thissen^{2*}, Linda Bekkers³,
Marten Geertsma⁴, Rian (C.A.T.) Pulles⁵, Henk Siepel^{6,7} & Linda J.E.A. van Turnhout⁸

¹ University of Applied Sciences HAS Den Bosch, P.O. Box 90108, NL-5200 MA 's-Hertogenbosch, the Netherlands

² Dutch Mammal Society, P.O. Box 6531, NL-6503 GA Nijmegen, the Netherlands,
e-mail: johan.thissen@zoogdiervereniging.nl

³ Jan Frankenstraat 38, 5246 VB Rosmalen, the Netherlands

⁴ Bargerveen Foundation, P.O. Box 9010, NL-6500 GL Nijmegen, the Netherlands

⁵ Meidoorn 129, NL-6226 WH Maastricht, the Netherlands

⁶ Department of Animal Ecology and Ecophysiology, Faculty of Science, Radboud University Nijmegen,
P.O. Box 9010, NL-6500 GL Nijmegen, the Netherlands

⁷ Alterra, Centre for Ecosystem Studies, Wageningen UR, P.O. Box 47, NL-6700 AA Wageningen, the Netherlands

⁸ Bas Dongen 9, NL-5101 BA Dongen, the Netherlands

Abstract: The food of the last remaining population of garden dormouse (*Eliomys quercinus*) in the Netherlands is studied by means of analysing faecal samples, collected in the summer and autumn of the year 2010. In total 139 scat samples were collected from 51 different nest boxes. The samples were visually analysed for the presence (or absence) of different animal and vegetable food items using a stereo microscope. Millipedes (Diplopoda), beetles (Coleoptera) and snails (Gastropoda) were found to be the main animal food sources. Important vegetable food remains were the fruit pulp of apples, pears and seeds. The identified seeds were the remains of blackberries (*Rubus* spp.) and elderberries (*Sambucus nigra*). The results were skewed by someone feeding the garden dormice with apples and pears. All the other food items were collected by the garden dormice themselves. These animal and vegetable food sources were present in more than 20% of the samples. Hymenoptera (Hymenoptera), earthworms (Lumbricidae), spiders (Araneae), harvestmen (Opiliones) and wood mice (*Apodemus sylvaticus*) were present in 5% to 20% of the samples. Flies (Diptera), true bugs (Heteroptera), woodlice (Isopoda), pseudoscorpions (Pseudoscorpiones), butterfly larvae (caterpillars) (Lepidoptera), songbirds (Passeriformes) and flowers were occasionally found. Invertebrates, especially millipedes, are the staple food during the entire active feeding period. In spring and early summer the garden dormouse eats relatively more vertebrates (possibly mainly the nestlings of birds and mice), gastropods, beetles and flowers, than in August-November. The first seeds of berries were identified in the beginning of August. The occurrence of seeds increased rapidly to 90% at the end of August and then decreased to 30% in September and 0% by the end of October. Garden dormice in woods seem to depend on the rich invertebrate fauna within the litter layer. Mesotrophic mull soils have a rich fauna of medium-sized to large invertebrates and these soils are disappearing from the Savelsbos as a result of traditional management practices being abandoned. Re-establishment of species-rich wood types that produce mesotrophic mull soils could be of benefit to the remnant population of garden dormouse in the Savelsbos.

Keywords: garden dormouse, *Eliomys quercinus*, dormice, faecal analysis, food.

Introduction

The garden dormouse (*Eliomys quercinus* Linnaeus 1766) is a critically endangered species in the Netherlands (Thissen et al. 2009). The only remaining and isolated Dutch population consists of about 70 animals and is located in the Savelsbos (Savel Wood) in southern Limburg. On the European Red List of mammals, the garden dormouse is classified as Near Threatened. This species has declined more than almost any other rodent in Europe and may have disappeared from as much as 50% of its former range over the last 30 years (Temple & Terry 2007). Diet studies can make an important contribution to developing appropriate management plans for this species (Litvaitis 2000). This was the rationale for carrying out a diet study in the Savelsbos during the summer and autumn of 2010.

Gil-Delgado et al. (2010) claim to be the first authors to report on seasonal variability in the food of the garden dormouse. They analysed a large number of faeces samples from Mediterranean Spain, a region with quite different conditions. A number of other authors have studied the food of garden dormice outside the Mediterranean region, but the diet was only studied for a limited period of the year or with little detail (Brosset & Heim de Balsac 1967, Holišová 1968, le Louarn & Spitz 1974, Gigirey & Rey 1999). These authors analysed the stomach contents of dead animals. Our study refrained from using lethal or invasive methods and used faecal analysis to acquire information on the diet of the garden dormouse.

Methods

Study area

The Savelsbos is a *Stellario-Carpinetum* woodland of 360 hectares in the extreme southeast of the Netherlands, situated on Maastrichtian limestone on the eastern slope of the Meuse valley near the town of Maastricht (Province of

Limburg). The last population of garden dormouse in the Netherlands lives at the bottom of the slope (60 to 90 m above sea level), in some 6 ha of land covering a portion of woodland and some adjacent agricultural land (50° 47' 24" N 5° 44' 15" E). The garden dormice of the Savelsbos are only active at night or during twilight, which is normal for the species. In summer 2009 two females with transmitters each had home ranges of 2.5 ha and a male had a home range of 3.4 ha (based on 95% minimum convex polygon; Dutch Mammal Society, unpublished data).

Nest boxes

Garden dormice use nest boxes as day roosts, for reproduction and even hibernation (Cortens & Verbeylen 2009a). Nest boxes for the garden dormouse have been provided in the study area since 2003. The design was developed by the Flemish organisation Natuurpunt (as described in Cortens & Verbeylen 2009b). A special feature of these boxes is that the entry is located at the back of the box, on the tree side. In 2007 the first garden dormice were detected in the nest boxes. In the summer and autumn of 2010, the year of this study, 84 nest boxes in the Savelsbos were checked for faecal matter.

Faecal samples

The faeces of garden dormouse are rather large, 2 to 4 mm wide and 7 to 15 mm long, sometimes even longer. They can be readily distinguished from those of other mammals which also use the nest boxes, such as wood mouse (*Apodemus sylvaticus*) and bank vole (*Myodes glareolus*).

All the faecal samples found inside or on top of a nest box were collected. Each sample contained all the faecal matter collected from a given nest box on one visit. The collecting method was similar to Gil-Delgado et al. (2010). From 25 June to 18 November 2010 samples were collected every week, except in

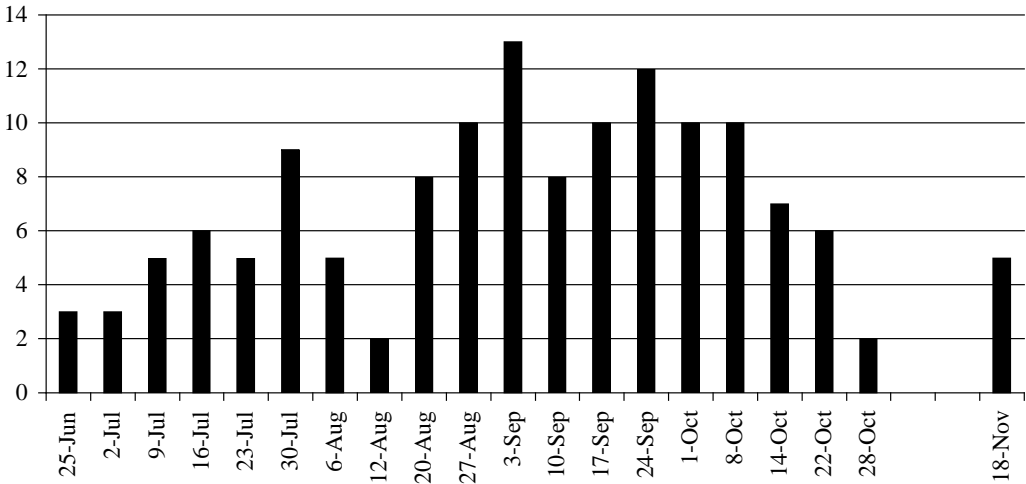


Figure 1. Number of faecal samples of garden dormouse collected per week in the Savelsbos in 2010.

the two first weeks of November. The samples were stored in 70% alcohol.

Faecal analysis

First, boiled lukewarm water was added to the samples to make them soft. The container was shaken gently and the fluid in the container above the faecal matter was removed. The samples were then pulled apart in a dish, into pieces smaller than 3 mm. Then a subsample of 0.4 ml was taken in a measuring cylinder. Seventy per cent alcohol was added to make a total volume of 5 ml. The faecal samples were then analysed using stereo microscopes with a magnification of between 10x and 63x and the presence of the different food items was determined.

Mosses were found in many samples, but these were considered not to have been consumed by the garden dormice. Many nest boxes contained nesting material, mainly mosses and feathers. While collecting excrements, these mosses must have been collected accidentally. For the same reason it was decided to only take feathers and hairs into account if there were many in the sample or if they were found in combination with bones. In some samples a few completely undamaged arthropods were found. These were

not taken into account, because these arthropods were presumed to have been inhabiting the nest boxes and collected accidentally.

Statistical analysis

In many weeks the number of samples collected was rather low. To get a clearer picture, periods of two weeks (and a last period of four weeks) were used to determine any seasonal variations. Data were expressed as the frequency of occurrence (i.e. percentage of samples containing a specific food item).

SPSS Statistics 17.0 was used for statistical analysis. Assuming independence among the samples, logistic binary regression was used to determine any decrease or increase in food items consumed during the research period. Tests were done for all food items separately, taking a probability limit of 1%.

Results

Food

In total 139 samples were collected from 51 different nest boxes. In more than half of the

Table 1. Occurrence (percentage) of food items (based on absence or presence) in 139 faecal samples of garden dormice in the Savelsbos in summer and autumn 2010.

Food item	%	Subcategory	%
Animal			
True bugs (Heteroptera)	4%		
Caterpillars (Lepidoptera larvae)	1%		
Flies (Diptera)	4%		
Hymenopterans (Hymenoptera)	11%	Parasitic wasps (Ichneumonidae)	1%
		Bees/bumblebees (Apidae)	4%
		Ants (Formicidae)	4%
		Not identified	2%
Beetles (Coleoptera)	35%	Ground beetles (Carabidae)	6%
		Click beetles (Elateridae)	1%
		Weevils (Curculionidae)	1%
		Carrion beetles (Silphidae)	1%
		Not identified	23%
		Coleoptera larvae	4%
Snails (Gastropoda)	22%		
Millipedes (Diplopoda)	70%		
Woodlice (Isopoda)	1%		
Spiders (Araneae)	7%		
Harvestmen (Opiliones)	7%		
Pseudoscorpions (Pseudoscorpiones)	1%		
Earthworms (Lumbricidae)	9%		
Songbirds (Passeriformes)	1%		
Wood mouse (<i>Apodemus sylvaticus</i>)	6%		
Plant			
Fruit pulp/peel	76%		
Green plant parts	66%		
Seeds	38%	Blackberry (<i>Rubus</i> ssp.)	22%
		Elder (<i>Sambucus nigra</i>)	5%
		Not identified	29%
Flowers	1%		

weeks less than six samples were collected (figure 1). In the two first weeks of November no samples were collected, as no field worker was available in that period.

Millipedes were the most frequent animal food item, followed by beetles and snails. Hymenopterans, earthworms, spiders, harvestmen and mice accounted for between 5 and 11% of the diet. Flies, true bugs, pseudoscorpions, woodlice, caterpillars and songbirds were occasionally present in the samples. The most frequently found vegetable food items were fruits, green plant parts and seeds (table 1).

Seasonal variation

Millipedes were an important food item during the entire season, although with relatively low frequencies by the end of August, when there was a high proportion of berry seeds (figure 2). The occurrence of beetles and mice decreased significantly in the course of the season (logistic binary regression, $P < 1\%$). Although statistically not significant, there also seemed to be a decrease in the occurrence of snails throughout the season. The animal part of the garden dormice's menu became

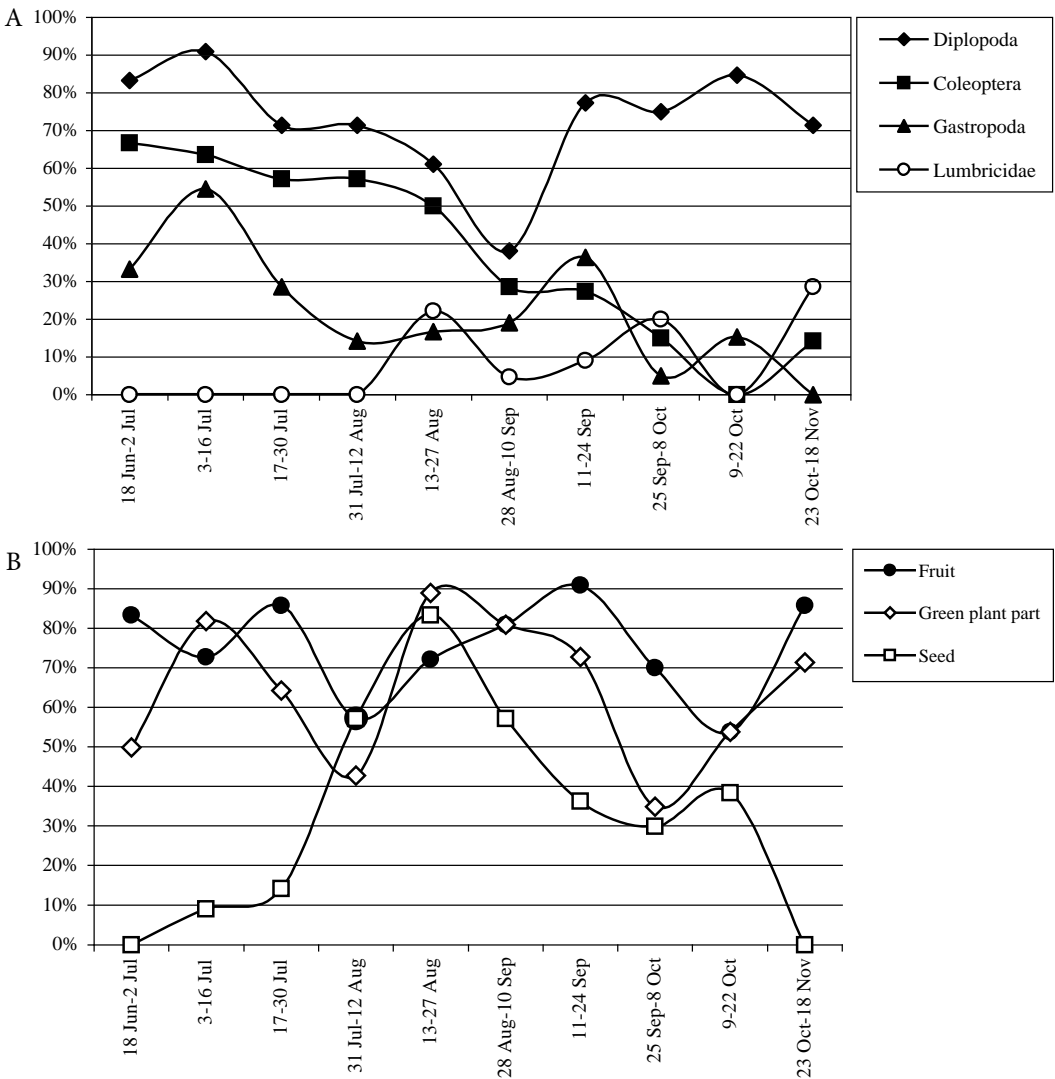


Figure 2. Seasonal variation of the occurrence (percentage) of main animal food items (A) and main plant food items (B) in faecal samples of garden dormice in the Savelsbos in summer and autumn 2010.

quite monotonous at the end of the season, by then mainly consisting of millipedes and earthworms. In June and July no earthworms were present in the food. Earthworm activity above the ground is correlated with rainfall (Darwin 1881). June was a very dry month and July had a normal amount of rainfall. Heavy rainfall occurred in the second half of August and from 6 to 14 November, and some rain fell from 23 September to 2 October.

The first berry seeds were identified in the beginning of August. The occurrence of seeds increased rapidly until the end of August, coinciding with the ripening of elderberries and blackberries. In September the occurrence decreased to 30% and was zero by the end of October.

The occurrence of fruit pulp stayed more or less constant during the course of the season. This seems illogical as fruit, like berries,

should be less available at the beginning of the year. We discovered that somebody had been feeding the garden dormice by putting apples and pears in the nest boxes. (Many remains of apples and pears were found in nest boxes). The occurrence of fruit pulp in the samples must have been strongly influenced by this artificial feeding. The dormice only consumed the pulp and peel but not the cores with the seeds. In fact it was not easy to recognise the remains of apples and pears in the samples of excrements. As far as we know, no other food was supplied.

Discussion

The garden dormouse is omnivorous, eating a large proportion of animal food (Storch 1978). Our study also found a high proportion of plant food (table 1). Fruit pulp and berries are known to be preferred food items (Brehm 1865, Gigirey & Rey 1999, Gil-Delgado et al. 2010). Green plant parts were frequently found in our samples, but in low quantities. In line with studies of stomach contents, such as that by Holišová (1968), we concluded that green plant parts are only of minor importance in the Savelsbos.

The results of our faecal analysis are in line with other studies on the food of garden dormice, which used stomach analysis (table 3). In table 3 we have arranged the studies from left to right, following a north-south gradient. Millipedes are the most frequent animal food item in woods in more northern regions. Holišová (1968) compared the food of four Gliridae in an oak-hornbeam wood on chalkstone in southern Slovakia, examining the stomachs of ten garden dormice. She found that garden dormice chiefly consume animal food throughout summer and autumn: about 90% of the stomach contents consisted of animal matter. This was a much higher rate than for edible dormouse (*Glis glis*), common dormouse (*Muscardinus avellanarius*) and forest dormouse (*Dryomys nitedula*). Gigirey &

Rey (1999) examined the stomachs of 20 garden dormice from a montane oak wood in the Sierra del Invernadeiro in north-western Spain in September and October 1985. Once more, millipedes were the most frequent food item. Apart from grasshoppers or crickets, spiders, hazelnuts and acorns, the diet they found was more or less similar to our results.

The three studies from Mediterranean Spain show quite a different picture from the three studies in woods in more temperate regions. The stomachs of 40 garden dormice collected in April 1970 on the Balearic island of Formentera showed high frequencies of snails, lizards and beetles and, to a lesser extent, mice (wood mouse and house mouse (*Mus musculus*)), spiders and ants (Formicidae) (Kahmann & Lau 1972). The high frequency of vertebrates in this study, which was carried out in spring, is remarkable. A study of twenty-seven stomachs – mainly from autumn – from Coto Doñana found high frequencies of beetles, hymenopterans (mainly honey bees (*Apis mellifera*) and ants), grasshoppers and crickets and Phoenician juniper (*Juniperus phoenicea*) berries (Palacios 1975). The third study in Spain (Gil-Delgado et al. 2010) was carried out in an orange plantation near Valencia. The method used here was quite different, and so the results have not been included in table 3. Garden dormice at this location are active the whole year round and even reproducing in autumn and winter, when their main food is oranges. In spring and summer, when there are no ripe oranges, the main food was arthropods. Gastropods were less frequently consumed. They did appear throughout the year in the faecal samples, but in low proportions in autumn.

It is remarkable that garden dormice eat so many millipedes especially since millipedes have odoriferous glands that produce chlorine, iodine, benzaldehyde and hydrogen cyanide, which leads most predators to avoid them. We surmise that garden dormice might have a general resistance to these poisonous substances. They are also very resistant to

Table 2. Occurrence (percentage) of the main food items of garden dormice, comparing this study with four other studies and the pilot study. Only food items that made up at least 10% of the total in one or more of the studies are included.

Source	Pilot study in the Savelsbos	This study	Holišová 1968	Gigirey & Rey 1999	Kahmann & Lau 1972	Palacios 1975
Method	Faeces	Faeces	Stomachs	Stomachs	Stomachs	Stomachs
Region		The Netherlands	Slovakia	NW Spain	Formentera	Coto Doñana
Number of samples	46	139	10	20	40	27
Time of year	Spring	Summer and autumn	Summer and autumn	Autumn	Spring	Mainly autumn
Millipedes	85%	70%	60%	65%	18%	11%
Centipedes (Chilopoda)					28%	11%
Beetles	65%	35%	20%	35%	90%	48%
Hymenopterans	28%	11%			53%	48%
Earthworms		9%	10%			
Snails		22%	10%	10%	100%	
Grasshoppers and crickets (Orthoptera)	2%			20%		26%
Spiders		7%		55%	60%	11%
Lizards (Lacertidae)					93%	
Mammals	11%	6%		20%	68%	11%
Song birds	13%	1%				
Hazelnuts, acorns, pine and maple seeds			10%	15%		7%
Blackberries and raspberries (<i>Rubus</i> spp.)		22%		60%		7%
Phoenician juniper berries (<i>Juniperus phoenicea</i>)						26%
Green plant parts	70%	66%	50%		?	11%
Fruit pulp	?	76%			?	
Flowers	43%	1%			?	

snake venom (Storch 1978).

Millipedes make up a large proportion of the food of garden dormice living in woods in Europe. Millipedes can reach high densities in woods on chalkstone soils. Kime (1992) recorded densities of more than 700 millipedes per m² in forests with mull soils on limestone in Belgium, for example in the Fouron Region, close to the Savelsbos. In forests on calcic mulls the burrowing julidans (Julida) and glomeridans (Glomerida) are strongly represented. In Europe, Atlantic forests are probably the most favourable habi-

tats for millipedes (Kime & Golovatch 2000). There is perhaps another reason why dormice eat millipedes. These arthropods contain 10-13% (dry matter) calcium; a hundred times more than other arthropods (Graveland & van Gijzen 1994). Vegetable matter, such as fruits, berries and acorns, has a much lower calcium content. Possibly millipedes are an important source of calcium for garden dormice.

We started to collect faecal samples from 25 June 2010. In the spring of 2010 a similar pilot study carried out in the same area, which



Figure 3. Remains of acorn, eaten by garden dormouse. Photograph: J. Scholten.

also analysed faecal samples. As the method employed was different, the unpublished results have not been included in the analysis within this article. The key findings of this study are worth discussing and are included in table 2. The study found a higher proportion of the remains of flowers and vertebrates, including bird eggs, and five birds. The flowers were possibly blackberry or raspberry (*Rubus* spp.). *Rubus* flowers are a common food item of the common dormouse in spring (Juškaitis 2007).

On 21 May 2010 two garden dormice were seen in a nest box in the Savelsbos, sitting on top of the remains of great tit (*Parus major*) nestlings. In other years similar observations of garden dormice eating the nestlings of birds have been made in spring. In Lithuania garden dormice have been recorded as eating the eggs and nestlings of birds in nest boxes and there were even three cases when adult starlings (*Sturnus vulgaris*), nesting in nest boxes, were killed by these rodents (Juskaitis 1999). In orange plantations in Spain, garden dormice were recorded as eating bird eggs, nestlings and adult birds, both from nest boxes and natural bird nests (Gil-Delgado et al. 2009).

Eight of our samples contained the remains of wood mouse, a species that regularly uses the nest boxes in the Savelsbos. After 10 September no wood mouse were found in the sam-

ples. It is possible that the garden dormouse predated (mainly young) wood mice. In fact it is long known that garden dormice kill and eat mice and birds (Brehm 1865, cf. Gil-Delgado et al. 2009). Occasionally they even eat rabbits (Palacios 1975).

The animal part of the menu of the garden dormice in this study became quite monotonous in autumn, but it may well be that they supplemented their food in that period with beech nuts (*Fagus sylvatica*) and acorns. Garden dormice are known to eat beech nuts and acorns (Brosset & Heim de Balsac 1967, Gigirey & Rey 1999). We found no remains of beech nuts in the faecal samples, but we did find remains of acorns eaten by garden dormice in the nest boxes (figure 3). Possibly their remains could not be identified in the samples.

Garden dormice mainly search for their food on the ground (Storch 1978, Bertolino et al. 2003). Their diet, containing many millipedes (figure 4A), ground beetles (figure 4B) and earthworms (figure 4B) confirms this. Garden dormice in woods depend on a rich invertebrate fauna that inhabits the litter layer. Areas with a large accumulation of litter have low densities of millipedes, whereas mesotrophic mull soils have very high densities (Kime 1992). Willers et al. (2012) describe that the depth of the layer of accumulated litter within the Savelsbos is inversely related to the local coverage by trees with fast decomposing leaves. Vegetation changes since 1955 indicate that mesotrophic mull soils are disappearing from the Savelsbos. In the middle of the slope, just above the small relict zone with garden dormice, rich types of *Stellario-Carpinetum* wood have changed into poorer wood types. It might be possible to re-establish species-rich wood types that produce mesotrophic mull soils by selectively felling beech and by planting tree species with good litter quality (elm and lime). Felling trees allows more light to reach the forest floor, leading to better decomposition of the accumulated litter (Bobbink et al. 2008). Traditionally the Savelsbos was managed as coppice-with-standards. Coppice man-

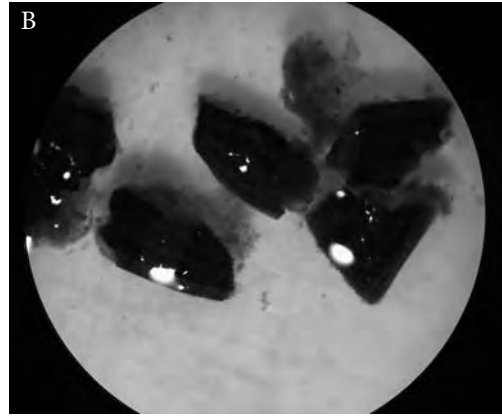
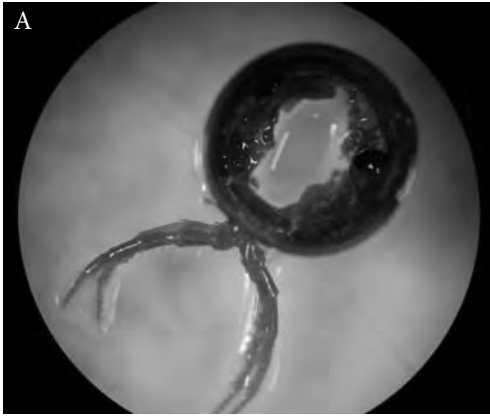


Figure 4. Segment with feet of a millipede (A), elytra fragments of a ground beetle (B), and bristles of earthworms (C), from faeces of garden dormouse. *Photographs: L. Kuipers en J. Scholten.*

agement favours a range of wildlife, often of species adapted to open woodland and shrubs.

Conclusions

Invertebrates, and especially millipedes were the staple food of the garden dormouse throughout the active feeding period. In spring and early summer more beetles, snails, vertebrates (possibly young) and flowers were eaten (compared to August-November). These latter food items were replaced from August by berries, especially blackberries, and earthworms. However, the feeding on earthworms from August may have been caused by the start of heavy rain in August.

The garden dormice in the Savelsbos seem to depend on the rich invertebrate fauna within the litter layer. Mesotrophic mull soils

have a rich fauna of medium-sized to large invertebrates. Management measures that focus on re-establishing species-rich wood types should be carried out in parts of the Savelsbos, adjacent to the relict zone at the bottom of the slope, in order to help maintain and encourage the remaining Dutch population of garden dormice.

Acknowledgements: Thanks to the State Forestry Service for permission to do fieldwork in the Savelsbos nature reserve. Karin van Dueren den Hollander was the tutor of Laura Kuipers and Janneke Scholten, who are students at the University of Applied Sciences HAS Den Bosch. We would like to thank Karin for her advice and feedback, and Osama Almalik of the same university, for advising us on statistics. Thanks also to: Wesley Overman of the Dutch Mammal Society for training us in identifying the hairs of mammals; Dr. Renée Bekker (National Authority for Data concerning Nature), who

identified several seeds; Dr. Edi Gittenberger (NCB Naturalis) and Stef Keulen, who assisted in identifying the remains of snails; Desmond Kime (Royal Belgian Institute of Natural Sciences) who provided valuable information on millipedes and Dr. Patrick Hommel (Alterra), who provided useful information on woodland management. We would also like to thank two anonymous referees for their useful comments.

References

- Brehm, A.E. 1865. *Illustriertes Thierleben: eine allgemeine Kunde des Thierreichs. Zweiter Band. Erste Abtheilung: Die Säugethiere. Zweite Hälfte: Beutethiere und Nager. Zahnarme, Hufthiere und Seesäugethiere.* Bibliographisches Institut, Hildburghausen, Germany.
- Bertolino, S., N. Cordero & I. Currado 2003. Home ranges and habitat use of the garden dormouse (*Eliomys quercinus*) in a mountain habitat in summer. *Acta Zoologica Academiae Scientiarum Hungaricae* 49, Supplement 1: 11–18.
- Bobbink, R., R.-J. Bijlsma, E. Brouwer, K. Eichhorn, R. Haveman, P. Hommel, T. van Noordwijk, J. Schaminée, W. Verberk, R. de Waal & M. Wallis de Vries 2008. Preadvies hellingbossen in Zuid-Limburg. Rapport DK 2008/094-O. Ministerie van Landbouw, Natuur en Voedselkwaliteit, Directie Kennis, Ede, the Netherlands.
- Brosset, A. & H. Heim de Balsac 1967. Les micromammifères du Vercors. *Mammalia* 31 (3): 325–346.
- Cortens J. & G. Verbeylen 2009a. Eikelmuisen in Vlaanderen. Verspreiding, bescherming en monitoring. *Natuur.focus* 8 (1): 4–10.
- Cortens J. & G. Verbeylen 2009b. De eikelmuis in Vlaanderen - Synthese van drie jaar inventarisieren en aanzet tot effectieve soortbescherming. Rapport Natuur.studie 2009/1. Natuurpunt Studie (Zoogdierenwerkgroep), Mechelen, Belgium.
- Darwin, C. 1881. The formation of vegetable mould, through the action of worms. John Murray, London, UK.
- Gigrey, A. & J.M. Rey 1999. Autumn diet of the garden dormouse (*Eliomys quercinus*) in the north-west Iberian Peninsula. *Mammalia* 63 (3): 372–374.
- Gil-Delgado, J.A., O. Mira, A. Viñals, J. Gómez, N. Banyuls & C. Vives-Ferrándiz 2010. Diet of the garden dormouse (*Eliomys quercinus* Linnaeus 1766) in orange groves: seasonal variation and use of available resources. *Mammalia* 74 (2): 147–151.
- Gil-Delgado, J.A., R. Tamarit, A. Viñals, J. Gómez & C. Vives-Ferrándiz 2009. Depredación sobre nidos, aves adultas y mamíferos por el lirón careto *Eliomys quercinus*. *Galemys* 21 (2): 3–11.
- Graveland, J. & T. van Gijzen 1994. Arthropods and seeds are not sufficient as calcium sources for shell formation and skeletal growth in passerines. *Ardea* 82 (2): 299–314.
- Holišová, V. 1968. Notes on the food of dormice (Gliridae). *Zoologické Listy* 17: 109–114.
- Juškaitis, R. 1999. Mammals occupying nest boxes for birds in Lithuania. *Acta Zoologica Lituanica* 9 (3): 19–23.
- Juškaitis, R. 2007. Feeding by the common dormouse (*Muscardinus avellanarius*). *Acta Zoologica Lituanica* 17 (2): 152–159.
- Kahmann, H. & G. Lau 1972. Der Gartenschäfer *Eliomys quercinus ophiusae* (Thomas, 1925) von der Pityuseninsel Formentera (Lebensführung). Veröffentlichungen der Zoologischen Staatssammlung München 16: 29–49.
- Kime, R.D. 1992. On abundance of West-European Millipedes (Diplopoda). *Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck, Supplement* 10: 393–399.
- Kime, R.D. & S.I. Golovatch 2000. Trends in the ecological strategies and evolution of millipedes (Diplopoda). *Biological Journal of the Linnean Society* 69: 333–349.
- le Louarn, H. & F. Spitz 1974. Biologie et écologie du lérot *Eliomys quercinus* L. dans les Hautes-Alpes. *La Terre et la Vie* 28: 544–563.
- Litvaitis, J.A. 2000. Investigating food habits of terrestrial vertebrates. In: L. Boitani & T.K. Fuller (eds.). *Research techniques in animal ecology: controversies and consequences*: 165–190. Columbia University Press, New York, USA.
- Palacios, F. 1975. Estudio ecológico del lirón careto grande (*Eliomys quercinus lusitanicus*) (Reuvenus, 1890), en la Reserva Biológica de Doñana. *Boletín de la Estación Central de Ecología* 4: 65–76.
- Storch, G. 1978. *Eliomys quercinus* (Linnaeus, 1766) – Gartenschläfer. In: J. Niethammer & F. Krapp

- (eds.). Handbuch der Säugetiere Europas, Band 1 – Nagetiere I: 208-225. Akademische Verlagsgesellschaft, Wiesbaden, Germany.
- Temple, H.J. & A. Terry (eds.) 2007. The Status and Distribution of European Mammals. Office for Official Publications of the European Communities, Luxemburg, Luxemburg.
- Thissen, J.B.M., D. Bal, H.H. de Jongh & A.J. van Strien 2009. The 2006 national Red List of mammals of the Netherlands and a IUCN Regional Red List. *Lutra* 52 (1): 23-35.
- Willers, B., P. Hommel & J. Schaminée 2012. Veranderingen in de zonerings van bosgemeenschappen in het Savelsbos. *Natuurhistorisch Maandblad* 101 (2): 24-31.

Samenvatting

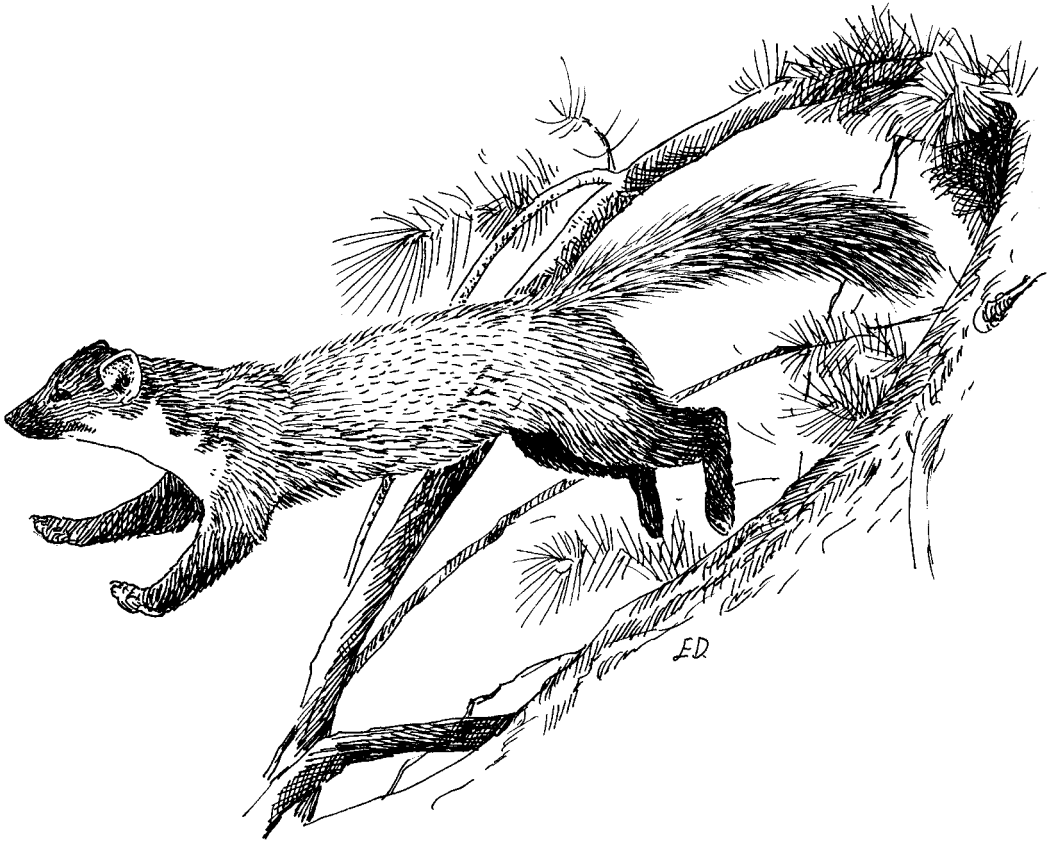
Het voedsel van de eikelmuis (*Eliomys quercinus*) in Nederland in zomer en herfst

Het voedsel van de enige Nederlandse populatie eikelmuisen is onderzocht door middel van analyse van uitwerpselen, verzameld in de zomer en de herfst van 2010. In totaal werden 139 monsters van uitwerpselen verzameld uit 51 verschillende nestkasten voor eikelmuisen. De monsters werden onderzocht op aan- of afwezigheid van diverse dierlijke en plantaardige voedselresten met behulp van een stereomicroscop. Miljoenpoten, kevers

en slakken bleken de meest frequent voorkomende, dierlijke voedselbronnen. Vruchtvlees en zaden waren veel voorkomende voedselresten, zoals zaden van braam en vlier. Helaas voerde iemand de eikelmuisen met appels en peren. De hierboven genoemde dierlijke en plantaardige voedseltypen kwamen alle voor in meer dan 20% van de monsters. Vliesvleugeligen (vooral bijen en mieren), regenwormen, spinnen, hooiwagens en bosmuizen zaten ieder in 5 tot 20% van de monsters. Ongewervelden, speciaal miljoenpoten, zijn stapelvoedsel. In het voorjaar eet de eikelmuis meer gewervelden, slakken, kevers en bloemen dan in het najaar. De eerste resten van zaden van bessen doken begin augustus op in de uitwerpselen. In de loop van augustus steeg het voorkomen van zaden tot 90%. Daarna zakte het aandeel van zaden weer sterk. Eikelmuisen in bossen lijken qua voedsel afhankelijk van een rijke ongewerveldenfauna van de strooisellaag. Mesotrofe bodems met goed door de bodem gemengde humus (mull bodems) hebben een rijke fauna van relatief grote ongewervelden. Het lijkt er op dat in het Savelsbos mesotrofe mull bodems aan het verdwijnen zijn. Dit kan tegengegaan worden door selectieve kap van beuken en aanplant van bomen met een goede bladkwaliteit, zoals iep en linde. Verder is het gewenst om door dunning meer licht toe te laten.

Received: 19 February 2012

Accepted: 24 April 2012



The effects of small rodent density fluctuations on the pine marten (*Martes martes*)

Henri J.W. Wijsman

Tony Offermansweg 6, NL-1251 KJ Laren, the Netherlands, email: hjwwijsman@tele2.nl

Abstract: Low mast production leads to winters that are scarce in small rodent prey for pine martens (*Martes martes*). As a result, litter size over the years 2005–2011, as studied in 193 marten litters in three areas in the central part of the Netherlands, decreased in the following spring. Moreover, births came one week later than in years of abundant prey. Certain females in consecutive years were consistently either late or early in giving birth, irrespective of the availability of prey. Pine martens turned to birds as alternative prey when rodents were scarce, resulting in an increased rate of raids on nest boxes. The connection between dearth of prey and delayed implantation is discussed.

Keywords: pine marten, *Martes martes*, litter size, population fluctuation, mast years, delayed implantation.

Introduction

In central and western Europe, mice and voles (Muridae and Microtidae, hereafter referred to as small rodents) represent a substantial part of the diet of the pine marten (*Martes martes*) (Marchesi & Mermod 1989, Jędrzejewski et al. 1993, Nitze 1998). Small rodent populations fluctuate in size (Pucek et al. 1993, Zalewski et al. 1995, Helldin 1999) according to fluctuations in the mast production of deciduous trees, mainly common oak (*Quercus robur*) and beech (*Fagus sylvatica*). In the central Netherlands, the mast production of beech and oak dips every two to three years (Wild-beheer Veluwe, unpublished data). The following winter will then often see a reduction in the small rodent population (Jędrzejewski et al. 1993); in times of rodent dearth, martens turn to alternative prey (Zalewski et al. 1995), such as birds or squirrels (the latter are seldom reported as prey in the Netherlands), so it is to be expected they will be indirectly affected by mast volume. In 2001, H. Kleef

(personal communication) observed indolent pine marten females in and around their dens, easily satisfied by short bouts of hunting, this in contrast to the activity in many other years such as 2002, when small rodents were at a low. He provisionally concluded that the levels of marten activity depended on differences in the availability of small rodent prey.

This study was an attempt to make a quantitative assessment of the influence of prey scarcity upon pine marten propagation. The study started in 2005, a year of abundant food for pine martens, and many nests were monitored. Several observers mentioned that bank voles (*Myodes glareolus*) literally crawled around their feet during observation bouts at various pine marten nests. By contrast, they were conspicuously absent in 2006 and in many a known territory, although the presence of a resident pine marten was deduced from observations of occasional scats or even observations at a tree hole, no nest was found even after intensive searching. In the nests that were found there was often only one kitten present. Additionally, more remnants of predated birds were found. Anecdotically, several observers reported that female martens were involved in

hunting for longer, and did so more frantically.

Between 2005 and 2011 data have been collected on mast, small prey availability, litter size and the date of birth in martens, and passerine nest boxes raided by martens. On the basis of these observations the hypothesis was launched that a shortage of small rodents, caused by poor (beech and oak) mast production in the preceding autumn, had led to smaller litter sizes, and even as late as April and May, a change in prey items to birds.

Preliminary results of this study have already been published in Dutch reports (Wijsman 2007a, Wijsman 2007b, Wijsman et al. 2010).

Material and methods

Study area

The study areas were situated in the Veluwe area (Province of Gelderland), the Utrechtse Heuvelrug area (Province of Utrecht) and, for 2008- 2011, in certain parts of Salland (Province of Overijssel) (figure 1). All the areas are characterised by relatively poor and acidic sandy soils. Beech forests and coniferous plantations are interspersed with heathland. Beech trees of more than 120 years, potentially very productive of beech nuts, are common. Common oaks and American oak (*Quercus rubra*) are widespread, while other trees bearing edible seeds, such as sweet chestnut (*Castanea sativa*), hazel (*Corylus avellana*) or hornbeam (*Carpinus betulus*), are quite scarce.

In most of the regions studied the beech marten (*Martes foina*) is absent, so that scats or other traces of marten activity can be safely ascribed to the pine marten.

Mast

Data on the production of mast have been kindly provided by Wildbeheer Veluwe (G.J. Spek); beech mast has been grouped into four classes: 3. mast plentiful, 2. mast normal, 1.

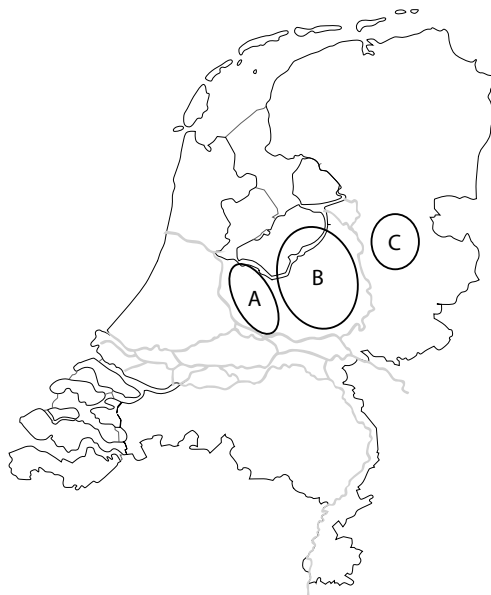


Figure 1. Map of the Netherlands showing the location of study areas. A=Utrechtse Heuvelrug; B=Veluwe; C=Salland.

mast locally, 0. no mast worth mentioning. Furthermore, Wildbeheer Veluwe produces a yearly assessment of the total seed production for beech, indigenous oak and American oak, by extrapolation expressed in kg for the Veluwe area, that is to say, around the area called Kroondomein (the area is dominated by “indigenous oak” with a great majority of *Quercus robur* interspersed with some *Q. petraea*). The Veluwe is located centrally in the study area, so it can be assumed that the data are more or less valid in the other provinces.

Mast production was assessed directly after the fruits ripened, that is, in the year before the effect of the amount of mast is felt in the mouse or vole populations. Therefore, I have allotted the mast of year n to the year $n+1$.

Abundance of small rodents

The relative abundance of wood mice (*Apodemus sylvaticus*) has been assessed by Bijlsma (2009, 2011) since 1993 on the basis of the fre-

quency of holes per 10x10 m². For the present study, Bijlsma communicated his original data on the wood mouse in February, and also made additional data for 2011 available.

Since data on the abundance of bank voles were not available, the breeding success of buzzards (*Buteo buteo*) and tawny owls (*Strix aluco*) (see below) was taken as an indicator of the abundance of small rodents in general. In the Gooi area (the northern part of the Utrechtse Heuvelrug) young buzzards have been ringed over a fairly long period to assess their distribution; their numbers were provided by H. Sevink (personal communication). Figures for the nest size of tawny owls nesting in large nest boxes in the same area were provided by Ballering & Beskers (2011), and, for 2011, R. Beskers (personal communication). De Graaff (in Wijsman et al. 2010) counted young tawny owls in the forestry Kootwijk.

Litter size

During 2005-2011, pine marten litter size was determined by small cameras with an infrared light set on a long pole and inserted into 193 nests (see Achterberg et al. 2012). Eleven members of the Werkgroep Boommarker Nederland (Dutch Pine Marten Working Group) collected the data. The cameras must be small in size, so as to enter holes with an entrance of 5 cm diameter. Nest inspection by cameras was introduced in 2004, and has been regularly applied from 2005 onwards.

Nearly all the nests inspected were situated in tree cavities, mainly woodpecker holes in beech trees, between 4 and 14 m above the ground. When the inspection is performed during the (early) nocturnal hours, the female is normally hunting. But even during the day, usually there is no practical disturbance of the nest, and the female may even simply continue nursing the kittens in the nest hole. In May, pine martens also go hunting in daylight (Broekhuizen & Müskens 2000, Kleef & Tydeman 2009), which makes it easy to monitor the kittens who take

little notice of the camera considering it, at the most, as an object to play with.

The kittens were counted on the first occasion possible after finding the nest, sometimes this was within days after birth, more often some weeks later. Litters of indeterminate size were not included in the analyses.

Identification of individuals

Individual pine martens can be distinguished on the basis of the pattern of brown spots in the yellow throat patch, with nearly all martens having a specific pattern (Stubbe 1993, author's observations of museum specimens). Cases are only listed when there was certainty as to the identification.

Date of birth

From 2008 onwards, the date of birth of litters was assessed by a combination of various methods: the very first observations of scats on or under the branches of the nest tree, the size and activity of the kittens, the development of the throat patch that contrasts in colour to the brown fur (two to three weeks) and the opening of the eyes (35-38 days). The estimates were often expressed in terms of weeks, these have been literally translated as seven days and expressed as ordinal dates, correcting for leap years (2008), i.e., adding one day. A margin of error of a few days may exist in the calculated days.

Predation on nest boxes for passerines

The pine marten is the most powerful of the predators that take eggs or young from a nest box, so cases where the lid of the box has been removed or the whole nest taken out and found on the ground, can be ascribed to pine martens. In many cases much of the nest material was hanging from the box opening and occasionally the marten left droppings on the roof of the box.

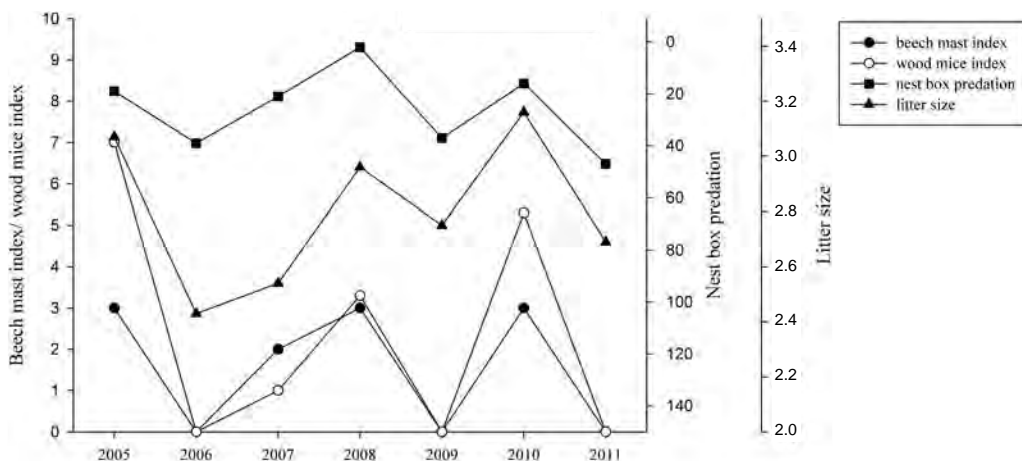


Figure 2. Beech mast (according to the index 0-3), wood mouse density in February (mean number of occupied holes per 10x10 m), mean pine marten litter size per year and nest box predation (percentage of young birds removed from nest boxes) in the Kootwijk area over 2005-2011. Note that the y-axis for nest box predation is inverted to stress the negative correlation with the other factors. Correlation coefficients (Spearman's Rho) are: litter size – beech mast: $\rho=0.77$ ($P=0.04$), litter size – wood mice: $\rho=0.96$ ($P=0.04$), litter size – nest box predation: $\rho=-0.71$ (n.s.), wood mice – beech mast: $\rho=0.96$ ($P<0.001$), wood mice – nest box predation: $\rho=-0.81$ ($P=0.04$), beech mast – nest box predation: $\rho=-0.92$ ($P=0.002$).

In the Noord-Ginkel (Veluwe) area, boxes were inspected in 2005 and 2006 (J. van Laar in Wijsman 2007b). For the other years data from Noord-Ginkel are not yet available. In the Gooi area R. Beskers (personal communication) carefully made the distinction between predation by greater spotted woodpecker (*Dendrocopos maior*) (which selectively removes the young without further damage), red squirrel (*Sciurus vulgaris*) (which leaves the nest in shreds and partially hanging out of the opening), and pine marten (when the box is often empty and the nest is on the ground; sometimes with a scat left on the top).

In the Kootwijk area approximately 180 to 220 nest boxes are monitored each year (courtesy of A. Mulder, personal communication). Kootwijk is located centrally in the Veluwe and, therefore, central to the study area.

Statistical analyses

Relations between litter size, mast, rodent abun-

dance, and nest box predation were quantified using Spearman's rank correlation coefficients.

As litter size does not follow a normal distribution, the effects of year and rodent years on litter size were tested using a generalised linear model (GLM) of litter size as a function of year and of rodent year as a factor (yes or no), with a log link function and a Poisson error distribution.

Birth dates followed a normal distribution, so differences in the date of birth of litters could be tested using an Analysis of Variance (ANOVA), followed by Tukey's post hoc test to see which years differed. Differences in nest box predation were tested using a Kruskal-Wallis signed rank test.

Results

Mast

Beech mast during 2005-2011 was estimated (figure 2). Figures for total mast (acorns and

Table 1. Total and oak mast (x 10,000 kg) in the Veluwe area, small rodent density (mean number of occupied holes per 10x10 m²), number of young buzzards ringed in the Gooi area and number of young fledged tawny owls over 2005-2011. Spearman's correlation coefficient between beech mast index and tawny owl breeding success was $\rho=0.77$ ($P=0.04$). nd = no data available.

Year	2005	2006	2007	2008	2009	2010	2011
Total mast (Veluwe area)	91	35	77	49	28	42	20
Oak mast (Veluwe area)	70	35	66	39	28	32	20
Small rodent density	7.0	0.0	1.0	3.3	0.0	5.3	0.0
Buzzards ringed	129	49	105	92	38	72	nd
Tawny owls fledged	17	2	19	13	8	72	4

Table 2. Litter size of pine martens during 2005-2011, in relation to the abundance of small rodent prey (holes per 10x10 m²). Litter sizes in the three small rodent peak years are significantly higher than in the three lows (Generalised Linear Model with log link function and Poisson error distribution, $P=0.03$, Nagelkerke's $R^2=0.08$).

Year	2005	2006	2007	2008	2009	2010	2011
Number of litters	28	23	24	33	29	30	26
Size 1	2	6	6	2	2	1	2
Size 2	9	4	7	9	7	5	8
Size 3	5	10	5	11	16	14	12
Size 4	9	3	6	10	4	8	4
Size 5	3	0	0	1	0	2	0
Average litter size	3.07	2.43	2.54	2.96	2.75	3.16	2.69
Rodent abundance	7.0	0.0	1.0	3.3	0.0	5.3	0.0

beech nuts combined) as well as oak mast (indigenous oak and American oak combined), can be found in table 1. Because the fluctuation in acorn production is much less pronounced than in beech nut production, beech mast is shown separately in the graph.

Abundance of small rodents

The relative abundance of wood mice peaked in the springs of 2005 and 2010, and was very low during the springs of 2006, 2009 and 2011 (figure 2, table 1).

The numbers of ringed nestling buzzards in the Gooi area over the years 2005-2011 are shown in table 1, as well as the numbers of fledged tawny owls. G. de Graaff (in Wijsman et al. 2010) confirmed that 2005 was a productive year for tawny owls in the Veluwe area, while in 2006 only a few young owls left the

nest. In the winter of 2008/2009 there were practically no acorns or beech nuts in the terrains he studies and this was followed by an unproductive owl year in 2009.

Litter size

Data about litter size in pine martens collected during the seven years of monitoring are summarised in table 2.

There was no significant increase or decrease in litter size over the years (GLM, $P=0.71$, table 2), although there were three peak years in litter size (2005, 2008, 2010) and three poor years (2006, 2009, 2011). The year 2007 was fairly low, but better than the preceding year. The differences in the average litter size between years of abundance or scarcity for small rodents are significant (GLM, $P=0.03$), but the explanatory power of the model is not

Table 3. Litter size of individual females (named after different areas). – litter size, if any, not determined; nd = no data available.

	Year	2005	2006	2007	2008	2009	2010	2011
Female								
Cronebos		4	1	1	3	-	-	-
Remmerstein		2	-	4	4	4	-	2
Galgenberg		3	3	-	-	3	-	nd
Beerenberg		2	1	1	-	4	-	2
Beverweert		nd	nd	nd	3	2	3	-
Bylaer		nd	nd	nd	nd	3	3	3

Table 4. Average date of birth. The numbers given here differ from those used in table 1: in some cases the kittens were actually observed and their age determined, but their number remained obscure. In other cases, kittens were counted but their age was not determined. Small rodent population: + = abundant, - = scarce.

Year	Average date (extremes)	n	Small rodent abundance
2008	6*April (20 March -12 April)	18	+
2009	15 April (4-30 April)	21	-
2010	6 April (25 March - 17 April)	23	+
2011	12 April (1-27 April)	23	-

*After correction for the leap year.

Table 5. Birth dates in individual females (named after different areas).

Female	Year	2005	2006	2007	2008	2009	2010	2011
Remmerstein		27 March		26 March	20 March	5 April		12 April
Beverweert					21 March	8 April		1 April
Bylaer						4 April	1 April	3 April
Zuiderbos						28 April		16 April

great (Nagelkerke's $R^2 = 0.08$).

Certain females, recognised on the basis of their throat pattern, were recorded in consecutive years (table 3). Apparently, the age of the female does not influence the size of her litter.

Date of birth

The mean date of birth, the spread in birth dates and the numbers of litters were assessed for the years 2008-2011, together with an indication of the abundance of small rodents in the relevant spring (table 4). In the poor

rodent springs of 2009 and 2011, the birth of marten kittens was about one week later than in the peak rodent springs of 2008 and 2010. The two sets of birth dates differ significantly (figure 3; ANOVA, $F_{1,85} = 10.157$, $P < 0.001$).

Certain of these individuals generally gave birth earlier than others in the cohort, although in years of dearth this was on a later date. Others were consistently late. Four individual marten females (named after the areas where they were observed), recognisable on the basis of their throat patch pattern were followed (although their nest was not found every year, see table 5).

Table 6. Young birds missing and presumably removed by pine martens from nest boxes in the Kootwijk area (Veluwe). The number of nest boxes varied between 220 and 180 from year to year.

Year	2005	2006	2007	2008	2009	2010	2011
Number of young birds missing	21	36	24	3	43	15	38
Total number of young birds	1127	972	1147	1298	1167	984	798
% of nest boxes raided	1.9	3.9	2.1	0.2	3.7	1.5	4.7

Change to passerine predation

Several observers commented on the many parts of bird feathers in marten scats in 2009 (in Wijsman et al. 2010) and other poor rodent years. In some of the study areas nest boxes for passerines have been installed and are regularly inspected. In the Noord-Ginkel (Veluwe) area, no boxes were raided in the peak rodent year of 2005, whilst in the low year of 2006, 57 out of 119 boxes were disturbed.

In the Gooi area, in the year 2010 (a plentiful year for small rodents) marten predation on nest boxes was negligible, while in 2009 (a poor year for small rodents) considerably more predation was noticed. In 2009 three species of tit, blue tit (*Cyanistes caeruleus*), coal tit (*Periparus ater*) and marsh tit (*Poecile palustris*) were particularly hard hit.

The percentages of raided nest boxes in the Kootwijk area, probably by pine martens (as judged from the damage), varied between years with a minimum of 0.2% in 2008 and a maximum of 4.9% in 2011 (table 6).

Discussion

Mast production

Data of beech mast production, density of wood mouse holes, litter size and the (inverted) percentages of predated nest boxes in the forestry Kootwijk show that the fluctuations in pine marten litter size correlate closely to those of mast production in the area and wood mouse abundance (figure 2). This can be considered a causal relationship, stemming from periodicity in mast produc-

tion. Oak mast was at its lowest in the years when beech mast was virtually absent (table 1). Studies in the Białowieża National Park, Poland, tend to stress the importance of acorns, but that is only because the beech does not occur in that area.

Small rodent abundance

It seems reasonable to take wood mouse abundance as a measure for small rodent abundance in general, as the wood mouse is an important food item for pine martens, in particular in the winter months.

Posluszny et al. (2007) analysed 155 pine marten scats, and found that wood mice made up 26% of the total prey of bank vole and wood mouse together. Similarly Marchesi & Mermod (1989) pointed to mice and voles as the most important food item in winter time, with no clearly discernible difference in the

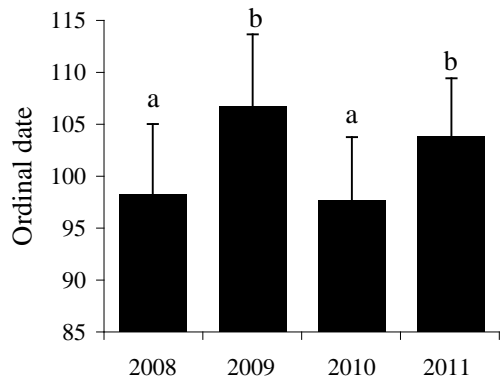


Figure 3. Date of birth (expressed as ordinal date) of pine martens in 2008-2011. Differences between 2008 + 2010 (a) and 2009 + 2011 (b) were tested using ANOVA, followed by Tukey's post hoc test ($F_{1,85}=10.157, P<0.001$).

relative importance of the two. Jędrzejewski et al. (1993: figure 2) showed that the wood mouse in the forest they studied made up about one third of rodent consumption. Although the bank vole appears in general to be the more important prey item (Zalewski 2007, Elmeros et al. 2008, Balestrieri 2011), it can be supposed that both species suffer to the same degree in years when mast is virtually absent. V. Dijkstra (unpublished results) has data from the Veluwe area that confirm this supposition.

While these authors calculate that the bank vole is the more important source of prey for pine marten, Nitze's study (1998) of a female and a male in a small woodland comes to a contrary conclusion. However, in Nitze's study a male in another small piece of woodland conformed to the pattern reported by other authors. Overall we can conclude that the wood mouse plays an important role in a marten's nutrition.

For buzzards and tawny owls, years with plenty of small rodents allow a rich increase in young that are fledged or ringed. Local variations in mast production and the reaction of small rodents, or possibly alternative prey, may have caused the years 2007 and 2008 to be both peak years. In the Gooi tawny owls, 2007 was a special year in that 19 young fledged, more than in 2008. The two years of 2007 and 2008 appear to take an intermediate position. This corresponds to the same years in the total mast production (table 1).

Dijkstra (in Wijsman et al. 2010) has been live trapping small rodents in the Veluwe area. Working under exactly the same circumstances he caught 200 animals in March 2008, compared to 3 in March 2009, which fits the picture obtained.

In retrospect, on the basis of anecdotal information, 2001 and 2003 have been good years for small rodents, in contrast to 2002 and 2004 (in 2004 also the buzzards also had a bad year; H. Sevink, personal communication).

Marten litter size

It is interesting to see the close correlation between wood mouse abundance in February and the litter size of the kittens born in March/April (figure 2). The marten delays implantation of the blastocysts, and the reproductive cycle is resumed in February. A food shortage in that month can be considered to influence the implantation process in the uterus, and thus litter size.

In central Sweden, Helldin (1999) investigated the number of corpora lutea and free blastocysts in the winter in carcasses obtained from trappers, and compared two winters, one with a high microtine density and one with a low one (the wood mouse does not occur in Central Sweden). Intra-uterine mortality (the difference between numbers of corpora lutea and blastocysts) did not differ significantly between the years. If this also holds for the females in the present study, we can conclude that it is rather the implantation process that is affected by an abundance of food. However, the later development of the embryo could also be the sensitive phase. What we discussed up to now as litter size seems to correspond to the number of young born, since we did not find any very young dead kittens. In a later phase of development, a small number of dead young were found, usually in the context of a change of den (unpublished data). This in itself seems to exclude the possibility that the female eats her dead kittens.

The relationship found between litter size and food availability during the winter could in itself be envisaged as an explanation for the mechanism of delayed implantation. Following the mating season in the summer, a winter rich in small rodents leads (statistically) to more successful implantation, whilst in poor winters resorption or rejection of blastocysts can take place, allowing the energy-consuming mating process to take place in the energetically favourable summer.

Mead (1994) only mentions the influence of a seasonal increase in the duration of daylight

in spring as determining blastocyst implantation. However, Douglas & Strickland (1987), referring to the fisher (*Martes pennanti*), speak of successful reproduction depending upon the condition of the females. A poor food supply (of the main prey) may result in little or no production of young.

It seems that, as in the Białowieża forest (Zalewski et al. 1995), adult pine martens in the Netherlands survive low rodent years without their numbers being affected. Zalewski & Jędrzejewski (2006) found that after exceptional years of rodent abundance (their peaks seem to be higher than in the current study) the actual number of pine martens increased (measured by an increase in snow tracks). This fits nicely, qualitatively, with a slightly increased rate of propagation in the previous year.

The data for individual females did not reveal any discernible trend (table 3). Hypothetically, giving birth for the first time might play a role in influencing these data; however, in 2005 some of these females had already had nests in previous years: Remmerstein gave birth in 2002 and 2003 to a litter of unknown size, Cronebos gave birth in 2002, 2003 and 2004 (three kittens), and Beerenberg had a litter of three in 2004 (unpublished results of A. and C. Achterberg (Remmerstein), V. Dijkstra (Beerenberg) and H.J.W. Wijsman (Cronebos)).

Date of birth

When food is abundant, birth occurs earlier. Although the date of birth can be only assessed with a margin of error of some days, our results suggest that the date of parturition was influenced by food availability in the previous winter.

It is interesting that some individuals seem genetically determined to give birth earlier, or later, than others (table 5). This can be confirmed by Kleef's data. Kleef's date of birth has carefully been determined as the day on

which the female remains in the nest hole for 24 hours or more (Kleef & Tydeman 2009), and is accordingly very precise. Our qualitative findings were that litters of five and births in March only occurred in rodent peak years. We only studied a small number of individual females, but our findings are supported by Kleef (unpublished results), who studied two females around Veenhuizen over five years. One was consistently three weeks ahead of the other with the litter (with one case of a small overlap). Four others, in the same region in Drenthe, consistently gave birth over 3, 4, even 7 years in a middle period compared with the Veenhuizen situation. The consistent timing of parturition among individual females in consecutive years seems to point to the influence of the mother's condition at the time of the implantation process rather than on embryo development, in view of the latter's more complex, random traits.

Alternative prey

In poor rodent years, martens take alternative prey, mainly birds. To obtain data on bird predation, files from nest box success were inspected. Data from the forestry Kootwijk supported the theory of increased predation upon young birds from boxes in years when small rodents were scarce (figure 2). In bountiful small rodent years the nest boxes were left alone, suggesting that martens must be quite desperate to change to preying from boxes. It follows that passerines do not fully compensate the shortage of mammalian prey.

Conclusions

Autumnal shortage of mast leads to a collapse in small rodents in winter time, which weakens the condition of marten females in February, the season when the foetus starts to develop. When this occurs the foetus devel-

ops later than usual and with reduced effectiveness of implantation in the uterus. This causal sequence provides an explanation for the delayed implantation as it combines mating in an energetically favourable season (summer) with the opportunity of reproductive success more than a half year later, at least in favourable years. Finally, even late in spring the shortage of rodent food leads to more birds being taken as prey.

It is recommended that future research pay more attention to the details of the consequences of a shortage of small rodents. This could involve more gathering of quantitative data related to: the occupation of known territories, litter size, birth date (all three with special interest paid to individual females); the proportion of birds among prey, differences in scat structure, dead youngsters left in the den, frequency of changing den, raids upon nest boxes, specific weather conditions (e.g. periods with very low temperature or snow, snow depth) and marten population density.

Acknowledgements: In relation to marten nests, I wish to thank all the colleagues observers who counted kittens: Bram Achterberg, Chris Achterberg, Ruud van den Akker, Harry van Diepen, Vilmar Dijkstra, Ben van den Horn, Robert Keizer, Olga van der Klis, Mark Ottens, Daniel Tuitert, for their diligent efforts and enthusiasm. Particular thanks go to Bram Achterberg who by now has obtained similar results in his own study terrain. Jan ten Böhmer, Wim Bomhof, Wilco Busstra, Margriet Hartman, Harry Hees, Tim Hofmeester, Rick van Kesteren, Dick Klees, Peter van der Leer, René van Lopik, Hans Teunissen, all assisted by finding nests. Special dispensation of the Flora and Fauna Law was kindly granted to the author by the Ministry of Agriculture, Nature Conservation and Food Quality, no. FF/75A/2009/013. All the owners of woodlands who were approached cooperated. For writing the paper, I am grateful in the first place to Rob Bijlsma for taking an interest and discussing data on mice and mast; next to Jacob van Olst for paving the way to cooperation and for moral support. Koen Van Den Berge, Sim Broekhuizen, Hans Kleef, Erwin van Maanen and Jasja Dekker gave helpful and expert

comments on the paper. Furthermore I am indebted to Jasja Dekker for statistical advice and digital support; to Hans Kleef and Florian Bijmold for moral support as well as many a discussion and to Hans also for being the first to see the link between rodent periodicity and marten behaviour and providing data on individual females. I thank Wildbeheer Veluwe and G.J. Spek for the quantitative data on mast; Hanneke Sevink for data on ringed young buzzards in the Gooi area; Ronald Beskers for data on fledged owls, on tits in nest boxes in the Gooi area, and for technical advice; G. de Graaff for data on tawny owls around Kootwijk; Aart Mulder and Jim van Laar for data on nest success in nest boxes on the Veluwe; Johan Thissen for moral support.

References

- Achterberg, B., C. Achterberg, R. van den Akker, H. van Diepen, V. Dijkstra, B. van den Horn, R. Keizer, O. van der Klis, M. Ottens, D. Tuitert & H. Wijsman 2012. Zeven jaren tellingen van jonge boommarters. *Marterpassen* 18: 60–65.
- Balestrieri, A., L. Remonti, A. Ruiz-González, M. Vergara, E. Capelli, B.J. Gómez-Moliner & C. Prigioni 2011. Food habits of genetically identified pine marten (*Martes martes*) expanding in agricultural lowlands (NW Italy). *Acta Theriologica* 56: 199–207.
- Ballerling, L. & R. Beskers 2011. Nestkastcontroles van de bosuil in 2010. *Uilen* 2: 14–19.
- Broekhuizen, S. & G.J.D.M. Müskens 2000. Utilization of rural and suburban habitat by pine marten *Martes martes* and beech marten *M. foina*: species-related potential and restrictions for adaptation. *Lutra* 43: 223–227.
- Bijlsma, R.G. 2009. Trends en broedresultaten van roofvogels in Nederland in 2008. *De Takkeling* 17 (1): 7–50 (with English summary).
- Bijlsma, R.G. 2011. Trends en broedresultaten van roofvogels in Nederland in 2010. *De Takkeling* 19 (1): 6–51 (with English summary).
- Douglas, C.W. & M.A. Strickland 1987. Fisher. In: M. Novak, J.A. Baker, M.E. Obbard & B. Malloch (eds.). *Wild furbearer management and conservation in North America*: 511–529. Ontario Trappers Association, North Bay, Ontario, Canada.

- Elmeros, M., M.M. Birch, A.B. Madsen, H.J. Baagøe & C. Pertoldi 2008. Skovmårens biologi og levevis i Danmark. Udredning om skovmårens økologi og forslag til fremtidig forskning og forvaltning. Faglig rapport fra DMU nr. 692. Danmarks Miljøundersøgelser, Aarhus Universitet, Denmark.
- Gurnell, J. 1993. Tree seed production and food conditions for rodents in an oak wood in southern England. *Forestry* 66: 291-315.
- Helldin, J.-O. 1999. Diet, body condition, and reproduction of Eurasian pine martens *Martes martes* during cycles in microtine density. *Ecography* 22: 324-336.
- Jędrzejewski, W., A. Zalewski & B. Jędrzejewska 1993. Foraging by pine marten *Martes martes* in relation to food resources in Białowieża National Park, Poland. *Acta Theriologica* 38: 405-426.
- Kleef, H.L. & P. Tydeman 2009. Natal den activity of female pine martens (*Martes martes*) in the Netherlands. *Lutra* 52: 3-14.
- Marchesi, P. & C. Mermod 1989. Régime alimentaire de la martre (*Martes martes* L) dans le Jura suisse (Mammalia: Mustelidae). *Revue suisse de Zoologie* 96: 127-146.
- Mead, R.A. 1994. Reproduction in *Martes*. In: S.W. Buskirk, A.S. Harestad, M.G. Raphael & R.A. Powell (eds.). *Martens, sables and fishers: biology and conservation*: 404-422. Cornell University Press, Ithaca, NY, USA.
- Nitze, M. 1998. Untersuchung zur Ernährungsbiologie des Baummarters (*Martes martes* L.) in Waldgebieten der Agrarlandschaft Südwest-Mecklenburgs. *Beiträge zur Jagd- und Wildforschung* 23: 193-218.
- Posluszny, M., M. Pilot, J. Goszczynski & B. Gralak 2007. Diet of sympatric pine marten (*Martes martes*) and stone marten (*Martes foina*) identified by genotyping of DNA from faeces. *Annales Zoologici Fennici* 44: 269-284.
- Pucek, Z., W. Jędrzejewski, B. Jędrzejewska & M. Pucek 1993. Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop and predation. *Acta Theriologica* 38: 199-232.
- Stubbe, M. 1993. *Martes martes* (Linné 1758). Baum-, Edelmarder. In: J. Niethammer & F. Krapp (eds.). *Handbuch der Säugetiere Europas*. Band 5: Raub-säuger – Carnivora (Fissipedia); Teil 1: Canidae, Ursidae, Procyonidae, Mustelidae 1: 374-426. Aula Verlag, Wiesbaden, Germany.
- Wijsman, H. 2007a. Muizenissen. *Marterpassen* 13: 35-36.
- Wijsman, H. 2007b. Hebben muizenjaren invloed op de voortplanting bij boommarters? *Zoogdier* 18 (3) 3-6.
- Wijsman H., B. Achterberg, C. Achterberg & B. van den Horn 2010. Worpgrootte en muizenjaar 2008/2009. *Marterpassen* 16: 44- 47.
- Zalewski, A. 2007. Does size dimorphism reduce competition between sexes? The diet of male and female pine martens at local and wider geographical scales. *Acta Theriologica* 52: 237-250.
- Zalewski, A. & W. Jędrzejewski 2006. Spatial organization and dynamics of the pine marten *Martes martes* population in Białowieża forest (E. Poland) compared with other European woodlands. *Ecography* 29: 31-43.
- Zalewski, A., W. Jędrzewski & B. Jędrzejewka 1995. Pine marten home ranges, numbers and predation on vertebrates in a deciduous forest (Białowieża National Park, Poland). *Annales Zoologici Fennici* 32: 131-144.

Samenvatting

De invloed van goede en slechte muizenjaren op boommarters (*Martes martes*)

Geringe productie van mast door eik en beuk leidt in de daarop volgende winter tot een afname van rosse woelmuizen en bosmuizen, belangrijke prooien voor de boomarter. Met name beuken zetten in bepaalde jaren helemaal geen vrucht. Gegevens over de jaren 2005-2011 van 193 marternesten op de Utrechtse Heuvelrug, op de Veluwe en in Salland laten zien dat de worpgrootte na slechte mastjaren in het voorjaar afnam en dat geboorten gemiddeld een week later plaatsvonden dan in jaren met veel aanbod van prooi. De muizensituatie in februari is de belangrijkste, omdat in die maand de ontwikkeling van de foetus hervat wordt. Bepaalde moertjes bleken consequent relatief vroeg

dan wel relatief laat te werpen, onafhankelijk van de beschikbaarheid van muizenprooi. In muizenarme jaren gingen de boommarters in toenemende mate over op predatie van vogels. In de boswachterij Kootwijk hield het plunde-

ren van nestkastjes gelijke tred met muizenarme jaren.

Received: 11 January 2012

Accepted: 12 April 2012

Courtship behaviour of western hedgehogs (*Erinaceus europaeus*) in a rural landscape in Ireland and the first appearance of offspring

Amy Haigh, Fidelma Butler & Ruth M. O’Riordan

School of Biological, Environmental and Earth Sciences (BEES), University College Cork, School of BEES, The Cooperage, Distillery Fields, North Mall, Cork, Ireland, e-mail: amyjoahaigh@yahoo.com

Abstract: A study was conducted to investigate the timing of the breeding season of western hedgehogs (*Erinaceus europaeus*) in a rural landscape in Ireland, their courtship activity and the first appearance and possible dispersal of juveniles. Between June 2008 and June 2010, 24 hedgehogs (18 ♂ and 6 ♀) were caught and monitored by radio tracking and direct following. A preponderance of males was recorded in both adults and juveniles at the study site and the sex ratio deviated significantly from a 1:1 ratio. Courtship behaviour took place between April and July and occurred almost exclusively in a nine ha pasture. An individual female paired with up to seven males in a season. The first appearance of juveniles was recorded in September (2008) and July (2009). The majority ($n=22$) of juvenile sightings, both alive and as road kill, occurred in July but they continued to be recorded up until November ($n=3$). The presence of juveniles at the study site in October 2008 and a pregnant female being found in September 2009 indicated that late litters occur in Ireland.

Keywords: sex biases, multiple pairings, juveniles, second litters, dispersal.

Introduction

The breeding season in the western hedgehog (*Erinaceus europaeus*) has been reported to begin soon after the hedgehog has emerged from hibernation in April until August, with peaks in activity varying depending on latitude (Morris 1961, Morris 1969, Kristiansson 1984, Riber 2006, Jackson 2006). In New Zealand, introduced hedgehogs have a breeding season centred around November-March (equivalent to the April-August breeding season in Europe), but the milder climate in New Zealand permits breeding well outside this core period (Parkes 1975).

Female western hedgehogs are polyoestrous and, in the male, spermatogenesis occurs

between early April and mid August peaking between mid April and June in the UK (Deanesly 1934). Courtship behaviour in hedgehogs is characterised by the male circling around the female with one or both sexes snorting loudly (Reeve & Morris 1986). According to Jackson (2006) this ritual may continue for over an hour, with the majority of displays failing to end in a successful mating.

According to Emlen & Oring (1977), in species where one sex is largely freed from parental care, as is the case with the western male hedgehog, individuals of this sex should remain active for the duration of the period during which members of the other sex become sexually receptive, in order to mate with as many females as possible. For a non-territorial animal, like a hedgehog, which remains receptive for the majority of its active period, the possibility to mate with multiple individuals

© 2012 Zoogdierveniging. Lutra articles also on the internet: <http://www.zoogdierveniging.nl>

is high. In previous studies individual males made mating attempts with several females, in some cases during the same night (Reeve 1981, Kristiansson 1984, Jackson 2006, Warwick et al. 2006). During the breeding season males' home ranges increase in order to cover the range of as many females as possible (Kristiansson 1984), and multiple paternity has been reported (Moran et al. 2009).

In the UK, following a pregnancy of 31-39 days (Morris 1961), during which females may accumulate a mass of 50-150 g (Jackson 2006); between 2-7 young are born (Morris 1961, Morris 1966, Jackson 2006). The number of offspring in New Zealand, also falls within this range (Parkes 1975). In Sweden, hedgehogs have a single litter, which is larger, with Kristiansson (1981) reporting a mean litter size of 5.2 with numbers ranging up to eleven. Kristiansson (1990) reported an equal sex ratio. However a preponderance of males was found by Morris (1969), Reeve (1981) and Riber (2006) in the UK and Denmark.

Possible late litter (any time after August) as suggested by Barrett-Hamilton & Hinton (1911), has been reported in the UK (Morris 1966, Jackson 2006) and matings can occur in late August and early September (Morris 1961). Courtship or pregnancies may therefore be found during most of the active year i.e. March-October (Reeve 1981). However, as the active period is short, it is unlikely that an individual female could successfully rear two litters and gain the required weight to survive hibernation (Reeve 1994). Jackson (2006) found that at least three females, who reared a second litter, died in an emaciated state soon after the young emerged. Therefore, most late litters are thought to be the result of a failed first litter or produced by females born in the preceding August or September, that might not be ready to breed until nearly a year old (Deanesly 1934). Morris (1961) and Morris (1966) found that mothers deprived of their earlier litter are highly fertile and will readily breed again during the same season. It is not known whether a second or late litter occurs amongst Irish hedgehogs.

Juveniles, in the UK, reach independence at six weeks of age at which time they weigh between 220-235 g (Reeve 1994). Hedgehogs have been recorded to reach sexual maturity between nine months (Allanson 1934) and two years of age (Kristiansson 1990). However, Deansley (1934) felt that they reach sexual maturity once they have reached a required weight. There is little known about the dispersal of young hedgehogs but Doncaster (1993) suggested that hedgehogs do not have a fixed natal territory from which to disperse, nor a clearly defined dispersal stage. However, Doncaster et al. (2001) observed that although natural dispersals were relatively rare events, hedgehogs were capable of travelling up to 3.8 km from a release point and up to 9.9 km in total.

With no previous data on the ecology of Irish hedgehogs, the breeding season, courtship behaviour and first appearance of juveniles in Ireland is unknown. Therefore the present study aimed to investigate patterns of courtship behaviour of a study group i.e. the number of mates, duration of courtship and the identity of pairings. The study also aimed to investigate the first appearance of juveniles, the timing of litters, the number of offspring and the possible patterns of dispersal by juveniles. It also aimed to test the following hypotheses that:

- Due to the increased home range of males during the breeding season, males would attempt to mate with multiple females.
- A late or second litter occurs amongst Irish hedgehogs and is evident amongst the study group and through the appearance of juvenile road kill
- In line with research in the UK, little dispersal occurs amongst juveniles.

Materials and methods

Site

The study was carried out between June and November 2008 on a site (51° 53' 59.5"N lati-

tude, 8° 29'03.7"W longitude) in SW-Ireland, 36.8 km from Cork city and 5.3 km from the nearest town of Bandon. The site of 97 ha consisted of 23% arable, 64% pasture, 7% residential garden, 1% scrub, 1% marsh, and 4% wood. Crops grown in the arable field consisted of barley and wheat, fungicides were applied once a year in May and the crop was cut in September. Pasture was grazed by horses. Hedgerow was maintained in all of these fields with each having a thick bramble understory. The walls around the various habitats did not appear to act as a boundary to the movement of hedgehogs and they were observed scaling these walls with little difficulty.

Capture and marking

Hedgehogs were captured by hand with the aid of spotlights. The animals were marked using a unique colour combination of 15 heat shrink plastic tubes (RS Components Ltd, Corby, UK) which were attached with glue (Evo-stik, Bostik Ltd, Leicester, UK) to a number of spines in three specific regions on the animal (left of head, centre and right of head). Reflective tape was also applied to one of the middle markers so that the head region could be identified while tracking. The tubes acted as a visual aid and minimised the need to recapture the animal for individual identification. The hedgehogs were also marked using passive integrated transponder (P.I.T.) tags inserted into the upper hind leg (Doncaster et al. 2001, Jackson et al. 2004). This allowed individuals to be re-identified after hibernation. All procedures were carried out in accordance with current regulations, with licenses being obtained from the Department of Environment, Heritage and Local Government.

All hedgehogs caught were classified as adult or juvenile, sexed and hind foot measurements were taken. Individuals were weighed weekly, using digital scales (Harvard Apparatus, Holliston, MA, USA), to assess weight changes associated with pregnancy and monitor juve-

niles. The hedgehog was considered to be a juvenile if it satisfied all of the following criteria: weight less than 600 g when first caught; hind foot length of less than 3.6 cm; and presence of growing spines all over the pelage.

Direct following

Spotlighting for hedgehogs took place between 26th June 2008 and 28th September 2008. Any hedgehogs caught during spotlighting nights were fitted with a tip light (MK IV, Murray and Co. Ltd, Cork, Ireland) placed on the back and monitored by direct observation using a UV filter placed over a spotlight. Fixes were taken at ten minute intervals using a Garmin GPS 60 (CH Marine, Cork, Ireland). Every ten minutes the behaviour and location of each hedgehog were recorded.

Radio tracking

All hedgehogs caught after 28 September 2008 were equipped with radio tags. Eight individuals were fitted with 173 MHz, R1-2B transmitters (Holohil Systems Ltd, Ontario, Canada) in 2008, 16 in 2009 and six in 2010. These tags were attached to the hedgehog as described in Jackson & Green (2000). The entire tag weighed 10 g. Individuals were then tracked using a SIKA receiver (Biotrack Ltd, Dorset, UK). When the hedgehog was located, its position was documented and a ten minute focal sample was conducted before locating the next tagged individual. In 2008, radio tracking was carried out from dusk until they returned to their nests at dawn. In 2009, individuals were monitored for either the first six hours of the night after emergence or the six hours before dawn.

Courtship behaviour

Courtship behaviour was identified based on the description by Reeve & Morris (1986), i.e.

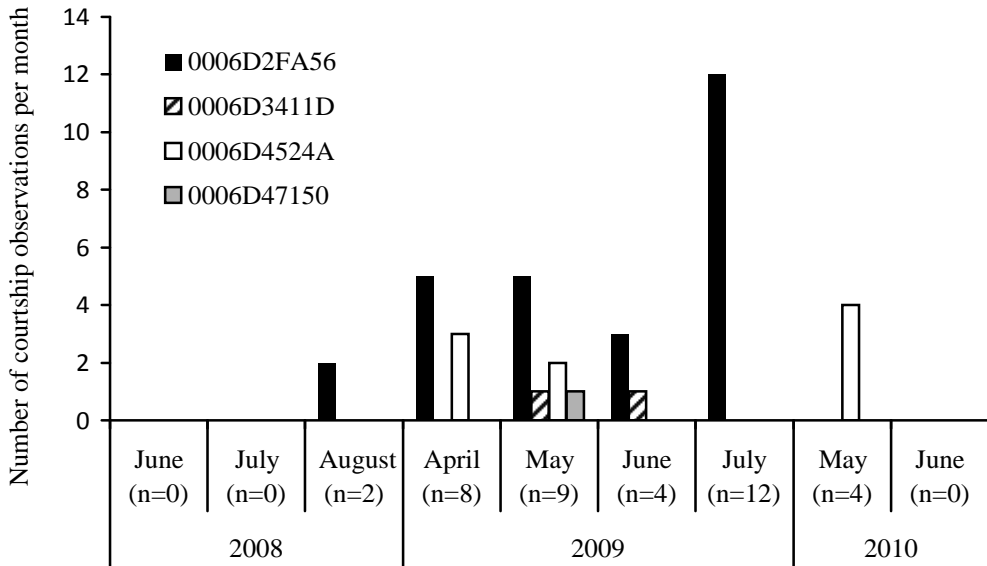


Figure 1. The months in which courtship behaviour was observed among the females (n =total number of observations of courtship).

“courtship involves the male circling closely around the female, with one or both sexes snorting loudly”. When courtship behaviour was observed, the identification of individuals involved was recorded, in addition to their location, the length of time which they spent engaged in courtship behaviour and whether the behaviour concluded in a successful mating.

Road kill

In March 2008, an appeal was sent out on the University College Cork website informing people about the project and appealing for carcasses. The public was also made aware of the project through the distribution of 320 surveys to agricultural colleges, gun clubs and rural areas, requesting records of hedgehog sightings (Haigh et al., in press). Carcasses of road kill were subsequently collected by both the authors and members of the public from all over Ireland. These were sexed, weighed and aged by one of the authors, using the same criteria as described previously. The time of year and the location

of the incident were also recorded. Carcasses of females were inspected for signs of lactation and if pregnant the numbers of foetuses were recorded.

Results

Sex ratio

Between June 2008 and June 2010, 24 hedgehogs (18 ♂ and 6 ♀) were caught at the site. The sex ratio of those caught was 3 (male) : 1 (female) which deviated significantly from 1:1 (Chi-squared test: $\chi^2=6.760$, $df=1$, $P<0.01$) ($\chi^2=6.8$ following Yates correction). Eight of these hedgehogs were juveniles (6 ♂ and 2 ♀) and as was the case with adults their sex ratio was also 3:1.

Courtship behaviour

Courtship behaviour was usually first obvious by the loud hisses of the female. The hedgehogs faced each other, the male attempting

to approach the female who would lunge forward, pushing her head underneath his body, while she forcefully pushed him away. The male would again edge forward and attempt to move behind the female, progressing in wide circles, and moving behind large clumps of grass. The female quickly circled around to avoid the male approaching behind her and again the hissing resumed.

Time of occurrence of courtship

In 2008, when 14 hedgehogs were monitored at the site for 375 hours over 81 nights from June to November 2008, there were only two observations of courtship behaviour, both in August (figure 1).

In 2009, 16 hedgehogs were observed for a total period of 624 hours over 104 nights, with twelve of these individuals being observed in courtship behaviour. From emergence in April until July 2009, there were 33 observations of courtship behaviour involving four adult females (figure 1), with no further observations of courtship behaviour after July.

In 2010, six hedgehogs were monitored for 76 hours over 38 nights. Courtship behaviour was first observed in May, and there was one female tagged at this time. Four incidents of courtship behaviour were observed between March and June, all taking place in May and involving this female. This female (524A) was killed on the road in June 2010 and no further courtship behaviour was observed (figure 1). Prior to this all courtship displays in 2010 had involved this female.

Duration of courtship events

Of the 39 observations of courtship behaviour over the entire study period, involving 16 individuals (4 ♀ and 12 ♂) no successful copulations were witnessed. Bouts of courtship behaviour had a mean duration of 60

(± 0.05) minutes. However, on one occasion in 2009 a bout lasted for up to 140 minutes. On this occasion, while one pair was involved in courtship behaviour in the pasture, two males approached from two different directions. One remained stationary behind a clump of grass for the duration of the interaction, while the other approached the female and attempted to mate with her.

Courtship always terminated with the male moving away and immediately starting to forage, while the female remained stationary until the male had moved away from the area.

Of the 1132 fixes from twelve (8 ♂ and 4 ♀) individuals obtained between April and July 2009, during 292 (26%) of these, hedgehogs were engaged in courtship behaviour. There was no significant variation in the number of fixes where courtship behaviour was observed for either sex ($\chi^2=2.381, df=1, P>0.05$). Out of 458 fixes obtained from females ($n=4$) between April and July 2009, in 139 (30%) of these, courtship behaviour was observed. In the same time period, out of 678 male ($n=8$) fixes, during 153 (23%) of these courtship behaviour was observed.

Identification of pairings

In 2008, there were two observations of courtship behaviour and they involved three of the tagged males and one female (FA56). In 2009, a male was observed paired with this same female on up to six different occasions (mean 2.4 ± 0.38 occasions per female). Males were observed in courtship behaviour with up to three different females during the breeding season (mean 1.6 ± 0.31 occasions per male) (figure 2). For example in 2009, male 8C88 was observed paired with female FA56 on three occasions, female 411D twice and once with female 524A. In 2010, female 524A was the only female observed at the site and all of the tagged males ($n=4$) were observed attempting to mate with her (figure 2).

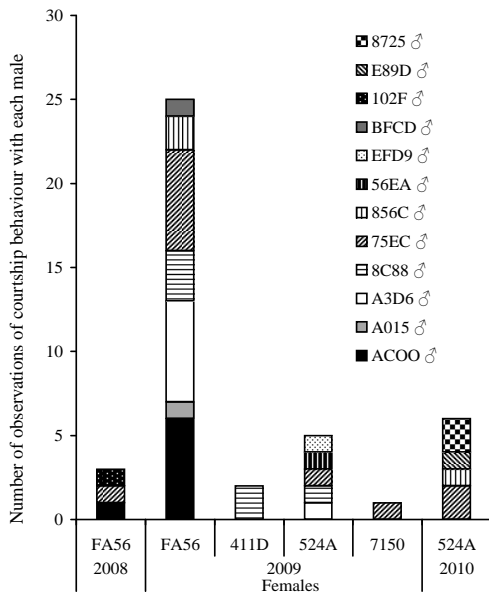


Figure 2. The number of times a female was observed paired with a particular male in 2009.

Location of courtship events

During the breeding season, both sexes concentrated their activity in pasture, and moved out of this area when the breeding season terminated. In total, 92.3% of courtship behaviour took place here, with only one observation in the marsh and two in the garden. Courtship behaviour in the garden occurred in August 2008, when breeding had terminated in the following two years. A female (411D) from the periphery of the site (*1 figure 3) moved down to the pasture (* figure 3) where all the courtship took place in May 2009. It was as she moved down into this area that a courtship event was observed in the marsh (*2 figure 3) between her and an adult male (8C88). Females occupied three neighbouring areas of pasture during the breeding season and this area was completely encompassed by the adult males. The pasture represented the core area of the females home range at this time in all years, and while their mean annual home range was 16.5 ± 0.49 ha ($n=3$ adult females), the males occupied 56.0

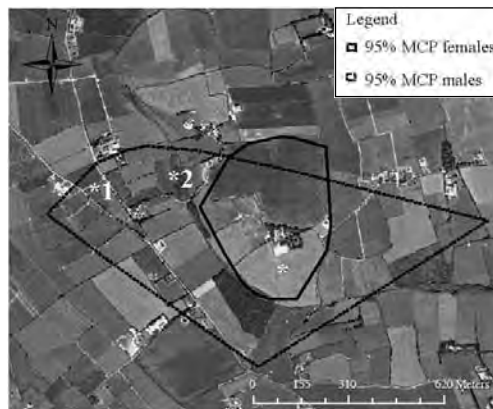


Figure 3. The home range of adult males and females (100% mcp).



Figure 4. Fixes of an adult female (524A) monitored over three years.

(± 0.67) ha ($n=4$ adult males) (Haigh 2011) (figure 3).

The most detailed information, over the three years, is available for adult female (524A). She was first caught in September 2008 in the arable field (1 in figure 4) and tagged until her death in June 2010. In the two consecutive years she moved away from the core area of her home range (2 in figure 4), at the end of May, after being involved in several courtship events (figures 1 and 2). At this time she moved into neighbouring pasture (0.53 km) (3 in figure 4). In September she moved back with the other adults (4 in

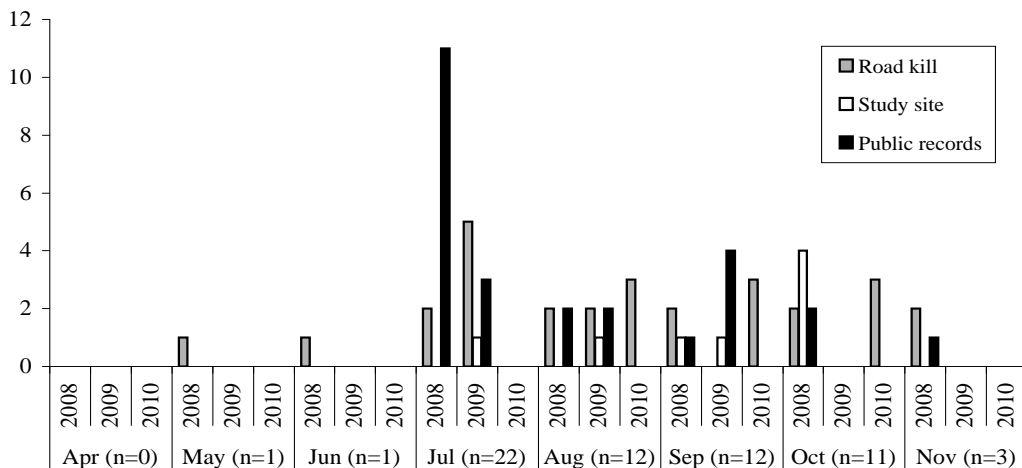


Figure 5. Month in which juveniles were either recorded alive (at the study site and by the public) or as road kill during the research period.

figure 4). In May 2009, her weight increased by 112 g in six days. When she was next seen active, and weighed, seven days later, she had lost 198 g, suggesting that she had given birth.

First appearance of juveniles

In 2008, the first juvenile (♀) was caught at the study site on 19 September. The remaining ($n=4$) juveniles were caught on 17 and 18 October of that year, their weight (244-281 g) indicating that they had just reached independence. In 2009, the first juveniles were caught at the site in July.

Four out of 35 road kill females collected as road kill (7 June, 23 June, 14 July and 6 September 2009), were pregnant when killed. In two of these cases the foetuses were well developed (between 4-7 g and 14-20 g and 2 cm long) with one female pregnant with five foetuses and the other with six. Only the litter of six could be accurately sexed and they showed a sex ratio of 1:1. None of the female carcasses showed obvious signs that they were lactating and none of the female carcasses collected in 2008 and 2010 were pregnant when killed.

Twenty-eight of the road casualties were

juveniles (figure 5) and 88 were adult, the remaining 29 were too damaged to accurately identify. The incidences of juveniles being killed on the road peaked in July, but they were found up until November (figure 5).

Movement of juveniles from natal nest

Juvenile movement in 2008

Juveniles made exploratory movements away from their natal nest, but returned and remained close to the area of their birth. There were 135 fixes obtained from juveniles in October and November 2008. In the first few days after tagging in October 2008, the four late juveniles (3 ♂ and 1 ♀) confined their activity to a small area of the arable field, and all of them returned to the same nest every morning. This is illustrated by one of these juveniles, a male (56EA) who was radio tagged (figure 6A). After the first week they all were observed foraging further into the field and occupied separate day nests, however they all remained in the arable field, where the adults were also foraging (figure 6B). The greatest distance moved was 0.20 km in October and 0.24 km in November. He remained in the



Figure 6. The movement patterns of a juvenile male (56EA) from first capture in October (A), November (B), March and April 2009 (C).

arable field throughout hibernation and did not leave this habitat until the following year. He emerged on 30 March 2009 and moved 0.06 km within the arable field. In April 2009 (figure 6C) he entered the nine ha area of pasture (0.50 km from first capture, 0.33 km from hibernacula).

Juvenile movement in 2009

The first juvenile of 2009 was again found in the arable field, but in July weighing 299 g. This animal, a male (ACD7) remained in the southern portion of the arable field for the first two months of independence. He gradually dispersed 0.23 km into the arable field, and was recorded on two occasions making exploratory trips into the neighbouring pasture in September (0.43 km) (figure 7). This individual was killed by a dog in the arable field at the end of September 2009.

Two more juveniles (both ♂) were found in three ha of pasture, at the site in August and September 2009. They remained in this area throughout the monitoring period. However, in October 2009 one of the juveniles (D89D) entered the arable field and built a hibernaculum there. Both of these hedgehogs were monitored throughout hibernation. One failed to emerge but the other (D89D) emerged in March 2010. This animal remained in the pas-

ture and despite making exploratory trips of 0.64 km (figure 7) into the neighbouring pasture returned to the core area of the pasture, where he was eventually killed by a mowing machine in June 2010.

Discussion

At the study site there was a sex bias in favour of males, for both adults and juveniles 3:1. Similarly, a strong preponderance of males in both juveniles (7:2) and adults (8:5) was noted by Reeve (1982) and Riber (2006), who caught 24 adult males and 7 females. However, Kristiansson (1990) in Sweden found an equal sex ratio. Reeve (1982) suggested that a male bias may be due to transient males, as he did not notice this bias amongst juveniles. This may partly explain the bias in the current study as four of these males were first caught between April and July 2009, at the height of the breeding season. Furthermore all of these individuals were first caught while trying to mate with tagged females. Two of the adult males were not seen again and the other two were known to have moved outside the core (56.0 ± 0.7 ha) home range after the breeding season ended in August 2009, with one returning again to attempt to mate in May 2010. It therefore must be considered that the strong male bias was

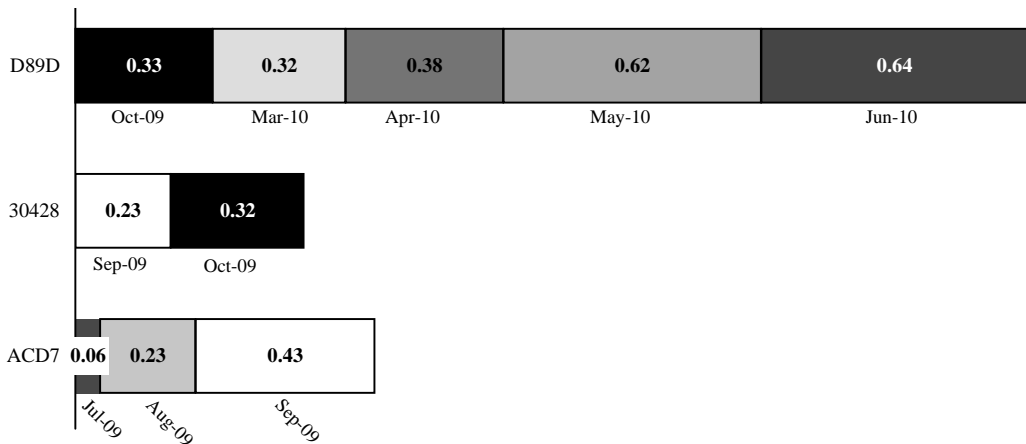


Figure 7. The greatest recorded distance (km) that a juvenile moved from the location where it was first captured to the furthest fix each month.

a result of the male's larger home range and small study area. It may therefore have not been as apparent if the study site was larger. However, in the present study a bias was also observed amongst juveniles in both years, with a litter of four juveniles in 2008 having just one female. In 2009, all of the three juveniles caught were male. Kristiansson (1990) noting the discrepancy between estimated litter size at birth (6.5) and the recruited number of juveniles per adult (2.79), and suggested a high mortality rate from birth to catchability. Therefore, mortality may be higher amongst female offspring as one of the litter of foetuses recovered from a pregnant female showed a sex ratio of 1:1. Clutton-Brock & Iason (1986) examined mammals increasing their fitness by varying the sex ratio of their progeny, in response to differences in the costs and benefits of producing males and females. They found that in species where males may disperse from their natal area, while females share their mother's home range, the female siblings are likely to compete for resources, so the mothers produce male biased sex ratios. However, as there is little information on whether juvenile hedgehogs disperse, it is unclear whether this could be the case in hedgehogs.

In the present study, a peak in sexual activ-

ity was observed in July which was similar to peaks in the UK (Reeve 1981, Jackson 2006) and Sweden (Kristiansson 1981). The breeding season of hedgehogs is often characterised by an increased movement of males in order to encompass the range of as many females as possible (Kristiansson 1984). The males who were tagged in the present study increased their range during the breeding season with one male covering an area of up to 30 ha, at its peak movement in July before reducing his range to eleven ha in August when breeding behaviour ceased (Haigh 2011).

Jackson (2006) reported that females were promiscuous and were estimated to have sexual encounters, though not necessarily matings, with at least five males. In the present study copulation was never observed, but 39 incidents of courtship behaviour were witnessed. Successful matings appear to be rare with Reeve & Morris (1986) reporting only five successful copulations in 76 courtship displays and Jackson (2006) only observing ten. Jackson (2006) felt that this reflected the brevity of mating (minutes) relative to the time spent courting (up to an hour or more). In shrews (*Sorex araneus*), as females cannot always distinguish between close kin they may copulate with several different males, thereby reducing the risk that all of their off-

spring will be sired by a close relative (Stockley et al. 1993). Multiple paternity, which has been reported in shrews and hedgehogs (Moran et al. 2009), may be a useful way for a non territorial animal, like the hedgehog, to reduce inbreeding depression and the need for dispersal.

Surprisingly, 92.3% of courtship events occurred in a core area of pasture. Potential prey was consistently poor in this habitat throughout the year (Haigh 2011), which may have meant that there was less distraction from breeding. Prey abundance was also lower here, than in areas of arable, which hedgehogs began to enter once the breeding season finished (Haigh 2011). Therefore, habitat selection appeared to be motivated by courtship behaviour at this time. They spent up to 35% of their time engaged in courtship behaviour and 26% of their time foraging (Haigh 2011). Three of the females concentrated their activity in this habitat during the breeding season and the fourth female (411D), moved down here from the periphery of the site. While, the reason for the selection of this pasture for courtship events is undetermined, it would appear that access to multiple mates is advantageous for both sexes. In other polyandrous species such as the marsupial *Antechinus agilis*, the female benefits through increased growth rates by mating with multiple males (Fisher et al. 2006). In the present study, females were found with up to seven different males and males were observed trying to mate with up to three different females. Over the breeding season an individual male attempted to mate with the same female up to six times. On two occasions the male attempted again to mate with the same female later in the same night. However, it was still unsuccessful. With animals that were tagged for more than one season, the same male attempted to mate with the same female the following year. This is in contrast to data from the UK, where Reeve (1981) and Jackson (2006) both reported that the probability of the male being found with the same part-

ner was low. In Reeve & Morris' (1986) study, ten of the 76 incidents involved partners who had been previously recorded together up to three times, but twelve of the females were courted by at least ten different partners. The high incidence of repeated pairings of the same individuals in the present study may be due to the high male bias and small number of females at the site, with only four adult females recorded in the two and a half year study. The two juvenile females caught in 2008 were not seen again after hibernation.

In all cases courtship behaviour was characterised by the aggressive behaviour of the female, in the same manner previously described by Reeve & Morris (1986) and Jackson (2006). Cox & Le Boeuf (1977) indicated that this behaviour, of rejecting a suitor, allows the female to test the vigour, tenacity and speed (indicators of fitness) of a potential suitor and select a union which results in optimal genetic consequences. Reeve (1994) too suggested that the courtship ritual allows plenty of time for a female to judge her suitor and less vigorous males may be displaced. In the present study a courting pair of hedgehogs was often approached by up to two other males. The males ran to the pair with their heads raised suggesting that they had been alerted to the pair either by the sound of the aggressive female or through her scent. Reeve (1994) suggested that odour plays an important part in hedgehogs' pre-mating behaviour, with males attracted to females in oestrus and certainly in this study this appeared to be the case with a male seen running towards a lone female from the other side of the nine ha pasture in June 2010. Aggressive female behaviour during mating has also been described in e.g. elephant seals (*Mirounga angustirostris*) that respond to male advances by loud vocalisations and escape movements, this alerts neighbouring males and competition ensues among males of varying ranks, with the result that the highest ranking male is selected (Cox & Le Boeuf 1977, Christenson & Le Boeuf 1978). As in the present study no observations

of courtship behaviour resulted in copulation, it is uncertain whether there was any effect of male dominance in the outcome of a mating attempt. However, in the present study on the two occasions when a male hedgehog, who was known to have been born the previous year, attempted to mate with a female, they were in both cases joined by an older male, who was aggressive towards the younger hedgehog that subsequently retreated.

According to Kristiansson (1990) female hedgehogs do not produce young until their third summer i.e. at about two years old. Jackson (2006) found that only four of 48 sub adults were found paired with a female, and none were definite sub adults. However, earlier estimates of sexual maturity have been reported, with Allanson (1934) suggesting nine months for males and Morris (1969) recording one female reaching an oestrus condition by the end of its first summer at an age of less than six months. Deansley (1934) suggested that hedgehogs reached sexual maturity once they have reached a required weight. The two males in the present study would have been seven months and ten months respectively, when found paired with a female, having both reached weights close to that of the adults at this time. However, as mentioned above, in both incidents of courtship behaviour, they were displaced by an older hedgehog.

In 2008, although spotlighting at the site began in June, juveniles were not seen at the site until September and October, 6-8 weeks after the only courtship displays had been observed in August 2008. On 17 October 2008, four juveniles were found with a mean weight of 259.5 g (\pm 0.99). In the UK Reeve (1994) reported weights of 200-235 g (about ten times) birth weight, at around 40 days and they are newly independent at about six weeks. Their size and the fact that these animals remained in close proximity to one another and returned to the same nest indicated that these animals were newly independent in October 2008. Although late in the year, second or late litters have been reported

in a number of studies (Barrett-Hamilton & Hinton 1911, Deansley 1934, Morris 1961, Morris 1966). Jackson (2006) found that 81% of females bred again in the later part of the season and in his study all nine adult females, that had failed early season breeding attempts, attempted to breed again. It is unlikely that all hedgehogs have two litters a year, since some, including parous animals, do not come into their first oestrus until June or even later (Deansley 1934). Animals born in the preceding August or September might not be ready to breed until nearly a year old, and these may account for some of the pregnancies in the second half of the breeding season (Deansley 1934). A late litter was also recorded in the present study in a hedgehog collected as road kill. A hedgehog killed on the 6th September 2009, was in the latter stages of pregnancy with six young. In 2009, courtship was observed from April onwards and similarly juveniles were found at the site earlier than in 2008, with the first observed in July, weighing 299 g. This coincided with the month in which there were peaks in newly independent juveniles collected as road kill.

According to Doncaster et al. (2001) hedgehogs do not have a fixed natal territory from which to disperse, nor a clearly defined dispersal stage. Becher & Griffiths (1998) examined genetic differentiation among local hedgehog populations in the UK, and found significant genetic differentiation, and restricted gene flow, among closely spaced hedgehog populations, indicating that dispersal among hedgehog populations occurs rarely. This therefore raises the question of the amount of genetic variation that exists between local populations and the effects of inbreeding. As a non territorial animal the hedgehog is largely free from the constraints of moving, to form new territories, and so may remain if there is a sufficient food and nest sites available. In the present study the late juveniles caught in 2008 were at first observed all returning to the same nest, but, as the week progressed they

gradually moved further into the 15 ha arable field and began occupying separate nests. One juvenile hedgehog was tagged throughout hibernation and for the first week after emergence in 2009, he remained in the arable field, before moving into the pasture that was occupied by all of the tagged adults. While two transient males were seen at the site in 2009 during the breeding season, all of the tagged hedgehogs remained in the study area for the duration of the study and occupied the same area each year. In the present study, a juvenile caught in 2009 occupied the same area in the first month after hibernation and then gradually made exploratory trips out of the core area. However, despite this he always returned to the central home range occupied by adults, until he was killed in June 2010. It therefore seems probable that although male hedgehogs may disperse during the breeding season, in order to encompass the range of as many females as possible, they will return to the core area of their home range if sufficient resources are available. The home range of males completely overlapped not only with one another, but also all of the adult females allowing the males to locate more females. In contrast females occupied mutually exclusive areas (Haigh 2011). In two consecutive years, the adult female whose range slightly overlapped that of another female, moved away from the core area at the end of May, before moving into the arable field in September with the other adults. In 2009, her weight and condition just prior to this time indicated that she was about to give birth, having put on 112 g. When she was next seen active (and weighed) she had lost 198 g. Jackson (2006) found that a female's mass increased by 50-150 g during pregnancy and dropped suddenly at birth. With respect to the female who was collected as road kill in the latter stages of pregnancy, the four foetuses were found to weigh 164 g in total. In the present study the movement of one of the females from her core home range area at the time she gave birth may have been a mechanism for regulating

numbers in her central home range, thereby reducing resource competition and the possibility of inbreeding. In rodents of the genus *Peromyscus*, home ranges are maintained by mutual avoidance at low densities and pregnant females will frequently abandon their home range and establish a new home range in a nearby habitat, suggesting that females are more instrumental than males in regulating recruitment (Wolff 1989).

Conclusion

This is the first record of courtship behaviour, sex biases and observations of offspring in Irish western hedgehogs. A strong male bias was observed amongst the study group, which could account for the high number of repeat pairings observed in the group, in comparison to studies elsewhere. Similar to research elsewhere in Europe, courtship behaviour was observed between April and July and males attempted to mate with multiple females. The presence of newly independent juveniles in October at the site and as road kill, indicate that, similar to the UK, late litters occur in Ireland. Little dispersal was observed amongst the study group, outside the breeding season and densities of hedgehogs at the site remained high, indicating that resources must be available to support this high density of hedgehogs.

Acknowledgements: The authors would gratefully like to acknowledge the assistance of the following people, Digger Jackson, Pat Morris, Nigel Reeve and Anouschka Hof for their invaluable advice on hedgehog research at the start of this work, Helen Bradley for all of her many hours of assistance with G.I.S. Padraig Whelan and all of the people who collected hedgehog carcasses. The Department of Environment, Heritage and local Government for granting licenses, the Crawford Hayes fund for PhD scholarship and all the staff and students in U.C.C who assisted in this study. We furthermore thank the two anonymous referees for their constructive comments. Finally this would not

have been possible without the assistance of the land owners, who co-operated throughout this study.

References

- Allanson, M. 1934. The reproductive processes of certain mammals. VII. Seasonal variation in the reproductive organs of the male hedgehog. Philosophical Transactions of the Royal Society of London Series B, Containing Papers of a Biological Character 223: 277-303.
- Barrett-Hamilton, G.E.H. & Hinton M 1911-1921. A history of British mammals. Volume 2, 748 pp. Gurney & Jackson, London, UK.
- Becher, S.A. & R. Griffiths 1998. Genetic differentiation among local populations of the European hedgehog (*Erinaceus europaeus*) in mosaic habitats. Molecular Ecology 7 (11): 1599-1604.
- Christenson, T. & B. Le Boeuf 1978. Aggression in the female northern elephant seal, *Mirounga angustirostris*. Behaviour 64 (1): 158-172.
- Clutton-Brock, T. & G. Iason 1986. Sex ratio variation in mammals. Quarterly Review of Biology 61 (3): 339-374.
- Cox, C.R. & B.J. Le Boeuf 1977. Female Incitation of male competition: a mechanism in sexual selection. The American Naturalist 111 (978): 317-335.
- Deanesly, R. 1934. The reproductive processes of certain mammals. Part VI. The reproductive cycle of the female hedgehog. Philosophical Transactions of the Royal Society of London Series B, Containing Papers of a Biological Character 223: 239-276.
- Doncaster, C. 1993. The influence of predation threat on foraging pattern: the hedgehog's gambit. Revue d'ecologie (La Terre et la Vie) 48: 207-213.
- Doncaster, C., C. Rondini & P. Johnson 2001. Field test for environmental correlates of dispersal in hedgehogs *Erinaceus europaeus*. Journal of Animal Ecology 70 (1): 33-46.
- Emlen, S.T. & L.W. Oring 1977. Ecology, Sexual Selection, and the Evolution of Mating Systems. Science 197 (4300): 215-223.
- Fisher, D.O., M.C. Double & B.D. Moore 2006. Number of mates and timing of mating affect offspring growth in the small marsupial *Antechinus agilis*. Animal Behaviour 71 (2): 289-297.
- Haigh, A. 2011. The ecology of the European hedgehog (*Erinaceus europaeus*) in rural Ireland. University College Cork, Cork, Ireland.
- Haigh, A., F. Butler & R. O'Riordan (in press). A review of techniques for detecting hedgehogs (*Erinaceus europaeus*) in a rural landscape. Journal of Negative Results.
- Jackson, D. 2006. Factors affecting the abundance of introduced hedgehogs (*Erinaceus europaeus*) to the Hebridean island of South Uist in the absence of natural predators and implications for nesting birds. Journal of Zoology 271 (2): 210-217.
- Jackson, D.B., R.J. Fuller & S.T. Campbell 2004. Long-term population changes among breeding shorebirds in the Outer Hebrides, Scotland, in relation to introduced hedgehogs (*Erinaceus europaeus*). Biological Conservation 117 (2): 151-166.
- Jackson, D.B. & R.E. Green 2000. The importance of the introduced hedgehog (*Erinaceus europaeus*) as a predator of the eggs of waders (Charadrii) on machair in South Uist, Scotland. Biological Conservation 93 (3): 333-348.
- Kristiansson, H. 1981. Distribution of the European Hedgehog (*Erinaceus europaeus* L.) in Sweden and Finland. Annales Zoologici Fennici 18 (2): 115-119.
- Kristiansson, H. 1984. Ecology of a hedgehog *Erinaceus europaeus* population in southern Sweden. University of Lund, Lund, Sweden.
- Kristiansson, H. 1990. Population variables and causes of mortality in a hedgehog (*Erinaceus europaeus*) population in southern Sweden. Journal of Zoology 220 (3): 391-404.
- Moran, S., P.D. Turner & C. O'Reilly 2009. Multiple paternity in the European hedgehog. Journal of Zoology 278 (4): 349-353.
- Morris, B. 1961. Some observations on the breeding season of the hedgehog and the rearing and handling of the young. Proceedings of the Zoological Society London 136 (2): 201-206.
- Morris, B. 1966. Breeding the European hedgehog *Erinaceus europaeus* in captivity. International Zoo Yearbook 6 (1): 141-146.
- Morris, P. 1969. Some Aspects on the ecology of the hedgehog (*Erinaceus europaeus*). University of London, UK.
- Parkes, J. 1975. Some aspects of the biology of the hedgehog (*Erinaceus europaeus* L.) in the Mana-

watu, New Zealand. *New Zealand Journal of Zoology* 2 (4): 463-472.

- Reeve, N.J. 1981. A field study of the hedgehog (*Erinaceus europaeus*) with particular reference to movements and behaviour. PhD thesis. University of London, London, UK.
- Reeve, N.J. 1982. The home range of the hedgehog as revealed by a radio tracking study. *Symposium of the Zoology Society, London* 49: 207-230.
- Reeve, N.J. 1994. Hedgehogs. Poyser, London, UK.
- Reeve, N.J. & P.A. Morris 1986. Mating Strategies in the hedgehog (*Erinaceus europaeus*). *Journal of Zoology* 210: 613-644.
- Riber, A.B. 2006. Habitat use and behaviour of European hedgehog *Erinaceus europaeus* in a Danish rural area. *Acta Theriologica* 51 (4): 363-371.
- Stockley, P., J. Searle, D. Macdonald & C. Jones 1993. Female multiple mating behaviour in the common shrew as a strategy to reduce inbreeding. *Proceedings: Biological Sciences* 254 (1341): 173-179.
- Warwick, H., P. Morris & D. Walker 2006. Survival and weight changes of hedgehogs (*Erinaceus europaeus*) translocated from the Hebrides to mainland Scotland. *Lutra* 49 (2): 89-102.
- Wolff, J.O. 1989. Social behavior. In: J.L. Kirkland & J.L. Lane (eds.). *Advances in the study of Peromyscus (Rodentia)*: 271-291. Texas Technical University Press, Lubbock, USA.

Samenvatting

Hofmakerij bij egels (*Erinaceus europaeus*) in een landelijke omgeving in

Ierland en het eerste moment van geboren worden van de jongen

Wij onderzochten het verloop in de tijd van het voortplantingsseizoen van egels in Ierland: het hofmaken, het eerste moment waarop de jongen worden geboren, en het mogelijk zich verplaatsen van de jongen. Tussen juli 2008 en juni 2010 ving we 24 egels (18 ♂ en 6 ♀), die we zenderden en volgden. Het laatste deden we ook door de dieren direct achterna te lopen. Mannetjes waren oververtegenwoordigd, zowel bij volwassen als bij jonge dieren, waarbij de geslachtsverhouding bij de adulten significant afweek van 1:1. Het hofmaken vond plaats tussen april en juni en bijna uitsluitend in een negen ha groot weidegebied dat onderdeel uitmaakt van het studiegebied. Eén vrouwtje paarde in een seizoen met zeven mannetjes. De eerste jongen werden in 2008 in september waargenomen en in 2009 in juli. In juli werden de meeste jongen waargenomen ($n=22$), hetzij als verkeersslachtoffer of als zichtwaarneming; de sterfte onder jongen door het verkeer liep door tot in november ($n=3$). De aanwezigheid van jongen in het onderzoeksgebied in oktober 2008 en de aanwezigheid van een zwanger vrouwtje in september 2009 toont aan dat in Ierland late worpen voorkomen.

Received: 14 April 2012

Accepted: 26 May 2012

Analyses of four centuries of bounty hunting on seals in Zeeland, SW-Netherlands

Kees G.N. de Vooy¹, Sophie M.J.M. Brasseur², Jaap van der Meer³ & Peter J.H. Reijnders^{2,4}

¹ NIOZ, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, NL-1790 AB Den Burg, Texel, the Netherlands, e-mail: cees.de.vooy@nioz.nl

² Institute for Marine Resources and Ecosystem Studies, dept. Ecosystems, P.O. Box 167, NL-1790 AD Den Burg, Texel, the Netherlands

³ NIOZ, Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, the Netherlands

⁴ Aquatic Ecology & Water Quality Group, Wageningen University, P.O. Box 9101, NL-6700 HB Wageningen, the Netherlands

Abstract: For centuries, bounty hunts for seals (*Phoca vitulina*) were conducted in the Province of Zeeland (SW-Netherlands). Records of bounties paid for seals hunted in that area have been archived by the province of Zeeland from the 16th until the 20th century. These hunting records were used to reconstruct the numbers of seals caught each year in order to subsequently investigate the effect of social and historical events on the hunt. Based on the type of records we discerned three periods in the bounty hunts: 16th until 19th century, 19th century, and 20th century. During these periods large fluctuations in numbers of seals killed were observed. In the first period, high yields were achieved when experienced hunters (Frisians) came to the area, whereas the presence of privateers - and to a much lesser extent war activities - lead to significant lower seal catches. The effects of these events on the hunt appear to be so significant that it impairs the reconstruction of the population size in the pre-20th century period. This is different for the 20th century. Besides the periods during the two World Wars, no large scale changes in environmental conditions occurred. Efficacy of hunting methods took effect from 1900 onwards, when firearms became increasingly accurate. When bounty payments stopped in 1934, the seal hunt still continued and catches were registered. When the hunt was finally closed in 1961, the population in the SW-Netherlands had been decreased to approximately five percent of its estimated size around 1900. It has not recovered since then, mainly due to lack of immigration, high mortality, excessive disturbance, and low reproduction.

Keywords: seal hunting, bounty scheme, SW-Netherlands, privateers, hunting methods, Zeeland.

Introduction

For centuries, harbour seals (*Phoca vitulina*) have been considered to impact fisheries. They were therefore hunted throughout their range of distribution, including the Netherlands, where hunting was encouraged by the provincial government by means of imposing bounties. There was a highly developed fishery in

the Province of Zeeland and seals were considered to be a threat, being by competition, gear damage or depredation. The authorities expected to promote seal hunting by providing bounties. The payment of bounties for each seal killed has a long history in the Netherlands. This was especially the case for the hunt in the waters around the Province of Zeeland (figure 1). This bounty system was particularly well documented and was introduced as early as 1591, continuing though with some interruptions, throughout the cen-

© 2012 Zoogdierverseniging. Lutra articles also on the internet: <http://www.zoogdierverseniging.nl>



Figure 1. Map of the Netherlands around 1800.

turies until 1934. Most of the information on the magnitude of the seal hunt presented here has been given in earlier publications written in Dutch (de Vooy et al. 1999, de Vooy 2003, de Vooy 2006). In theory, this data could be used to analyse changes in the local seal population, assuming a relation between population size and hunting success (Reijnders 1992). However, next to the population size, the success of these bounty hunts aimed at strongly reducing the seal population might have been affected by social and historical events. This would render it impossible to estimate the population size in historic times, solely based on numbers of seals killed and retrieved. Therefore we study here the possible effects of prevailing social and historical events in Zeeland on the bounty hunt during four centuries. The usage of the word

seal or seals refers to harbour seals, as in the time period covered there were no observations on occurrence of other seal species such as the grey seal (*Halichoerus grypus*).

Material and methods

data sources

The main source of data used to determine the seal hunting activities in Zeeland are the bounty payments recorded in the archives of the Province of Zeeland. The different types of archives are the basis for the separation into three periods.

For the first period of bounties in the 16th, 17th and 18th centuries (1591 until 1810) we

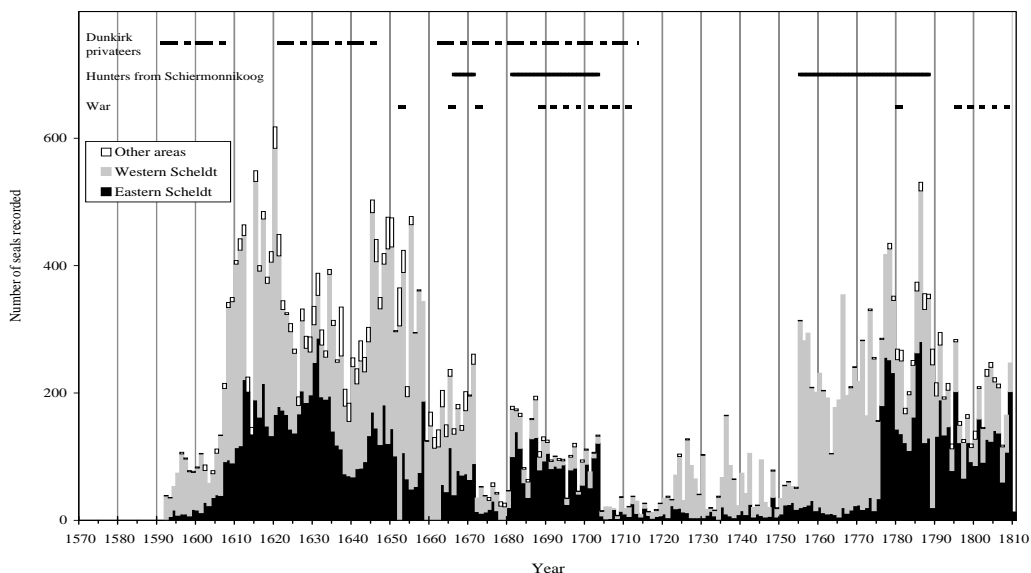


Figure 2. Number of harbour seals killed for bounties in the 17th and 18th centuries in Zeeland. Factors influencing numbers caught are indicated.

used the general archive of Zeeland (Zeeuws Archief, Middelburg). For the 17th and 18th centuries they can be found under the numbers: Rekenkamer (Audit-office) van Zeeland 1319-1805, Rekenkamer B (ZA No. 505), Rekenkamer II (ZA No. 512), Rekenkamer varia (ZA No. 513). These archives contain the receipts of the bounties paid to the hunters. In the 19th century (1825) the Fishery Board of Zeeland (*Bestuur der visscherijen op de Schelde en de Zeeuwse Stroomen*) was founded. From then on (second period, 1826-1856), bounties were paid for each seal or harbour porpoise (*Phocoena phocoena*) killed. This was considered the second period. Until 1840 seals were recorded separately. However after that, only the total amount of animals killed (seals and porpoises together) was registered. Bounties were paid for each seal or porpoise caught. Registrations of payment of these bounties were preserved in the Zeeuws Archief (17.1): No. 838 (1825-1844) and No. 839: (1845-1867). For these years the number of seals killed could be estimated based on the reported total seal catch in the period 1840-1849 and for the

period 1850 -1856 we assumed that the ratio seals-to-porpoises was similar to the period before (de Vooy 2003).

For the third period of bounties, from 1900-1934, payments for captured seals were recorded, now for the whole of the Netherlands. The numbers for the Wadden Sea in the north, and Zeeland, were given separately in the yearly reports on Dutch fisheries. Registration of bounties paid in the 20th century can be found in: Verslag van den Staat der Nederlandse Zeevisscherijen (1900-1910); Jaarverslagen der Visscherijinspectie (1911-1920) and from 1920 onwards: Verslagen en Mededelingen van de afdeling visserijen, Departement van Landbouw, Nijverheid en Handel .

Historical Background

Presumably, seal hunting was never the only source of income of a person involved, even when bounty systems were operative. However, it could have been a lucrative supplementary income. Discussions were held repeatedly

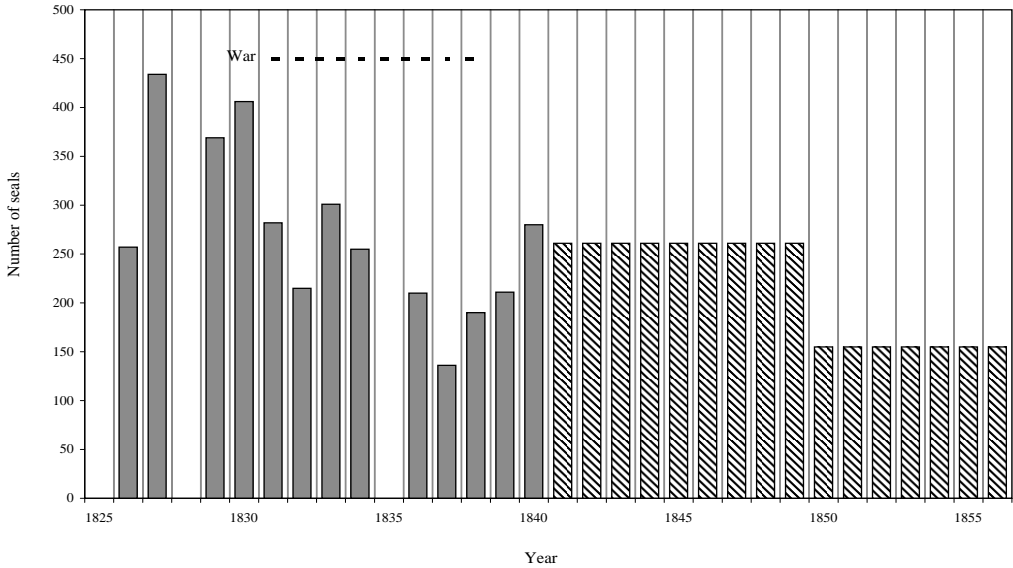


Figure 3. Number of harbour seals killed for bounties in the 19th century in Zeeland. Filled bars are registered numbers of harbour seals killed and hatched bars are estimated numbers of harbour seals killed. --- Period of Belgian Independence War.

Table 1. Privateers and Naval wars which restricted and were destructive for Dutch fishery and merchant fleet (Boxer 1977).

	Period	Under protection of / against	Duration (years)
Dunkirk Privateers	1583-1609	Spain	26
	1621-1646	Spain	25
	1662-1713	France	51
Naval wars	1652-1654	England	2
	1665-1667	England	2
	1672-1674	England & France	2
	1701-1713	France	12
	1780-1784	England	4
	1795-1813	England	18
	Belgian revolt	1830-1839	Belgium

in the parliament on the efficacy of the bounty system (de Vooy 2006). It was questioned whether the bounty system would contribute significantly to seal hunting to generate a sound source of income. As an example, reference was made to a small business in West-ernieland (Province of Groningen, the Netherlands) which existed from 1860-1905 and caught about 200 seals per year without bounties. However, this company did not depend

solely on seal hunting. The people involved were primarily fishermen and salvage workers (de Vooy et al. 1999).

Seal hunting in Zeeland is assumed to have been influenced by the varying social and historical events occurring in the area during the study period. In 1581 the Seven United Provinces proclaimed independence from the government of the Habsburg King Philips II, King of Spain. The war ended in 1648, when

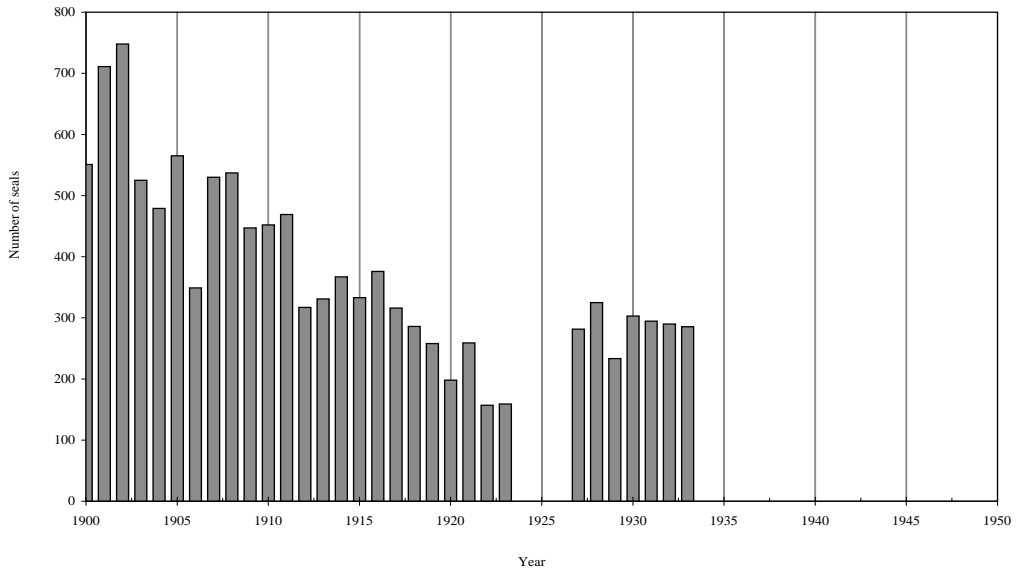


Figure 4. Number of harbour seals killed for bounties in the 20th century in Zeeland.

Dutch independence was recognised by the Spanish government. During this period, the Spanish commander-in-chief Parma founded an Admiralty in Dunkirk aimed at causing maximal damage to the Dutch merchant fleet and fishery (Boxer 1977). An overview of the historical events is presented in table 1.

The Admiralty succeeded to damage the Dutch fleet considerably and this continued until 1646, when the French occupied Dunkirk. Before that, this practice had only been interrupted during the “twelve year truce” lasting from 1609–1621 (van Vliet 2004). In 1662 however, the privateers started again, now under French protection and this lasted until 1713.

On top of these privateer activities, the seal hunt could also have been affected by the four naval battles the Netherlands fought with England, and the two battles against France during the 17th and 18th centuries (table 1). During these wars Dutch fishery and coastal activities were practically impossible, as for example curfews were in effect.

The Congress of Vienna in 1815 united the Netherlands and present-day Belgium into one country under King William I of Orange. However, the Belgians revolted against the

Dutch government in 1830. After nine years, a peace treaty was concluded on 19 April 1839. During the war the Western Scheldt was closed by English and French warships, and shipping at night on the Western Scheldt was forbidden (van den Broeke & Paul 2004). As seal hunting was often carried out with nets, and often practiced at night, hunting in the Western Scheldt must have been severely hampered. On the other hand, seal hunting in the Eastern Scheldt could have continued unhindered in that period.

Interestingly, from the mid-17th century to the second half of the 18th century the majority of seals were caught by Frisians coming from the island of Schiermonnikoog in the North of the Netherlands, and not by local people. This could be deduced from the receipts in the archives in Zeeland as well as the archives of Schiermonnikoog. The naval wars and especially privateer activity, must have also affected the traveling of the Frisian fishermen to Zeeland. The presence of Frisian hunters was only recorded reliably for the period after 1666.

The number of hunters and the amount of bounties paid out to each of them is known

Table 2. Analysis of Deviance. Terms added sequentially (first to last); Df = degrees of freedom, Resid. Df. = residual degrees of freedom, Resid. Dev. = residual deviance.

	Df	Deviance	Resid. Df	Resid. Dev
NULL		287.0		19134.0
Area	1	268.9	286	18865.1
Frisians	1	8109.0	285	10756.1
Privateers	1	1466.2	284	9290.0
War	1	120.8	283	9169.2
Area : War	1	229.0	282	8940.2
Area : Privateers	1	178.0	281	8762.1
Area : Frisians	1	5.6	280	8756.5

in the 19th and 20th centuries (de Vooyo 2006), but not in the 17th and 18th centuries.

Statistical Treatment

In order to determine how historical events affected the number of harbour seals harvested in Zeeland, data for the first period up to 1810 was analysed. The number of seals caught was related to the binary factors Area (East or West, representing respectively the districts Eastern Scheldt and Western Scheldt, as defined in 't Hart 2007), War (Yes or No), Privateers (Yes or No) and presence of Frisian hunters (Yes or No).

A log-linear model was fitted using main effects and first-order interactions with the factor Area. These interactions were included in order to examine whether the factors War, Privateers and Frisian hunters differed between Areas. A Poisson-like error was assumed and a correction for overdispersion was made (Crawley 2005, R Development Core Team 2009).

Reliable information on the presence of Frisian hunters was only available for the period after 1666. Data before 1666 was therefore excluded from the statistical analysis.

Results

Annual yields for the period 1590-1934 are given in figures 2-4. Data show that for all

centuries considered, large variations in yearly yields occur, from a maximum of about 700 per year to almost none in some years.

Effects of historical events

For the first period of bounties, the analysis of deviance showed that all main effects and the interactions Area : War and Area : Privateers were significant ($\alpha=0.01$, $\chi^2=6.64$, and table 2). The contributions of the main effect War and of all its interaction effects Area : War and Area : Privateers were, however, small and difficult to interpret. For example, the number of seals caught increased slightly during a war period in the West but decreased slightly in the East (figure 5). As we are dealing with time series where the data are probably auto-correlated, the risk of over-fitting is large and we have therefore chosen to leave the main effect War and all interaction effects out of the final model. For the entire period, the coefficients of the final model point to an average number of 50 seals caught per year in the Western Scheldt district (West) and 41 in the Eastern Scheldt district (East), bringing the total to over 90 seals. But this holds only for those periods when neither privateers nor Frisians were around. When privateers were active the total number caught decreases to an average of 47 seals compared to the situation when privateers were absent. When Frisians were around many more seals, 354, were caught (almost 4 times as much)

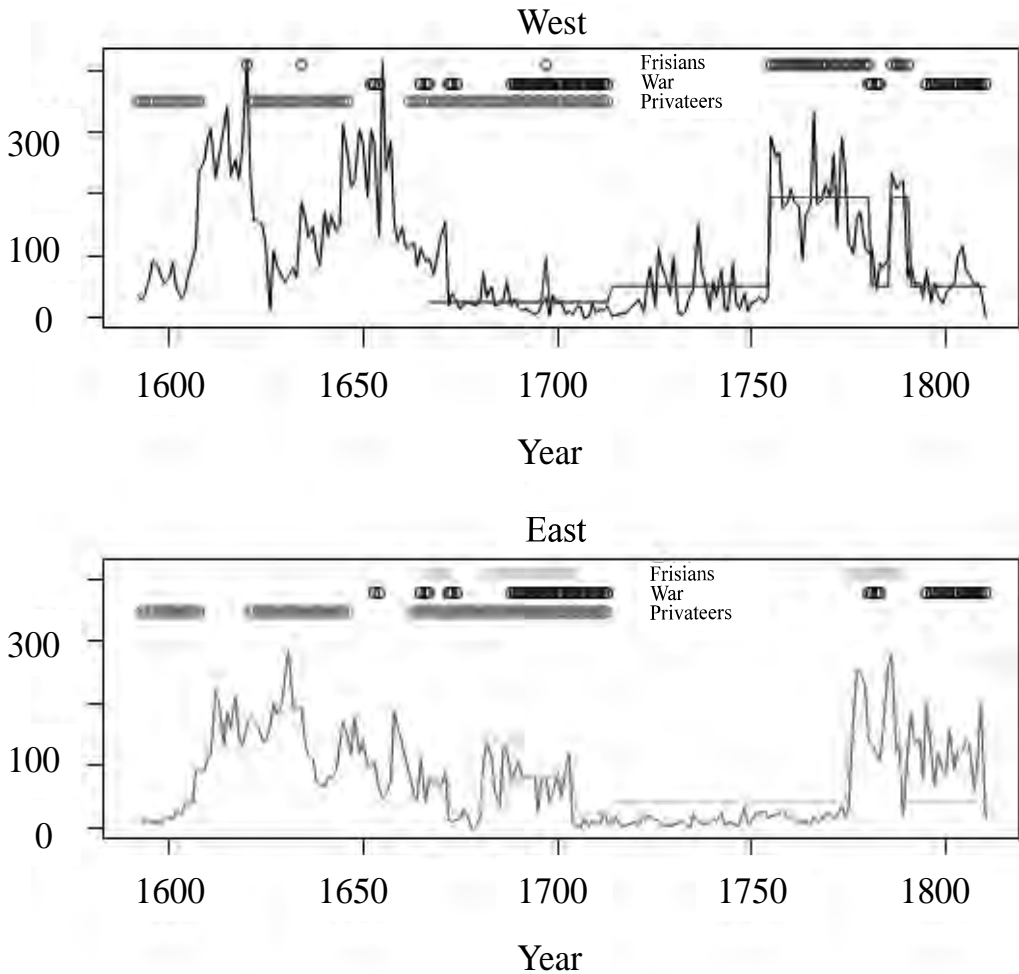


Figure 5. The number of harbour seals caught versus time in the West and the East, with data and model predictions. Straight lines represent model outcome.

compared to the situation when these hunters were absent. Figure 5 shows the data and the model fit for both areas separately.

For the second period of bounties, which was not subject to the statistical analysis, the influence of the Belgian Independence War and subsequent tumult (1830-1839) seem to have suppressed the yield (figure 3).

In the third period of bounties, the reported numbers caught strongly decreased over time (figure 4).

Records for the 19th and 20th centuries were given in more detail. They show that seal hunt-

ing effort was concentrated around the third quarter of the year (figure 5). This coincides with the pupping and moulting period of the harbour seals. During the late summer, the animals spend relatively more time on the sandbanks as they attend to their young and subsequently moult. Seal hunting was therefore a seasonal activity.

Discussion

The analyses of bounty payments in rela-

tion to circumstances during the first period of bounties show that a dominant influence was exerted by both Frisians coming to the southern Delta area to hunt and privateers who posed a threat to vessels sailing in the area. The influence of the naval wars on the seal hunt was less, as can be deduced from the deviances in table 2. This is also the case for differences between areas. The model does not fit well in all periods. Apparently, other factors must have played a role here. Shifts of interest could explain the relative low yields of seals in the Netherlands in part of the 18th century. Next to seals, bounties were paid for several other species of mammals and birds in Zeeland from 1712 onwards. This also applies to the Province of Friesland from 1720 onwards, and in the Province of Groningen from 1703 onwards (‘t Hart 2007).

In the second period of seal bounties a decrease in the yield can be observed from 1831 to 1838. This could have been influenced by war. During the revolt of the Belgians (1830-1839), fishing in the Western Scheldt was prohibited during the night. This might have hindered seal hunting as well (Broeke & Paul 2004).

The large variations in hunting yield seen in the Netherlands are not unique. Similar large fluctuations are known for the long-term harvest of Cape fur seals (*Arctocephalus pusillus*) in South Africa. Reconstruction of that harvest operating from 1653-1899 revealed that hunting effort was the dominant factor influencing the yield (David & van Sittert 2008). The low fur seal yields in the period 1840-1860 could be explained by high prices of guano occurring in the same region, and local people shifted to guano collection instead of seal hunting.

Changes in hunting methods – from clubbing and netting to firearms - might have played a role in the hunting efficacy, and hence yield during the centuries studied. Clubbing can be effective when seals can be taken by surprise or when they are less mobile, for instance when mothers are accompanied by

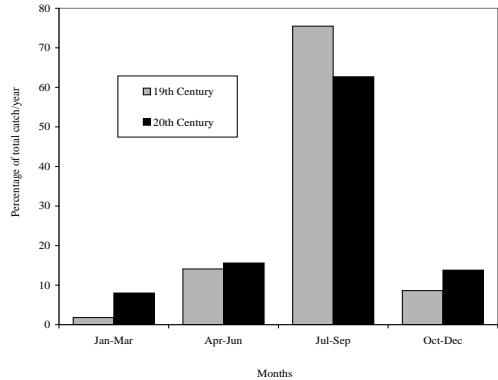


Figure 6. Percentages of total catch of harbour seals in different seasons in the 19th and 20th centuries.

a young pup. Until the beginning of the 20th century in the Netherlands hunting with nets was often practiced (Anonymus 1852, Kuelper 1912). In the 19th and the beginning of the 20th century seals were sometimes caught alive, and could be sold to zoological gardens and circuses (Anonymus 1852). In Germany seals were hunted in the Elbe estuary and the coast of Schleswig-Holstein. Here old sturgeon-nets were used. Different hunting techniques were used, depending on the width and depth of the gully and the strength of the current. If the gully could be closed off at low tide, seals would be caught in the net. In wider gullies, nets were used to contour the seals on the bank, and when the seals flush into the water, the net would be tightened. When the depth of the gully extended beyond the depth of the net, the current was used to float the net along the seal bank. When the net reached the bottom, the seals are hunted into the water and the net was contracted.

Hunting of seals by means of firearms was hardly practiced before the end of the 19th century, and only seals on sandbanks were shot. Both the precision of the firearms (often muskets) and the quality of the ammunition was rather inferior. Only after 1900 rifles became increasingly effective. With the improved firearms seals could be killed when swimming in the water, and this could increase the catch. The efficiency of the new

firearms could account for the relative high number of seals killed in the beginning of the 20th century onwards, when bounties were re-introduced (third period of seal bounties 1900-1923). Firearms gradually superseded older hunting methods. The hunt was so efficient that it affected the population size. This could explain the decrease in catch from 1920 onwards (figure 4).

After termination of bounties in 1934, hunting on seals was continued, licensed under the Dutch Hunting Law of 1954. But the character of hunting changed. After the Second World War many seals, especially young ones, were killed for the fabrication of fur coats. Finally, the seal hunt was banned in the SW-Netherlands in 1961 and in the Dutch Wadden Sea in 1962. The extent of this hunt had a devastating influence on the seal population (Reijnders 1976).

Currently, the estimation of the size of seal populations is carried out based on aerial or boat surveys. In the Netherlands, seal counts have been conducted from the late 1950s onwards. In addition, back calculations using hunting statistics to estimate more historical population sizes have been carried out for the Dutch Wadden Sea (Reijnders 1992) and Zeeland (Reijnders 1994). These techniques have enabled back calculations to 1900. The size of the harbour seal population in the SW-Netherlands in 1900 will have been close to 11,500 animals.

Similar studies were carried out in the Skagerrak-Kattegat (Heide-Jørgensen & Härkönen 1988, Marboe 2004) and show a negative influence of hunting on population size.

To go further back to estimate the seal population in Zeeland, a definite link had to be made between the yield of the hunt and the seal population size. In this study we show that human societal factors were in times determinant for the number of seals taken. Therefore we deem it not possible to estimate the size of the population for the 17th, 18th or 19th century in Zeeland.

Calculations estimating population size

in retrospect, using hunting statistics have been carried out for the 20th century. These showed clearly that hunting as carried out in the mid-20th century was not sustainable for the seal population. When the hunt stopped in the SW-Netherlands in 1961, the size of the population was then less than 5 percent of its estimated size around 1900, and only 350 harbour seals were counted (Reijnders 1994). Given the centuries long period of bounty hunt with strongly fluctuating but generally relatively low number caught, it is unlikely that the hunt in the preceding centuries would have had a similar impact. Probably the inefficacy of hunting techniques, and the further complications rendering the hunt sometimes impossible, prevented a significant decimation of the seal population throughout the centuries.

Contrary to the Wadden Sea harbour seal population, which recovered during the 20th century after the complete ban of hunting including Denmark and Germany in the mid-1970s, the seal population in the SW-Netherlands did not recover (Reijnders 1994). Particularly disturbance and lack of immigration are considered initial causes hampering recovery from overhunting. In addition a general lack of reproduction and extremely high mortality in the area prevents recovery.

Conclusion

Here we show that social and historical events such as long periods of war, privateers and visiting hunters have had a strong influence on the success of hunting harbour seals in the Province of Zeeland. Despite the excellent records of the seal bounty hunt in that area, spanning more than three centuries, it appears that the bounty records cannot be linked to population size in these periods. For seal populations in the Netherlands in the 20th century, and in other areas, it was possible to use bounty records to back-calculate the original population size. This was possible, as



Frans Snyders. Flemish Fish market, depicting a.o. two harbour seals and a harbour porpoise. Painted 1618-1621. Royal Museum of Fine Arts, Antwerp, Belgium © Lukas - Art in Flanders vzw. *Photograph: Hugo Maertens.*

a few independent population estimates enabled checking of the calculated population trajectories. One can however conclude tentatively that in these earlier days the population must have been extremely large, to sustain, sometimes years on end, the loss of hundreds of animals per year. However, the intensified and efficient hunt in the first half of 20th century was apparently unsustainable, from which the population could not recover until now.

References

- Anonymus 1852. De robbenvangst. Sloet's Tijdschrift voor Staathuishoudkunde en Statistiek 7: 195-208.
- Boxer, C.R. 1977. The Dutch seaborne empire 1600-1800. Hutchinson & Co, London, UK.
- Crawley, M.J. 2005. Statistics: An introduction using R. John Wiley, Chichester, UK.
- David, J. & L. van Sittert 2008. A reconstruction of the Cape (South African) fur seal harvest 1653-1899 and a comparison with the 20th century harvest. South African Journal of Science 104: 107-110.
- de Vooyo, C.G.N. 2003. Premies voor de jacht op zeehonden in Zeeland, 1826-1856. Nehalennia 142: 34-39.
- de Vooyo, C.G.N. 2006. Zeehondenjacht in Zeeland: het effect van premies. Zoogdier 17 (3): 9-12.
- de Vooyo, C.G.N., S.M.J.M. Brasseur & P.J.H. Reijnders 1999. Visserij en zeehonden in de vorige eeuw. Waddenbulletin 34 (3): 40-41.
- Hart, P. 't 2007. Zeehondenjacht in Nederland 1591-1962. PhD Thesis. Vrije Universiteit, Amsterdam, the Netherlands.
- Heide-Jørgensen, M.P. & T. Härkönen 1988. Rebuilding seal stocks in the Kattegat-Skagerrak. Marine Mammal Science 4: 231-246.
- Kuelper, W. 1912. Der Seehundsfang an der deutschen Nordseeküste. Mitteilungen Deutschen Seefischer-Vereins 28: 245-258.
- Marboe, A.H. 2004. Seals, Seal Hunting and Fishermen - The seal population in Denmark's Coastal Waters, c. 1750-1889. In: P.J. Moree, A. Poldervaart, A.P. van Vliet & J.P. Voort (eds.). Fish, War and Politics, 1300-2003, International Conference Amsterdam/Middelburg. Network, Jaarboek Visserijmuseum 15: 120-126. Visserijmuseum, Vlaardingeng, the Netherlands.
- R Development Core Team 2009. R: A language and

- environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reijnders, P.J.H. 1976. The harbour seal (*Phoca vitulina*) population in the Dutch Wadden Sea: size and composition. *Netherlands Journal of Sea Research* 10: 164-179.
- Reijnders, P.J.H. 1985. On the extinction of the Southern Dutch harbour seal population. *Biological Conservation* 31 (1): 75-84.
- Reijnders, P.J.H. 1992. Retrospective Population Analysis and Related Future Management Perspectives for the Harbour Seal *Phoca vitulina* in the Wadden Sea. *Netherlands Institute for Sea Research Publication Series* 20: 193-197.
- Reijnders, P.J.H. 1994. Historical population size of the harbour seal, *Phoca vitulina*, in the Delta area, SW Netherlands. *Hydrobiologia* 283: 557-560.
- van den Broeke, W. & P. Busse 2004. De betekenis van de visserij voor de Zeeuwse economie in de periode 1795-1849: niets dan vel en graat? In: P.J. Moree, A. Poldervaart, A.P. van Vliet & J.P. Voort (eds.). *Fish, War and Politics, 1300-2003*. International Conference Amsterdam / Middelburg. Network, Jaarboek Visserijmuseum 15: 59-69. Visserijmuseum, Vlaardingen, the Netherlands.
- van Vliet, A.P. 2004. Vissen in oorlogstijd. De Zeeuwse zeevisserij in de zestiende en zeventiende eeuw. In: P.J. Moree, A. Poldervaart, A.P. van Vliet & J.P. Voort (eds.), *Fish, War and Politics, 1300-2003*. International Conference Amsterdam / Middelburg. Network, Jaarboek Visserijmuseum 15: 50-58. Visserijmuseum, Vlaardingen, the Netherlands.

Samenvatting

Het verloop van vier eeuwen premiejacht op zeehonden in Zeeuwse wateren

Eeuwenlang vond in de Zeeuwse wateren premiejacht op zeehonden plaats. De uitbe-

taalde premies van de in de 16^e tot in de 20^e eeuw buitgemaakte dieren werden geregistreerd in Zeeuwse archieven. In deze studie worden die jachtstatistieken gebruikt om het aantal jaarlijks geschoten dieren te reconstrueren. Vervolgens wordt het effect van sociale en historische gebeurtenissen op het jachtsucces onderzocht. Er worden drie perioden van premiejacht onderscheiden op basis van het systeem van registratie: 16^e tot begin 19^e eeuw, de 19^e en de 20^e eeuw. Gedurende deze periodes treden grote fluctuaties op in het geregistreerde aantal gedode zeehonden. In de eerste periode waren er hoge opbrengsten wanneer ervaren jagers (Friezen) in het gebied kwamen, terwijl de aanwezigheid van kapers en in veel mindere mate oorlogsactiviteiten, leidden tot significant lagere vangsten. De invloed van die gebeurtenissen op de vangstopbrengst was in de periode 16de tot 20ste eeuw dermate groot, dat het niet mogelijk is op basis van de jachtgegevens een reconstructie van de populatiegrootte voor die tijd uit te voeren. Dat is anders voor de 20ste eeuw. Afgezien van de duur van de twee wereldoorlogen waren er geen grootschalige veranderingen in omgevingsomstandigheden. Wel nam de doelmatigheid van de jachtmethoden toe vanaf circa 1900, toen vuurwapens steeds nauwkeuriger werden. Ondanks het stoppen van de premiebetalingen in 1934, werd de zeehondenjacht toch voortgezet en werden de aantallen gedode zeehonden geregistreerd. Toen de jacht in 1961 tenslotte werd gesloten, was de populatie in ZW-Nederland gedaald tot ongeveer 5% van de geschatte omvang omstreeks 1900. Die heeft zich sindsdien amper hersteld, hoofdzakelijk door het ontbreken van immigratie, verstoring, hoge mortaliteit en lage reproductie.

Received: 20 April 2012

Accepted: 4 June 2012

The harbour porpoise in the Netherlands: will it get the care it deserves? An urgent conservation plan

Conservation plan for the Harbour Porpoise *Phocoena phocoena* in the Netherlands: towards a favourable conservation status.

Kees (C.J.) Camphuysen & Marije L. Siemmensma 2011. NIOZ Report 2011-07. Royal Netherlands Institute for Sea Research, Texel, the Netherlands. 183 pp.

In the past few decades, several reports and recommendations concerning the status and conservation of the harbour porpoise in Dutch waters have been issued; and in numerous publications, both scientific and popular, the plight of the only truly indigenous cetacean in the southern North Sea has been discussed. As usual regarding species that were once common, not much attention had been paid to the harbour porpoise by (marine) biologists in the past, until an alarming decline became apparent in the 1950s and particularly the 1960s, culminating into the near disappearance of the species from Dutch coastal waters. The alarm having been raised, it turned out that there were hardly any useful references to the situation in the first half of the 20th century, let alone further back in time. The harbour porpoise had always been considered commonplace, its occurrence taken for granted, and nobody could foresee that this might ever change. But then, all of a sudden, the animals were gone.

Thus, in the 1970s and 1980s interest in the harbour porpoise increased and, slowly and haltingly, research came off the ground: field observations started, at first as a by-product of bird-watchers, and stranded animals were registered, collected and studied. Gradually,

field recordings became organised in a more systematic way, so that they could be corrected for effort; and the scope of activities extended from watching animals from coastal sites to dedicated surveys from ships and aeroplanes. The Dutch strandings network was intensified, and the study of carcasses gradually developed into a multi-disciplinary affair, with attention being paid to food, reproduction, age composition, pathology, parasitology, bacteriology, virology, toxicology, genetics and, very importantly, to evidence of by-catch in fisheries. Live-stranded porpoises were taken to marine mammal parks, where studies on behaviour, physiology and acoustics could be carried out. Similarly, researchers in other countries also turned their attention to the harbour porpoise and other small cetaceans. And now, at the beginning of the 21st century, a great amount of knowledge has accumulated, though at the same time we have come to realise how little we still understand of the life of this elusive species.

On many occasions, scientists and conservationists have expressed concern about the harbour porpoise in Dutch waters, seen in the light of the deteriorated ecological state of the North Sea, particularly with respect to pollution and (over)fishing. However, little action has been taken, and it seemed that reports and recommendations tended to disappear into the proverbial drawers, physical or electronic. One of the main obstacles to a consistent and sustainable management of the Dutch marine environment and its biodiversity is that several different ministries and other administrative bodies in the Netherlands are or were at different times responsible for different aspects of such management, with often contradictory short-term interests and goals. Another drawback has always been the fact that, within those various authorities, the responsible departments and officials were and still are subject to frequent reorgan-

isations and reshuffling of staff, which time and again resulted into a stunning loss of collective memory, repeated shifts of priorities, and consequently into a weak, fragmented and inconsistent policy. Compared to several other North Sea countries, the Netherlands has been lagging far behind in setting up serious research and taking other action aimed at a better understanding and conservation of the harbour porpoise.

Therefore, the initiative by the Dutch Ministry of Economy, Innovation and Agriculture (another novelty – also responsible for nature conservation) for this conservation plan has been timely and most welcome. The task was commissioned to the Royal Netherlands Institute for Sea Research (NIOZ) and carried out by Kees Camphuysen and Marije Siemensma; a great many others were involved in its preparation. They have done an excellent job. In the preface, the circumstances that led to this initiative are briefly mentioned. Among those are the various international conventions and agreements signed and ratified by the Netherlands, under which the participating countries are obliged to take conservation measures for the marine environment at large and small cetaceans in particular. Then there is the problem of fisheries, with the by-catch of porpoises, which is causing great concern. Added to this are the continuing problems of pollution and, in recent decades, of acoustic disturbance by underwater noise generated by industrial activities. And finally, quite another, seemingly contradictory, phenomenon has appeared: the spectacular increase in the numbers of harbour porpoises visiting Dutch waters, which started in the 1990s and resulted in peak numbers in the first decade of the 21st century. Just like the earlier disappearance of the species, nobody had foreseen its “return”.

The conservation plan lying before us is a very thorough publication, in which all aspects of porpoise biology and conservation are treated. On the whole, it is well written and edited (there are few typing errors)

and nicely illustrated, and gives an admirably complete overview of the state of our knowledge. It starts with three summaries (chapter 1): a short one in English and in Dutch, followed by an extensive full summary of eleven pages. After the preface and the introduction (chapters 2, 3) there are sections reviewing the current knowledge of the harbour porpoise, the observed threats, the existing mitigation measures, the policy and legislative context of the situation in the North Sea and particularly in Dutch waters, a “stakeholder” consultation (some management jargon seems unavoidable), and a chapter containing proposals for action, such as further, directed research and “concrete” conservation measures. The report ends with a final discussion and conclusions, after which there are the acknowledgements and, very important, a most impressive list of references, covering 23 pages.

For those who do not readily have the time or patience to read through more than 150 pages of text, the full summary gives an excellent condensation of the contents. Here, officials and politicians pressed for time can find virtually everything they need for grasping the matter, for proper policy-making and taking the right action, though one may hope that many will read further for gaining a sound background knowledge and deeper understanding of the problems. It is there to be used! In the following, some comments on each chapter will be given.

Chapters 3 and 4 (Introduction; Current knowledge) draw a clear picture of the history and present situation. The decline of the harbour porpoise off the Dutch coast since the middle of the 20th century is illustrated by the very low numbers of animals washed ashore during the period 1970-1985 (p. 22); it should be emphasised that these are in reality low numbers of *reported* animals, as the strandings network (“observer effort”) was still poorly developed in this period and only improved during the 1980s. Nonetheless, the species had indeed become quite rare in those days. The authors calculate a world population

of at least 700,000 harbour porpoises, by adding up the results of estimates made in various parts of the world (p. 31). Of course, "at least" is inflatable, but given the lack of information from many areas, this outcome seems far too low. The two SCANS-surveys in 1994 and 2005 arrived at an estimated 231,000-268,500 porpoises in the North Sea alone (though within very wide confidence limits), which in this light would amount to roughly one third of the world population. Further on (p. 33), an estimate of 150,000 is given for the southwestern North Sea (management unit 9: see figure 8, p. 32), which is now flatly stated to represent one fifth of the world population. This is not credible. The hypothesis that two populations may be distinguished in the North Sea: a northeastern and a southwestern one (management units 8 and 9) is interesting, though the evidence is still rather weak and the borders are not clear (pp. 32-33). If true, this would be consistent with the authors' view that the recent increase in Dutch waters is largely the result of migration of animals from the northwestern North Sea to the Southern Bight, possibly caused by a depletion of food resources in Scottish waters. On the whole, strandings records and field observations from coastal sites run nicely parallel over the years, both showing a gradual increase since the 1990s, with a particularly sharp rise during the first decade of the 21st century. But then, the authors suggest that strandings data are biased towards younger animals and/or either sex, probably meaning as compared to the assumed natural mortality, mainly basing themselves on differences in Danish samples obtained from strandings and by-catches, respectively (pp. 47, 55). This is not elaborated and hence not convincing: one should realise that in any animal population, (natural) mortality among young individuals is much greater than in adults. If anything, it would seem that samples from by-catches are more biased than those from strandings, though in a different direction.

Chapter 5 (Observed threats) deals with

all thinkable factors that may have adverse effects on the harbour porpoise in the North Sea. The authors lay a very strong emphasis on the by-catch problem, particularly the suspected by-catches in bottom-set gillnets. But here they have a serious problem. In all countries around the North Sea and elsewhere in the North Atlantic (Norway, Iceland, Canada), data on by-catches of harbour porpoises are being or have been collected in close co-operation with fisheries. The only striking exception is the Netherlands, where such co-operation has proved impossible till now, for whatever reason, but the weak policy of the responsible ministry seems the main cause of this inexcusable omission. This has the unfortunate consequence that all discussions on by-catches in Dutch waters are based on indirect evidence obtained during autopsies of stranded animals. The percentage of by-catches among these carcasses is high: most studies specifically directed at identifying by-catch, carried out by different teams using varying methods, have arrived at close to or even far over 50% by-caught or probably by-caught animals among the stranded samples (pp. 61-63). One study, published in 2008, arrived at a much lower percentage (table 4, p. 61). The authors discuss that outcome without questioning (p. 62). Therefore, it may be said here that this particular study was unprofessional in many respects: it was carried out by an institute that chose not to co-operate with other teams despite promises and obligations, used inadequate methods and references which made the results incomparable with those of others and, moreover, the by-catch study was partly financed by the Dutch Fisheries Association. The mere fact that such a thing was allowed to happen in the Netherlands is another consequence of the lack of a firm policy and implementation of regulations and agreements by the Dutch authorities. But whatever the outcome of the various studies, it is clear that by-catch is a serious problem off the Dutch coast, as it is elsewhere, though exact numbers and proportions and

hence the effects of this mortality on the population can only be guessed.

The lack of direct reports on by-catches in Dutch fisheries has caused that the (thorough) discussion of this topic remains somewhat speculative, with no firm proof and with rather unsatisfactory conclusions (pp. 70-72). The authors regard bottom-set gillnets as the main culprits, but for this had to base themselves on studies in other countries. The emphasis on bottom-set nets has distracted their attention from other types of fisheries such as bottom-trawling, which they consider less dangerous to porpoises. This may be so, but the many documented cases of by-catches in beam-trawls do warrant a closer look into that kind of fishery: one should not exclude this beforehand (as the authors repeatedly state: one should go by facts and not by preconceived ideas). Without proper and obligatory monitoring of all types of fisheries, hard as this may be to organise, the opportunities for denying or belittling the problem by the "stakeholders" remain too favourable. Fishermen and the authorities have thus manoeuvred themselves into the comfortable position that proof lies with the scientists, who are handicapped as long as necessary data are withheld to them, or not even collected. The realms of cetacean researchers and fisheries thus remain wide apart, and the authors realise that no "concrete" measures can be taken if this hide-and-seek game will continue. Shame upon the Netherlands!

Many other things are put forward as "observed threats", which give reason for some remarks. Ample attention is paid to signs of acoustic disturbance caused by shipping and all kinds of industrial activities (pp. 75-80) but, apart from local and temporary effects, these do not seem to affect the North Sea population as a whole to a significant extent. Nonetheless this should indeed be closely monitored, as of some small cetaceans it is known or suspected that favourable areas for feeding and calving are (temporarily) deserted if they become too noisy. Depletion of poten-

tial food resources would seem more detrimental, but this is discussed only summarily (pp. 85-86). The supposed effects of climate change on the stocks of sandeels (*Ammodytidae*) in the northwestern North Sea do receive attention, since the decrease of these fish is suspected to lie at the base of the recent invasion of porpoises into Dutch waters. But nothing is said about possible (over)fishing of this and other prey species, though the effects of earlier overexploitation of sandeels on seabird populations in Scottish waters has been well documented, and has been suspected for porpoises. The authors express concern over the fact that many stranded porpoises are in poor nutritive condition. However, natural selection among young individuals is heavy in any animal population, and usually takes effect through starvation. Disease and parasites (pp. 87-90) too, are natural phenomena and hence tools of natural selection. But then, contamination with organic and inorganic pollutants, and particularly pcb's, has been proved to have serious negative effects on the immune system and reproduction of marine mammals, and can lead to more diseases than would naturally occur. However, the important subject of pollution is discussed rather briefly (pp. 83-85). All these factors are treated as seemingly independent threats, and the probable and complicated interaction between them is not sufficiently taken into account. It is good to realise that strandings samples may be biased in one way or another and may not exactly mirror the mortality that occurs farther at sea. But to call them "a suspect subset of material" (p. 93) is taking things too far. And, whatever the drawbacks, this is what we have.

It is obvious that future research on stranded or by-caught porpoises should consist of an integral, multidisciplinary study by an international team of specialists, in which all the above-mentioned factors and their interactions are thoroughly investigated. Close co-ordination and co-operation with all countries neighbouring the Netherlands

is imperative. The authors are right in stating that current research of dead porpoises in the Netherlands has been too fragmentary. The summary of missing information (p. 93) clearly illustrates these shortcomings. Lack of funds is given as one of the principal obstacles. There should be no misunderstanding that in-depth research will have to be long-term and expensive.

Chapter 6 gives an overview of the mitigation measures in the North Sea and elsewhere that have become available up to now. This is thoroughly done. The chapter concentrates on efforts to reduce by-catch and the adverse effects of industrial activities. Regarding by-catch: “pingers”, devices that are set on nets and produce acoustic signals meant to scare off porpoises, are regarded as promising, though there are still many doubts and problems and unwanted side-effects. Thus, one could imagine that porpoises may leave good feeding grounds if pinger-noise would become overriding. Once more the authors emphasise that first of all, one has to identify the type of fishing gear in which most by-catch occurs, before expensive measures are imposed. Fortunately, experiments in Dutch waters have now started, with the co-operation of fishermen, which is one positive thing. Elsewhere, modification of gear or change to less detrimental fishing methods have proved effective. As for industrial activities: these consist mainly of seismic surveys for oil- and gas-prospecting and the construction of windfarms; concerning the latter, particularly the phase of pile-driving is disturbing. Less detrimental methods are discussed; some of those have already been implemented in German waters, so it is hard to understand why these have not become standard practice throughout the North Sea.

Chapter 7 (Policy and legislative context) gives a most useful review of the truly amazing jungle of international, European and national treaties, laws, regulations and action plans that touch upon management and conservation of the North Sea, its natu-

ral resources and biodiversity. In all these, the harbour porpoise and other small cetaceans are given the highest protective status. Naturally, however, many of those regulations contain contradictory elements and discrepancies, making it all too easy to evade unpopular and politically sensitive measures. Thus, though it would seem that no marine area in the world is better managed than the North Sea, there is a shrill contrast with reality. The Netherlands does not heed many of its obligations and commitments including its own national laws, regulations, action plans or whatever. This is no wonder in the light of this legal and administrative chaos, involving so many different and often antagonistic authorities, even within the same ministry (e.g., fisheries versus conservation), and with a government that gives little or no priority to habitat and species protection. The discussion on the legality or illegality of by-catch (pp. 124-125) poses a staggering and kafkaesk example; it would be hilarious, if the matter were not so sad. It is one of the reasons why fishermen are not really encouraged (to put it mildly) to bring in by-caught porpoises.

Chapter 8 (Stakeholder consultation: two pages) shows the prudent way in which this plan has been composed: all parties involved received ample opportunity to contribute and criticise during the process.

Chapter 9 (Concrete measures) summarises all things that are being done or should be done, in the way of research and protective (mitigation) measures. After an explanation of the needs and problems, research activities and proposals are summarised in a table (pp. 138-139) and given priority marks ranging from 1 to 4, each followed by a brief statement explaining the need. Priorities 1 are (letters given by the reviewer):

- a. Better and regular population assessments by “state of the art” (jargon again) aerial surveys.
- b. Research into hearing damage caused by underwater noise.
- c. Assessing by-catch rates in various types

of fishing gear and evaluating mitigation measures.

- d. A study of the interaction between nutritive status of animals and pollution levels. Here we come upon a stumbling block. This will only be meaningful if it includes studies of the age, health and reproductive condition of each animal which, very strangely, are given priority 2, though all of these will interact. The authors seem to overlook that the purpose of a thorough necropsy should not be restricted to establishing the cause of death (a common misconception, even among veterinarians), but rather to give an overall picture of the health and reproductive status of an animal, to be followed by analyses of samples in various laboratories. Nutritive condition and pollution burden are necessary components of this integral approach. It is evident that this should be combined with identifying by-catch and, perhaps, hearing damage. Of course, such a study will be difficult, time-consuming, long-term, will have to involve several disciplines and institutes within and outside the Netherlands, and hence will be expensive. But only that is the very kind of research we need and, considering what they say on pp. 134-135, the authors appear to realise this very well. What should be avoided is that one or more links in a chain of partial and interdependent studies would break by lack of finances, and thus obstruct the whole research process. One may then end up with freezers or jars full of the finest samples, which cannot be studied; see again the list of "missing information" given on p. 93. Finally, *all* institutes in the Netherlands should be forced to co-operate in such a programme: there can be no place for withholding material or data for petty private interests and hidden agendas.
- e. Formation of a national scientific research steering group, which should develop and oversee research projects. This is very important in the light of what has been said above. But it should be stressed once more

that only national *and* international co-ordination and co-operation will be able to raise research on the harbour porpoise to a sound scientific standard. At present, too many projects in the North Sea countries seem to be carried out on a national level only (or not even that!), and too many researchers work in isolation. However, porpoises have no knowledge of borders, and we are dealing with "management units" that extend over several jurisdictions, which are all equally responsible for the care of the very same animals. Research and conservation should be truly, well co-ordinated international affairs.

There will, of course, always be debate on priorities, and unexpected problems may suddenly appear. The practical feasibility of the ideas and proposals listed in this chapter is not always considered and, with the present lack of finances and co-ordination, some things may not be realistic, at least not for now. This section ends with a list of main action points (p. 140) which, however, do not quite follow the priority ranking given before.

The second part of chapter 9 reviews the existing and recommended mitigation measures. These too, are summarised in an excellent concluding table, for each point indicating which authorities are responsible: a bewildering assortment. Again, this is followed by a list of main action points, concentrated on reducing by-catch and underwater noise (pp. 150-151).

Chapter 10 (Discussion and conclusions, six pages) is in fact a good and useful recapitulation of the contents of the report. One might even start reading this before plunging into the other chapters. This too, culminates in a re-iteration of the main action points regarding research and mitigation measures, the latter once more covering by-catch and underwater noise. One striking point: despite the authors' doubts about samples obtained from strandings, the importance of safeguarding data and material from stranded animals is stressed here as an important goal: no valu-

able material should get lost; even a special “strandings co-ordinator” is recommended. Collection of by-caught animals too, should be organised, as has been done in other countries.

This will do. Despite the few critical comments given above, this conservation plan is to be praised and highly recommended, and the authors are to be congratulated. Although the report necessarily concentrates on the situation in the Netherlands, it can be a great stimulus to upgrade the work that is already done here and, above all, must be done, to a more international level. The Netherlands is still far behind in many respects and should

make a truly Olympic effort to gain an honourable position in the international team of cetacean scientists and conservationists. We can only hope that this plan will generate further action, and that the various Dutch authorities will join forces without squabbling over budgets and responsibilities.

Chris Smeenk

Emeritus Curator of Mammals
National Museum of Natural History (now
NCB Naturalis)
P.O. Box 9517
NL-2300 RA Leiden
The Netherlands