LUTRA

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LUTRA

Journal of the Society for the Study
and Conservation of Mammals

Volume 50 – Number 2 – December 2007

L U T R A

Volume *Deel* 50 – Number *Nummer* 2 – December 2007

Lutra is a scientific journal published by the Society for the Study and Conservation of Mammals (VZZ). The society is dedicated to the study and protection of native mammals in Europe. Lutra publishes peer -reviewed scientific papers on mammals across all disciplines, but tends to focus on ecology, biogeography, behaviour and morphology. Although exceptions are made in some cases, Lutra generally publishes articles on mammal species native to Europe, including marine mammals. Lutra publishes full articles as well as short notes which may include novel research methods or remarkable observations of mammals. In addition Lutra publishes book reviews, and compilations of recent literature on mammals. Lutra publishes in British English as well as Dutch. Lutra publishes two issues per year and Lutra is indexed in 'Biological Abstracts' and 'Zoological Record' and 'Artik'.

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When you prepare a manuscript for Lutra please comply with the guidelines set out below. For additional information on style and format please consult a recent issue and the "How to submit a paper to Lutra" document that is available in English as well as Dutch from the internet (http://www.vzz.nl) or VZZ office (address see 18).

1. Lutra publishes in British English as well as Dutch.
2. Choose an informative title for the manuscript that does not exceed 15 words.
3. Use 200-250 words for the abstract of a full article. For short notes an abstract is not required, but if desired it should be 100-150 words. Add a Dutch summary (400 words maximum for a full article, 250 for a short note).
4. Use up to ten different key words or short phrases that best identify the manuscript.
5. A manuscript should generally follow a standard scientific format. When appropriate you may subdivide the text with second or even third level headings.
6. When you name a species for the first time in the text use the English or Dutch name, depending on the language of the article, followed by the scientific name between brackets and in italics: pine marten (Martes martes).
7. When you report the findings in the results section avoid repetition from tables or figures, but do integrate the most important or interesting aspects in the text.
8. Use digits for numbers from 13 and up, and use words for numbers up to twelve. If a number is part of a measurement unit use digits: 7 g or 2.5 km.
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11. Reference citations in the text are normally placed at the end of a sentence. Use "et al." for three authors or more. The references are first arranged in chronological order and then in alphabetical order: (Reeve & Huijser 1999, Broekhuizen et al. 2000, Jansman & Broekhuizen 2000).
12. List the references in alphabetical order and then by year of publication. Do not prepare your manuscript with tabs here. Please provide the full name of a journal. For books only name the first location if a publisher has offices in more than one city. Use the full name of the country, but abbreviate United Kingdom and United States of America: UK and USA. Only refer to a site on the internet if you are reasonably sure the site concerned has a relatively long life span. Please review the following examples
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    Bergers, P.J.M. 1997. Versnippering door railinfra structuur. Een verkennende studie. Report 262. Instituut voor Bos- en Natuuronderzoek, Wageningen, The Netherlands.
    Clarke, G.P., P.C.L. White & S. Harris 1998. Effects of roads on badger Meles meles populations in south-west England. Biological Conservation 86: 117-124.
    Clevenger, A.P. 1998. Permeability of the Trans-Canada Highway to wildlife in Banff National Park: importance of crossing structures and factors influencing their effectiveness. In: G.L. Evink, P. Garrett, D. Zeigler & J. Berry (eds.). Proceedings of the international conference on wildlife ecology and transportation: 109-119. FL-ER-69-98. Florida Department of Transportation, Tallahassee, USA.
    Shkedy, Y. & B. Shalmon 1997. Evaluating open land scapes in the Negev Desert, and the implications on military activity. Nature Reserves Authority, Jerusalem, Israel. (In Hebrew with English summary).
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Editorial

50 Volumes of Lutra (2)

This year Lutra celebrates its 50th Volume. This provides a good moment to both look back at what has happened on the pages of our journal and ahead and try to recognise the challenges facing Lutra and possible new directions that it may take in the near future. In the editorial of Lutra 50-1 we provided an overview of the establishment and organisation of Lutra and its editorial history. Here we take a closer look at what has been published and identify key trends in the origin or content of the articles that we have published. Over the following pages we present some statistics on Lutra that provide a symbolic closure of roughly half a century of Lutra but which we hope will also inspire all of us, authors and editors, to continue producing interesting papers on the study and conservation of mammals.

The first 50 volumes of Lutra contained 1145 contributions, an average of almost 23 contributions per volume. 520 of them can be categorised as research papers, opinion papers or short notes, which are collectively referred to as ‘articles’ in this editorial (as opposed to other contributions such as announcements, bibliographies or book reviews). The first article printed in Lutra was a short note on the den system of moles, written in French by Van den Brink (Lutra 1, 1953). The first full research papers appeared in Lutra 2 (1960) with the contributions from Kortenbout van der Sluijs on fossil finds of pleistocene mammals and from Naaktgeboren on observations of brown rats giving birth in laboratories. However these three papers were not representative of the articles published in the following years. Although the mole was the focus of nine further articles, articles on insectivores in general form a relative small proportion of the articles published in Lutra. The same applies for articles on pleistocene mammals: until 1990 papers on giant deer, sabre-toothed cat and cave bears were only occasionally published and in the last seventeen years only one paper in this field, about the aurochs (van Vuure, Lutra 45, 2002) has been published. The brown rat made only one more appearance in the pages of Lutra since then, when Keijl discussed the development of brown rat populations on the islands of Vlieland and Terschelling (Lutra 43, 2000). The lengthiest of all contributions was the voluminous paper of Van Wijngaarden et al. on the occurrence and distribution of the Dutch mammal fauna (Lutra 13, 1971), which ran to 105 pages.

Figure 1 provides an overview of the general picture in terms of the species groups and species discussed in Lutra. Over the years carnivores have been the most written about group, followed by rodents and bats. Since 2000 these three mammal groups have accounted for 83% of all published papers. Special editions of Lutra, such as the ones on pine martens (Lutra 43-2), rodents (Lutra 45-2) and beavers (Lutra 46-2) in this period no doubt contributed to the high score of these mammal groups, but even in earlier periods these species drew much attention. Many articles have also been written about whales and dolphins over the years, but apart from recent

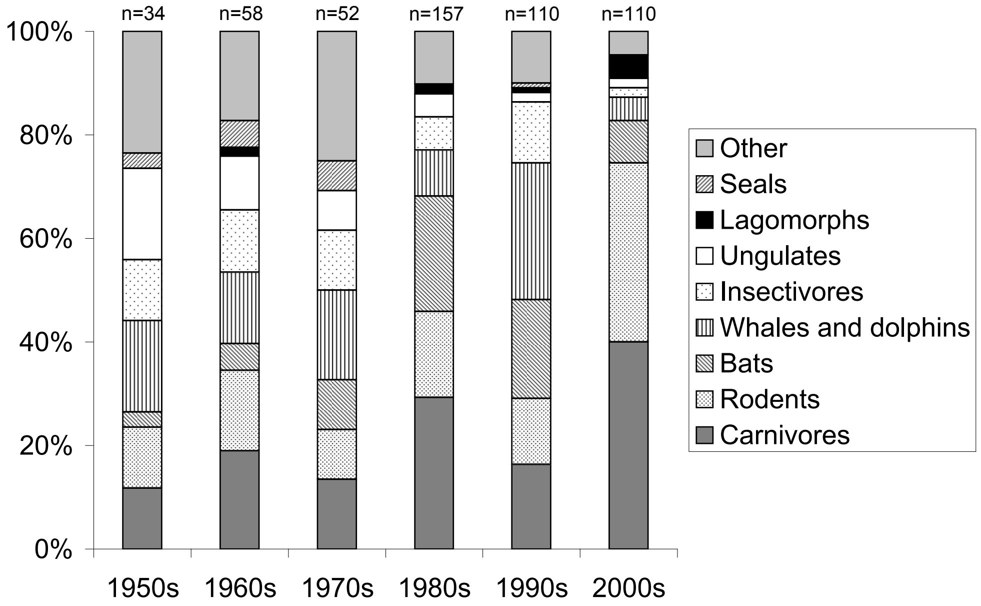

Figure 1. Shifts in the relative frequency of articles on different mammal groups published in the first 50 volumes of Lutra. The “Other” category includes cattle species, extinct hominid species and elephant species, as well as papers that discussed more than one species group.

contributions about stranding records on the Dutch and Belgian coasts, there have been fewer of these since 2000. The main years for articles on insectivores were the 1980s (10 papers) and 1990s (13 papers, including nine in the Lutra special on hedgehogs - Lutra 42, 1999). Ungulates drew most attention in the 1950s, 1960s and 1980s, but always in low numbers. Just two papers have been published on this mammal group in each of the last two decades, the most recent one by Groot Bruinderink on the possibilities of creating a trans-national ecological network for red deer (Lutra 45, 2002). Even fewer articles have been published on lagomorphs (10 papers over 50 volumes) and seals (8 papers over 50 volumes). This is not due to an absence of research on species within these groups. Rabbits and hares have been extensively studied over the last four decades, as illustrated by the recently published book “Wilde konijnen” (“Wild rabbits” - Drees et al. 2007) which describes some of the major research activities on rabbits and hares within the Netherlands. Equally much research has been done on seals within the Netherlands, although most of this research has been published elsewhere.

If we zoom in on the species themselves there is an obvious ‘winner’ in terms of number of articles: Fittingly, Lutra most often publishes articles about *Lutra lutra*! In total Lutra has published 40 articles about the otter, exactly twice the number of articles published on the second species in the ranking list, the beaver, with 20 papers over 50 volumes (figure 2). We will never know whether this is due to a providential choice of title when the journal was launched or whether the journal attracts papers on the species because of its title. It is clear that the otter is much loved as a subject of research and that Lutra has been one of the main avenues for communicating research results about this species. These articles are not limited to studies conducted in the Netherlands or Belgium, but also originate from many other European countries, including Luxembourg, Germany, the UK, Ireland, Denmark,

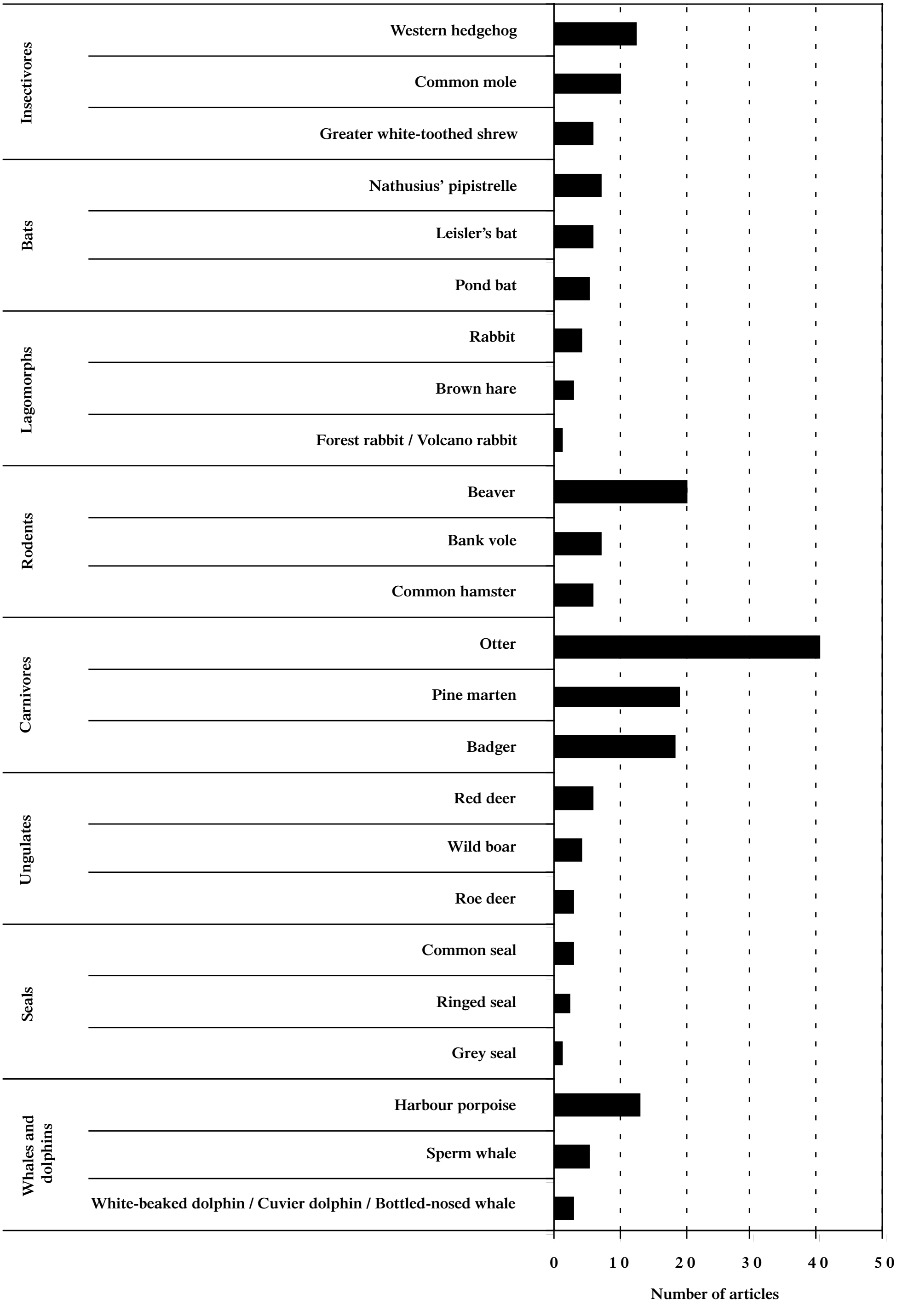

Figure 2. Number of articles in the first 50 volumes of Lutra about the three highest ranking species in each mammal group.

Finland, Austria, Spain, Poland, and Belarus. Although most of these papers fall within the fields of biogeography and ecology, others have been published from the fields of morphology, physiology, embryology, genetics, toxicology, palaeontology, population dynamics, policy and law, research techniques and nature management and nature conservation, including several papers on (re)introductions.

Besides otters, the carnivorous pine martens and badgers also rank highly in terms of published papers with 19 and 18 articles respectively published in the first 50 volumes of Lutra. For the pine marten this is mainly the result of the Lutra special (Lutra 43-2), which carried fifteen articles on this species. These included several in depth articles, such as the paper on sex-dependent dispersal by Broekhuizen and Müskens, one on natal den attendance of female pine martens by Kleef, and one on day-hides of a male pine marten by Müskens, Klees and Broekhuizen. The story for the badger is different. Publications about this species have been more or less evenly distributed over the years, with voluminous monographs about distribution and population trends in the Netherlands by Van Wijngaarden and Van de Peppel (Lutra 6, 1964), Wiertz and Vink (Lutra 29, 1986), Wiertz (Lutra 32, 1992) and Van Moll (Lutra 48, 2005) providing a "red thread" through the history of Lutra.

The beaver has been the most written about rodent species in Lutra articles. As with the pine marten this is mainly the result of the publication of a Lutra special in 2003, in which 14 of the total 20 articles on beavers were published. The bank vole and hamster are the second and third most written about rodent species, with most articles published since the 1980s. The harbour porpoise is the most commonly written about marine mammal, with 13 articles published over 50 volumes. These mostly address morphological aspects and the distribution/population trends of the species. Articles worthy of mention in this respect include those of Smeenk (Lutra 30, 1987), Camphuysen and Leopold (Lutra 36, 1993), Addink and Smeenk (Lutra 41, 1999),

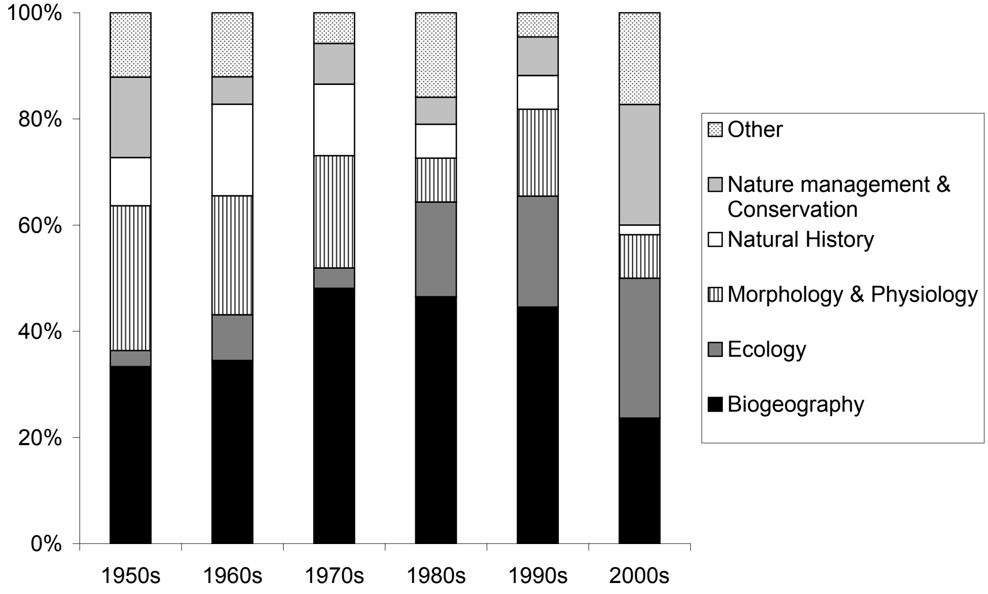

Figure 3. Shifts in the relative frequency in the disciplinary focus of articles published in the first fifty volumes of Lutra. The "Other" category includes taxonomy, animal welfare and ethology, population dynamics, genetics, research techniques, toxicology, and policy and law.

Camphuysen (Lutra 47, 2004) and all the stranding reports which provide exhaustive data about the harbour porpoise. Together this group of papers makes a valuable contribution to our growing knowledge on this species in Dutch waters.

In terms of research fields, articles on the biogeography of species have been the most numerous (figure 3). Almost 40% of the articles published in the first 50 volumes of Lutra describe the distribution of a species within Europe, a country or a region, the finding of a specimen, roost, wintering place or new location for a species. Memorable contributions in this respect are the papers on the distribution of the beaver (van Wijngaarden, Lutra 8, 1966) otter (van Wijngaarden, Lutra 10, 1970) and hazel dormouse (van Laar, Lutra 27, 1984) in the Netherlands. Ecology is the second most important research field, with 17% of all articles. However, whereas the biogeographical contributions have declined somewhat (slightly in the 1980s and 1990s and more rapidly since 2000), papers on ecology only started to seriously enter the journal in the 1980s (28 papers in the 1980s as opposed to 2 in the 1970s) and their number is still increasing. The same applies for articles in the field of nature management and conservation. From the 1980s onwards there has been a growth in this type of article - with papers on e.g. conservation measures for badgers along roads (Derckx, Lutra 29, 1986), management measures by the International Whaling Commission (van Beek, Lutra 30, 1987), threats to mammals in wetlands (van Apeldoorn, Lutra 37, 1994) and management measures to benefit mammals in agricultural landscapes (Huijser, Lutra 44, 2001), to name a few. The fourth most frequent research field is morphology and physiology, contributions from which have been rather stable, with an average of 12 articles (min. 9; max. 18) in each ten year period. There has been a marked decline in the number of papers from the field of natural history, including palaeontological studies, with just two papers published in the most recent period. Notably 88% of all articles published in Lutra describe studies on, or observations of, mammals in the wild, showing that Lutra remains a journal that primarily publishes field based studies. The remaining articles (12%) involve the study of mammals in an enclosure, animal rescue centre, zoo, laboratory, or farm, or are based on (museum) collections and/or the literature.

Table 1. “Top 10” authors, based on the number of scientific articles published in the first 50 volumes of Lutra.

Ranking	Author	Number of articles
1	van Laar	17
2	Lina	16
3	Broekhuizen	13
4	van Wijngaarden	9
5	van Bree	8
6	Bekker J.P.	8
7	Van der Straeten	7
8	Mostert	7
9	Hoekstra	7
10	Kompanje	6

There is no journal without authors. So let us also take a closer look at some statistics about the authors who contributed to the first 50 volumes of Lutra. In total there have been 396 first named authors that published in the journal. Of these, 293 published a scientific article. Eighty six of these authors have used Lutra as a platform to disseminate two or more articles, a pleasing 30% of all authors who have published a scientific article in Lutra. Of these 86, about half published two articles in Lutra, with the remainder contributing more than two manuscripts. Van Laar holds the record for the most publications with 17 (table 1). It is also encouraging that more than half of the authors in this ‘top-10’ continue to be active and frequently submit new papers to Lutra, as illustrated by the two papers by Broekhuizen in this issue. Authors’ appreciation of Lutra as a means of informing their peers about their observations and research findings can not only be measured by the number of articles per author, but also by the time period between the publication of the first and most recent articles published by the same authors. Again a ‘top-10’ can be

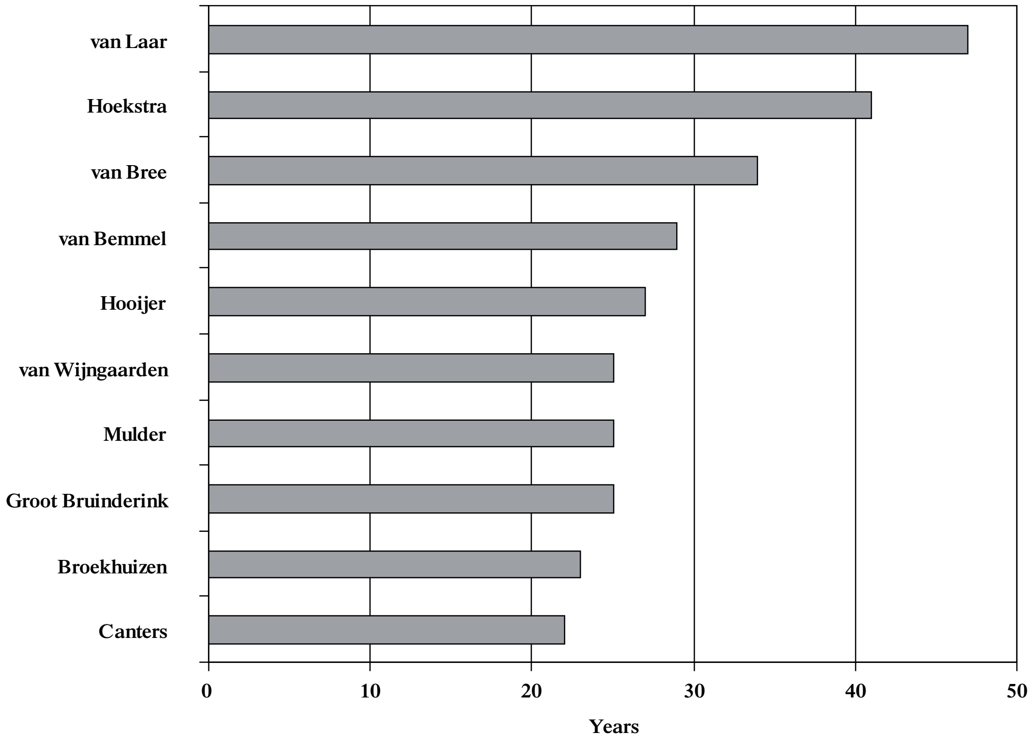

Figure 4. “Top 10” authors, based on the period between the publication of their first and their most recent articles.

made of this phenomenon of “loyalty to Lutra” (figure 4) with Van Laar, whose articles span a period of no less than 47 years, coming out again as the winner. His first article on small mammals in bird pellets in 1959 appeared in the very first volume of Lutra and his most recent contribution (jointly with Hemmelder) in 2006 describes population trends of hare and rabbit and the occurrence of other mammals at Schothorst, a city park in Amersfoort (Lutra 49).

Analysis of the data on authors in the first 50 volumes of Lutra also shows the evolution of the journal from a small society newsletter into a more comprehensive scientific journal. In the early years of Lutra most authors contributed under their personal title whereas nowadays contributions increasingly originate from authors at research institutes and universities (figure 5). This is not to imply that articles written by private individuals are of less value or scientific quality, but rather that the growing number of authors affiliated with professional scientific institutions shows an increasing recognition of Lutra as a professional medium for communicating scientific research results. Figure 7 also shows some other interesting shifts in the background of authors. In the first period, when Lutra was still a newsletter, most contributions were made under a personal title. In the 1960s an increasing number of articles were published by authors affiliated with museums. This trend continued until a sudden drop in the late 1990s, since when only occasional manuscripts from museum scientists have been received. The start of *Cranium* in 1984 – a new journal of the Dutch Working Group on Pleistocene Mammals – may partly explain this decrease yet, as early as the early 1970s, we were receiving fewer palaeontological articles from museum-based authors. Another reason may be the shift in interest of mammalogists from morphological studies, usually conducted and/or facilitated by museums, towards studies on ecology

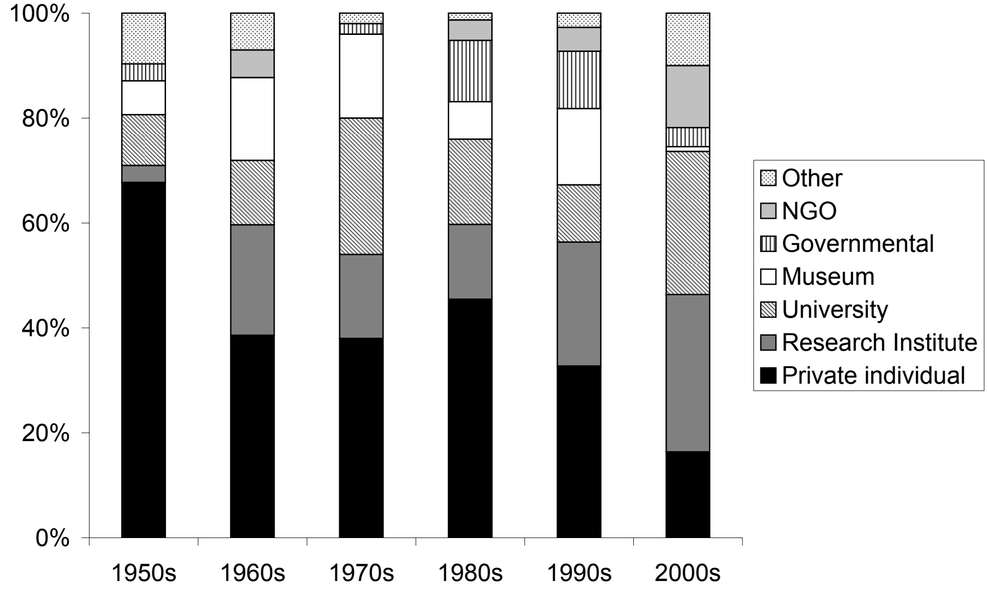

Figure 5. Affiliation of authors published in the first 50 volumes of Lutra. The "Other" category includes authors from nature management organisations, private (consulting) companies and zoos or animal care centres.

and wildlife management, which are more often conducted by universities and research institutes. But, perhaps the most logical explanation is the change in the composition of the editorial board, as described in the editorial of Lutra 50-1. Many articles from museums in the 1980s and 1990s were, without any doubt, the result of Smeenk's involvement as managing editor with the journal. Employed by the "Rijksmuseum van Natuurlijke Historie" (nowadays the Natural History Museum "Naturalis") in Leiden at that time, he was responsible for numerous contributions himself, including four research papers, and also encouraged his colleagues to publish their work in Lutra. This is well illustrated by the 16 articles, published by authors from museums between 1991 and 1999: 15 of which were about marine mammals, Smeenk's main field of research. Two other shifts in the background of authors are worth mentioning. One is the decrease in contributions from governmental organisations in the late 1990s and the other is the increase in contributions from NGOs in the same period. The first trend is somewhat worrisome as it may imply that civil servants are less involved in conducting and publishing studies on mammals, which may possibly indicate a widening gab between science and policy making. The second trend is more gratifying, as it shows the more professional approach of NGOs, including the Society for the Study and Conservation of Mammals (VZZ), for whom contract research is becoming 'standard procedure' and apparently contributing to an increase in scientific publications.

The evolution of Lutra into a mature scientific journal can also be seen in the shift between the types of contributions over the years (figure 6): with fewer "other" contributions – primarily dealing with society business, such as meeting minutes, travel reports, summaries of presentations, announcements or requests – and more full research articles. It is our wish that this trend continues and it is hoped that the recent decisions to open Lutra up for opinion articles (Lutra 47, 2004), which is intended to initiate scientific debate about current issues, and to transfer the bibliographies to other, more appropriate, media (such as the website) will both contribute to this process. When comparing the types of contributions

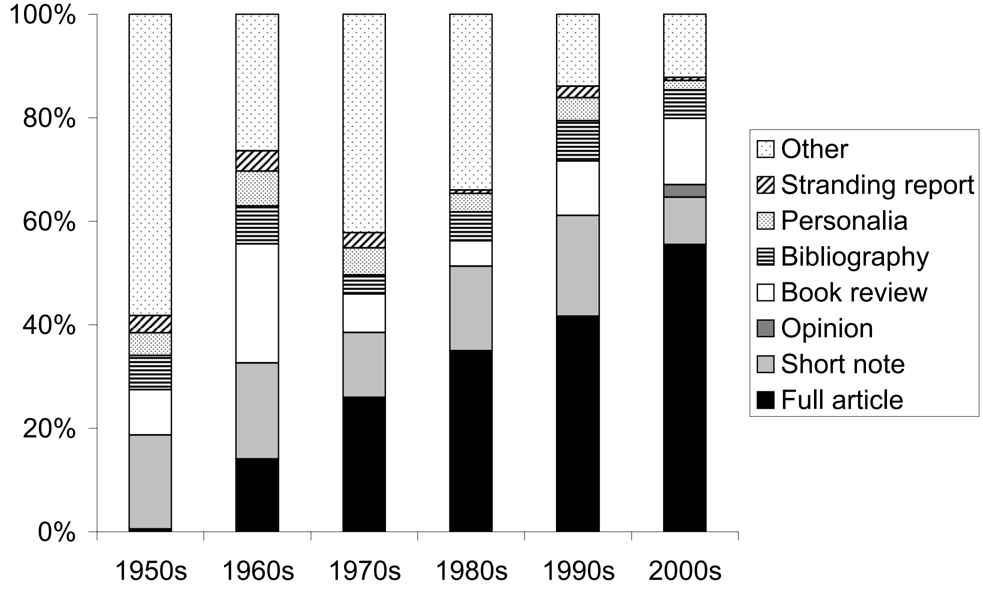

Figure 6. Shift in the type of contributions in the first 50 volumes of Lutra. The “Other” category includes editorials, summaries of presentations, minutes of meetings/workshops, announcements, previews of books, movies, conferences and meetings, news messages, requests, travel reports, reactions, and the publication of the statutes of the Society for the Study and Conservation of Mammals (VZZ).

in Lutra over the years one striking feature is the fairly constant number of book reviews, a form of contribution that is always much appreciated by the editors, as these inform us about up to date and important new publications on mammals. In total Lutra has published 122 book reviews, written by 46 different authors. Please, keep sending us those book reviews to enable us to highlight new findings on mammals published elsewhere! Another constant factor in Lutra has been the stranding reports that have been submitted over the years by Van Deinse (Lutra 1-8, 1953-1966), Van Utrecht (Lutra 10, 1968), Husson (Lutra 14 and 18, 1972/1976), Van Bree (Lutra 16, 20 and 25, 1974/1978/1982), and Smeenk (Lutra 32, 35, 38 and 46, 1989/1992/1995/2003) for the Netherlands and by Van Gompel for Belgium (Lutra 34 and 39, 1991/1996).

Lutra has not only become more ‘mature’ in terms of a significant increase in full research papers, but has also become more international. This can be seen in several shifting trends, relating to the language, origin of authors and countries where the published research was undertaken. As already described in the editorial for Lutra 50-1, a considerable move towards English papers has occurred since the late 1980s. This shift has been encouraged and was formalised in 2001 when English officially became the preferred language for Lutra. This ensures that Lutra can reach a wider audience and is more in line with scientific standards. There has also been a notable increase in publications from authors from outside the Netherlands and Belgium in recent years, with most of them originating from other European countries (figure 7). From the fifteen or so manuscripts currently being reviewed for future issues we see that this trend continues. Simultaneously there has been a shift in countries where the studies took place, with more research from European countries apart from the Netherlands and Belgium being published. This has resulted in more articles on species that do not occur in the Netherlands or Belgium, although still many of these ‘foreign’ articles are about species that do occur here.

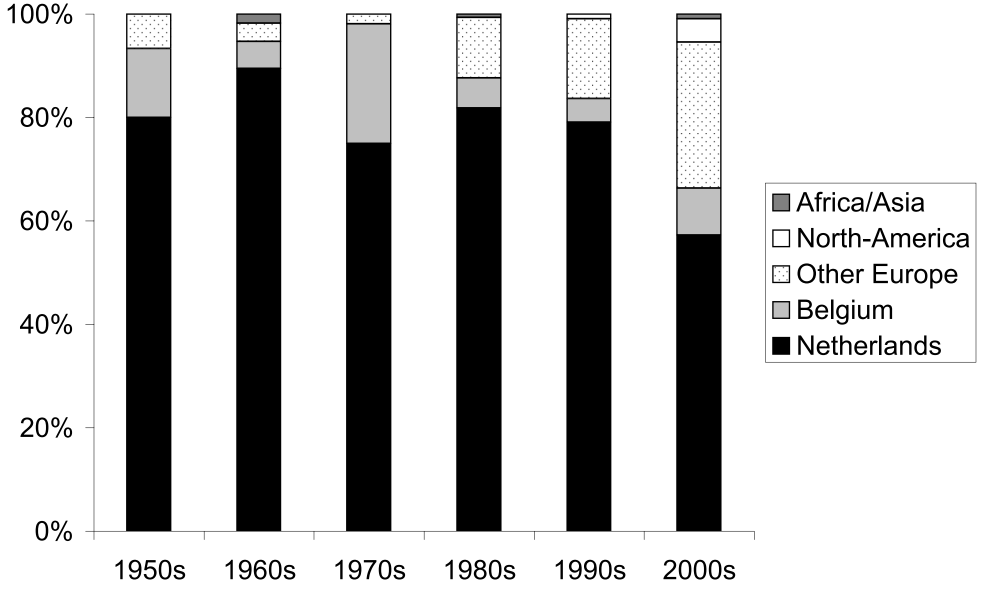

Figure 7. Shift in the residence of first named authors of articles published in the first 50 volumes of Lutra.

There have also been some papers on mammals from other continents, such as those on Salim Ali's fruit bat in India by Vanitharani et al. (Lutra 47, 2004) and the forest rabbit in Surinam by Hoogmoed (Lutra 26, 1983). This is not an entirely new phenomenon though: in the early days Lutra carried a report of a safari in Kenya by Koeman (Lutra 11, 1969). The primary focus of Lutra remains on European mammal species. We hope to more strongly position ourselves as a more international journal on European mammals and believe that the step we took in 2005, in publishing the full text of Lutra for free on the web, (see Lutra 48-2) will help us reach that objective. We intend to report about this in more detail in a future editorial. In the meantime we look forward to fifty volumes more of publishing a wide range of articles addressing all species groups, from large ungulates to shrews, and research fields, from ecology to genetics.

Correction

In the Editorial of issue 50-1 we credited the 'Société Française pour l'Etude et la Protection des Mammifères' (SFEPM) as the publisher of the journal *Mammalia*. This was incorrect. *Mammalia* is published by the 'Muséum National d'Histoire Naturelle' in Paris. The SFEPM publishes the journal *Arvicola*.


E.D.

The least weasel (*Mustela nivalis nivalis*) in north-western Taimyr, Siberia, during a lemming cycle

Sim Broekhuizen[1], Jaap L. Mulder[2], Gerard J.D.M. Müskens[1] & Igor Yu. Popov[3]

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Abstract: During the summers of 2005-2007 the least weasel (*Mustela nivalis nivalis*) near Mys Vostochniy, NW Taimyr, Siberia, was studied in relation to the fluctuating abundance of the Siberian lemming (*Lemmus sibiricus*). The number of lemmings largely determines the reproductive success of birds and predatory mammals on the tundra. The 2005 expedition to Mys Vostochniy occurred in a peak lemming year and was the only one out of nine carried out in the preceding 14 years in which least weasels were observed. They were abundant on the mainland, but were not observed on the nearby islands. A search plot of 1.5 ha was selected in order to gain an impression of the intensity of the predation on lemmings by weasels. 107 lemming winter nests with a diameter of ≥14 cm were found within the search plot, of which 52% showed signs of predation by weasels. Smaller lemming nests showed no signs of predation. This predation of lemmings corresponded with about 127 days on this particular search plot over winter, suggesting the presence of just one weasel. In 2006 no new lemming winter nests were built on the search plot. 6.5% of the lemming nests (*n*=92) checked in the wide surroundings showed signs of predation by weasels, indicating a continuing but limited presence of weasels in the winter of 2005-06. However, no weasel was spotted in 2006. In 2007, a build-up year of the lemming cycle, 36 new lemming winter nests were found within the search plot, but none showed signs of predation by weasels and no signs of the presence of weasels were found outside the search plot. In 2005 we found some dead weasels and we were able to catch others. We collected these data as we had found no published data about weasel from the Taimyr-part of Siberia. The weight of two males in moulting coat exceeded the maximum weight mentioned in the literature, and this was presumably related to the optimal food situation during the lemming peak in the spring of 2005. Two females were checked for litter size, 14 and 10 respectively. The reason for the sudden abundance of weasels near Mys Vostochniy in 2005 remains unexplained; either the first animals moved in from the south at the beginning of the lemming peak, or there was a very small, and hence hitherto unnoticed population, which was able to suddenly flourish. Weasels do not seem to have a major function in maintaining the multi-annual cycle of lemmings in Taimyr.

Keywords: least weasel, *Mustela nivalis*, Siberian lemming, *Lemmus sibiricus*, lemming cycle, moulting, reproduction, predation, tundra, Taimyr.

Introduction

Between 1990 and 2005 the Dutch Institute for Nature Research (now Alterra) in Wageningen organised nine expeditions to Mys Vostochniy (East Cape) on the northern side of the Pyasina delta, western Taimyr, about 200 km east of the town of Dikson, Siberia (figure 1). The purpose of these expeditions was to study the factors that influence the breeding success of the black bellied Brent goose (*Branta bernicla nigricans*) which shows a high annual variability, that has been shown to be related to the number of Siberian lemmings (*Lemmus sibiricus*) (Greenwood 1987, Summers & Underhill 1987). During peak lemming years, predators, such as the arctic fox (*Alopex lagopus*), the snowy owl (*Nyctea scandiaca*) and the Taimyr herring gull (*Larus argentatus*), that would normally feed on geese eggs and chicks, concentrate on lemmings as food, leaving the geese the opportunity of breeding relatively undisturbed.

Figure 1. Location of the study area in Taimyr, on the northern side of the Pyasina delta.

Figure 2. Least weasel near the camp site at Mys Vostochniy. *Photograph: Vasily Grabovskiy.*

It is not only the predators of geese nests that benefit from peak lemming years, other species also predate lemmings. Among these is the weasel (*Mustela nivalis*) which has a wide distribution on the Taimyr Peninsula (Yudin 1980). Of the different subspecies of weasel, the least weasel *Mustela nivalis nivalis* inhabits the northwest of Siberia and its presence in the Pyasina delta was recorded by Nowak and Pavlov (1995). However, during the nine preceding expeditions before 2005 the least weasel was not ever seen in the vicinity of Mys Vostochniy, even in the peak lemming years of 1991 and 1994 (Rykhlikova & Popov 1995). Dr Y. Kokorev, a biologist in Norilsk, who has visited the Pyasina delta every summer since 1978, had never seen least weasels in this area, but had sometimes observed a stoat (Y. Kokorev, personal communication). When the first expedition members arrived on 9 June 2005, it became immediately apparent that 2005 was a peak lemming year (Popov 2006) and they were surprised to find that there were weasels present, especially around the campsite (figure 2) and in the rocky outcrops of the tundra.

The questions arose as to when and from where these least weasels had colonised the area around Mys Vostochniy, and the role that they would play in the local ecosystem. A peak lemming year is usually followed by a low year and then by a build up year. To understand how the weasel population had reacted to the drastic change in the number of lemmings, the locations where weasels were spotted or caught in 2005 were checked again in 2006. In 2007 there was not enough time to do this.

Materials and methods

Taxonomic status of the least weasel

In order to compare data from the weasels we collected near Mys Vostochniy with data from previous literature, we had to decide which subspecies of *Mustela nivalis* these weasels belong to.

Figure 3. Least weasel showing the straight boundary line between the brown back and the white belly. *Photograph: Sim Broekhuizen.*

Within the genus *Mustela* the weasel shows one of the largest variations in body size. Apart from a clear sexual dimorphism, body size generally increases from north to south (King & Powell 2006), in contrast to what one would expect from the Bergmann rule (1847) and the Allen rule (1877). The same is true of skull size and tail length in relation to body length (Abramov & Baryshnikov 2000). This latter characteristic and the coat colouration have given rise to a large variety of subspecies being described. Reichstein (1993) listed 13 subspecies for Europe, Abramov and Baryshnikov (2000) described another nine for Asia, one for North Africa and, conform to Hall (1951) four for North America. According to the description of the typical *Mustela nivalis nivalis*, (made by Linnaeus in 1766 and based on specimens from northern Switzerland) the subspecies is white in winter and in summer has a white ventral side and brown dorsal side with the border between the two being almost straight (figure 3). These features differentiate this subspecies from *Mustela nivalis vulgaris* (Erxleben 1777) which occurs in Western and Central Europe. In this species the border between the brown and white in the coat is generally irregular, and the white ventral side may show small and irregular brown spots. Normally this subspecies does not turn white in winter, but within its range of distribution, some individuals are found with a 'nivalis' appearance (Reichstein 1993). Similarly the 'vulgaris' appearance is found now and then in animals that normally exhibit the 'nivalis' characteristics (Abramov & Baryshnikov 2000).

According to Abramov and Baryshnikov (2000) Siberia is inhabited by *Mustela nivalis nivalis*, except in the north-eastern part (east of the Omolon river) where the weasels are generally a little smaller and have a somewhat shorter relative tail length. Therefore they are regarded as a separate subspecies, *Mustela nivalis pygmaea* (Allen 1903). From the north-western part of Siberia Abramov and Baryshnikov (2000) mention *Mustela nivalis nivalis* from the Yamal peninsula. Volokh (1995) has identified this subspecies in the north-eastern part of the Gydan peninsula, west of Dikson.

Some authors before, however, are of the opinion that almost all of Siberia is inhabited by *Mustela nivalis pygmaea* (Gromov et al. 1963, Chernyavskii 1984), while Parovshchikov (1963) stated that "the northern or snow weasel, *Mustela nivalis nivalis*, is not similar to the Siberian, tundra or little weasel (short-tailed), *Mustela nivalis pygmaea*, which lives in the tundras", and: "(t)he southern boundary of distribution is the northern limits of the taiga and the forest tundras", while in the northeastern part of Russia, the tundras of Malozemel'skaja and Bol'shezemel'skaja, was inhabited by *Mustela nivalis pygmaea*, bordered in the south by a zone of hybridisation with *Mustela nivalis nivalis*. Ternovsky (1977) does not speak about the aspect of subspecies in *Mustela nivalis*, but rather mentions that the weasels living on the tundra are smaller compared to those from the taiga and suggests that this is due to the poor conditions on the tundra.

Parovshchikov (1963) describes the summer coat of *Mustela nivalis nivalis* as very dark-brown to brown on the back and pure white on the belly, while the summer coat of *Mustela nivalis pygmaea* is pale brownish with a rusty hue on the back. As all weasels in summer coat that were spotted during the expedition to Mys Vostochniy in 2005, had dark brown to brown dorsal fur (figure 4), we follow Abramov and Baryshnikov (2000) and recognise these weasels as being specimens of *Mustela nivalis nivalis*.

Of the four subspecies of the weasel in North America, *Mustela nivalis rixosa* most closely resembles *Mustela nivalis nivalis*, in terms of body size and coat colouration (Abramov & Baryshnikov 2000). We follow after several other authors (e.g. Blomquist et al. 1981, Frank 1974) in considering *Mustela nivalis rixosa* as being identical to *Mustela nivalis nivalis*.

Features of the weasels collected

In 2005, all the weasel observations by the expedition members were collected together, together with data about all the dead weasels found in the field and in fox dens, (the later probably killed by arctic foxes). Some weasels were killed inadvertently, mainly in snap-traps used for lemming monitoring and one weasel drowned in a bucket of water on the campsite. During the last three weeks of the expedition in 2005, from 28 July to 15 August, weasels were live trapped during 44 trap days using self made 'seesaw-traps' with a tilting and closing floor, on the campsite, in rocky outcrops and on the beach, among the driftwood. These live trapped animals were individually marked with marker pens (figure 5).

In 2006, between 28 June and 21 July, for a period of seven days two or three live traps were placed every where that weasels had been caught or seen in 2005, except on the 'Vysokaya' hill, about 5 km from the camp. One trap was placed on two small rocky outcrops on the tundra. New live traps had been made for this purpose. To ensure that the trapping results were not influenced by the characteristics of the new traps, on most trap sites one or two new traps were placed together with a trap used in 2005. In total 140 trap days were involved.

Dead weasels were weighed, and the extent of winter whitening of the brown fur was noted. If possible, body length, and the length of the skull, tail, ear and hind foot were measured. From the males, the weight of the baculum was taken, and from the females the uterus was examined for embryos or placental scars. Usually only sex and body weight (sometimes also tail length) could be obtained from the live trapped individuals, since anaesthetics were not available on the 2005 expedition and live weasels are difficult to handle.

Weasel predation search plot

To estimate the extent of lemming predation by weasels, a search plot of 73-102 m wide and 172–191 m long, covering a total of about 1.5 ha, was systematically searched for the winter nests of lemmings and prey remains, such as fur, skulls and other skeletal remains. Most of the braincases of skulls of juvenile and sub-adult lemmings eaten by weasels were only opened on the back, in contrast to those of lemming skulls found in the pellets of the snowy owl (*Nyctea scandiaca*) and the pomarine skua (*Stercorarius pomarinus*), which were mostly heavily damaged (figure 6). At some of the lemming nests with lemming remains one or more weasel latrines with piles of faeces, were found. These faeces contained only lemming hair.

The search plot lay within a shallow, sloping valley with a high density of lemming nests. The vegetation was classified as 'grass-sedge marshy tundra', characterised by *Carex concolor, Carex bigelowii, Arcagrostis latifolia, Poa arctica, Salix reptans* and *Sphagnum sp.*, changing on both sides into 'moss-sedge-*Cassiopa* tundra' with small hummocks that was characterised by *Cassiopa tetragona, Eryophorum polystachium* and *Chandonantus setiforme* (Rykhlikova & Popov 1995) (figure 7). All the lemming nests were marked with a numbered stick.

In July 2006 and 2007 the search plot was checked again for lemming winter nests and signs of predation. In addition, during random walks on the tundra, a much larger area was searched for fresh lemming nests and signs of predation.

To gain an impression of the age of the lemmings killed by weasels, the remains of lemming skulls were collected from the nests in the search plot. As a relative indication of the lemming's age the size of the diastema (distance between incisors and molars) in the upper jaw was measured whenever possible.

Results

Distribution of weasel observations

Figure 8 shows the locations of the weasel observations in 2005. The dead individuals recovered from the arctic fox den on the Vysokaya hill were probably caught near the den, as the foxes were harassed intensively by pomarine skuas during their foraging trips on the tundra. In 2005 the skua territories completely covered the lower tundra. On the higher hilly parts, where the fox dens were located, this was far less the

Figure 4. Three least weasels in summer coat (above), and one weasel moulting from winter to summer coat, found dead near Mys Vostochniy in 2005. *Photograph: Sim Broekhuizen.*

Figure 5. Weasel individually marked with – in this case – a blue stripe on the white throat. *Photograph: Sim Broekhuizen.*

Figure 6. Skulls of Siberian lemmings killed and eaten by the snowy owl (upper row), pomarine skua (central row) and weasels (bottom row). *Photograph: Sim Broekhuizen.*

Figure 7. Part of the sloping valley in which lemming winter nests were checked for the remains of lemmings killed by weasels. *Photograph: Sim Broekhuizen.*

case. There were 15 weasel catches (twelve different individuals) in the live weasel traps and eleven different weasels were caught in the lemming traps. The numbers in figure 8 indicate the minimum number of different individuals caught and observed in each location, the latter mostly by chance.

In 2005 we also checked lemming nests on the islands of Farwatterniy (110 nests) and Vyerkhniy (several dozens) (see figure 1). In none of these were the remains of lemmings killed by weasels found. In 2006 and 2007 no weasels, weasel tracks or other weasel signs were observed at all, either on the tundra, around the camp, or on either island.

Coat colour

With the exception of three individuals, all the weasels observed in 2005 were in summer coat, with the characteristic unicoloured brown dorsal fur separated by a straight line from the white fur on the ventral side. On 4 July the only least weasel in white winter coat (figure 9) was observed at a small mound of loose rocks. This individual then disappeared underground and for some time the sounds of a social gathering could be heard, indicating an encounter with one or more juveniles. Thus this was probably an adult female with a litter at that site.

On 8 July 2005 a dead male least weasel was found in a food cache of an arctic fox den on 'Vysokaya' hill. The coat of this specimen showed brown as well as white fur on its back, suggesting that it was moulting from its winter to summer coat (figure 10). Its date of death is unknown: in such cold conditions it could have been killed long before the date of recovery.

In the night of 14 / 15 July 2005 another moulting male weasel was inadvertently caught in a lemming trap; the central part of the fur on its back was already brown, while the edges were still white (figure 4, bottom). A visit to the Darwin Museum in Moscow (figure 11) with its collection of specimens and paintings suggested that this pattern of moult is the more common of the two. In England the moult to the summer coat also starts with a central brown band over the head and back (King 1979). All the other least weasels spotted after 15 July were in full summer coat.

Measurements

Data and measurements taken from live trapped or dead least weasels collected in 2005 are listed in appendices 1 and 2.

The body weight of the weasel males near Mys Vostochniy varied between 63 and 124 g, and that of the adult females between 75 and 55 g. The two heaviest males were both in moult from winter to summer coat and weighed 115 and 124 g. The next heaviest males were those found on 7 and 8 July: 103 and 94 g. The smallest female, weighing only 36 g, had no visible nipples and had the 'soft-faced' appearance of a juvenile. Figure 12 shows the measurements of body weight plotted against time.

The head-body length of the two moulting males from Mys Vostochniy were 20.0 and 20.2 cm respectively, so these were not only the heaviest, but also the largest, individuals. The length of males in summer coat varied from 16.5 to 18.9 cm (*n*=16).

One of the two females with embryos had had her head bitten off by an arctic fox. The other one had a head-body length of 16.5 cm and a total body length (including tail) of 18.0 cm. None of the other females could be measured, since they were all caught alive and no anaesthetic was available to be able to handle them comfortably.

Reproduction

In 2005 we were able to examine the reproductive status of two females: one found dead on 25 June in an arctic fox den, and the other caught unintentionally in a lemming trap on 7 July. Both females were pregnant with 14 and 10 embryos respectively. The uterus swellings were ca. 10 and 11 mm in diameter. The reproductive state of the other females could not be detemined as they were captured alive and were difficult to handle.

In mid June seven small individuals were seen together on one of the rocky outcrops on the tundra. They clearly belonged to one litter (R. Bom and M. La Haye, personal communication), but it is uncertain whether they were the entire litter.

Predation of lemmings in or near winter nests in 2005

Predation and size of the lemming nests

On the search plot in 2005 remains of dead lemmings were only found in lemming winter nests with a diameter ≥14 cm. Of the 107 nests of that size that were inspected, one or more tufts of lemming fur were found in 56 (52 %). In 47 of these nests other remains of lemmings were also found, mostly parts of skulls (see figure 13). A total of 150 skulls were collected, apparently from lemmings killed and eaten by weasels, an average of 2.7 lemmings per nest with signs of predation. If all these lemmings lived inside the search plot, the predation rate during the winter of 2004-05 would have been 100 lemmings per hectare from an unknown period of weasel presence there.

In addition about 200 smaller lemming nests were found (diameter <14 cm), that had apparently been only in use for a short time. Of these, 41 were inspected for lemming remains, but in none of them were remains of dead lemmings found.

During the snow thaw in the beginning of June 2006 quite a number of wet lemming carcasses emerged from under the snow and were immediately eaten by gulls. Around 26 July 2006 a very fresh scat of an arctic fox was found containing lemming hair (S. Bakker, personal communication). This indicates that there were still lemmings present when the snow covered the tundra in the autumn of 2005. The number of fresh winter nests found in 2006, however, was much less than the year before and not a single winter nest was found within the search plot area. During walks across the tundra 92 lemming winter nests, which looked fresh enough to originate from the previous winter (2005-06), were checked for lemming remains. According to Sittler (1995) it is not always possible to distinguish nests of the past winter from nests of the year before, so there could have been some misjudgements. For comparison the nests on the search plot, that were marked in 2005, were still available. None of these nests looked really fresh, but, as the plot was located in a shallow valley, they may have been more exposed to wet conditions. Nevertheless, from the presence of nests in good condition outside the search plot (figure 14), we conclude that lemmings were still present when the tundra was covered with snow in the autumn of 2005.

Of the 92 lemming winter nests inspected during the summer of 2006, 42 had a diameter of ≥14 cm, four (9.5%) of these contained lemming fur and two of these also contained parts of a lemming skull. From the 50 nests with a diameter of <14 cm only one (2%) contained lemming fur. Next to two of the nests with lemming remains there was a weasel latrine. These observations indicate that not only did several lemmings survive until the tundra became covered with snow in the autumn of 2005, but that there were still some weasels present then. The percentage of predated winter nests in 2006 was, however, much lower than in the winter nests of the 2005 plot.

In the summer of 2006 only one lemming was seen and none were caught during the regular lemming inventory.

In June-July 2007, 38 new lemming winter nests were found in the search area, indicating re-colonisation of the plot. Of these nests, 28 had a diameter of ≥14 cm and 10 a diameter of <14 cm. In none of these nests was any sign of predation by weasels found, nor were any signs of weasel presence detected beyond the search area, during the three week expedition.

Use of lemming nests by weasels

On the 2005 search plot a weasel latrine was found in close proximity to 13 of the 56 nests with lemming remains, and more than one latrine was found near seven of these nests (figure 15). Such an accumulation of weasel faeces indicates that the lemming nest had been used or visited for at least several days by one or more weasels.

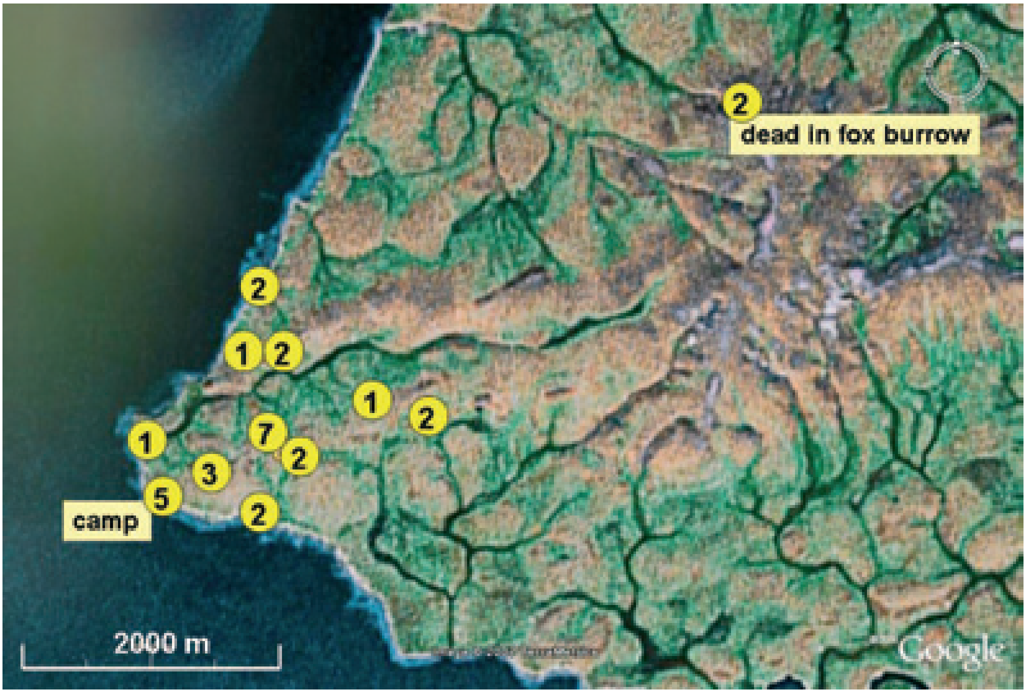

Figure 8. Map of the surroundings of Mys Vostochniy, with the locations of weasel observations and the minimum number of different individuals concerned.

Figure 9. Least weasel in winter coat, observed on 4 July 2005 near Mys Vostochniy. *Photograph: Sim Broekhuizen.*

Figure 10. Two male least weasels: left with two-coloured coat on the back. *Photograph: Sim Broekhuizen.*

Figure 11. Painting by K.A. Komarov in the Darwin Museum in Moscow of a least weasel and a stoat, both moulting from winter to summer coat.

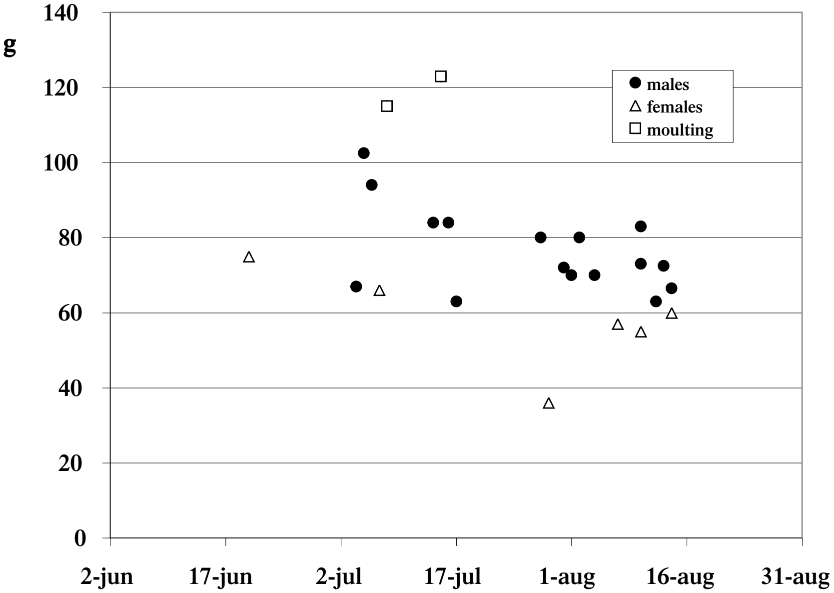

Figure 12: Body weight (g) of least weasels caught or found dead near Mys Vostochniy in 2005.

In 2005 three lemming nests lined with a thick layer of lemming fur were found on the search plot (figure 16). MacLean et al. (1974) found evidence that weasels occupy lemming nests during periods of inactivity and will increase the insulation properties of the nest by lining it with lemming fur. These nests may also have been used by a weasel for raising its young. Two of these lined nests contained the most lemming skulls, indicating that they were also used for catching prey. These nests were 52 m apart. The third lined nest contained only three lemming skulls and was located 42 m and 32 m respectively away from the two other nests. The three fur lined nests may have been used by three different female weasels, but it is also possible that one weasel used all three nests in succession. No other lemming nests with a lining of fur were found in the adjacent part of the valley, but the search was less intensive there than within the search plot area itself.

In 2006 one fresh small lemming nest, with a diameter of 13 cm, was found with a lining of lemming fur, in this case outside the 2005 search plot. The lining was relatively thin, compared to the linings found in 2005, making it unlikely this nest had been used by a female weasel for reproduction.

Age of the lemmings eaten by weasels

A total of 99 of the 150 skulls collected on the search plot in 2005 could be used as an indication of the age of the lemmings, by measuring the diastema, i.e. the gap between incisors and molars (figure 17).

The most common size of the diastema was between 9.0 and 9.5 mm and the majority (66%) of the values were between 8.0 and 10.0 mm. As the diastema of two dissected adult and reproductive females was 10.5 and 10.8 mm, and those of two adult reproductive males 11.5 and 11.9 mm, it seems that most of the lemmings killed by weasels were juvenile or sub-adult. The number of very young lemmings in the example is probably underrepresented, as the skull bones of very young lemmings are not yet fused, so they disintegrate after death.

Discussion

Origin of the weasels

The question of where all the least weasels in 2005 came from, while none were ever seen before, remains unanswered. The presence of adult animals in winter or moulting coat, and probably born in 2004, does not provide an answer to the question of whether they were already present in the area around Mys Vostochniy during the summer of 2004 (or even earlier) or, alternatively, whether they colonised the area shortly before or during the winter of 2004-05. If they were already there in summer, their numbers must have been so low that their presence was not detected during the short expedition, from 3 to 20 July in 2004.

Weasels can cover large distances in a short time. The white animal seen on 4 July was spotted running across the tundra covering a distance of about 400 m, which took only a mere few minutes. King and MacMillan (1982) mention recoveries of young males over distances of more than 20 km in the course of only a couple of weeks. In Oklahoma the range of distribution of the weasel expanded by 300 miles (483 km) in a period of a few years (Choate et al. 1979, cited by King & Powell 2006). Ternovsky (1977) points out the benefit of the white winter fur, as he observed weasels moving across the snow cover over distances of 1–3 km (at temperatures of -42 to -47 ºC) before they went under the snow again. So, theoretically, it is possible that in 2004 the area around Mys Vostochniy was colonised after the expedition left. The first colonisers may have travelled hundreds of kilometres.

On the other hand, and probably more likely, weasels may have been present in the area already, but at such a low density that they were not observed during the earlier expeditions. This might also have been the case in 2006, when no more weasels were observed after the high number observed in 2005. Indirect evidence for survival of some weasels was found in the several lemming winter nests with tufts of lemming fur including one with a small weasel latrine nearby and one lined with lemming fur. To detect such signs one has to have a trained eye, so it is possible that former expeditions missed these less obvious signs of weasel presence. In 2006 we also found two predated nests of snow buntings (*Plectrophenax nivalis*) in places tucked away between rocks that appeared inaccessible to any avian predator or to the arctic fox.

The least weasel situation near Mys Vostochniy in the years 2005-2007 seems very similar to the situation near Point Barrow (North-Alaska) in 1969 and the following years, where MacLean et al. (1974) studied the relationship between least weasels and brown lemmings (*Lemmus trimucronatus*). During the winter of 1968-69 there was a peak density of both lemmings and weasels, with 34.7% of the lemming nests occupied by weasels. In the summer of 1969 ten weasels were collected. In spring 1970 no lemming nests were found and nest predation could be considered as zero. A remarkable increase in lemming abundance occurred over the next winter, 1970-71, with 41.7 nests/ha in search areas, only 5.6% of which had been occupied by weasels. However, no weasels were seen. During the 1971-72 winter a decline in lemming breeding activity was observed (27.5 winter nests/ha), and during the summer of 1972 only 1.1% of the lemming nests examined showed evidence of weasel predation. Again, not a single weasel was seen during the summer of 1972. During the winter of 1972-73 there was another over-winter decline (14.4 nests/ha). In 1973 a single weasel was seen and none were caught, despite operating 49 trap sites during the season. Thus, it is not exceptional that least weasels remain unnoticed for several years and only become conspicuously present in peak lemming years.

Coat colour

The fur coat of the male weasel, still with a white crest but with (light) brown patches on its side as well (figure 10), and another weasel in complete white winter coat observed on 4 June (figure 9), illustrate a remarkable variation in moulting pattern and moulting time. This variation is also mentioned by Ternovsky (1977), who shows a photograph of two siblings, one already in

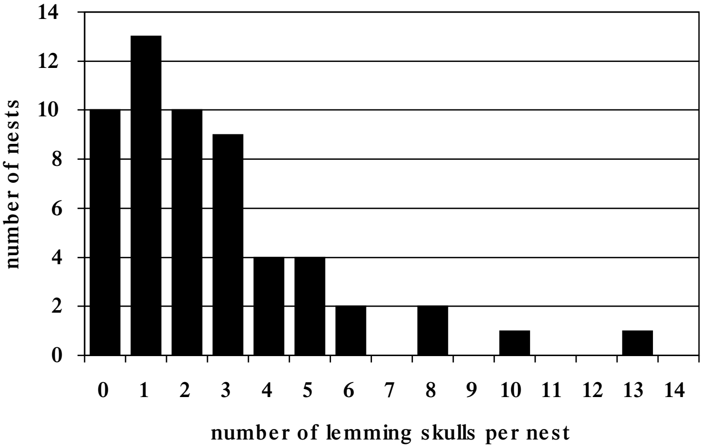

Figure 13. Distribution of the number of Siberian lemming skulls found on and in a lemming nest.

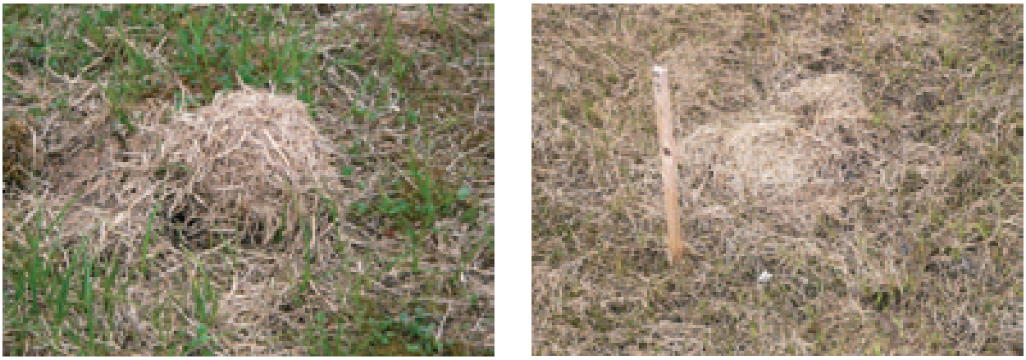

Figure 14. Lemming winter nests: left a nest most probably originating from the winter 2005-06, found in July 2006; right the freshest looking nest on the 2005 search plot, also found in July 2006. *Photographs: Sim Broekhuizen.*

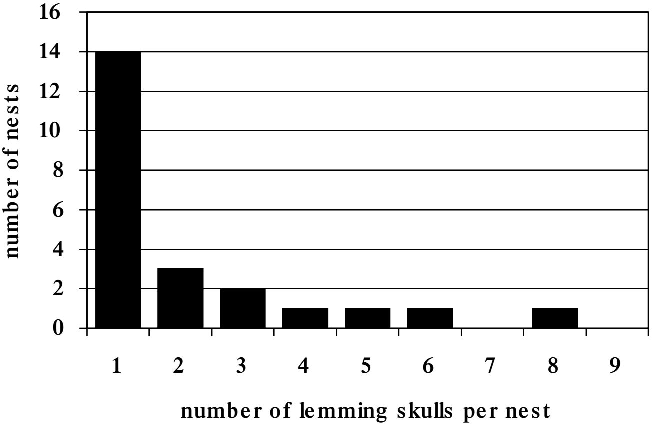

Figure 15. Frequency of the number of weasel latrines near lemming nests with remains of lemming skulls.

Figure 16. Lemming winter nest from the winter 2004-05, lined with a thick layer of lemming fur. *Photograph: Sim Broekhuizen.*

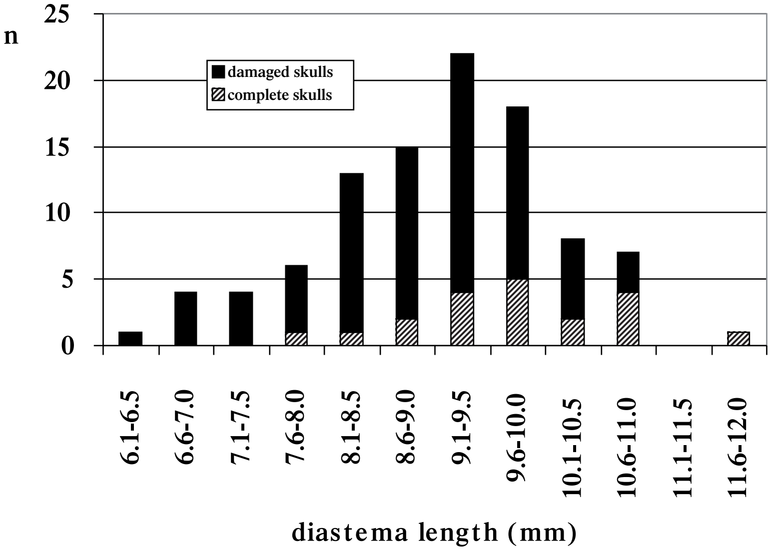

Figure 17. Distribution of diastema size of the Siberian lemming skulls found in lemming nests on the search plot in 2005.

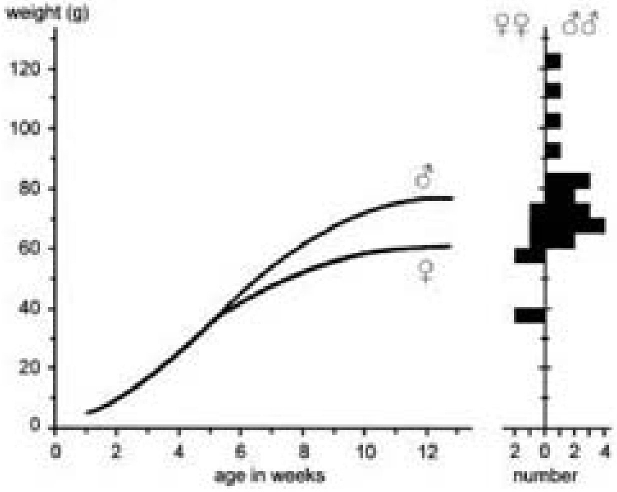

Figure 18. Body weights of least weasels from Mys Vostochniy (on the right), compared to the growth curves of a male and a female least weasel kept in captivity (on the left); curves after Heidt (1970).

moulting coat, the other still in white winter coat, indicating that the variation in moulting time is not just determined by age or external factors.

Weight and size

The body weights of the weasels near Mys Vostochniy in 2005 were high, compared to the data in the literature. The males we caught were considerably heavier than the previously measured maximum weight of 90 g, published by Stolt (1979) for males in northern Sweden, which is again higher than for males of *Mustela nivalis rixosa* from North America (table 1). Heptner et al. (1967, cited by King & Powell 2006) mention an average body weight for *Mustela nivalis nivalis* from Siberia of a mere 53 g.

The female weasels were also relatively heavy. The body weight of five of the six individuals (55-75 g) was more than the body weights published for *Mustela nivalis rixosa* (table 1). Heptner et al. (1967, cited by King & Powell 2006) give an average body weight of 41 g for female weasels from Siberia. However, the body weight of the two adult females with small embryos in their uterus (66 and 75 g) is similar to that of two pregnant least weasels caught by MacLean et al. (1974) in Alaska (69.0 and 70.2 g).

Figure 18 depicts quite a close resemblance between the body weight of the adult least weasels from Mys Vostochniy in 2005 (except for the four heaviest males) to the body weight shown on Heidt's growth curve (1970) of a male and female weasel, kept in captivity and probably well fed.

The measurements of the head-body length are inside the range given by Abramov and Baryshnikov (2000) for male weasels from Siberia: 14.2-20.0 cm. Barnfield (1974) recorded head-body lengths of 18.3-21.7 cm for male *Mustela nivalis rixosa*. Thus the males in our sample were not particularly long (see table 2). Similarly the only adult female measured was not extremely large compared to published records. This shows that the weasels we encountered were in relative good condition, especially those males moulting from winter to summer coat. The latter had gone through the lemming peak, which may have been at its highest during spring, just before the melting of the snow. This supports the opinion of Ternovsky (1977) that the body weight of weasels in the north of Siberia is determined mainly by the available food resources.

Table 1. Some ranges of body weight (g) of adult *Mustela nivalis*, mentioned in the literature.

Region	(Sub-)species*	Author(s)	Males	Females
N-Sweden	*M. n. nivalis*	Stolt 1979	- 90	
E-Siberia	*M. n. pygmaea*	Chernjasvsky 1984	36.0 - 60.5	23.5 - 32.5
Canada	*M. n. rixosa*	Banfield 1981	34.5 - 63.5	25 - 58
N-America	*M. rixosa*	Burt & Grossenheider 1976	39 - 63	28 - 39
Michigan	*M. rixosa*	Burt 1957	40 - 50	40 - 49
Michigan**	*M. nivalis*	Heidt 1970	75	60

* name used by the author(s)
** animals in captivity; data taken from graph.

Table 2. Some ranges of head-body length (cm) of adult *Mustela nivalis*, mentioned in the literature.

Region	(Sub-)species*)	Author(s)	Males	Females
Siberia	*M. n. nivalis*	Abramov & Baryshnikov 2000	14.2 – 20.0	
E-Siberia	*M. n. pygmaea*	Chernyavskii 1984	14.8 – 16.5	13.1 – 14.0
Canada	*M. n. rixosa*	Banfield 1974	18.3 – 21.7	17.0 – 18.1
N-America	*M. rixosa*	Burt & Grossenheider 1976	15.0 – 16.5	14.0 – 15.2
Michigan	*M. rixosa*	Burt 1957 (tail incl.)	18.9 – 20.5	17.2 – 17.6
Michigan**	*M. nivalis*	Heidt 1970 (tail incl.)	17.8	16.3

* name used by the author(s)
** animals in captivity; data taken from graph.

The variation in size and weight of the other males may be partly the result of age differences. The low weight of the bacula of the males caught on 4 and 16 July (see appendix 1) indicates that they were sub-adult. The variation in size and weight in the remaining males may also be the result of age differences, probably induced by differences in food availability during their juvenile development, as the lemming population was already decreasing at the time of arrival of the expedition, on 9 June 2005. In juvenile weasels the fastest period of weight increase is in their first two months (Delattre 1987).

Potential population growth

In contrast to the West European weasel *Mustela nivalis vulgaris*, the least weasel from North America is able to become pregnant and have litters during most months of the year (Hall 1951, Heidt 1970). During lemming peaks on the tundra they also have litters under the snow (Fitzgerald 1981). Frank (1974, cited by King & Powell 2006) found that the period of pregnancy was the same in *Mustela nivalis nivalis* as in *Mustela nivalis vulgaris* (about five weeks), but that the former, the least weasels, were already able to get into oestrus again five weeks after the birth of their last litter, whereas in the common weasel this happened only after weaning at eight to nine weeks. Providing conditions are optimal, female least weasels can thus become pregnant while still suckling the young of their last litter, and may thus have a new litter every 2.5 months. This is quite different from the stoat (*Mustela erminea*) which shows a delayed response to changes in prey density as it can have only one litter a year (King & Powell 2006). This delayed response in reproduction, and thus in predation, is thought to be the driving force in maintaining the regular four-year lemming cycle, as observed in the collared lemming in Greenland (Gilg et al. 2003), where the stoat is the main mammalian weasel predator. The least weasel is able to respond more quickly through reproduction to an increase in food resources.

The litter size of the least weasel can be large. King and Powell (2006) show that the number of embryos born in the wild may vary from 3-19 (Fitzgerald 1981: Alaska 7-16; Heptner et al.:

Mongolia 5-19; Danilov & Tumanov: USSR 4-10). Sundell (2003) mentions a slight increase of litter size from south to north and found the largest litter (14) in her Finnish breeding stock was born to the individual with the northernmost origin.

Assuming an average litter size of twelve around Mys Vostochniy, an age of sexual maturity of three months, a period of five weeks between litters and no pre- and postpartum mortality, one pair of adult least weasels may have produced a population of 264 individuals between the beginning of September 2004 (after the departure of the expedition, during which no weasels were observed) and the end of June 2005. In the Pyasina delta the conditions for the growth of the lemming population were favourable in 2004: with a good season for vegetation growth and the first snowfall at the end of September, which probably remained through to the following season (Y. Kokorev, personal communication). As shown by Mullen (1968) these factors promote a rapid growth in the lemming population, which in turn is favourable for the growth of the weasel population.

Although the maximum theoretical population growth will not have been reached, the large number of weasels in the summer of 2005 may have consisted of the offspring of a very sparse and previously undetected population of weasels in 2004. Ims and Fuglei (2005) stated: “A weakness of our present knowledge of the role of small mustelids in arctic ecosystems is that no quantitative population data (e.g. population density and demographic rates) are available”. In this respect our 2005-2007 visits to Mys Vostochniy did not contribute in filling this gap.

In the absence of lemmings in the summer of 2006 the lack of observations of weasels was not surprising. However, the question remains whether there were no weasels at all, or whether some rare survivors remained unnoticed.

Influence on the ecosystem

The fact that in the former peak lemming years 1991 and 1994, when expeditions were at Mys Vostochniy, there were no weasels observed, suggests that weasel predation alone can not be a decisive factor in the cyclic fluctuations in lemming abundance, and supports the opinion of Lambin et al. (2006) that multiannual population cycles in rodents can not be explained exclusively by the interaction with specialist predators. Turchin et al. (2000) even argue that, in contradistinction to voles, population oscillations in lemmings are not caused by predation, but by the depletion of certain moss species, their main food resource in the critical winter period. Krebs (1964) describes a sharp decline in populations of the brown lemming (*Lemmus trimucronatus*) at Baker Lake (Northwest Territories, Canada) in 1960, in the virtual absence of predators.

This does not mean that weasel predation has no effect at all. During the snow cover period in the winter of 2004-05, when at least half of the larger lemming winter nests on the search plot were visited by weasels, their predation may have been the most important mortality factor for lemmings. It may have levelled off the top of the lemming’s abundance, shortened the length of the period of winter reproduction, and accelerated the spring decline. At high prey densities least weasels kill more animals than needed to meet their known energy demands, a phenomenon known as “surplus killing” (Sundell et al. 2000). Equally when important avian lemming predators, such as Taimyr gulls and pomarine skuas, explored the area around Mys Vostochniy in the spring of 2005 and decided to reproduce there, the lemming population density must still have been very high. From that moment on the lemming predation by the least weasel was probably merely a minor factor in the total lemming mortality due to predation, because of the large array and high density of other predators: Taimyr gulls, pomarine skuas, snowy owls, roughlegged buzzards (*Buteo lagopus*) and arctic foxes. Both Krebs (1964) and Clough (1968), in a study of a population crash of the Norwegian lemming (*Lemmus lemmus*), have suggested that heavy predation may prolong the length of the low phase. On the other hand, an experimental vole study by Norrdahl and Korpimäki (1995) points out that excluding avian predation did not affect the synchrony of population fluctuation with those in control areas, but only caused a lesser amplitude.

The functional effect of predation by weasels on the ecosystem around Mys Vostochniy remains unclear. The weasel's predation will have influenced the number of lemmings and, possibly, also that of eggs and chicks of breeding waders and other birds. The large number of lemmings known to have been killed by weasels (*n*=150) from the skull remains found in lemming winter nests on the search plot, may seem impressive, but we have no data of the population size of the lemmings or the total period of the weasels' predation. In fact, we lack much data that would be needed for a thorough understanding of the predation rate, such as the possible migration of lemmings in and out of the search plot, the number of weasels present and their range of activity under the snow. There may have been only one individual weasel active in and around the search plot that used the three fur lined nests in succession. In captivity a single weasel of about 80 grams has a daily food intake of about 28-32 g (East & Lockie 1964, Gillingham 1984, Moors 1977, Short 1961). The average weight of adult lemmings caught near Mys Vostochny in 2005 was about 85 g (I.Yu. Popov, unpublished data). MacLean at al. (1974), however, estimated that a 65-g least w easel living at an ambient temperature of -20 ºC would require about two 50-gram lemmings each day to satisfy its demand, but the snow cover and the insulation by the lemming nests will diminish the effect of the outside temperature. The 150 lemmings eaten on the search plot would represent about 127 weasel-days, provided all the lemmings had been adult, which was not the case. This reasoning suggests that between September 2004 and June 2005 there might well have been only one weasel on the search plot.

We can only speculate about the number of weasels present around Mys Vostochniy in the summer of 2005. We did not catch any males with a body weight less than 70 g and we caught only one female under 50 g. This may indicate a poor reproduction after June 2005, resulting in the apparent absence of the species in 2006. It is not clear whether there were really no weasels present; Sittler (1995) mentions the absence of direct observations of stoats in a study area in the Karupelv Valley (NE Greenland) in a year (1991) when 10 % of the 282 winter nests of the collared lemmings had been occupied by stoats.

In the summers of 2006 and 2007, when no weasels were observed in the area, the number of breeding small songbirds, such as Lapland longspurs (*Calcarius lapponicus*), snow buntings and horned larks (*Eremophila alpestris*), was much higher than in 2005. We can only speculate as to whether this increase in the number of breeding birds was related to the possible absence of weasels in those years.

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Samenvatting

De dwergwezel (*Mustela nivalis nivalis*) in noordwest Taimyr, Siberië, tijdens een lemmingcyclus (2005-2007)

In de zomers van de jaren 2005, 2006 en 2007 werd bij Mys Vostochny (Kaap West) in het noordwesten van het Siberische schiereiland Taimyr het voorkomen van de dwergwezel (*Mustela nivalis nivalis*) onderzocht. De belangrijkste prooisoort van de dwergwezel is hier de Siberische lemming (*Lemmus sibiricus*). De mate van aanwezigheid van lemmingen is bepalend voor het broedsucces van een aantal andere predatoren, zoals poolvos, sneeuwuil, ruigpootbuizerd, middelste jager en ook Taimyr zilvermeeuw. Wat betreft de lemming was 2005 een uitgesproken piekjaar, 2006 een even uitgesproken daljaar en 2007 een opbouwjaar. 2005 was het eerste jaar dat rond Mys Vostochny dwergwezels werden gezien, hoewel in de voorgaande 15 jaar negen expedities naar het gebied waren geweest, ook in de lemming piekjaren 1991 en 1994.

In 2005 werd een aantal morfologische gegevens van de dwergwezels verzameld aan de hand van zowel dieren die dood werden aangetroffen – veelal slachtoffers van poolvossen – als van dieren die met ter plaatse gemaakte wipvalletjes werden gevangen. Deze gegevens worden vergeleken met die uit de literatuur, waarbij de Amerikaanse ondersoort *Mustela nivalis rixosa* als identiek met de Eurazische dwergwezel wordt beschouwd.

De dwergwezel onderscheidt zich van de gewone wezel (*Mustela nivalis vulgaris*) doordat hij – net als de hermelijn - in de winter een witte vacht krijgt. Van de dieren die in 2005 tussen 17 juni en 16 augustus werden gezien of gevangen was op 4 juli een vrouwtje nog in winterkleed en twee mannetjes in de eerste helft van juli in overgangskleed. Deze mannetjes waren met lichaamsgewichten van 115 en 125 gram extreem zwaar, wellicht doordat ze opgroeiden bij een overvloed aan voedsel. Twee dood gevonden vrouwtjes waren drachtig van resp. 14 en 10 jongen, wat ook de gunstige voedselsituatie weergeeft.

Om een indruk te krijgen van de invloed van de wezels op de lemmingpopulatie werd in 2005 in een grazig dalletje met relatief veel winternesten van lemmingen een plot van ca. 1,5 ha uitgezet. Hierin werden 107 lemmingnesten met een diameter ≥14 cm gevonden, waarvan 52% tekenen van wezelpredatie vertoonden: ze bevatten haar en/of botten, meest schedels, van lemmingen. Bij kleinere nesten ontbraken predatiesporen. Uit de nesten werden 150 lemmingschedels verzameld, gemiddeld 2,7 per gepredeerd nest en 100 dieren per ha. Literatuurgegevens over de voedselbehoefte van wezels maken duidelijk dat al deze lemmingen gegeten zouden kunnen zijn door één enkele dwergwezel gedurende de hele winterperiode.

Gedurende de zomer van 2005 stortte de lemmingpopulatie in, mede als gevolg van de grote predatiedruk door middelste jagers die dat jaar alom aanwezig waren. In 2006 werden in het onderzoeksplot geen nieuwe lemmingnesten aangetroffen. Tijdens het verblijf van de expeditie werd slechts één levende lemming gezien, alhoewel uit onderzoek van lemmingnesten buiten het onderzoeksplot bleek dat er gedurende de winter 2005-06 nog wel lemmingen aanwezig waren en er ook nog predatie door dwergwezels had plaatsgevonden. Tijdens ons verblijf in 2006 werden echter geen dwergwezels gezien, gevangen of gespeurd.

In 2007 werden in het onderzoeksplot weer nieuwe winternesten van lemmingen aangetroffen: 28 met een diameter ≥14 cm en tien kleinere. In geen van deze nesten werden tekenen van predatie door wezels gevonden. Ook buiten het plot werden geen wezels of sporen van wezels waargenomen. Dit wil echter niet zeggen dat er beslist geen wezels aanwezig waren: onderzoek in Groenland heeft aangetoond dat in een lemmingdaljaar de aanwezigheid van hermelijnen daar alleen bleek uit vondsten van latrines, terwijl er geen dieren werden gezien of gevangen. Het speuren naar latrines van dwergwezels vraagt een getrainde blik en het is mogelijk dat daar tijdens voorgaande expedities onvoldoende aandacht aan is besteed.

Dwergwezels hebben een groot voortplantingsvermogen en ze kunnen daardoor snel op veranderingen in het voedselaanbod reageren. Dat ze daardoor ook verantwoordelijk zijn voor de vaak cyclische fluctuaties in de lemmingpopulaties is niet waarschijnlijk. In de lemmingpiekjaren 1991 en 1994 werden, in tegenstelling tot het piekjaar 2005, geen dwergwezels waargenomen. In de winter van 2004-05 was er beduidende predatie op de lemmingen door dwergwezels, maar in het begin van de zomer werd hun predatie overvleugeld door de predatie door middelste jagers. De mate van aanwezigheid van dwergwezels lijkt eerder volgend ten opzichte van de omvang van de lemmingpopulatie dan dat die de veroorzaker is van de fluctuaties in de aantallen lemmingen.

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Appendix 1. Measurements of male least weasel *(Mustela nivalis nivalis)*, collected between 19 June and 15 August 2005 near Mys Vostochniy.

Collection date	Location	Fur on back	Body weight (g)	Head-body (mm)	Tail (mm)	Tail/head-body (%)	Ear (mm)	Hind foot (mm)	CBL*	Baculum weight (g)	Remarks
June 19	tundra	brown							38.0		partly eaten
July 4	trap	brown	67	165	11.8	7.2	13.6	24.0	32.7	0.013	
July 5	trap	brown	104	188	20.2	10.7	12.4	25.6	35.7		
July 7	trap	brown	94	183	15.4	8.4	14.0	24.8	34.6	0.027	
July 8	fox den	moulting	115	200	15.0	7.5	15.0	26.0	39.0	0.029	
July 15	camp	brown	84	186	15.5	8.3	14.1	25.0		0.018	drowned in bucket
July 15	trap	moulting	124	200	16.6	8.3	15	26.8		0.035	
July 15	trap	brown	84	186	14.5	7.8	14.1	23.6		0.028	
July 16	trap	brown	63	165	17.8	10.8	12.9	22.5		0.011	
July 29	live trap	brown	80								released
July 31	live trap	brown	72								released
Aug. 1	live trap	brown	70								released
Aug. 2	live trap	brown	80								released
Aug. 4	live trap	brown	70								released
Aug. 6	trap	brown		176	19.7	11.2	13.9	25.5	35.9	0.022	partly eaten
Aug. 10	live trap	brown	73					22			released
Aug. 10	live trap	brown	83	189	20	10.6	13	27		0.032	died after recapture
Aug. 12	live trap	brown	63					22			released
Aug. 13	live trap	brown	72								released
Aug. 14	live trap	brown	67	171	22	12.9	12.8	*24.4*		0.020	died in trap
mean			81	183	17.1	9.4	13.7	24.6	36.0	0.025	

* *condylobasal length (mm)*

Appendix 2. Measurements of female *Mustela nivalis nivalis*, collected between 19 June and 15 August 2005 near Mys Vostochniy.

Collection date	Location	Fur on back	Body weight (g)	Head-body (mm)	Tail (mm)	Tail/head-body (%)	Ear (mm)	Hind foot (mm)	CBL*	Embryos *(n)*	Remarks
June 20	fox den	brown	75							14	
July 7	trap	brown	66	165	15.0	9.1	12.5	20.4	30.6	10	
July 17	live trap	brown									lactating
July 29	live trap	brown	36								juvenile
Aug. 7	live trap	brown	57								
Aug. 10	live trap	brown	55					19			
Aug. 14	live trap	brown	60								
mean			58								

* *condylobasal length (mm)*

Hunting strategy and tympanate moth predation by the pond bat (*Myotis dasycneme*)

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Abstract: Visual observations of moth predation by pond bats *(Myotis dasycneme)* are described and related to typical secondary echolocation and flight behaviour patterns. When hunting over canals and rivers, the common search phase of pond bats combines low-level flight over the water surface with an quasi uninterrupted series of frequency modulated echolocation calls. During the season that moths become available the bats gradually switch to a faster and linear search flight, regularly interrupted by sudden rises and attacks upon moths. Observations of power dives of moths upon bat approaches reveal that these attacks are often aimed at tympanate moths. The bats counter the moths' escape reactions by additional aerial attacks or by an immediate switch from aerial hawking to trawling in response to the power-diving prey dropping to the water surface. During these search flights, bats switch between two distinct echolocation signals, the first predominantly frequency modulated, the second having a more pronounced QCF ending, with both differing from the basic trawling echolocation signal. In this fast aerial hawking search phase, pond bats typically switch between sequences of high intensity pulses and sequences of silences or possible stealth/whispering mode, creating a discontinuous call pattern. These sound sequences always include narrowband signals of a high intensity and long duration, increasing the detection distance to larger prey items. We assume that this discontinuous echolocation pattern facilitates the bats in successfully approaching tympanate moths by delaying or counteracting the moths ability to identify bats from a distance.

Keywords: pond bat, *Myotis dasycneme,* Chiroptera, tympanate moths, power dive, waterways, echolocation.

Introduction

The Palaearctic insectivorous pond bat *(Myotis dasycneme)* occurs mainly in lowland areas in cool and humid climates, often in open landscapes with abundant large, calm water surfaces (Kapteyn 1995, Mostert 1997, Horáček 1999, Limpens et al. 1999). This bat takes prey from the water surface with its large feet or tail membrane in pointed dips, a strategy also found in other trawling *Myotis* (Jones & Rayner 1988, 1991, Britton et al. 1997). Pond bats also feed by aerial hawking and use a variety of echolocation signals from brief broadband FM to long narrowband FM-QCF-FM (Ahlén 1990, Kapteyn 1993, Limpens & Roschen 1995, Britton et al. 1997, Ahlén & Baagøe 1999). Several authors have reported sudden rises and quick pursuits of insects by this species.

Although the pond bat is basically a trawling bat, some morphological aspects, such as its wing shape and tragus length, as well as aspects of its echolocation (the narrowband signal components) reveal striking similarities with open space aerial hawking bats (Norberg & Rayner 1987, Schober & Grimmberger 1998).

Food analyses in the Netherlands and Germany revealed small Diptera as the bulk of prey (76 and 70% of volume respectively). Lepidoptera (11 and 3% respectively), Trichoptera (1.5 and 27% respectively) and Coleoptera (11% in the Netherlands only) have been found in lower quantities (Britton et al. 1997, Sommer & Sommer 1997).

Many larger species of Lepidoptera: Noctuidae, Arctiidae, Notodontidae, Geometridae and

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Pyralidae possess tympanal organs which are sensitive to ultrasounds in the range of 20-60 kHz and enable them to detect the echolocation signals of most aerial hawking bats (Roeder 1966, Rydell & Young 2002).

Tympanate moths move away from the sound source when they detect echolocation calls of a low intensity at a low repetition rate (far-bat reactions) and react to calls of a high intensity and high repetition rate by unpredictable escape manoeuvres such as spirals, loops or power dives (near-bat reactions; Roeder 1967, Waters & Jones 1996). In spite of these defences, several gleaning and aerial hawking bat species feed heavily on eared moths. Aerial hawking species specialised in moth hunting emit echolocation calls with peak frequencies that are below or above the optimum hearing range of tympanate moths (allotonic frequency hypothesis; Fullard 1987). In general few moths are found in the diet of aerial hawking bats that use peak frequencies that are within the moths' optimum hearing range (Bogdanowicz et al. 1999).

This manuscript describes a special moth hunting technique ("fast aerial hawking low over water" - FH) used by the pond bat and compares this strategy to the typical midge ("trawling" T) hunting technique. This fast aerial hawking behaviour was found to be associated with feeding on tympanate moths 0.5-3 m over water. We discuss the hypothesis that the significant gaps in the echolocation pattern facilitate the bats' hunting of tympanate moths.

Materials and methods

Bat observations

Bat observations and recordings were carried out between 1998 and 2005 in Flanders (Belgium) at town moats, ponds, canals and lowland rivers. A monocular image intensifier ITT Night Mariner 150, supported by a powerful infrared light (Vision Nachtzicht Techniek), was used for combined visual-acoustic field observations. The infrared light contains 49 GaAs light emitting diodes with a wavelength of 880 nm, a radiation angle of 20 degrees and a range of 30-50 m. With these tools, water surfaces remain dark, but bats and large insects are seen as bright objects. Infrared illumination does not influence bat and moth activities (Arlettaz et al. 2001, Fullard & Napoleone 2001). Visual observations covered a total of 91 nights (field survey duration 0.5-1.5 h per night), about 450 observed bat passes and about 40 visual observations of sudden climb attacks.

Insect trapping

A mercury vapour light trap (Skinner trap, Alana Ecology Ltd.) with a HQL 125W (MBF-U) ultraviolet light was used for insect sampling along the banks. Insects were identified to family level, or species level where possible, using Chinery (1986). Insect trapping was done over 12 nights between March and October of 2005. The sessions lasted 1.5–2 h per night, starting one hour after sunset. The method is semi-quantitative and cannot replace a full range of insect trapping, which would have to include land-based as well as water-based trap methods. However, Brack & La Val (2006) showed that, based on a large scale faecal analysis and land-based light trapping comparison, diet and insect availability correspond largely in at least *Myotis grisescens*, a Nearctic bat feeding over water.

Ultrasound recordings

We identified pond bats directly in the field, based on heterodyne sounds. Identification was made only when at least some of the species' characteristic sounds were perceived (QCF at 32-35 kHz). Bats only using FM signals during the entire bat pass were not identified because of possible confusion with sympatric Daubenton's bat (*Myotis daubentonii*) (Ahlén 1990, Limpens & Roschen 1995).

A Pettersson D240 ultrasound detector was used for heterodyne and time expansion recordings in the field. All recordings were made at fixed observation points as close to the waterway as possible (<3 m). Recordings were stored on a Sony minidisc MZ-R35 stereo recorder at a sampling

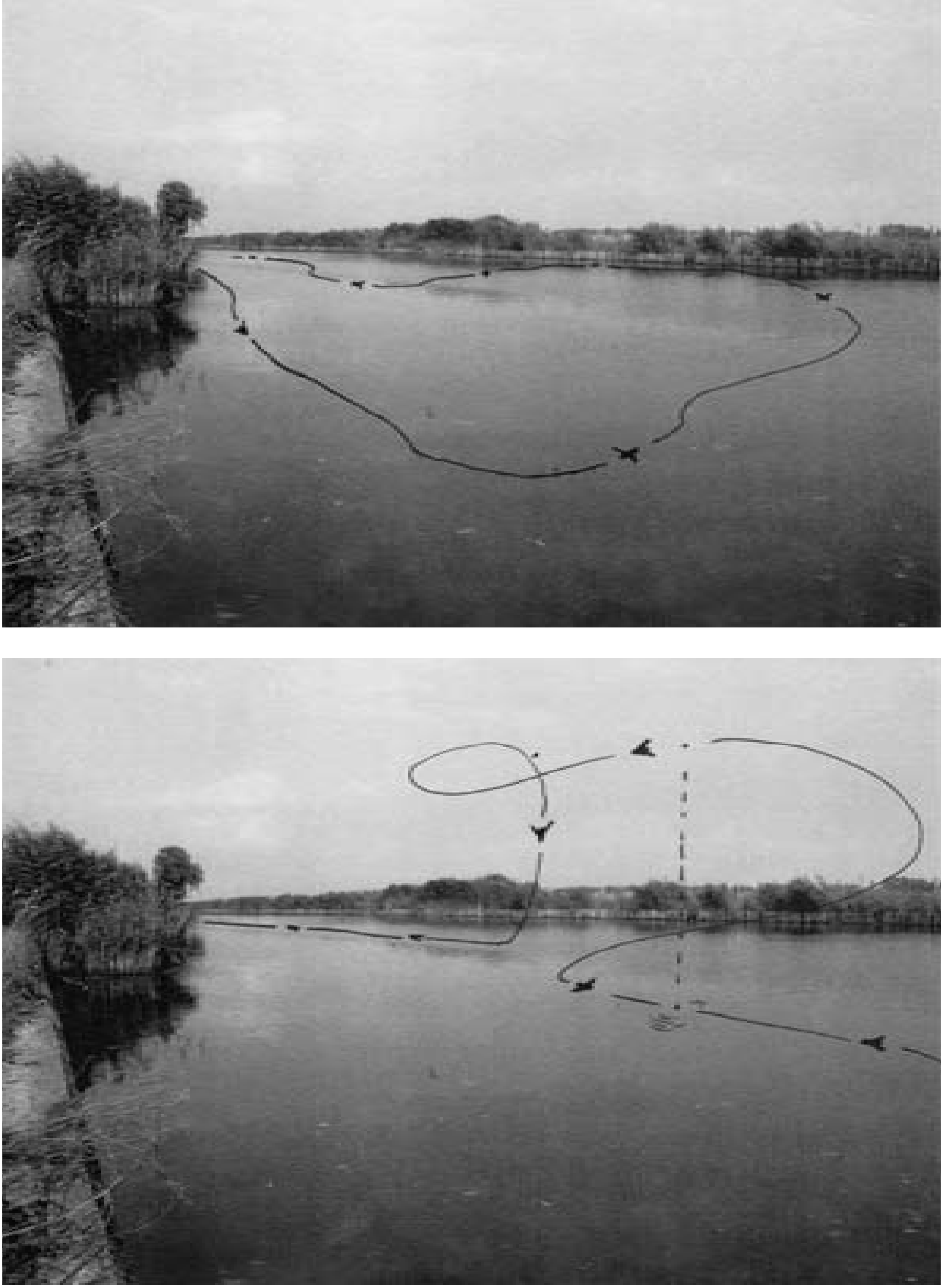

Figure 1. a (above): T-style: permanent low flight, ever changing directionality with distance, sometimes close to the banks. b (below): FH-style: rapid linear search flight over the midline of a canal, sudden climb, attack on a moth, moth escape (power dive) and final capture of a floating moth. *Photographs: Marc Van de Sijpe.*

rate of 44 kHz and transferred to the BatSound programme (Pettersson Elektronik AB).

In total, 60 call sequences were analysed in heterodyne, corresponding to 2656 pulses within a time frame of three years. Calls were recorded at four different geographically separate regions (minimum 50 km apart). Based on the numbers of commuting bats at least 1-30 individuals were present in each region. Calls were recorded at random within the regions. Ninety-four call sequences were analysed in time expansion, corresponding to 1084 pulses.

The time expansion mode was used to determine pulse length (PL), pulse interval (PI), QCF-frequency and peak frequency. The pulse interval PI is defined as the time between two consecutive pulses. We excluded intervals of <50 and >150 ms from our analysis. We assumed a PI of >150 ms to be indicative of an omission of one or more pulses, and a PI of <50 to correspond to an approach phase, possibly preceding a buzz and a catch.

Omitting pulses leads to considerable gaps between the series of pulses, which can be either silences or sequences of whispering calls which are not detected at distances of about 10 m. Both silence or stealth mode serve the same purpose of making the bat inconspicuous to tympanate prey. Gap length (GL) is defined as a period corresponding to more than five consecutively omitted/undetected pulses. The time interval of sound sequences between two consecutive gaps is called sequence length (SL). Silence/stealth mode gaps are not the result of temporally gliding sequences of the bats. Visual observations confirm that passing bats were beating their wings while being silent. The duration of approach phases and feeding buzzes was measured using heterodyne recordings because the time expansion recording capacity of the D240 detector was too short. The onset of the approach phase was defined as the signal with a PI at least 30% shorter than the typical search phase PI. The end of the buzz sequence was the first pulse following the post buzz silence (Kalko & Schnitzler 1998). Catch sequences are defined as the time interval between the start of the first approach phase and the final capture or abandonment of the insect. These sequences can include several buzzes and approach phases.

Results

Flight behaviour over large waterways

Acoustic and visual observations over large linear waterways (width 20-50 m) revealed two hunting strategies, referred to below as “Trawling” (T; figure 1a) and “Fast aerial Hawking at low heights over water” (FH; figure 1b). The two styles were separated by differences in echolocation: T = continuous pattern and absence of signals of long duration (>15 ms) and FH = discon-

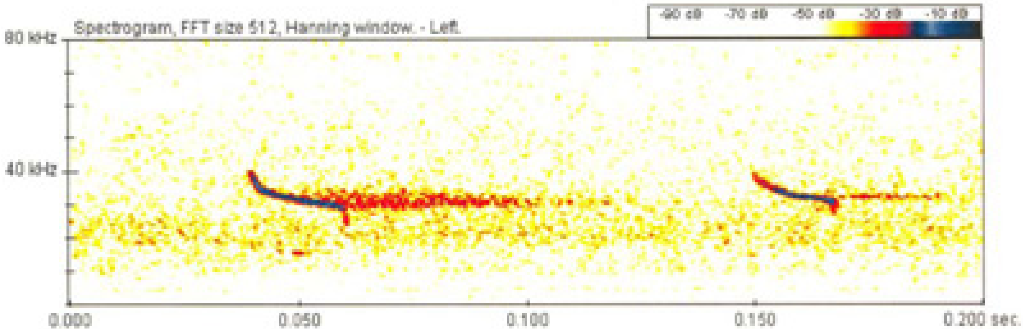

Figure 2. BatSound spectrogram of a time expansion recording: first two narrowband signals of a sound sequence (emitted after a silence/stealth mode gap) from a pond bat hunting in FH-style. Pulse lengths of 21 and 18 ms respectively.

tinuous pattern with calls of both short and long duration (figure 2).

In the T-style the bats fly in both straight and circular paths at a low height over water, sometimes even close to the banks (1-2 m). Visual observations revealed that the bats foraged on emerging midges.

The FH-flight was straight, often over the midline of the waterway, parallel to the banks and low over the water surface (height <0.5 m). In this way the bats patrol the waterways, covering stretches of 100-200 m, for periods up to one hour. During FH-search flights, the bats maintained a distance of at least 10 m from the nearest clutter producing bank. FH-style pond bat hunting was not observed over small canals (the minimum canal width for this activity was approximately 20 m). In FH-style, the bats regularly and suddenly change their flight track in order to climb and chase large insects (figure 2b). The flight speed during the search phase was variable (estimate: max 30 km/h), but considerably faster than in the Trawling T-style. This visually observed speed difference between T and FH was confirmed by the lower pulse repetition rate of the FH style, as aerodynamic models predict that flight speed is inversely proportional to wing beat frequency, hence also to pulse repetition rate (see below). In early spring the T-style was the only flight style observed, with the FH-style gradually replaced the T-style hunting as the season proceeded (figure 3).

Visual observations of bat – moth interactions

Visual observations revealed both successful and unsuccessful attacks on moths, together with moth power dives and other evasive reactions (erratic flight, escaping to the banks and gaining height). Moth hunting was only observed when the bats hunted in the FH-style. Insects were identified as moths (Lepidoptera), as opposed to lacewings (Neuroptera), caddis flies (Trichoptera) or beetles (Coleoptera) on the basis of their appearance, flight style and escape reactions,.

Light trap results

Several thousand Chironomids were caught, along with 153 larger insects. Insect sampling revealed that small Diptera (Nematocera, mainly Chironomidae) were, by two orders of magni-

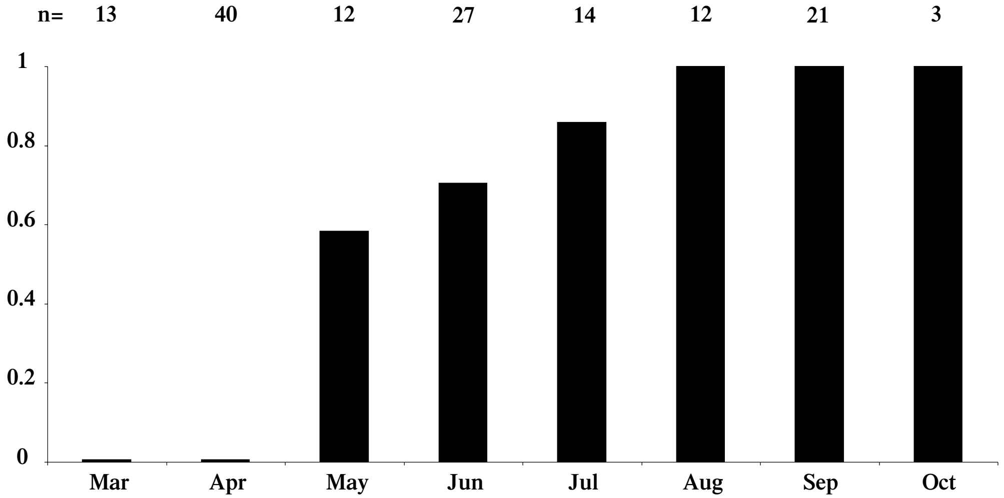

Figure 3. Proportion of hunting nights with positive visual and/or acoustical identification for FH type hunting (qualitative approach, pooled data 1998-2005). FH: Fast aerial hawking at low heights over water; *n*: number of hunting nights with positively identified hunting activity of pond bats; total surveys: 142 (0.5-1.5 h).

Table 1. Semi-quantitative results of light trapped insects, trapped on pond bat hunting sites during 2005, identified on family or order level; number of insects per 1.5–2h sessions. Total Lepidoptera: sum of the three major and other families identified. Chironomidae: >500, may include up to several thousand midges.

		31 Mar	3 Apr	5 Apr	7 Apr	12 Apr	2 Aug	4 Aug	6 Aug	7 Aug	25 Sep	26 Sep	3 Oct
Diptera	Chironomidae	23	23	20	4	>100	>500	>500	>500	>500	>100	>100	>100
Coleoptera			1				1	1		1	1		1
Trichoptera								2					
Lepidoptera	Noctuidae	4		1	1		12	5	18	11	4	4	6
	Arctiidae						1	2	2				
	Geometridae						2	1	1	2		4	
	Total Lepidoptera	4	0	1	1	0	15	10	23	17	4	8	6

tude, the most abundant insect group (table 1). There was a clear distinction between the densities of insects caught between mid April and early August (4 to 23 per catch versus >100 to >500). Larger insects such as Trichoptera, Coleoptera and Lepidoptera were found in lower numbers, with higher densities from the beginning of August (0 to 4 per catch versus 0 to 23). No samples were taken in the period May-July.

Heterodyne results

A heterodyne analysis was used to identify differences between T and FH flight patterns. For both T and FH flights, 30 bat passes of between 3.4 and 11.9 s were analysed. The pond bat's T-style hunting is characterized by an absence of larger gaps (>5 omitted pulses), with at most three consecutively omitted pulses (figure 4a). FH sonar is highly discontinuous with long silences between sound sequences (figure 4b). The majority of FH bat passes are characterized by short pulse sequences consisting of a small number of emitted pulses per sequence. Per bat pass there were 1-3 gaps and 1-3 pulse sequences. Gaps for FH-style hunting were long, up to 3570 ms, corresponding to 34 missing/undetected pulses. It is possible that the gaps in the echolocation pattern

Table 2. Heterodyne analysis of T- and FH-styles pond bat passes. PI average pulse interval (excluded intervals <50 and >150 ms), GL: gap length (FH-style only), SL: sound sequence length (FH style only), emitted N (SL): number of pulses in the sound sequences (FH-style only), % omitted: percentage of omitted/undetected pulses (total per bat pass).

	T Mean ± sd Median (Min-Max)	FH Mean ± sd Median (Min-Max)	Statistical testing T versus FH Mann-Whitney U
Total number of bat passes (n)	30	30	
Total number of pulses	2055	601	
Bat pass duration (s)	7.7 ± 1.6	6.2 ± 1.7	
PI (ms)	102 ± 4 103 (93-107)	117 ± 5 118 (104-124)	*** $P< 0.001$
GL (ms)	-	1963 ± 758 (*n*=43)	
SL (ms)	- -	1537 ± 861 (*n*=65) 1370 (470-5090)	
emitted N (SL)	-	8 ± 4 (*n*=65) 7 (3-27)	
% omitted	11 ± 9 (*n*=30) 8 (0-29)	61 ± 9 (*n*=30) 63 (38-74)	*** $P< 0.001$

are not real silences but a series of low-intensity/whispering calls that remained completely undetected at distances of 10 m due to atmospheric attenuation and spherical spreading. On a few occasions, single steep FM signals of very weak intensity were recorded in the FH gaps. T and FH call series tested as highly significant different (Mann-Whitney $P<0.01$) for pulse interval lengths and number and percentage of omitted/undetected pulses (table 2).

Time expansion results

Time expansion was used to describe the T and FH echolocation call parameters: 783 (T) and 301 (FH) echolocation calls were analysed (table 3). The analysis of FH bat passes always started with the first call emitted after a silence and in this type of analysis, only search phase calls were used with approach phase calls and catch buzz sequences being omitted.

FH calls were separated in two distinct groups based on pulse length, with FH1 calls having a pulse length of ≤12 ms and FH2 signals one of >12 ms (figure 5). FH1 calls were aimed at midges over water and FH2 calls at larger insects.

The most noticeable observation is that in general the T and FH1 call patterns, expressed as pulse length and slope of the call, are very similar (figure 6). Both are short calls with a steep slope, although the call duration and therefore the duration of the QCF-part in T-style calls may vary considerably (T median PL 8 ms).

FH2 style calls are significantly longer (median 18 ms) with a pronounced QCF-part. T and FH2 calls have similar ending frequencies (median 27.0 and 26.6 kHz) and these are significantly different from the median FH1 ending frequency (30.6 kHz, $P<0.001$). FH2 QCF-frequencies and peak frequencies are closer to T-style than to FH1 style calls (table 3). The difference in PI between T and FH-styles found in the heterodyne analyses is confirmed in time expansion (table 3). Assuming a 1/1 link between wing beat and pulse emission, the median T-style PI of 103 ms

Table 3. Time expansion analysis of search signals for bat passes in T- and FH-styles: T, FH1 and FH2. Parameters are all highly significantly different (Mann-Whitney $P \leq 0.001$), except for pairs of data marked # which do not score significantly different even at a $P<0.05$ level.

	T	FH	
Total number of bat passes	55	39	
Total number of pulses	783	301	
		FH1	FH2
	Mean ± sd Median (Min-Max)	Mean ± sd Median (Min-Max)	Mean ± sd Median (Min-Max)
Total number of pulses		96	205
Starting frequency (kHz)	54.5 ± 7.1	48.8 ± 4.0	44.1 ± 3.1
	55.4 (37.2-77.7)	48.8 (39.6-63.4)	43.6 (35.1-59.4
Ending frequency (kHz)	26.9 ± 2.3	30.9 ± 2.5	26.7 ± 1.5
	27.0 (19.3-34.4) #	30.6 (25.2-36.5)	26.6 (21.6-32.5) #
Bandwidth (kHz)	27.6 ± 7.8	17.9 ± 5.1	17.3 ± 3.3
	28.0 (9.8-59.0)	17.9 (7.9-31.5) #	17.2 (9.3-31.9) #
QCF-frequency (kHz)	33.4 ± 0.8	35.0 ± 1.1	32.8 ± 0.9
	33.4 (31.2-35.9)	35.1 (32.7-37.6)	32.7 (29.9-35.5)
Peak frequency (kHz)	35.9 ± 1.9	37.9 ± 2.1	33.6 ± 1.6
	35.4 (28.8-43.3)	37.6 (33.8-43.3)	33.3 (28.3-41.0)
PI (ms)	101 ± 16	121 ± 8	117 ± 13
	103 (53-149)	121 (105-140) #	117 (74-144) #
PL (ms)	7.7 ± 2.4	6.8 ± 2.7	17.6 ± 2.3
	8.0 (2.0-17.0) #	7.0 (1.0-12.0) #	18.0 (13.0-23.0)

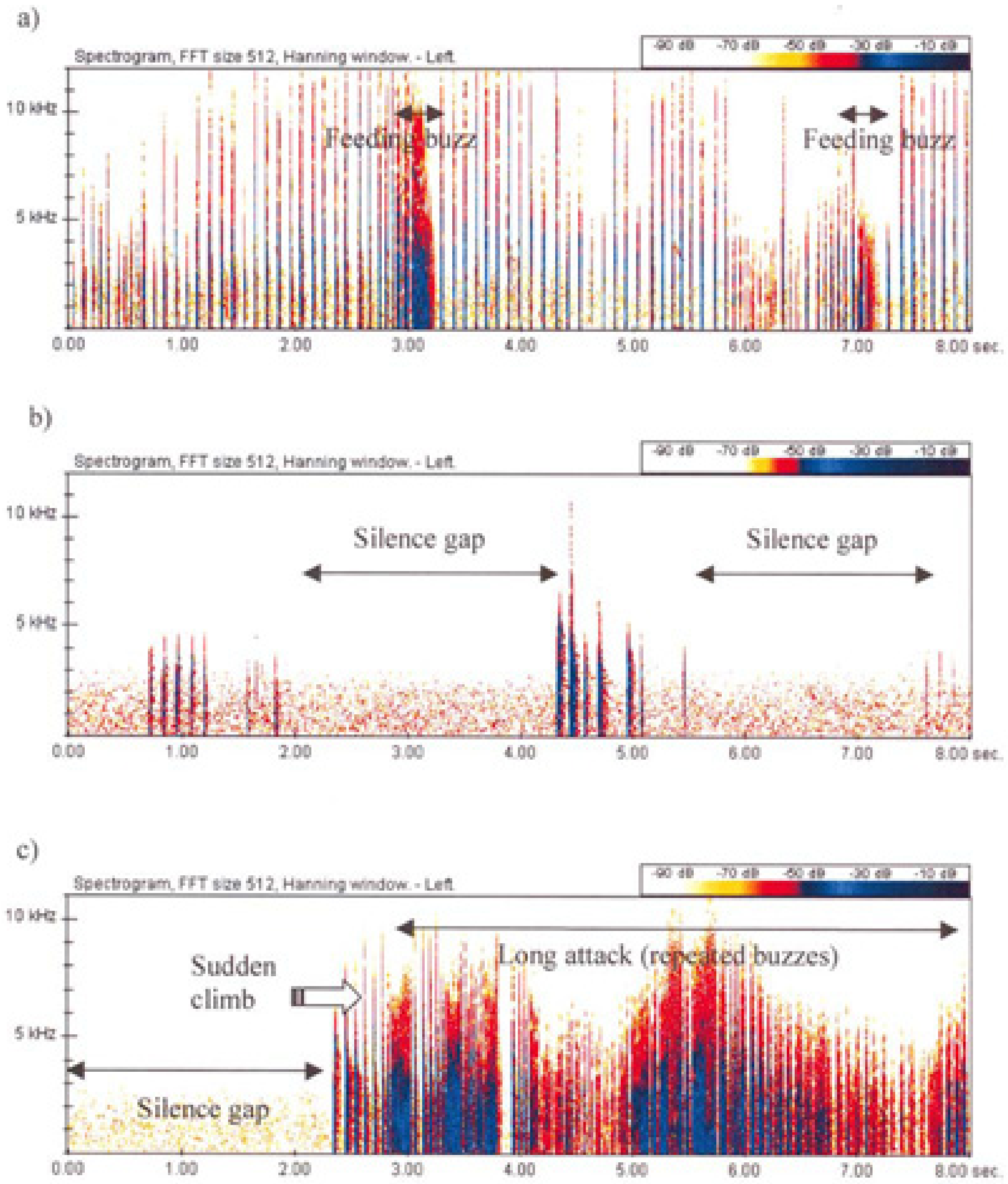

Figure 4. BatSound spectrograms of heterodyne recordings:
a) T-style search phase; echolocation is almost continuous (no gaps). Now and then short feeding buzzes occur (attacks on Chironomids on the water surface).
b) FH-style search phase; echolocation is highly discontinuous: 3 groups of pulses separated by long silence/ stealth mode gaps.
c) FH-style, from left to right: part of silence/stealth mode gap (0–2.3 s), start of sound emission at 2.3 s, start of approach phase at 2.7 s, coinciding with a sudden attack on a moth (2.7–8 s) involving several approach phases and feeding buzzes.

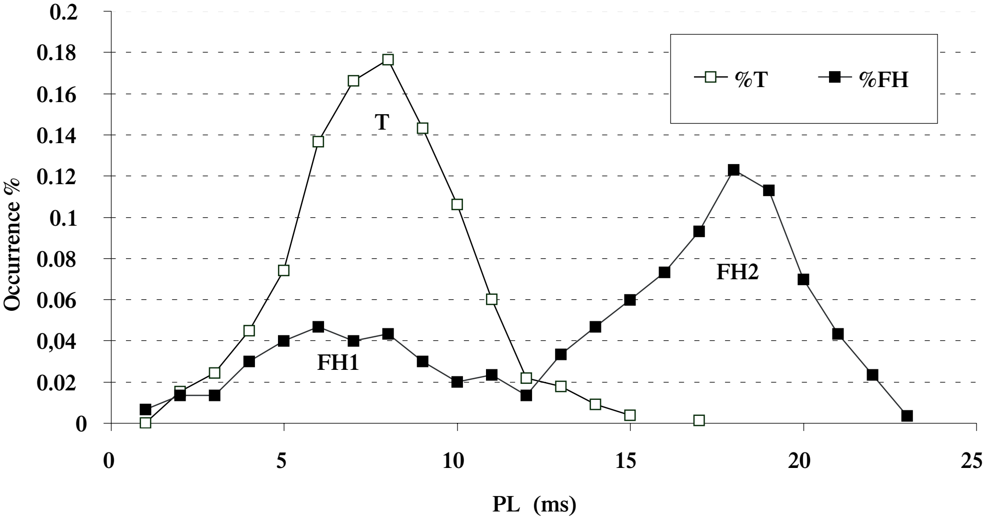

Figure 5. Distribution of pulse length (ms) of T-style (*n*=783) and FH-style (*n*=301) search phases of the pond bat for typical T, FH1 and FH2 calls.

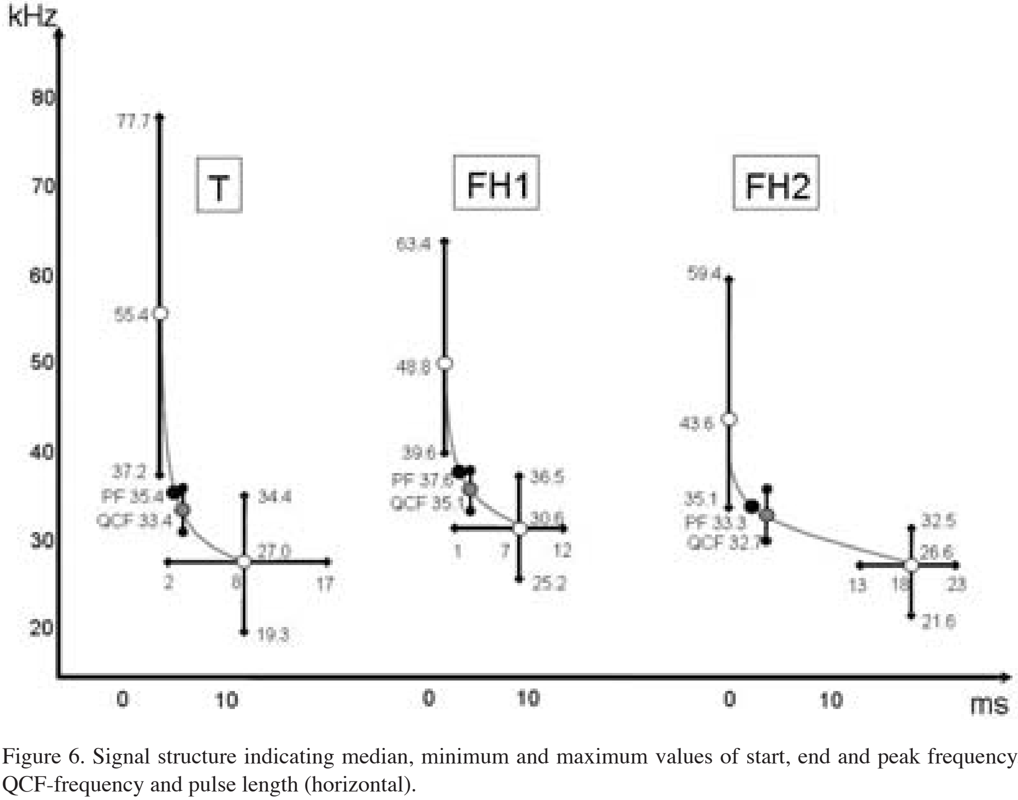

Figure 6. Signal structure indicating median, minimum and maximum values of start, end and peak frequency, QCF-frequency and pulse length (horizontal).

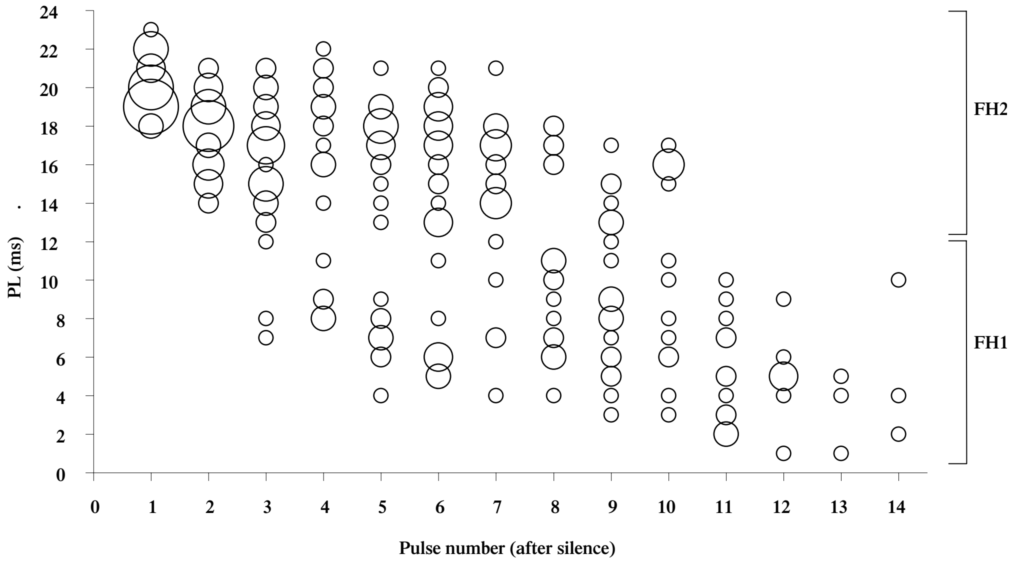

Figure 7. Change of pulse length (ms) versus pulse number in FH call series (pulse nr 1 corresponds to the first pulse emitted after a gap, pulse nr 2 with the second pulse, etc.).

corresponds with a flight speed of approx. 2.8 m/s, and the median FH1-style PI of 117 ms with a flight speed of 7.5 m/s for a pond bat of 17 g, according to the formula given by Bullen & McKenzie (2002).

FH-style hunting call pattern change

Figure 7 shows the pulse lengths for sequences of pulses in FH-style hunting, starting each time after a silence/stealth mode gap. The first two pulses of the sequences are always FH2 (>12 ms) and are gradually replaced by a mixture of FH1 (<12 ms) and FH2 type calls (9-68% FH1, 32-91% FH2). The mixing of FH1 and FH2 calls is random and this was obvious from the field recordings. Also it should be highlighted that, the FH2 calls are clearly stronger in amplitude than the following call FH1-style. Towards the end of the sequence (above a wing beat of 11), calls are exclusively FH1 style, which is considered to be a typical trawling call. After some time, this ends in a new, long gap.

Approach phase and feeding buzz durations

Table 4 compares the duration of the catch sequences for the pond bat's different hunting styles

Table 4. Approach phase + feeding buzz durations from heterodyne recordings of pond bats in T and FH styles and of Daubenton's bats (2000) and common serotines (1998) as a reference (own data), n: number of sequences analysed.

Species	Hunting style	Type of attack	n	Duration appr + buzz phase (ms)	
				Mean ± sd	Median (Min-Max)
M. daubentonii	T	trawling, slow flight	7	451 ± 67	440 (380-590)
M. dasycneme	T	trawling, slow flight	10	615 ± 162	605 (390-920)
M. dasycneme	FH1	sudden rise & pursuit in the air, fast flight	10	3402 ± 2335	3070 (1010-9410)
M. dasycneme	FH2	low catch over water / trawling, fast flight	5	538 ± 254	440 (340-1040)
E. serotinus	Aerial hawking	pursuit around street light	7	1646 ± 774	1250 (840-2980)

(T and FH), and compares this to similar sequences for Daubenton's bat and the common serotine (*Eptesicus serotinus*) (own data analysis).

In the FH-hunting strategy both long and short catch sequences occur. The long catch sequences (mean 3402 ± 2335 ms), are associated with FH2 search pulses and aerial hawking. Sudden climbs often include a lot of manoeuvring in order to catch a moth or another larger prey (figures 2b and 4c). Catch sequences as long as 25 s are reported in *Lasiurus borealis*, a Nearctic aerial hawking and moth hunter (Reddy & Fenton 2003). The pond bat's long catch sequences are comparable with those of the common serotine when chasing moths around street lights (average time 1646 ± 774 ms). Short buzzes associated with FH1 (538 ± 254 ms) and T-style (615 ± 162 ms) hunting are significantly shorter in duration and compare to the sequences of trawling Daubenton's bat (451 ± 67 ms). Even though the duration of an approach and catch of an FH1-style compares to the duration of a T-style trawling, it is associated with a faster search flight.

Discussion

Signal design

Short broadband FM signals (T and FH1) are typical for trawling behaviour (Jones & Rayner 1988, 1991, Britton et al. 1997). A short broadband FM signal, which quickly sweeps through many frequencies, improves spatial orientation (Schnitzler & Kalko 2001, Schnitzler et al. 2003) and assures an adequate separation of overlapping echoes (Boonman & Ostwald 2007) ensuring the detection of prey close to clutter producing objects. The short duration of calls limits the forward masking zone, allowing a search for small prey items.

Although the QCF part in the long T-style calls is uncommon in trawling bats (Siemers et al. 2001), these calls are also related to trawling behaviour involving the detection and capture of chironomid midges near to and on the water surface. In the FH-style hunting, the majority of search signals (FH2) have a much longer QCF part, resulting in pulse lengths up to 23 ms. QCF-calls are also documented in trawling *Rynchonycteris naso*, a Neotropical Emballonurid bat species (Jung et al. 2007), and in the Nearctic *Myotis volans*, known to forage over trees, cliffs and water (Fenton & Bell 1981). Both Neotropical trawling Noctilio species also emit mixed QCF-FM calls (Schnitzler et al. 1994, Kalko et al. 1998). These species are documented as hunting on larger prey.

QCF-components increase the detection distance because the bat's neuronal filter tuned to the QCF frequency is activated for a longer period, thereby enabling the detection of weak echoes (Schnitzler & Kalko 2001). In addition, long duration calls increase the detection distance by improving the chances of receiving acoustic glints of fluttering insects at moments when the insect's wings are perpendicular to the sound beam (Schnitzler & Kalko 1998). If acoustic glints play a role in target detection, it is likely to happen right at the beginning of the sound emissions after the silence/stealth mode gaps, at moments when the bats emit their longest pulses. Lepidoptera have typical wing beat frequencies of 5-85 Hz and small Diptera one of 100-1000 Hz (Knospe 1998). Average FH2 calls at the start of call series (PL 20 ms / PI 108 ms) yield a glint rate of one glint/pulse for an insect fluttering at 50 Hz.

FH2 calls: long range echolocation at low height

When flying close to clutter generating objects such as trees or the ground, bats need to shorten their calls to keep an overlap-free window open for prey detection (Jensen & Miller 1999). Aerial hawking bats use long QCF calls when hunting high over the ground in the open. When occasionally foraging at lower heights these bats shorten their calls and reduce or omit the QCF-part. Unlike structured land surfaces, smooth water surfaces do not generate clutter echoes for bats flying close to the surface. Ensonifying the surface from a sharp angle causes the sound beam to reflect away from the bat (Boonman et al. 1998, Rydell et al. 1999, Siemers et al. 2001). In this particular situation the canal banks are the only sources of clutter echoes. If the bat maintains enough distance from the banks, it will experience an acoustically open environment in which the emission of narrowband signals of long duration becomes possible. Reflection from the water surface results in an interference pattern in the recordings, which can be seen as a sinusoidal amplitude modulation in each call. In the FH style, which seems to be a special case of open space aerial hawking, the pond bat combines the advantages of low flight height, increased flight speed and long range echolocation in order to optimise the detection, pursuit and capture of large, fast flying prey in the lower air. Interestingly, Kalko et al. (1998) observed moth hunting over water by the predominantly insectivorous *Noctilio albiventris*, including power dives of moths and counter attacks involving trawling manoeuvres by the bat.

Verboom et al. (1999) found that commuting pond bats emitted calls with a longer pulse length and pulse interval when flying over the midline of larger canals, suggesting that the canal banks play a role as acoustic landmarks when navigating through a landscape. FH2 type calls therefore may also play a role in spatial orientation, in detecting distant banks when flying over large open water surfaces. However these authors also describe long QCF in bats flying more than 100 m from the shore, suggesting these calls serve for more than spatial orientation. Britton et al. (1997) associated the emission of long QCF calls with hunting behaviour over a large lake. We assume therefore that our observations of FH behaviour are associated with hunting behaviour. Sudden rises are always associated with groups of FH2 calls. We never observed rises during the silence/stealth mode. Open space aerial hawkers, e.g. *Nyctalus* and *Vespertilio*, are also known to use long QCF calls while hunting on large prey at high altitude.

Maximum detection distances

Although detection distances are longer for prey low over water, than for the same prey in open air (Siemers et al. 2005), long duration FH2-type signals are probably not well suited for the detection of individual small prey items (e.g. midges) because, for an aerial hawking bat, the maximum detection distance (2 m at 35 kHz for Culicidae) is typically shorter than the actual forward masking zone (3 m for 18 ms signals) (Waters et al. 1995). Such small targets can better be detected with the shorter T- and FH1-style pulses because the forward masking zone is smaller (1.4 m for 8 ms signals). The longer FH2-signals are well suited for detecting larger prey items (e.g. moths) because of their greater target strengths and larger detection distances (maximum 12 m at 35 kHz for *Noctua pronuba*) (Waters et al. 1995, Britton et al. 1997). Because the first few signals after a silence are always the long FH2 type, the bat's interest at that particular moment is focussed solely on detection of large prey at a distance and/or landscape elements (navigation). If no large prey is revealed after the emission of the first long pulses, the bat continues its fast flight and typical FH sonar emissions. However, over time, more and more shorter pulses appear within the sequences, seeming to indicate a switch of the bat's interest towards potential smaller prey at a close range.

Discontinuous sound emission pattern

Tympanate moths are especially sensitive to ultrasounds in the range 30-40 kHz, with the detection threshold decreasing with increasing pulse length (Surlykke et al. 1999, Norman & Jones 2000). According to Surlykke et al. (1999), tympanate moths can detect approaching bats at up to a maximum of 30-90 m. Bat using frequencies around 35 kHz can detect large moths at up to a maximum of 12 m (Waters et al. 1995). Detection distances on both sides are highly dependent on amplitude, frequency and size. If the bats emit continuous pulse series, tympanate moths will detect them long before they can be detected themselves. Since moths have lower flight speeds than bats, they need larger detection distances to stay outside the sound beam of approaching bats. However, silence/stealth mode gaps in the FH-style might delay far-bat escape reactions and increase the chances for an unnoticed approach. Silences of 2000 ms correspond with a travelled pathway of approx. 17 m at a bat's flight speed of 30 km/h. In this way the gaps in calls seem to be a strategy by the bats to counter the tympanate moth's ability to evade distant bats.

If economizing were an issue, we would expect the bat to more frequently omit single pulses as observed among species that hunt in the open, rather than omitting a large number of pulses consecutively.

The faint signals that sometimes occur in the silences leave the impression of a whispering sonar. Trawling bats scanning smooth water surfaces for aquatic insects have to use high intensity FM signals in order to detect small sized prey and even then they operate at low signal-to-noise ratios (Rydell et al. 1999). Because the scattered signals in the silences are so faint even at relatively short distances (10 m) it is unlikely that they are intended for prey detection. It is possible that these signals provide short-range spatial orientation to prevent collisions with (unpredictable) obstacles e.g. other bats or floating water birds. Daubenton's bats passing over water at similar distances emit a continuous pulse series of loud FM calls that are easily heard with a bat detector, in contrast to the few faint calls of the pond bat during an otherwise silent flight.

Pond bat diet

The few available food analyses indicate quite low percentages of Lepidoptera in the diet of the pond bat (Britton et al. 1997, Sommer & Sommer 1997). However, our visual observations showed that this bat does approach and catch tympanate moths over water. One needs to be extremely careful when analysing Lepidoptera in bat droppings, as the legs and wings may well be removed before ingestion, leaving only few possible traces of larger Lepidoptera in the droppings.

In early spring the absence or scarcity of large insects in general, and also over open water, apparently influences pond bats to use only the trawling technique (T-style). The yearly reappearance of FH behaviour in May and the growing frequency of this behaviour up to September/October seems to coincide with the emergence of most large nocturnal insects, including many Lepidoptera (Emmet 1992).

The majority of bat-moth interactions were observed over linear water elements, including canals and rivers, of 20-45 m width. The density of basically terrestrial insects may be higher over these linear elements than over large lakes due to a closer contact surface with the surrounding terrestrial habitat. Many Lepidoptera, especially Noctuidae, live on food plants which are common in canal and river banks, e.g. willow, common reed, reed mace, yellow iris, grasses, nettle and many other herbaceous plants (Emmet 1992). The light trap experiments confirm the presence of a wide variety of Lepidoptera.

Conclusion

The pond bat uses different hunting techniques when foraging low over water, the choice of these is highly dependent on the available food resources: a 'classical' trawling T-technique allows exploitation of motionless or slow flying aquatic insects near to and on the water surface. An alternative FH fast aerial hawking strategy through it's FH2 calls provides access to larger, faster prey items (including tympanate moths) flying in the lower air. This is a unique strategy because it combines a relatively fast flight at low height over large smooth water surfaces with long range echolocation calls. The prominent silence/stealth mode gaps in the echolocation pattern, the emission of long QCF calls immediately after each silence and the simultaneous visual observations of moth attacks and typical moth evasive reactions reveal that the pond bat is at least an occasional tympanate moth predator. As soon as these moths are available in sufficient numbers in their specific habitat (larger water surfaces) and when weather conditions are favourable, pond bats readily switch from slow T to fast FH hunting strategy.

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Samenvatting

Predatie op motten met tympanale organen door de meervleermuis (*Myotis dasycneme*) door middel van een speciale jachtstrategie

Dit artikel beschrijft zichtwaarnemingen van het jachtgedrag van de meervleermuis op motten met tympanale organen en legt een verband met

de echolocatie en het vlieggedrag. Wanneer de vleermuizen op motten jagen boven brede kanalen en rivieren vliegen ze snel en rechtlijnig heen en weer, laag boven het wateroppervlak, ver van obstakels die nevenecho's veroorzaken (oeverlijnen). Regelmatig wordt deze vlucht onderbroken waarbij de vleermuizen plots steil omhoog schieten en prooien achtervolgen hoger boven het water. Waarnemingen van motten die zich pijlsnel naar beneden laten vallen (de zogenaamde 'power dives') tonen aan dat minstens een deel van de aanvallen gericht is op motten met tympanale organen. De vleermuizen omzeilen de vluchtreacties van de motten door de grillig vliegende mot herhaaldelijk in de lucht aan te vallen of door onmiddellijk over te schakelen van aerial hawking naar trawling, zodra de mot na een duikvlucht op het wateroppervlak terecht komt. In de zoekfase wisselen de vleermuizen reeksen luide echolocatiepulsen af met stilteperioden of reeksen van zeer zwakke echolocatiepulsen, waardoor een discontinu patroon ontstaat. De reeksen echolocatiegeluiden die volgen op de stilteperioden bevatten steeds lange, smalbandige FM-QCF-FM signalen van hoge intensiteit, in het bijzonder aan het begin van elke pulsreeks. Dit signaaltype levert een grotere detectieafstand op in vergelijking met de typische korte FM-signalen van trawling vleermuizen, maar kunnen allicht enkel dienen voor waarneming van grote prooien. Wij beargumenteren dat de discontinue sonar het benaderen van motten met tympanale organen vergemakkelijkt door het vertragen of uitschakelen van de afweerreacties van de motten tegen verafgelegen ultrasone bronnen (de zogenaamde 'far-bat reacties'). De echolocatie van het jachtgedrag op motten, dat wij in dit artikel omschrijven als 'snel luchtscheppen laag boven open water' wordt vergeleken met het klassieke harken (trawling).

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Rare or underestimated? – The distribution and abundance of the pond bat (*Myotis dasycneme*) in Poland

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Abstract: The paper summarises the distribution and abundance of the globally vulnerable and nationally endangered pond bat *(Myotis dasycneme)* in Poland and is based on all the available published and unpublished data. The species was recorded in 105 UTM squares, scattered across almost the whole of Poland. In addition fossil remains, mostly from the Holocene age, were found in 13 squares. Evidence of pond bat breeding (nursing) was obtained from 10 UTM squares, restricted to the lakelands of northern Poland and the valleys of the large rivers in the central part of the country. Only two nursery roosts, used respectively by a maximum of 481 and 391 individuals, were found. The remaining summer records (41 UTM squares) were sightings or captures of adult males, non-breeding females or unsexed individuals and were widely dispersed in areas located far from known reproduction sites. The summer roosts (*n*=21) were located mainly in buildings, bridge crevices and bird and bat boxes. Sixty-seven hibernation sites of pond bat were found, mainly in old fortifications, cellars and caves. 63% (*n*=42) of them were used by single individuals and only three held 10 or more individuals (maximum *n*=34). In the two regularly monitored sites the number of pond bats has fluctuated in recent years and in one site it even increased. Most of the available bat data (winter censuses, bird and bat boxes, owl pellets, road casualties, fossil remains, mist netting) shows that pond bats account for less than 1% of the Polish bat assemblages. However this figure reached 2.1 - 2.7% (and in one instance 17.5%) of the total number of bats netted in some regions of the northern lakelands. Many areas that are potentially attractive for breeding populations of pond bat have not yet been surveyed, suggesting that the species in Poland may be much more common and numerous than previously thought.

Keywords: bats, Chiroptera, Vespertilionidae, endangered species, conservation status, riparian habitats.

Introduction

In Europe the distribution range of the pond bat (*Myotis dasycneme* Boie, 1825) extends from southern Sweden, Finland and Russia in the north, to Belgium and France in the west and Croatia, Serbia, Bulgaria and Ukraine in the south (Horáček 1999, Limpens et al. 2000, Benda et al. 2003, Siivonen & Wermundsen 2003). A vagrant individual was recently also found in Great Britain (Hutson 2005). Within this distribution range, reproduction (i.e. nursing) has been observed in the Netherlands, Denmark, northern Germany, Hungary, Latvia, Estonia and Russia (Limpens et al. 2000). The pond bat is a stenotopic species that prefers a lowland landscape with a dense network of patches of still or slow-moving freshwater and uses a specialised hunting tactic (trawling). Its continued survival is a high conservation priority (Horáček & Hanák 1989, Limpens et al. 2000) and it was included in the 1996 IUCN Red List of Threatened Animals and classified as vulnerable (VU) in the Palearctic Region (Hutson et al. 2001). As a result the pond bat is included in Appendix II of the EC Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora

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(92/43/EEC) as a species that demands creation of special areas of conservation (SAC) within the Natura 2000 Network. It is legally protected at the international level through the Bern Convention on the Conservation of European Wildlife and Natural Habitats, the Bonn Convention on the Conservation of Migratory Species of Wild Animals and the Agreement on the Conservation of Populations of European Bats (EUROBATS) and is nationally protected in all European countries. While generally considered as a rare, patchily distributed and seriously threatened species in Western and Central Europe, it is one of the most abundant bat species within its Russian range (Strelkov & Iljin 1990, Bolshakov & Orlov 2000).

In 1986 it was thought that the population of the pond bat was as small as 3,000 in Western Europe and that the world population was about 7,000 individuals (Stebbings & Griffith 1986). More recently the number of pond bats in countries designated as population centres, i.e. Hungary, Latvia, the Netherlands and Russia, has been estimated as between 100-200,000 (Limpens et al. 2000), indicating a substantial earlier underestimation. This discrepancy was largely caused by a lack of surveys on the occurrence and abundance of the pond bat over most of its range (Limpens et al. 2000). In Western Europe, the only available data concerning long-term population changes are from the Netherlands. Population trends based on calculations by Statistics Netherlands (CBS) indicate that the numbers in hibernation sites have more than doubled between 1986 and 2005 (Verboom 2006). A similar increase was also found earlier in Estonia (Piusa Caves; Lutsar et al. 2000) and recent information from other parts of Europe within the range of the pond bat indicate that the numbers are stable or slightly increasing (e.g. Baagøe 2001).

In Poland the pond bat has traditionally been treated as a rare species confined to lowland areas with an abundance of water (Kowalski 1955, Kowalski & Ruprecht 1981). The first comprehensive review of the distribution of Polish mammals listed 33 localities of pond bat (Ruprecht 1983) but made no clear distinction between winter and summer locations. About half of the distribution data were drawn from pond bat remains found in owl pellets. There were no confirmations of the species breeding in Poland in the 20th century even though it was suspected that this occurred in some areas. An earlier claim by Horáček and Hanák (1989), that Krzanowski (1956) provided direct evidence of the reproduction, appears to be a misunderstanding (Ciechanowski et al. 2002). Horáček and Hanák (1989) also speculated that the pond bat avoids large areas of the Polish lakelands (e.g. the Masurian and Pomeranian regions) as it prefers linear water bodies (canals, blind river branches) rather than large lakes. The “Action Plan for the Conservation of the Pond Bat *Myotis dasycneme* in Europe” (Limpens et al. 2000) estimated roughly 1,000 individual pond bats in Poland. The species is classified as an endangered species (EN) in the National Red Data Book (Wołoszyn 2001) but the statement that it had strongly declined in recent years is not supported by any literature or original field data. Recently, localities of pond bat have been identified in almost all regions of Poland (Sachanowicz et al. 2006) although there has been no up-to-date review of the species’ distribution and status in the country, which is essential for planning national conservation measures. This review seeks to fill this gap by presenting the current state of knowledge on the distribution, abundance and status of the pond bat in Poland.

Material and methods

In describing the distribution of the pond bat in Poland, we have used all the available data, including both published (81 publications, 262 records) and unpublished reports (39 Polish and foreign bat workers, 88 records). These include both recent and historical information (from the C19th to June 2007). This information was obtained trough a variety of methods: mist netting, surveys of summer and winter roosts, radio-tracking individuals captured in their summer colonies, ultrasound detection and observations of foraging or commuting bats and

Table 1. The total number of localities and UTM squares, where the pond bat has been recorded. [1] Nurseries, captures or findings of lactating females and juveniles in May–August; [2] Swarming sites were included, however all of them appeared to also be hibernacula. March–April and September–October were considered as transitional periods.

Type of record	Number of localities	Number of UTM squares
summer breeding[1]	13	10
summer non-breeding	47	41
winter and transitional quarters[2]	69	39
undetermined period	26	26
owl pellets	13	13
museum specimens	5	5
total	171	105

collecting dead specimens and owl pellets (see Limpens 2001 for review on methods). Here we apply the terms 'breeding' and 'reproduction' as synonyms for nursing, so breeding is only acknowledged if a nursery roost, lactating female or juvenile individual was recorded in a particular site. Three localities where the pond bat was claimed to be present were rejected as doubtful, either because the method used was insufficient to recognise the species (Sitowski 1948) or the author did not provide any details about the place, date and method (Čmak 1968). In addition we separately review fossil records of the species. A complete synopsis of all these records and their references is given in Annexes 1-5. All localities were attributed to the particular UTM coordinates, using Gnomon 3.3 software (Desmodus, Poland). We also analysed the use of particular types of roosts used by pond bats, as well as the percentage of pond bats within available bat samples – netted, counted in roosts, collected as road casualties, extracted from owl pellets and fossil material (only samples where *n*>100 individuals were included).

Results

General and summer distribution

In total, the pond bat has been recorded as present at 171 sites, located in 105 UTM squares (table 1). These sites were spread across the whole of the country, with no limit of distribution and no clear distribution pattern (figure 1). Concentrations of records (Warsaw area, the Upper Narew and Biebrza Basins) and those regions where any recorded localities are lacking (including some parts of the Northern Lakelands) were associated with different intensity of bat surveys conducted in these areas. However, some distinct distribution patterns can be found when summer and winter records are separately considered. In summer almost all the records were obtained from the low-lying parts of the country, with only three records from localities in the Southern Uplands and one from mountainous areas (the Sudety Mountains) (figure 2). The lack of records from the Carpathians was not due to a low intensity of survey efforts, but rather to the avoidance of higher altitudes by pond bats in summer. We cannot, however, exclude the incidental occurrence of pond bat in the Polish Carpathians outside of its hibernation period, as the species has been discovered in the Slovakian part of the Tatra Mountains and foothills, both at foraging sites and cave entrances (Pjenčák et al. 2003).

Evidence of breeding was found in only ten UTM squares (Annex 1), all concentrated in the lakelands (Masurian, Pomeranian) or large river valleys (Vistula, Warta). Recent breeding records (1990-2005) are restricted to the northern and central parts of the country (figure 2). Two currently active nursery roosts, one

Figure 1. Distribution of the pond bat in Poland. Grey circles – records before 1939, grey squares – records from 1939 to 1983; black circles – new records since publication of Ruprecht (1983); black squares – sites where the presence of pond bat was recorded before 1983 and confirmed later. Complete list of numbered localities and records in Annexes 1-4.

in the wooden church in Jeleniewo (Suwałki Lakeland, UTM FF 20) and the other in an old forester's lodge in Lubnia (Pomeranian Lakeland, UTM XV 88) (Wojciechowski et al. 1999, Ciechanowski et al. 2003a) were used by maximum numbers of 481 and 391 individuals, respectively. Both of these roosts are protected as Natura 2000 sites (PLH 200001 and PLH 220015 respectively). In the 19th century, a third nursery roost was reported in an old church in Trześnia (Sandomierska Forest, southern Poland, Jachno 1868) but no data about its size are available. The remaining breeding records relate to lactating females and juveniles that were mist-netted above rivers (five localities), feeding grounds of radio-tracked lactating females (two localities), a juvenile killed in a road accident (one locality) and a historical record of a female with a juvenile in a tree hole, probably a satellite roost, in Sokolniki near Trześnia. Analysis of the data (figure 2) indicates the presence of at least three other

Figure 2. Summer distribution of the pond bat in Poland. Large black circles – breeding sites recorded between 1990 and 2007, large grey circle – historical breeding site from 19th century, small open squares – non-breeding records. Known and suspected nursery colonies: 1 – Jeleniewo, 2 - Lubnia and the environs of Wdzydze Lake, 3 – Trześnia, 4 – Iława Lake Region, 5 – Vistula river valley near Warsaw, 6 – Upper Warta river valley; recorded colonies of males: 7 – Puławy, 8 – Golesze, 9 – Żłobek.

nursery roosts situated in Iława Lake Region, the Vistula river valley (near Warsaw) and the Upper Warta river valley. The largest concentration of breeding records was noted around Wdzydze Lake (Pomeranian Lakeland, UTM XV 88, 89, 98), where, apart from the nursery colony in Lubnia, 14 lactating females and 6 juvenile individuals were netted over the Wda river at four distant localities (Ciechanowski et al. 2006b).

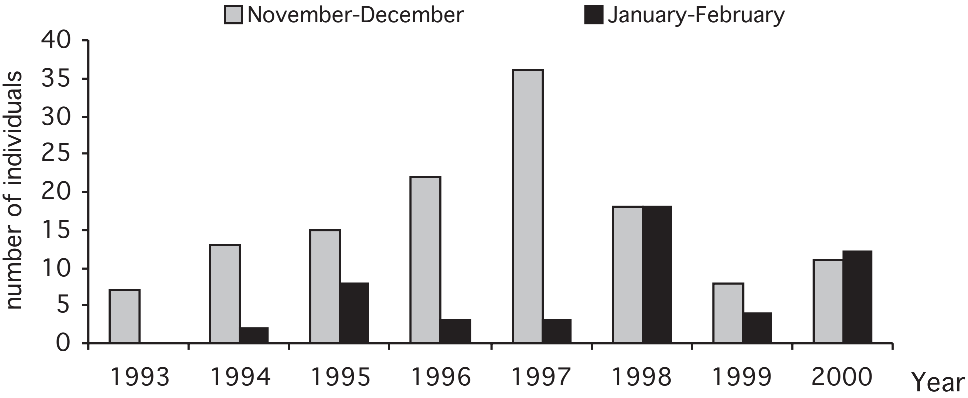
The remaining summer records were mostly of single adult males (both netted and found in roosts) and were widely distributed across the low-lying parts of Poland (figure 2). Non-lactating or non-pregnant adult females were recorded in just four localities. Some individuals found in roosts remained unsexed or the original publications did not provide data about their sex and status. In three instances (Puławy, Golesze, Żłobek), small summer colonies of 9-12 males

Figure 3. Winter distribution of the pond bat in Poland. Size of circles reflects maximum number of individuals counted during one census.

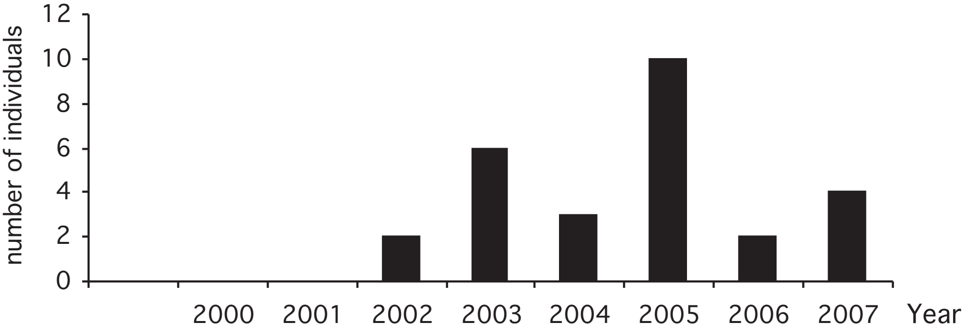
were found (Annex 2). The distribution of non-breeding individuals seems to be unaffected by the size and density of water systems and they even occur in the dry lowlands and uplands of southern Poland. In ten summer localities the occurrence of pond bat was determined by the use of ultrasound detectors and observations of flying individuals, mostly in the typically-preferred biotope of large water surfaces. Some historical data on foraging individuals over the fish ponds of Lower Silesia (Pax 1925) and the Dunajec River in the Pieniny Mountains (Sitowski 1948) should be regarded as doubtful (e.g. Kowalski 1955) as they were based exclusively on visual observations.

Winter distribution and abundance

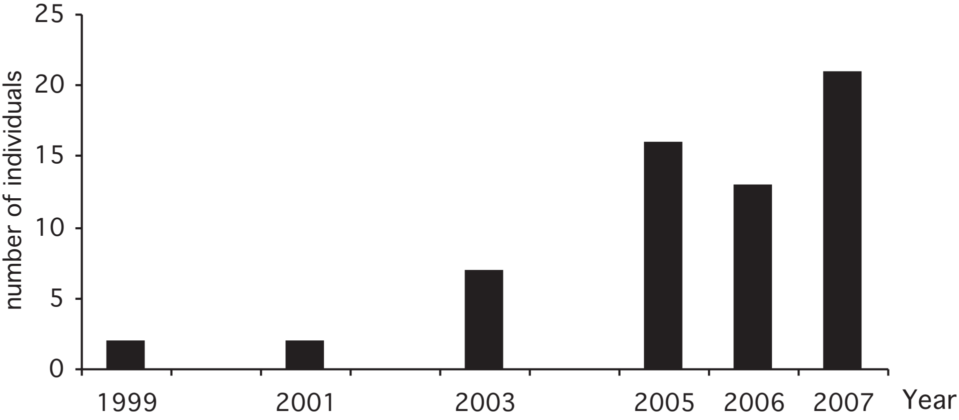
Hibernacula, spring and autumn transitional roosts and underground swarming sites associated with these bats are widely, although unevenly, distributed across the country (figure 3). In most winter roosts (*n*=42, 63%) single individuals were found and only in 13 hibernacula (19%) were two bats counted simultaneously. Larger winter sites are even rarer: occurrence of 3-5 in-



Biebrza and Narew river basins (northeastern Poland)



Fort Carré of the Wisłoujście Fortress (northern Poland)



"Nietoperek" bat reserve (western Poland)

Figure 4. Changes of pond bat numbers in the largest Polish hibernacula. Data from all the regularly monitored sites in the Biebrza and Narew river basins (Osowiec, Piątnica, Drozdowo, Trzcianne, Downary) were pooled together.

dividuals was found in seven roosts (10%), 6-9 individuals in three roosts (4%), while only three sites (4%) were used by 10 or more hibernating pond bats (Annex 3).

All the main hibernacula of the pond bat are located in lowland river valleys or in lakeland areas (figure 3). The site with the most wintering individuals is in Fort Osowiec II in the Biebrza Valley (up to 34 bats); with the other large winter sites being the underground corridors of the "Nietoperek" bat reserve (up to 21) and the Wisłoujście Fortress on the Baltic Sea coast (up to eleven). The biggest concentration of hibernacula and hibernating individuals, consisting of 16 different roosts, is around the swampy surrounds of the Biebrza and the Upper Narew River Basins. These accounted for 9.7% (n=165) of all hibernacula surveyed in that region (Kowalski et al., 2003). The Międzyrzecki Fortified Front accounts for relatively large numbers of pond bats, wintering not only in the main underground fortification system (see above) but also in three smaller bunkers, where an additional ten individuals were found in 2001. Several individuals were regularly captured in this area during autumn swarming (Łupicki et al. 2001). Several winter sites of the pond bat have also been found in the karstic uplands and mountainous areas in the south of the country, which is rich in caves and abandoned mines (figure 3). In most cases these contained only 1-2 hibernating individuals. Although the species was recorded in 7.9% (n=132) of the caves in the Kraków-Częstochowa Upland and Sudety Mountains these 16 localities are dispersed across an area more than twice the size of the Upper Narew and Biebrza Basins (Nowak & Kozakiewicz 2000, Postawa & Zygmunt 2000, Furmankiewicz & Furmankiewicz 2002, Nowak et al. 2002). Between 1999 and 2007 the number of pond bats at the "Nietoperek" bat reserve increased. Strong fluctuations in numbers were observed and between 1993 and 2000 at the five sites in the Upper Narew and Biebrza basins between 2000-2007 at Fort Carré / Wisłoujście Fortress (figure 4). Significantly more pond bats were counted in November-December than in January-February in the latter area (Wilcoxon test, T=1.00, Z=2.20, P<0.03).

The species hibernates in the Carpathians only incidentally and this exclusively in the highest part, the Tatra Mountains. The highest recorded recent European sightings of pond bat are all located here; in the Magurska, Psia and Miętusia Wyżnia caves (at 1465, 1410, and 1393 masl, respectively – Nowak et al. 2001). There are no winter records of the species from any other parts of the Carpathians (e.g. the Beskidy Mountains), although numerous surveys have been conducted in the sandstone tectonic caves in that region (Mleczek 2002), or amongst the winter bat colonies of Western Pomerania (Dzięgielewska 2002, Bernard & Samoląg 2002, Gawlak et al. 2002).

Fossil occurrence

The distribution of fossil and sub-fossil records (28 localities, 13 UTM squares) is restricted to upland and mountainous regions where cave deposits occur (figure 5). Remains that resemble the pond bat were described as *M. dasycneme subtilis* from the basal Pliocene of the Kraków-Częstochowa Upland by Kowalski (1956), although this was later considered as conspecific with *Myotis delicatus* Heller, 1936 (Horáček and Hanák 1989). Pond bat was also found in late Pliocene deposits in two localities in the same region (Annex 5). Remains of the pond bat, which were identical with recent species, were also found in 4 Pleistocene and 21 post-glacial (Holocene) sites in the Kraków-Częstochowa and Roztocze Uplands and in the Świętokrzyskie, Sudety, Tatra and Pieniny Mountains (figure 5). In the Holocene period, pond bats reached even higher altitudes than they nowadays, visiting the caves that are now located above the tree-line in the Tatra Mountains (in the Nad Dachem, Studnia w Kazalnicy and Ptasia Caves at 1570, 1545 and 1627 masl respectively – Piksa & Wołoszyn 2001). Recently three Polish caves containing post-glacial remains of the pond bat have been used by the species for hibernation (Postawa 2004).

Figure 5. Distribution of fossil remains of the pond bat in Poland. Black circles – Holocene sites, grey circles – Pleistocene, grey squares – sites from the Pleistocene and Pliocene periods, black squares – sites from the Holocene, Pleistocene and Pliocene periods. Complete list of numbered localities and records in Annex 5.

Percentage of the species in bat assemblages

The pond bat appears to be one of the rarest bat species in Poland. In bat assemblages it usually constitutes less than 1% of all bats, irrespective of the sampling method employed. In national banding programmes it accounted for 0.44% of the total bat number in 1939-1953 (Kowalski et al. 1957), 0.38% in 1950-1960 (Krzanowski 1960) and 0.59% in 1975-1994 (Harmata 1996). It constitutes 0.73% of the 1,240 bat remains found in barn owl (*Tyto alba*) (Ruprecht 1979) pellets and 0.58% of the 172 bat remains in the food of tawny owl (*Strix aluco*) (Ruprecht 1979, Kowalski & Lesiński 1990, Ruprecht 1990, Kowalski & Lesiński 2002), collected across all of Poland. Among the 4,334 bats found in Polish bird and bat boxes 0.30% were identified as pond bats. Pond bats used this type of roost only in the north-eastern part of the country, where they accounted for 0.93% of 1,401 records (Kowalski & Lesiński 1994). Among the 157 bat road casualties on Polish roads, 1.3% belonged to the pond bat (Lesiński 2007).

The species was also rare in bat assemblages in the Holocene period. It accounts for just 0.19% of sub-fossil bat remains found in cave sediments in the Kraków-Częstochowa Uplands (Postawa 2004), 0.34% in those in the Tatra Mountains (Piksa & Wołoszyn 2001) and 0.56% in the Pieniny Mountains (Alexandrowicz et al. 1985, Ochman & Wołoszyn 2003).

Pond bat is also an uncommon species during bat winter censuses, constituting about 0.02% of the 139,959 bat winter records between 1988 and 1992 (Wołoszyn 1994) and 0.2% of 1,221 bats hibernating in small village cellars throughout the country (Lesiński et al. 2004). The occurrence of pond bat in winter assemblages during February censuses varied between regions, from 0.04-0.05% in the caves of the Tatra Mountains (Piksa & Nowak 2000) and the fortifications of the Masurian Lakeland (Fuszara et al. 2002) to 0.15% in caves in the Sudety Mountains (Furmankiewicz & Furmankiewicz 2002), 0.29% in caves of the Wieluń Uplands (Kowalski et al. 2002) and 1.70% in anthropogenic underground sites in the Biebrza and Narew valleys (Lesiński & Kowalski 2002). In post-Soviet military bunkers in the Podlasie Lowland pond bats constituted just 0.1% of bats counted between December and February, although it reached 1.8% in September-November (Sachanowicz 2007). Exceptionally high proportions of pond bat were observed in winter samples from the bunkers at the Międzyrzecki Fortified Front, away from the main underground system (2.78%; Szkudlarek et al. 2001), in the November-December sample from the Biebrza and Narew Valleys (5.4%; Lesiński & Kowalski 2002) and in autumn and winter samples from the Wisłoujście Fortress (5.2% and 3.0%, respectively; Ciechanowski et al. 2006a). In the largest Polish hibernaculum, the underground system of the "Nietoperek" bat reserve, only 0.05% (16 out of 32,200) of bats counted in the 2004/2005 winter season were identified as the pond bat (authors' unpublished data).

The percentage of pond bats among bats captured in mist nests over water bodies in Poland is generally low. It varies from none in most areas of southern and central Poland (Kowalski et al. 1996, Rachwald et al. 2001, Mysłajek 2002, Mysłajek et al. 2002, Sachanowicz & Krasnodębski 2003) to 0.5% in Western Pomerania (Wojtaszyn 2002) and 2.1-2.7% in the eastern part of the Northern Lakeland belt (Ciechanowski et al. 2002, Postawa & Gas 2003). The summer assemblage of bats in the Wdzydze Landscape Park (Eastern Pomerania) appears to be unique in Poland, as the pond bat constitutes 17.5% of all bats captured there in mist nets above the rivers and is the second most numerous species recorded by this method (Ciechanowski et al. 2006b). There is little data about the numbers of pond bat among bats swarming at the entrances of underground roosts, figures vary from none in mountainous areas (Furmankiewicz & Górniak 2002, Węgiel et al. 2004) to 1.1%-3.3% in the Międzyrzecki Fortified Front on the western lowlands (Łupicki & Kowalcze-Łupicka 1999, Łupicki et al. 2001).

Habitat use

No systematic survey on habitat selection by pond bats in Poland has been conducted, but some conclusions may be drawn from the material reviewed in this paper (Annexes 1-4 in supplementary material). Summer roosts, including all nurseries and male colonies, are mostly located in buildings (lofts, spaces inside roofs and wall cavities: 8 sites). Non-breeding individuals were observed in bird and bat boxes, bridge crevices and, exceptionally, in caves (table 2). The only two observations of pond bats roosting in tree holes were made in the 19th century. One of them, made in August 1861 in a hollow hornbeam tree in Kaskada Park in Warszawa, could have been a mating roost (Wałecki 1881). Pond bats in Poland only hibernate in underground shelters, mainly in fortifications and caves, small cellars (in north-eastern Poland), sporadically in mines, underground quarries and once in a village well (table 2). Exceptionally, the species has been found in a greenhouse in winter (Krzanowski 1963) and in a sewer pipe on 17th September (7 ♂♂, unknown locality; Krzanowski 1959b). Observations of copulating individuals, hidden in crevices in the internal brick walls of the Wisłoujście Fortress (autumn 2002) were evidence that some hibernacula may also be used as mating roosts (Sachanowicz & Ciechanowski 2005).

Observations and captures of foraging or commuting pond bats have been made on large and medium-sized rivers (*n*=10), lakes (*n*=9), small rivers and streams (*n*=7), fish ponds (*n*=5), canals (*n*=4), oxbow river branches (*n*=2), a campsite near a river (*n*=1), artificial reservoirs (*n*=1) and an old park (*n*=1). Initial radio-tracking observations conducted in Jeleniewo (*n*=5 ♀♀ ad. tagged) revealed that the feeding grounds were located 2.2 - 4.8 km from the nursery roost, exclusively over large mesotrophic lakes (Kokurewicz & Furmankiewicz, unpublished data).

Discussion

Although the pond bat is considered as endangered in Poland (Wołoszyn 2001) it seems to be quite widespread in all of the lowland parts of the country and is recorded as breeding in five areas (figure 2). Other large areas are utilised mostly by non-breeding individuals that may live solitarily and disperse much more widely than breeding females. Another water-surface forager, daubenton's bat (*Myotis daubentonii* (Kuhl, 1817)) reveals local sex segregation in summer, when pregnant and lactating females occupy areas much closer to optimal foraging sites than adult males (Encarnação et al. 2006). the pond bat appears to express a similar pattern on a much wider geographical scale. This discontinuous distribution of pond bat has also been observed in the rest of its European range. The concentrations of maternity roosts are known in only a few European regions (mainly the lowlands of the Netherlands and Belgium, Eastern Jutland in Denmark, the northern German lakelands and the Tisza river basin in Hungary) which are commonly recognised as the reproduction centres, while there are regular non-breeding bat records from other regions (Horáček & Hanák 1989, Limpens et al. 2000, Van de Sijpe et al. 2004). Occurrence of the species in small, partially isolated, areas as is observed in Western and Central Europe seems to be characteristic only in the edge zone of the species' distribution range. It is difficult to decide if the widespread occurrence of the pond bat in Latvia (Pētersons & Vintulis 1998) indicates that this might also be another reproduction centre or rather the Latvian population is an extension of a continuous core range, that also covers large areas of Russia, where the pond bat is one of the dominant species in bat assemblages (see Strelkov & Iljin 1990, Bolshakov & Orlov 2000, Chistyakov 2001).

Scattered, spatially restricted populations of habitat specialists are generally recognised to be in serious threat of extinction and it has often been suggested in the past that this was the situation faced by the pond bat, especially as there was evidence that these islands of distribution have shrunk seriously in the past (as indicated by sub-fossil materials from some European countries, Horáček & Hanák 1989). However, the pond bat in Poland seems to be much more common and much less threatened than previously stated (Limpens et al. 2000, Wołoszyn 2001). No long-term population trends of the species could be traced in Poland, largely because national bat monitoring is mainly based on winter censuses of the underground roosts (Wołoszyn 1994) in which only a few dozen individual hibernating pond bats are usually counted. Such a small sample is highly sensitive to stochastic phenomena (e.g. accidental deaths of particular individuals) and cannot reflect any more general trends in the population at large. Moreover, estimating bat numbers from winter roosts, where censuses traditionally take place in January and February, can be inappropriate for the pond bat, which reaches much higher numbers in autumn (Lesiński & Kowalski 2002) and later probably hides in inaccessible places. Wintering pond bats observed in Poland usually hibernate in deep and narrow crevices (authors' observations) so might often be overlooked in some site censuses. The total number of individuals inhabiting the two known maternity roosts is several times higher than in all recently visited hibernacula – so we do not know where most of the Polish pond bats spend the winter. This situation is very similar to that observed in the Netherlands, where the known summer population of pond bats is 20 times higher than the winter one (Limpens et al. 2000). Overall, there is no evidence to suggest any recent decline of the species in Poland, as the winter counts reveal only fluctuations or even possibly a periodic increase in the numbers of pond bats.

There are however, much more important reasons for rejecting the hypothesis about any decline in this species. Firstly, the abundance of the pond bat in Poland seems to be strongly underestimated, as it was previously in the Netherlands, where systematic and goal-directed surveys between 1986 and 1993 revealed a population 4-5 times larger than previously estimated (Limpens et al. 2000). Low dominance indices (<1%) for pond bats obtained from most Polish samples might imply that it is a rare species. Most of the intensive bat surveys, however, have been carried out in regions that do not have the optimal habitat conditions for pond bats. In some localities, the species is both common and numerous, as netting surveys in the Wdzydze area and Biebrza basin have recently shown. Although mist netting appears to be an effective method for pond bat surveys, it may only work well under specific conditions, where medium-sized rivers and canals serve as commuting corridors (cf. Limpens 2001). In other regions that are potentially suitable for the pond bat, surveys need to be based on inspections of lofts and attics and on ultrasound detection, combined with visual observations of foraging individuals. These surveys need to be conducted by people familiar with the species (Limpens 2001). No such studies have yet been carried out in most of the lakeland or fishpond regions of Poland and there has been no systematic bat survey done in either Żuławy Wiślane (delta of the Vistula river) or the delta of Odra river regions, where the landscapes, rich in canals, ditches and blind river branches are suitable for pond bats.

In addition, the range of optimal hunting habitats for pond bats is much wider than has been previously suggested (Horáček & Hanák, 1989). Both the known Polish nurseries for the pond bat are located in young, post-glacial lakeland landscapes, which are only rich in lakes (mesotrophic rather than eutrophic) but without any broad canals or slowly flowing, large rivers. Such landscapes, formerly considered as unfavorable for the species, resemble the habitat utilised by the Latvian population (Pētersons & Vintulis 1998) which has one of the highest population densities in the European Union (Limpens et al. 2000). In the light of this knowledge, breeding populations of pond bat can sustain themselves in any areas rich in large water bodies, and it is very likely that other maternity roosts will be discovered in geographically similar other regions of Poland (e.g. the Lubuskie Lakeland, the southern part of Pomerania or Polesie) that have not yet been properly surveyed. Given this possibility and recent records, it is possible that Poland could be recognised as another European reproduction centre in Europe, joining those already identified by Limpens et al. (2000). Equally it may be possible to treat Polish breeding colonies as stepping stones within a larger, continuous, reproduction area that ranges from northern Germany, across the Baltic States and onto the Russian populations. There is however one gap in this distribution, in Lithuania, where despite frequent summer records the only known nursery is in the north-east of the country and possibly represents an extension of the large Latvian population (Mickevičiene et al. 1999). In southern Lithuania, bordering Poland, the pond bat appears to be a rare bat, and there are only a few records of non-breeding bats (Pauža & Paužiene 1999), although these do include the largest hibernaculum in the country, the Paneriai tunnel in Vilnius, used by about 85 individuals (Baranauskas 2006).

Any hypothesis about numerous, but locally distributed and mostly undiscovered, summer populations of pond bats in Poland is not necessarily shaken by a lack of large winter aggregations, even though mass hibernation of the species (500-1700 in one site) is known from Denmark (Baagøe 2001) and Russia (Bolshakov & Orlov 2000). Only in Danish Jutland, there is evidence of one population of pond bats reproducing and hibernating in the same area (Baagøe 2001). In general the species has strong migratory tendencies (with female movements up to 300 km). A large part of the lowland Dutch population migrates to the hilly area of Limburg and German mountains, where there are optimal hibernacula (Roer 2001). Similarly, Polish summer populations could leave the country for winter. Equally, the Polish main hibernacula could be simply still remain undiscovered because of their observed tendency to aggregate in large numbers in a just few of many available sites (cf. Bolshakov & Orlov 2000).

It is not possible to predict whether any natural or anthropogenic factors could lead to a serious decline of the pond bat in Poland in the near future. The pond bat, as a synanthropic species, makes great use of buildings as maternity roosts in the summertime. Recent renovation, rebuilding and demolition activities could be a threat for the pond bat, as old houses, with deep crevices, slowly disappear from the Polish landscape. A second threat could be increasing and uncontrolled disturbance of hibernation sites by tourists. Despite the legal protection that bats are afforded in Poland and the designation of the largest hibernacula as Natura 2000 sites, sight-seeing in underground sites in winter is still possible and in some places, such as the "Nietoperek" bat reserve, it is steadily increasing (authors' unpublished data).

Wołoszyn (2001) suggested water pollution as the main threat for the species and this was partially confirmed by field studies by Van de Sijpe et al. (2004), who recorded higher pond bat activity over waterways with mild and moderate pollution than over heavily polluted ones. Yet this result may also be influenced by other unstudied factors (e.g. proximity of roosts) and the methodological issues associated with calculating hunting activity solely from qualitative data (presence/absence in the number of surveys). In polluted areas there is evidence of heavy metals, PCBs and pesticides being absorbed by the aquatic chironomid flies which are the main prey of the pond bat. Dead pond bats, collected in less contaminated areas, contained PCBs at concentrations known to inhibit reproduction among some other mammals (Reinhold et al. 1999). However, water quality has improved in some Polish waters in recent years including in Wdzydze Lake, which is part of the Pomeranian refuge of the pond bat (Żmudziński 1997). On the other hand many of waters in northern Poland are still heavily polluted by untreated sewage effluents.

Even if the picture of the status of pond bat in Poland painted here appears more optimistic than earlier thought, this should not diminish conservation efforts. In future, the emphasis of these might change towards focusing on protecting an internationally important population rather than a local peculiarity. The conservation of unevenly distributed species on a European scale should focus on those regions with the strongest and most viable populations, where the pond bat is still common and widespread. This is in line with the goals of the Habitat Directive and Natura 2000 Network, which recommend prioritising the protection of populations / areas with Pan-European significance (Hoffman et al. 2004). However, establishing such areas for pond bats requires developing comparable data, based on extensive inventories, which are far from complete in most of the countries that acceded to the EU between 2004 and 2007 (cf. Limpens 2001).

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Samenvatting

Zeldzaam of onderschat? - Het voorkomen van de meervleermuis (*Myotis dasycneme*) in Polen

Dit artikel geeft een overzicht van het voorkomen van de meervleermuis (*Myotis dasycneme*) in Polen, gebaseerd op alle beschikbare gepubliceerde en ongepubliceerde gegevens. De soort is waargenomen in 105 UTM-hokken, verspreid over een groot deel van Polen. Daarnaast zijn fossiele resten, vooral uit het Holoceen, gevonden in 13 UTM-hokken. Voortplanting is vastgesteld in 10 UTM-hokken, uitsluitend in het noordelijk merengebied en in de riviervalleien van het centrale deel van Polen. Er zijn slechts twee kraamkolonies gevonden, met respectievelijk 481 en 391 individuen. De overige zomerwaarnemingen (41 UTM-hokken) zijn verspreid door het land gedaan, ook in delen ver verwijderd van de voortplantingsgebieden. Het gaat hier om zichtwaarnemingen en vangsten van volwassen mannetjes, vrouwtjes die niet aan de voortplanting deelnamen of dieren waarvan het geslacht onbekend was. Zomerverblijven (*n*=21) waren vooral gevestigd in gebouwen, holtes in bruggen en vogel- en vleermuiskasten. Winterverblijfplaatsen (*n*=67) van de meervleermuis bevonden zich hoofdzakelijk in oude forten, kelders en grotten. Hiervan werd 63% (*n*=42) bezet door één dier, terwijl in slechts drie verblijven tien of meer (maximaal 34) dieren werden gevonden. In twee verblijven waar regelmatig werd geinventariseerd fluctueerden de aantallen meervleermuizen in de laatste jaren, in een ander winterverblijf namen de aantallen zelfs toe. Het merendeel van de beschikbare data (wintertellingen, vogel- en vleermuiskasten, braakballen van uilen, verkeersslachtoffers, fossiele resten, mistnet-vangsten) laat zien dat meervleermuizen minder dan 1% uitmaken van de vleermuizen in Polen. In enkele delen van het merengebied van noordelijk Polen is het percentage meervleermuizen in mistnet-vangsten echter hoger, 2,1 - 2,7%, in één geval zelfs 17,5%. Veel gebieden die in potentie geschikt zijn als leefgebied voor de meervleermuis zijn nog niet onderzocht. Dit suggereert dat de meervleermuis in Polen wel eens veel algemener zou kunnen zijn dan tot dusver werd gedacht.

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Annex 1. Breeding records of the pond bat in Poland. Explanations: r. – river, l. – lake(s), rs – survey of roost, nt – netting, tr – radiotracking of individuals from Jeleniewo nursery, ad. – adult, juv. – juvenile, lact. – lactating, act. – sexually active. If no symbol is given, the numbers refer to the unsexed individuals or that no data about sex and age are available. Capital italics (e.g. *AP*) represent the initials of unpublished data owners (explained in the acknowledgements) or of the authors (*MC* – Mateusz Ciechanowski, *KS* – Konrad Sachanowicz, *TK* – Tomasz Kokurewicz).

UTM square	Locality	Method	Date	Number and status of bats	Source
XV 88	Lubnia, forester's lodge	rs (nursery)	17.07.2002	107[1]	Ciechanowski et al. 2003a
			19.07.2003	160	*MC & KS*
			07.07.2004	321[2]	*MC* & *AP*
			07.07.2005	391[3]	*MC* & *AP*
			15.07.2006	252[4]	*MC*
			27.06.2007	231[5]	*MC*
XV 89	Loryniec, Wda r.	nt	11.07.2002	9 ♀♀ ad. lact., 1 ♀ juv., 1 ♂ juv.	Ciechanowski et al. 2003a
XV 89	Schodno l., outflow of Wda	nt	23.08.2004	1 ♀ ad. lact.	Ciechanowski et al. 2006
			01.09.2004	2 ♀♀ juv.	Ciechanowski et al. 2006
			27.07.2005	1 ♂ juv.	Ciechanowski et al. 2006
XV 89	Płocice, Wda r.	nt	15.07.2002	1 ♀ juv.	Ciechanowski et al. 2006
XV 98	Borsk, Wda r.	nt	12.07.2003	5 ♀♀ ad. (4 lact.)	Ciechanowski et al. 2006
CC 33	Mikołajewice, old branch of Warta r.	nt	26.06.2004	1 ♀ ad. lact.	*MI*
DC 99	Łomianki, on road	found dead	12.08.1997	1 ♀ juv.	Lesiński 2003
DE 05	stream between Januszewskie and Czerwica l.	nt	11.07.1999	1 ♀ juv.	Ciechanowski et al. 2002
EB 51	Trześnia, church loft	rs (nursery)	06.1867	*large number*	Jachno 1868
EB 51	Sokolniki tree hole	rs	25.06.1867	1 ♀ with juv.	Jachno 1868
FF 20	Jeleniewo, church loft	rs (nursery)	09.07.1997	476	*MW*
			10.07.1999	481 (♀♀ ad. + juv.)	Wojciechowski et al. 1999
			25.07.2002	467 (♀♀ ad. + juv.)	*TK & JF*
			31.07.2002	315	*TK & JF*
FF 20	Szelment Wielki l.	tr	24.07 - 04.08.2002	11	*TK & JF*
FF 21	Szurpiły l.	tr	24.07 - 04.08.2002	12	*TK & JF*

[1]nt: 1 ♀ juv., 1 ♂♂ juv.; [2]nt: 2 ♀♀ ad. lact., 1 ♂ juv.; [3]nt: 2 ♀♀ ad. (1 lact.), 1 ♂ juv.; [4]nt: 1 ♀ ad. lact., 1 ♀ juv.; [5]nt: 2 ♀♀ ad. lact., 1 ♂ juv.

Annex 2. Non-breeding summer records of the pond bat in Poland[1]. Explanations: r. – river, l. – lake(s), f.d. – forest district, dt – foraging or commuting bat, observed with ultrasound detector, rs – survey of roost, nt – netting, ad. – adult, juv. – juvenile, act. – sexually active. If no symbol is given, the numbers refer to the unsexed individuals or that no data about sex and age are available. Capital italics (e.g. *MW*) represent the initials of unpublished data owners (explained in the acknowledgements) or of the authors (*MC* – Mateusz Ciechanowski, *KS* – Konrad Sachanowicz, *TK* – Tomasz Kokurewicz).

UTM square	Locality	Method	Date	Number and status of bats	Source
VU 46	Bielinek, Old Odra r.	dt	1999		Szkudlarek & Dzięgielewska 2003
VV 60	Lower Odra Valley, canals	dt	2001		*RS*
WR 88	Kudowa Zdrój	dt	07.1999		*RS* in: Mikusek & Pikulska 1999
WU 30	Międzyrzecz Fortified Front (“Nietoperek” bat reserve), undergrounds	nt	31.07.2001	1 ♂	*TK* et al.
WU 96	Trzcianka, narrow between Długie l. & fish ponds	nt	13.05.2000	1 ♂	Wojtaszyn 2002
XS 09	Tarchalice, old branch of Odra r.	dt	2003		*JF*
XS 46	Odra r. near Wrocław	dt	2001		*RS*
XV 76	Struga Siedmiu Jezior, between Płęsno and Skrzynka l.	nt	14.08.2002	1 ♂ ad.	*MK*
CB 90	Wielkanocna Cave	rs	15.08.1998	3 (1 ♂ ad.)	*MI*
CC 33	Jeziorsko reservoir	nt	07.1995	1 ♂ ad.	*JH*
CC 33	Warta II, Mazur ox-bow lake, crevice in a bridge	rs	20.07.2003	2	Ignaczak & Manias 2004
CC 42	Nobela, Niniwka r., crevice in a bridge	rs	12.10.2003	1	Ignaczak & Manias 2004
CC 42	Kolasa, Niniwka r., crevice in a bridge	rs	08.06.2003	1	Ignaczak & Manias 2004
CC 50	Brody, Grabia r., crevice in a bridge	rs	20.05.2003	1	Ignaczak & Manias 2004
CD 82	Gociąż l., bird box	rs	29.06.1993	1 ♂ ad.	Kasprzyk & Ruczyński 2001
CE 95	Fabianki, Liwa r.	nt	07.1997	2	Ciechanowski et al. 2002
CE 99	“Lake Drużno” nature reserve	dt	29.07.2001	1	*MC*
		nt	26.08.2002	1	*CN* (photo), *MC* (det.)
CF 25	Wejherowo, Reda r.	nt	21.08.2002	1 ♂ ad.	*MC*
			21.08.2004	1 ♂ ad.	*MC*
CF 52	Gdańsk-Sobieszewo, bat box	rs	30.07.2006	1 ♂ ad.	*MC*
DB 87	Chlewiska, church	rs	11.06.1993	1 ♂ ad.	*SC & MK*
DC 16	Rydwan and Okręt fish ponds	nt	07.1972	1	*ZW*
DC 20	Golesze, building loft	rs (colony)	1997-1998	up to 10 ♂♂	*SZ*
DC 30	Tomaszów Mazowiecki, Pilica r.	nt	03.09.1999	2 ♂♂ ad.	*JH, WP* & *RJ*
DC 71	Wólka Magierowa, Drzewiczka r.	nt	04.08.1995	1 ♂ ad. act.	*MK, GL & AO-K*
DD 60	Kromnów f.d., Kampinos Forest, bird box	rs	03.08.1989	1 ♂ ad.	Kowalski & Lesiński 1995
DD 80	Łomna, church loft	rs	21.07.1984	1 ♂ ad.	Kowalski & Lesiński 1995
			15.06.1991	1 ♂ ad.	Kowalski & Lesiński 1995
DD 80	Kiełpin, on road	found dead	22.09.1999	1	Lesiński 2003
DE 05	canal between Twaruczek and Płaskie l.	nt	11.07.1999	1 ♀ ad.	Ciechanowski et al. 2002
DE 21	Kostkowo f.d., bat box	rs	26.07.2005	1 ♂ ad.	*JG & AS*
EB 69	Puławy, loft of forester’s lodge,	rs (colony)	1952	9 ♂♂, 1 ♀	Krzanowski 1956
EC 08	Warszawa-Marymont, Kaskada Park, hollow *Carpinus betulus* tree	rs	08.1861	1 ♂, 1 ♀	Wałecki 1881
EC 15	Czersk, church loft	rs	25.07.1992	1	*IK*
ED 79	Motyka, bat box	rs	09.06.2004	1 ♂ ad.	*MK & TN*
ED 99	Wierciszewo, campsite near Biebrza r.	dt	30.08.2004		*GA & AJH*
EE 35	Mikołajskie l.	dt	08.08.1994		*BV & HH*
EE 46	canal between Łuknajno and Śniardwy l.	dt	09.08.1994		*BV & HH*
FB 30	Zwierzyniec, city park	nt	03.07.1989	1 ♂ ad.	Jurczyszyn 1994
FC 70	Żłobek, barn	rs (colony)	07.2000	12 ♂♂	*MP*
FD 94	Białowieża Forest, Hwoźna r., bridge	nt	02.06.2007	1 ♂ ad.	*IR*
FE 01	Gugny, bird boxes	rs	30.06.1987	7 (3 ♂♂)	Lesiński 2001
			05.08.1988	4 ♂♂ ad.	Lesiński 2001
FE 15	Dręstwo l.	dt	15.08.1994		*BV & HH* in: Lesiński 2001
FE 27	Rospuda r., bridge	nt	03.06.2007	1 ♂ ad.	*BK*
FE 37	bridge between Necko and Białe l.	dt	02.06.2007		*BK*

UTM square	Locality	Method	Date	Number and status of bats	Source
FE 39	narrow between Okrągłe and Wigry l.	nt	07.07.1995	1	Postawa & Gas 2003
			04.07.1996	1	Postawa & Gas 2003
			07.07.1996	1	Postawa & Gas 2003
FE 39	narrow between Białe and Wigry l.	nt	11.07.1995	1	Postawa & Gas 2003
FE 47	Augustowski Canal	nt	25.08.1996	1 ♂ ad. act.	*RD*
FF 21	Jaczno water-mill	nt	04.07.1998	1 ♂	Ciechanowski et al. 2003b

[1] After checking the final proof of this paper, we found an unmentioned publication providing another record of the pond bat, fitting into the time frames of our review. On 17 August 1980 one female was found in an abandoned beehive on the island of Komosa Pond, “Krasne” nature reserve (UTM FD 59; Kupryjanowicz, J. & A.L. Ruprecht 2006. Beitrag zur Fledermausfauna (Chiroptera) des Knyszyn-Waldes (NO-Polen). Nyctalus (N.F.) 11 (4): 335-343). Thus, the number of localities of the pond bat in Poland increased to 172 (48 summer non-breeding) and the number of occupied UTM squares to 106 (42 summer non-breeding).

Annex 3. Hibernacula (November-February), transitional roosts (March-April, September-October) and associated swarming sites (netting)of the pond bat in Poland. Explanations: rs – survey of roost, nt – netting at the entrance, ad. – adult. If no symbol is given, the numbers refer to unsexed individuals. Capital italics (e.g. *MW*) represent the initials of unpublished data owners (explained in the acknowledgements) or of the authors (*MC* – Mateusz Ciechanowski, *KS* – Konrad Sachanowicz, *TK* – Tomasz Kokurewicz).

UTM square	Locality	Method	Date	Number and status of bats	Source
VV 71	Szczecin, near the pier of the bridge on the Berlin-Szczecin motorway	found grounded	12.03.1988	1	Janyszak & Jurczyszyn 1989
WS 62	Kowary, adit near Hydromech	rs	01.1998	3	Szkudlarek & Paszkiewicz 1999
			11.1998	3	Szkudlarek & Paszkiewicz 1999
			11.1999	3	Szkudlarek & Paszkiewicz 1999
			01.1999	4	Szkudlarek & Paszkiewicz 1999
			16.12.1999	3	Furmankiewicz et al. 2001
			16.03.2000	3	Furmankiewicz et al. 2001
WS 93	Książ, under the castle	rs	1972-1974	1 ♂	Haitlinger 1976
WS 94	Północna Duża Cave	rs	01.11.1964	1 ♂	Wołoszyn 1968, 1971
			21.03.1971	1 ♂, 1 ♀	Haitlinger 1976
			23.01.1972	2 ♂♂	Haitlinger 1976
			05.02.1973	2 ♂♂	Haitlinger 1976
			03.12.1973	1 ♂	Haitlinger 1976
			15.01.2000	1 ♀	Kliś et al. 2001
WS 94	Nowa Cave	rs	23.01.1972	1 ♂	Haitlinger 1976
			01.04.1973	1 ♀	Haitlinger 1976
			17.03.1974	1 ♂, 1 ♀	Haitlinger 1976
WS 94	Szczelina Wojcieszowska Cave	rs	02.02.2001	1	Kliś et al. 2001
WU 30	Międzyrzecz Fortified Front (“Nietoperek” bat reserve), underground	rs	31.10.1975	1	Bagrowska-Urbańczyk & Urbańczyk 1983
			03.01.1975	1	Bagrowska-Urbańczyk & Urbańczyk 1983
			07-08.12.1985	1	Lesiński 1988a
			1989	2	Urbańczyk & Gólski 1994
			1991	2	Urbańczyk & Gólski 1994
			1992	3	Urbańczyk & Gólski 1994
			01.02.1995	3	*KS* et al.
			22.11.1998	3	*TK* et al.
			06.01.1999	2	*TK* et al.
			20.01.2001	2	*TK* et al.
			18.01.2003	7	*TK* et al.
			15.01.2005	16	*TK* et al.
			14.01.2006	13	*TK* et al.
			13.01.2007	21	*TK* et al.
		nt[1]	12.08-24.09.1994	1	Łupicki & Kowalcze-Łupicka 1999
			18.08-10.09.1995	10	Łupicki & Kowalcze-Łupicka 1999
			08.09.2000	3	Łupicki et al. 2001
			13.10.2000	3	Łupicki et al. 2001
WU 30	Pieski, bunker PzW 741	rs	21.11.1998	1	Szkudlarek et al. 2001
			17.01.1999	3	Szkudlarek et al. 2001
			26.01.2000	4	Szkudlarek et al. 2001
			14.02.2001	5	Szkudlarek et al. 2001

UTM square	Locality	Method	Date	Number and status of bats	Source
			25.03.2001	8	Szkudlarek et al. 2001
			21.02.2002	2	*MW & TK*
		nt	17.08.1999	4	Łupicki et al. 2001
			10.09.1999	2	Łupicki et al. 2001
			24.09.1999	2	Łupicki et al. 2001
			10.10.1999	1	Łupicki et al. 2001
			16.08.2000	2	Łupicki et al. 2001
			02.09.2000	1	Łupicki et al. 2001
			19.09.2000	2	Łupicki et al. 2001
WU 30	Wysoka, military tunnel	rs	14.02.2001	3	Szkudlarek et al. 2001
			24.03.2001	1	Szkudlarek et al. 2001
			20.02.2001	1	*MW & TK*
WU 30	Stare Kursko, bunker PzW 754-757	rs	13.10.1998	1	Szkudlarek et al. 2001
			26.01.2000	2	Szkudlarek et al. 2001
			14.02.2001	1	Szkudlarek et al. 2001
WU 30	Pieski, bunker PzW 743	rs	26.01.2000	1	Szkudlarek et al. 2001
			25.03.2001	1	Szkudlarek et al. 2001
WA 70	Koszalin, air-raid shelter	rs	31.01.2005	1	Wojtaszyn et al. 2006
XR 07	Młoty, Obiegowa Adit	rs	05.03.2005	1	*PK*
XU 30	Poznań Fortress, Fort I	rs	09.12.1995	1 ♂	Gawlak 1996
CB 45	Szachownica Cave	rs	28.03.1981	1 ♂	Lesiński 1983
			06.03.1982	2 ♂♂	Lesiński 1983
			29.01.1982	1 ♂, 1 ♀	Lesiński 1983
			29.01.1983	1 ♂	Lesiński 1983
			29.01.1994	4	*MK, MI & KS*
			1993/94	max. 3	Hejduk & Radzicki 1996
			1994/95	max. 3	Hejduk & Radzicki 1996
			29.01.1995	2	*MI*
			29.01.1996	6	Kowalski *et al.* 2002
			29.01.2000	4	*MI*
			29.01.2001	4	*MI*
			29.01.2002	5	*MI*
		nt	07.09.2002	3 ♂♂ ad.	*MI*
			28.09.2002	1 ♂	*MI*
CB 46	Stalagmitowa Cave	rs	28.11.1982	1 ♂	Lesiński 1983
CB 72	Towarna Cave	nt	11.05.2000	1	*TP & AW*
CB 72	Pod Sokolą Górą Cave	rs	21.11.1993	2	Postawa & Zygmunt 2000
			20.11.1977	1	Postawa & Zygmunt 2000
			07.11.1993	1	Postawa & Zygmunt 2000
			05.02.1994	1	Postawa & Zygmunt 2000
			02.02.1995	1	Postawa & Zygmunt 2000
			27.10.1993	1	Postawa & Zygmunt 2000
CB 72	Koralowa Cave	rs	28.10.1951	1 ♀	Kowalski 1953
CB 72	Studnisko Cave	rs	02.03.2001	1	Gas & Postawa 2001
CB 81	Wiercica Cave	rs	06.11.1963	1	Skuratowicz 1968
			10.11.1996	1	Postawa & Zygmunt 2000
			12.02.1998	1	Postawa & Zygmunt 2000
			14.02.1998	1	Postawa & Zygmunt 2000
CD 37	Toruń, Fort V	rs	03.2000	max. 3	*KK*

UTM square	Locality	Method	Date	Number and status of bats	Source
			31.01.2003	1	*KK*
CF 43	Gdańsk, Wisłoujście Fortress, Fort Carré	rs	11.02.2002	2	Ciechanowski et al. 2006a
			14.09.2002	8	Ciechanowski et al. 2006a
			24.09.2002	2	Ciechanowski et al. 2006a
			24.10.2002	1	Ciechanowski et al. 2006a
			21.11.2002	6	Ciechanowski et al. 2006a
			21.12.2002	6	Ciechanowski et al. 2006a
			21.01.2003	4	Ciechanowski et al. 2006a
			16.02.2003	6	Ciechanowski et al. 2006a
			22.03.2003	5	Ciechanowski et al. 2006a
			18.09.2003	6	*MC* & *KS*
			19.12.2003	4	*MC* & *AP*
			24.02.2004	3	*MC* & *AP*
			18.02.2005	10	Ciechanowski et al. 2006a
			08.02.2006	2	Ciechanowski et al. 2006a
			05.02.2007	4	Ciechanowski et al. 2006a
		nt	06.10.2000	4 ♂♂	Ciechanowski & Przesmycka 2001
			21.10.2000	1 ♀	Ciechanowski & Przesmycka 2001
			14.09.2002	1 ♂	*MC* & *KS*
			14.09.2003	5 ♂♂	*MC* & *KS*
CF 43	Gdańsk, Wisłoujście Fortress, Prochownia	rs	24.02.2004	1	*MC* & *AP*
			18.02.2005	1	Ciechanowski et al. 2006a
			08.02.2006	5	Ciechanowski et al. 2006a
			05.02.2007	1	Ciechanowski et al. 2006a
		nt	15.10.2006	1 ♀	*MC*
DV 15	Psia Cave	rs	17.03.2000	2	Nowak et al. 2001
			02.03 -25.04.2000	1	Nowak et al. 2001
DV 15	Miętusia Wyżnia Cave	rs	11.02.2001	1	Nowak et al. 2001
DV 25	Magurska Cave	rs	31.12.1998	2	Nowak et al. 2001
			07.01.2001	1	Nowak et al. 2001
			10.03.2000	1	Nowak et al. 2001
DA 08	Zegar Cave	rs	29.01.1998	2	Postawa & Zygmunt 2000
			10.02.1998	2	Postawa & Zygmunt 2000
			11.02.1999	2	Postawa & Zygmunt 2000
			11.03.1998	2	Postawa & Zygmunt 2000
DA 16	Biała Cave	rs	1985	1	Godawa 1995
DA 16	Nietoperzowa Cave	rs	08.03.1987	1	Godawa & Wołoszyn 1990
			12.03.1988	1	Godawa & Wołoszyn 1990
			10.02.1995	3	Kozakiewicz & Strzałka 1996
DA 16	Łokietka Cave	rs	11.02.1997	2	Nowak & Kozakiewicz 2000
DA 16	Jama Ani Cave	rs	15.02.2001	1	Nowak et al. 2002
DA 16	Zbójecka Cave	rs	27.02.2001	1	Nowak et al. 2002
			2003	3	Grzywiński et al. 2004
DB 53	Adit in Miedzianka	rs	26.09.1960	2	Wołoszyn 1962
			29.12.1960	2	Wołoszyn 1962
			13.02.1961	1	Wołoszyn 1962
			04.01.1963	1 ♂	Wołoszyn 1964

UTM square	Locality	Method	Date	Number and status of bats	Source
DB 84	Bukowa Góra, adit	rs	15.02.2000	2	*MG*
DD 70	Fort Cybulice I	rs	25.10.1984	1 ♂ ad.	Kowalski & Lesiński 1995
DD 71	Fort Goławice	rs	05.12.1979	1 ♂ dead	Lesiński 1988b, Ruprecht 1983
			22.12.1981	1 ♂	Lesiński 1988b
DD 71	Fort Strubiny	rs	17.11.1981	1 ♀	Lesiński 1988b
DD 71	Modlin, citadel	rs	07.04.1998	1	*GL*
DD 71	Fort Henrysin	rs	23.11.1996	1	*MF & GL*
DD 80	Fort Janówek III	rs	02.02.1997	1	*GL & PHCL*
			29.03.1998	1	*GL*
			10.02.1998	2	Gulatowska & Kowalski 2004
			07.12.2003	3	Gulatowska & Kowalski 2004
			27.12.2003	4	Gulatowska & Kowalski 2004
			30.01.2004	5	Gulatowska & Kowalski 2004
			27.02.2004	7	Gulatowska & Kowalski 2004
			11.12.2005	9	*JG & MK*
DD 81	Fort Czarnowo	rs	13.11.1987	1 ♀	Lesiński 1988b
			29.11.1987	1 ♀	Lesiński 1988b
EB 02	Łagów, Zbójecka Cave	rs	02.02.1960	1	Wołoszyn 1962
EB 68	Bochotnica, artificial cave	rs	30.11.1987	1 ♀	*MK*
			03.02.1988	1 ♂	*MK*
			13.02.1989	1 ♂	*JPC*
			08.02.1992	2	Kowalski & Dróżdż 2002
			02.2000	3	*MP & MU*
			02.2001	2	*MP*
			09.03.1991	1 ♀	*MK*
			26.03.2002	1	*MP & MU*
EB 69	Puławy artificial cave	rs	02.01.1952	1 ♀	Krzanowski 1956, 1959a
EB 69	Puławy, cellar of the Sybilla Temple	rs	25.11.1954	1 ♂	Krzanowski 1956
EB 69	Puławy, greenhouse	rs	?	1	Krzanowski 1963
ED 79	Piątnica, fort	rs	02.12.1990	1	Kowalski et al. 2003
			02.12.1992	1	Kowalski et al. 2003
			09.12.1996	1	Kowalski et al. 2003
ED 79	Kalinowo, cellar	rs	24.01.2002	1	Kowalski et al. 2003
ED 79	Drozdowo, cellars of brewery	rs	01.12.1993	1	Kowalski et al. 2003
			04.02.1994	1	Kowalski et al. 2003
			05.12.2000	1	Kowalski et al. 2003
			03.12.2002	1	Kowalski et al. 2003
			09.12.2003	1	Kowalski et al. 2003
ED 79	Drozdowo, Dolna Street, cellar	rs	05.12.2000	1	Kowalski et al. 2003
			31.01.2001	1	Kowalski et al. 2003
ED 79	Drozdowo, Kraska Street	rs	29.11.1999	1	Kowalski et al. 2003
			04.02.2000	1	Kowalski et al. 2003
ED 88	Pniewo, cellar	rs	17.12.2002	1	Kowalski et al. 2003
ED 89	Żelechy, village well	rs	27.01.2002	1	Kowalski et al. 2003
ED 89	Żelechy, cellar	rs	09.12.2003	1	Kowalski et al. 2003
EE 48	Giżycko, Boyen Fortress	rs	1992-1999	1	Fuszara et al. 2002
EE 93	Łojki, cellar	rs	14.02.2003	1	Kowalski et al. 2003
FB 40	Senderki, artificial caves	rs	20.02.2002	2	*MP & MU*
FD 30	Anusin, bunker SM AN 2	rs	29.10.1994	1	Sachanowicz 2003

UTM square	Locality	Method	Date	Number and status of bats	Source
FD 30	Anusin, bunker SM AN 7	rs	28.10.1995	1 ♂	Sachanowicz 2003
			02.12.1995	1	Sachanowicz 2003
FD 30	Anusin, bunker SM AN 11	rs	26.10.1996	1	Sachanowicz 2003
			13.02.1999	2	Sachanowicz 2003
FD 30	Anusin, bunker SM AN 14	rs	26.10.1996	1 ♀	Sachanowicz 2003
			28.12.1995	1	Sachanowicz 2003
FE 02	Osowiec, Fort Zarzeczny	rs	14.12.2003	1	Kowalski et al. 2003
FE 11	Trzcianne, cellar	rs	09.12.1997	1	Lesiński 2001
			06.02.1998	1	Lesiński 2001
			19.01.1999	1	Lesiński 2001
			08.12.2002	1	Lesiński 2001
			11.02.2003	1	Kowalski et al. 2003
FE 12	Downary, cellar	rs	07.02.1992	1	Lesiński 2001
			04.02.1997	1	Lesiński 2001
			09.12.1997	1	Lesiński 2001
			06.02.1998	1	Lesiński 2001
			22.01.1999	1	Lesiński 2001
			04.01.1992	1	Kowalski et al. 2003
			30.01.1999	1	Kowalski et al. 2003
			15.02.2000	1	Kowalski et al. 2003
			20.11.2000	1	Kowalski et al. 2003
			29.11.2001	1	Kowalski et al. 2003
			04.02.2002	1	Kowalski et al. 2003
			18.02.2002	1	Kowalski et al. 2003
FE 12	Osowiec, Fort Centralny	rs	26.11.1993	6	Lesiński 2001
			03.02.1994	2	Lesiński 2001
			05.12.1994	13	Lesiński 2001
			13.02.1995	8	Lesiński 2001
			23.11.1995	15	Lesiński 2001
			01.02.1996	2	Lesiński 2001
			26.11.1996	21	Lesiński 2001
			09.12.1997	34	Lesiński 2001
			04.02.1997	2	Lesiński 2001
			06.02.1998	16	Lesiński 2001
			11-12.1998	18	Lesiński 2001
			02.1999	2	Lesiński 2001
			11-12.1999	8	Lesiński 2001
			02.2000	11	Lesiński 2001
			29.11.2000	9	Lesiński 2001
FE 45	Hamulka, cellar	rs	10.02.2003	2	Kowalski et al. 2003
FE 45	Trzyrzeczki, cellar	rs	30.12.2000	1	Lesiński 2001
FE 55	Kamienna Stara, bunker 84	rs	10.02.2003	1	Kowalski et al. 2003

[1] entrance A64 (Wysoka)

Annex 4. Localities of the pond bat in Poland with undetermined status or dates. Explanations: f. i. – forest inspectorate, f. d. – forest district, obs – visual observation of foraging or commuting individuals, pl – remains extracted from owl pellets, rs – survey of roost, juv. – juvenile, coll – collected (museum) specimen (UAM – Adam Mickiewicz University of Poznań; ISEZ – Institute of Animal Systematics and Evolution PAS, Kraków; MIZ – Museum and Institute of Zoology PAS, Warszawa). If no abbreviation is given, the numbers refer to unsexed individuals or that no data about sex, age and reproduction status are available. Capital italics (e.g. *KK*) represent the initials of unpublished data owners (explained in the acknowledgements).

UTM square	Locality	Method	Date	Number and status of bats	Source
WS 43	Cieplice, fish ponds	obs		frequently recorded	Pax, 1925
WU 86	Folsztyn	pl (*Tyto alba*)	07.05.1984	1	Ruprecht 1990
XT 19	Jeziory f. i.	coll (UAM)	1965	1	Ruprecht 1983
XT 51	Milicz, fish ponds	obs, coll (UAM)		1	Pax 1925
XS 81	Niemodlin, fish ponds	obs		frequently recorded	Pax 1925
YU 01	Hutka f. d., Skorzęcin f. i., bat boxes	rs	1950-1951	3 times	Kozikowski & Niedzielski 1954
CB 45	Szachownica Cave	pl (*Strix aluco*)	01-02.1987 -1988	1	Kowalski & Lesiński 1990
CD 18	Solec Kujawski	pl	1964		Ruprecht 1979b, 1983
CD 56	Ciechocinek	pl (*Tyto alba*)	1960		Ruprecht 1964 in: Ruprecht, 1983
CD 66	Sumin	pl	1971		Ruprecht 1983
CE 52	Grudziądz, The Citadel	rs	05.02.2003	1 (mummified)	*KK*
CE 53	Pokrzywno, the old castle	pl (*Strix aluco*)	10.04.2001	1	*KK*
EC 90	Michów	pl	1961		Nikodem 1982, Ruprecht 1983
DV 57	Pieniny, Dunajec river[1]	obs			Sitowski 1948
DA 16	Biała Cave	coll (ISEZ)		1	Ruprecht 1983
DB 93	Świętokrzyski National Park[2]				Čmak 1968
DB 94	Świętokrzyski National Park[2]				Čmak 1968
DC 99	Warszawa-Marymont	coll (MIZ)	XIX century	1	Ruprecht 1983
DD 71	Fort Janowo	pl (*Tyto alba*)	14.10.1984	1	Kowalski & Lesiński 1986
EB 69	Włostowice	pl	1955		Ruprecht 1983
EE 08	Reszel	pl	1961		Ruprecht 1983
EE 18	Święta Lipka	pl	1961		Ruprecht 1983
EE 55	Kociołek	pl	1961		Ruprecht 1983
EE 77	Zelki	pl	1961		Ruprecht 1983
FB 79	Osowa, game-keeper's cottage	pl (*Strix aluco*)	1990-1991	1	Styka 2000
FD 48	Białystok	coll	1979	1	J. Kupryjanowicz in: Ruprecht 1983
CA 53	Pszczyna, fish ponds	obs		frequently recorded	Pax 1925
CA 78	Tuliszów	coll	1866	1 juv.	Wałecki 1881
EC 07	Jeziorna	coll (MIZ)	XIX century	1	Ruprecht 1983

[1] doubtful according to Kowalski (1955), thus not included in the analysis

[2] no details on date, status nor localities were given, thus we regarded these records as doubtful and rejected them from the analysis

Annex 5. Fossil records of the pond bat in Poland

UTM square	Locality	Period	Source
WS 94	Wschodnia Cave	Pleistocene	Zotz 1939 in: Wołoszyn 1987
CB 72	Maurycego Cave	Holocene	Postawa 2004
CB 72	Pod Sokolą Górą Cave	Holocene	Postawa 2004
CB 72	Studnisko Cave	Holocene	Postawa 2004
		Pleistocene	Bednarczyk in: Horáček & Hanák 1989
CB 72	Urwista Cave	Pliocene	Horáček & Hanák 1989
CB 72	Zamkowa Dolna Cave	Pliocene	Wołoszyn 1987
CB 81	Trzebniowska Cave	Holocene	Postawa 2004
CB 90	Studnia Szpatowców Cave	Pliocene[1]	Kowalski 1956
CB 90	Żabia Cave	Pleistocene	Horáček & Hanák 1989
CB 91	Kryształowa Cave	Holocene	Postawa 2004
DV 15	Czarna Cave	Holocene	Piksa & Wołoszyn 2001
DV 15	Nad Dachem Cave	Holocene	Piksa & Wołoszyn 2001
DV 15	Piwnica Miętusia Cave	Holocene	Piksa & Wołoszyn 2001
DV 15	Ptasia Cave	Holocene	Piksa & Wołoszyn 2001
DV 15	Studnia w Kazalnicy Cave	Holocene	Piksa & Wołoszyn 2001
DV 15	Szczelina Chochołowska Cave	Holocene	Piksa & Wołoszyn 2001
DV 15	Wysoka Cave	Holocene	Piksa & Wołoszyn 2001
DV 15	Zimna Cave	Holocene	Piksa & Wołoszyn 2001
DV 37	Obłazowa Cave	Holocene	Ochman & Wołoszyn 2003
DV 57	cave in Szopczański Gorge	Holocene	Alexandrowicz et al. 1985
DA 16	Bramka Cave	Holocene	Madeyska 1981
DA 16	Na Tomaszówkach Dolnych Cave	Holocene	Postawa 2004
DB 56	Kozi Grzbiet	Pleistocene	Wołoszyn 1987
DB 63	Raj Cave	Holocene	Wołoszyn 1987
EB 02	Zbójecka Cave in Łagów	Holocene	Wołoszyn 1989
FA 43	Józefów, karst fissures	Holocene	Kowalski et al. 1963

[1] as *Myotis dasycneme subtilis*

Re-mating in otter *(Lutra lutra)*

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Abstract: After the first observation of three morulas in the uterus of an otter (*Lutra lutra*) (Broekhuizen et al. 2004) a second observation of three morulas, together with three early-stage blastocysts, was made in April 2005. In the light of the short period of delayed implantation of blastocysts in the mucous membrane of the uterus we discuss the probability of this indicating re-mating and compared the evidence with the more frequent occurrence of superfoetation in the American mink. (*Mustela vison*).

Keywords: otter, Eurasian otter, *Lutra lutra*, re-mating, delayed implantation, superfoetation, morula, blastocyst.

Introduction

The female otter (*Lutra lutra*) is known to be polyoestrous, having a succession of oestrous periods and no specific breeding season. This mustelid does not have the several months long delayed implantation of ova in the mucous membrane of the uterus that is found in the martens (*Martes spp.*), the badger (*Meles meles*), the American mink (*Mustela vison*), the stoat (*Mustela erminea*), the American long-tailed weasel (*Mustela frenata*) or the American river otter (*Lontra canadensis*). In those species fertilised ova develop into morulas during their passage in the oviduct, the stage in which the lump of cells becomes surrounded by a thick layer of protective mucus, the zona pellucida. At around the time that the morula enters the uterus, a cavity is formed within the morula and the zona pellucida disappears. The morula then becomes a blastocyst, which consists of one layer of wall cells around the cavity and the remaining lump of inner cell mass from which the embryo (the embryoblast) will develop. During delayed implantation the blastocyst remains in the uterus, where it is unattached to the uterus wall and grows slowly by enlarging the central cavity.

We might generalise from the discovery of three morulas in the uterus of an otter (Broekhuizen et al. 2004) that the ova of this species develop more slowly during their passage in the oviduct than is the case with other related species (in which the ova have already developed to the blastula stage upon entering the uterus). In the case described here, the morulas still had a thick zona pellucida after entering the uterus.

Although the otter does not have a delayed implantation of several months, this species belongs to a group of mustelids in which the pre-implantation period is longer than in many other mammal species. In otters this pre-implantation period lasts 12 days or more after mating (Mead & Wright 1983), in the weasel (*Mustela nivalis*) it lasts about 11 days (Heidt 1970), in the ferret (*Mustela putorius furo*) it occurs after 10 days (Strahl 1906, cited in Hansson 1947) and in the American mink after about 16 days (Hansson 1947). This means the chances of finding blastocysts in the uterus of these species is greater than in mammal species with a ‘normal’ pre-implantation time of about three days.

After the first finding of morulas in the uterus of a female otter, checking the uterus of otters for morulas has became part of the routine autopsy procedure for females found dead.

Observation

Since 2002 otters have been reintroduced into the Netherlands (Lammertsma et al. 2006), but the species remains rare. Several cases of reproduction have been established, but the number of otters is being reduced by road traffic victims. On April 30, 2005 a female otter was killed on the road close to where she was released on June 25, 2004, after having been caught along the river Tirza in Latvia on May 24 2004. At that time her body weight was 5.9 kg and her age was estimated (based on the tooth wear) as 3-4 years old. When she died her condition was quite good and her body weight was 6.45 kg. Both uterus horns had a placental scar, indicating that she had littered before. As the nipples were visible but not very pronounced, her last litter had already been weaned.

When the uterus horns were flushed three morulas, with a thick zona pellucida, were found, as well as three blastulas with a still thin zona pellucida (figure 1). Two morulas and one blastula were found in the left horn and one morula and two blastulas in the right one. Only three corpora lutea were visible, two in the left ovary and one in the right one.

Discussion

For otters we have no information about how long after entering the uterus the morulas lose the zona pellucida. The thin remains of the zona pellucida still present around the blastulas found in the uterus suggest that these blastulas did not stay there for long before the morulas arrived, although this is not certain. The question arises

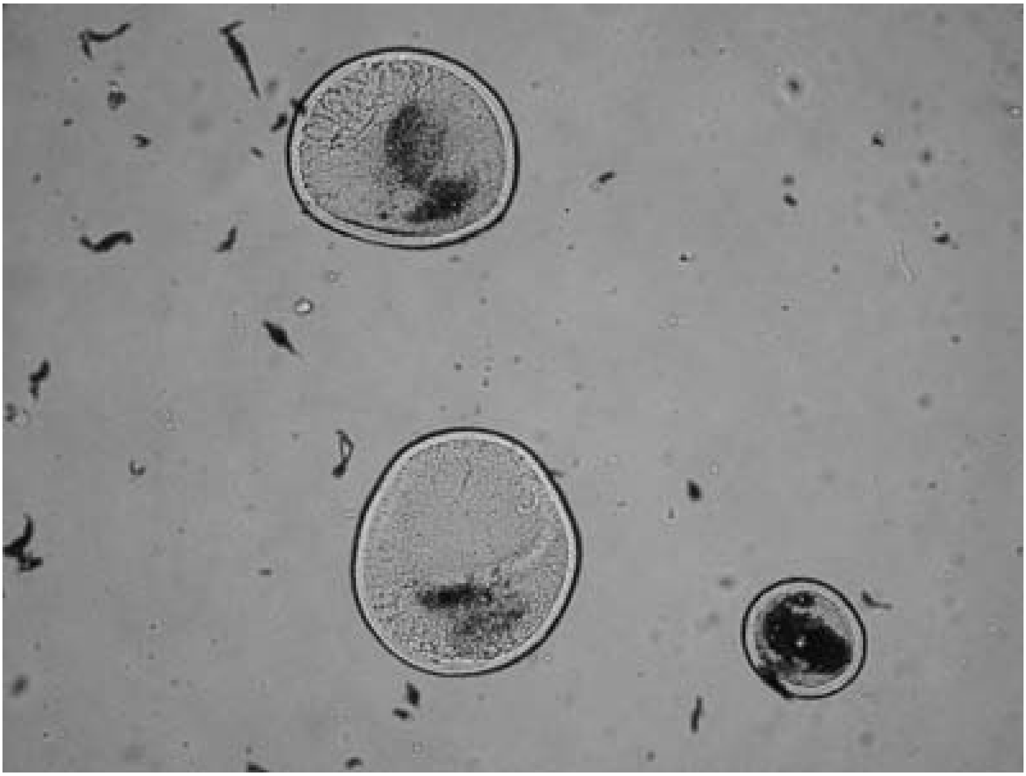

Figure 1. One morula and two blastocysts found in one of the uterus horns of an otter. *Photograph: Wim Dimmers, Alterra.*

of the possible cause of the simultaneous presence of these two stages of development of ova. Several possibilities can be hypothesised.

One hypothesis is that both stages of development resulted from the same bout of ovulation, but there was some variation in the rate of development of the ova. In the mink it takes the ova about 6.5 days after ovulation until the stage of morula has been reached (Hansson 1947). Normally the litter size of the otter is small, mostly two or three and rarely four (Wayer 1979, Kruuk 2006). Occasionally, however, litters of five have been reported (Van Wijngaarden & Van de Peppel 1970, Hauer et al. 2002). Harris (1968) and Baruš & Zejda (1981) mention rare cases of six cubs. An argument against the possibility of one ovulation and a variation in the rate of development of the ova is that all three morulas and all of the three blastulas were in almost exactly the same stages of development.

Another possibility is the fertilisation of ova from two different ovulations within the same period of oestrus. Female otters come into oestrus every 30-45 days (Gorman et al. 1978, Wayer 1979) and remain so for about two weeks (Wayer 1979). Within these periods of oestrus the female appears to be an induced ovulator (Jorga et al. 2004). Reuter (1993) found that among female captive otters successful impregnation was nearly always achieved as soon as a male was admitted to the female.

We have no information about the occurrence of repeated ovulation after a successful mating during the likely period of two weeks of oestrus of the female or of re-mating during that period. Green et al. (1984) found in a pair of radio-monitored free ranging otters that after copulation the male appeared to continue to attempt further matings, but that the female's interest had waned.

Hansson (1947) found that female American minks allow several matings at intervals of between 1-2 and 7-10 days. Ovulation occurs 36-37 hours after mating (Dunstone (1993) mentions a variation of 36-42 hours). Hansson (1947) also found that female minks frequently ovulate for a second time after re-mating. This observation was based on the autopsies of females that had been mated twice, among which two sets of corpora lutea were found which histologically appeared to be of different ages. If this also holds true for the otter, the different stages of development of the ova that we found could be the result of two matings. Among mink Shackleford (1952) found consecutive matings, usually seven days apart. In nearly 15% of the females that he allowed to mate twice within this period the mating resulted in a litter containing offspring from different males, based on the different colourings of the fathers. More recently Yamaguchi et al. (2004), using microsatellite markers, confirmed the occurrence of multi-paternity in free-ranging American minks.

Shackleford (1952) considered mink litters resulting from fertilisation of ova of different ovulations as cases of superfoetation, as distinct from superfecundation, i.e. the fertilisation by successive matings of ova from the same period of ovulation. Superfoetation is known among the badger, where females sometimes become impregnated for a second time during the, less intensive, autumn mating-season, after having already been impregnated during the main mating-period in late winter or early spring (Harris & Neal 1956, Cresswell et al. 1992). As the growth of the blastocysts is more or less asymptotical, the blastocysts of the second impregnation may be similar in size at the moment of implantation, resulting in a mixed litter, possibly sired by different males.

It is not known whether the simultaneous presence of morulas and blastocysts within the uterus of the female otter originated from one and the same ovulation (superfecundation) or from two different ovulations (superfoetation). The repeated impregnation might be the result of mixed paternity, as otters are probably both polygynous and polyandrous (Kruuk 2006). However, it is unknown whether litters with cubs sired by different fathers occur in nature.

Although a litter size of six is exceptional for otters, this does not imply that ovulation of six ova is equally rare. Hauer et al. (2002) found prenatal losses of foetuses, e.g. three foetuses in a litter of five among otters in Eastern Germany. In the American mink superfoetation results in a larger litter size. Possibly, some of the larger litters in otters result from superfoetation. In cases of mixed paternity among minks only a small proportion of the ova from the first ovulation succeed in implantation in the uterus wall (Shackleford 1952).

As an incidental observation, when slicing the ovaria by hand, we only found three thriving corpora lutea. According to Hauer et al. (2002), thriving corpora lutea will fill about 75% of the ovaria, so it is unlikely that we missed three corpora lutea. We have no real explanation for this discrepancy. Possibly, it was a consequence of multi-oocytic follicles (MOFs), characterised by two or more oocytes surrounded by a common follicular envelope. MOFs have been reported at low but variable frequencies in mammal species from different orders, with the frequency increasing with oestrogenic contaminants in the environment (Guillette & Moore 2006). It is speculative whether this is a factor in this case.

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Samenvatting

Dubbele bevruchting bij een otter (*Lutra lutra*)

Na de eerste waarneming van de aanwezigheid van drie morula's in de baarmoederhoorns van een otter (Broekhuizen et al. 2004), werden bij een in mei 2005 doodgereden otter (*Lutra lutra*) naast drie morula's ook drie blastocysten in de baarmoeder aangetroffen. Dit gelijktijdig voorkomen van verschillende ontwikkelingsstadia van bevruchte eicellen duidt op herhaalde bevruchting in verschillende perioden van oestrus (superfoetatie). Het optreden van superfoetatie is mogelijk doordat otters een, zij het korte (ruim 12 dagen), periode van uitgestelde implantatie van de blastocysten hebben. Het voorkomen van superfoetatie bij otters wordt vergeleken met dat bij Amerikaanse nertsen (*Mustela vison*), waarbij de aanwezigheid van gemengde worpen afkomstig van opeenvolgende paringen met verschillende mannetjes ook in het wild is vastgesteld.

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Book Reviews

Cetaceans in the North Sea

Whales and dolphins of the North Sea. C.J. Camphuysen & G.H. Peet 2006. Fontaine Uitgevers BV, 's Graveland, The Netherlands. 159 pp. ISBN-10: 90 5956 2216 or ISBN 13: 978 98 5956 2219 [in English]. ISBN-10: 90 5996 157 or ISBN-13: 978 90 5956 1 [in Dutch].

In recent years there has been a surge of public interest in cetaceans in the Netherlands and Belgium, not the least because of the growing number of sightings and strandings of cetaceans in the southern North Sea. These events have been documented in specialised journals such as Lutra and the Journal of Applied Ecology but, until now, a more popular publication for a broader audience has been lacking. At the start of the International Year of the Dolphin a new book by Kees Camphuysen and Gerard Peet, *Walvissen en dolfijnen in de Noordzee*, meets this demand. The book was initiated by the North Sea Foundation (Stichting De Noordzee) and presents an up to date review of the occurrence and distribution of cetaceans in the Dutch and Flemish parts of the North Sea. It is illustrated with numerous photographs and with drawings by Frits-Jan Maas, who had already worked with Gerard Peet on their earlier book (Peet, G., H. Nijkamp, P.-H. Nelissen & F.-J. Maas 1992. Bruinvissen, dolfijnen en walvissen van de Noordzee. M.& P., Weert, the Netherlands). Much however has changed since the publication of that book.

This new book contains an interesting introduction, followed by accounts of the different species. The introduction describes the North Sea environment from its genesis onwards. It discusses fossil records of cetaceans and gives a brief history of the transition from whale hunting to dedicated research which now provides the (primary) source of information. This section illustrates how the monitoring of living cetaceans is more or less a by-product of a nationwide sea watching scheme supported since the early 1970s by dedicated volunteer birdwatchers.

The species accounts are divided in four sections. These are based on abundance, ranging from common residents (three species: harbour porpoise (*Phocoena phocoena*), common bottlenose dolphin (*Tursiops truncatus*) and white-beaked dolphin (*Lagenorhynchus albirostris*)) to extinct (one species: gray whale (*Eschrichtius robistus*)). Depending on the status of the species and available data, the authors describe seasonal and distributional patterns in the (southern) North Sea, illustrated with graphs and distribution maps. In addition they provide a brief summary of how to identify the species, their ecology and distribution in the (Northeast) Atlantic. The resulting species accounts are rather extensive, with, for instance, two pages devoted even to the extinct gray whale.

The occurrence of species is described for different periods: the ancient past, before 1900, 1900-1960, and 1960-2005. Though highly anecdotal, descriptions from the past provide a historical context. Not surprisingly, the most recent data are the most detailed. Most species are only known from strandings, clearly showing that the shallow North Sea is not a prime habitat for most cetaceans.

Reading the species accounts, one thing is striking: how the identification, even of easily identifiable species, frequently poses a problem. The publication of a Dutch identification guide might help address this. Perhaps Kees Camphuysen could update his 1987 identification guide, the "Handleiding voor de determinatie van walvisachtigen (cetacea) in het Noordoost-Atlantisch gebied." ("Handbook for the identification of cetacea in the Northeast Atlantic")

Compared to Gerard Peet et al's earlier book on cetaceans, this new book contains more detailed information, especially on the distribution and seasonal occurrence of live animals. Overall, this book is a pleasure to read, containing a plethora of information on cetaceans.

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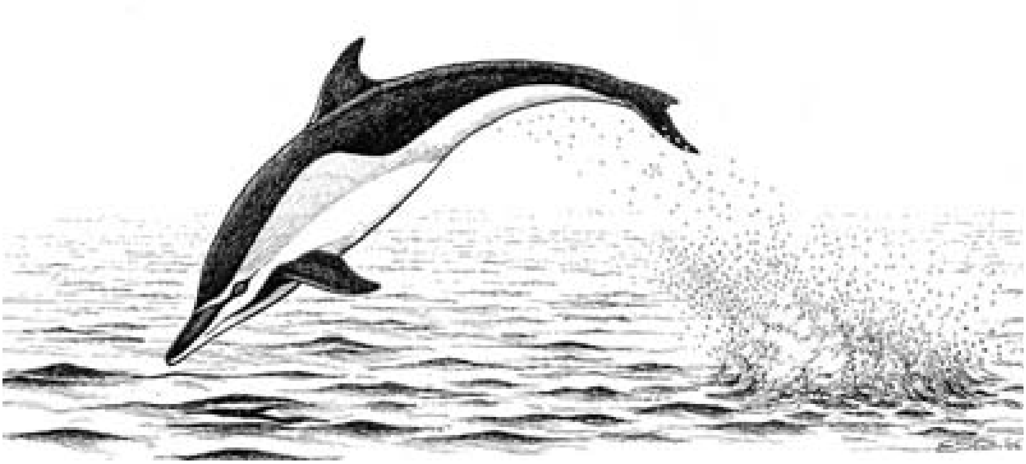

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