L U T R A

Volume *Deel* 47 – Number *Nummer* 2 – December 2004

Contents *Inhoud*

Editorial / Redactioneel

Contributed Papers / Artikelen

Short Notes / Korte Berichten

Opinion / Opinie

Recent Publications / Recente Publicaties

Index

Printed by Grafisch bedrijf Ponsen & Looijen bv, Wageningen
ISSN 0024-7634

LUTRA

Journal of the Society for the Study
and Conservation of Mammals

Volume 47 – Number 2 – December 2004

LUTRA

Volume *Deel* 47 – Number *Nummer* 2 – December 2004

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’, ‘Zoological Record’ and ‘Artik’.

Editorial board *Redactie*	Kees J. Canters (editor-in-chief), Jasja Dekker (secretary), Edgar A. van der Grift, Jan Piet Bekker, Kamiel Spoelstra, Goedele Verbeylen, Ben Verboom (managing editor)
Editorial assistant *Redactie-assistent*	Steve Geelhoed
Address *Adres*	Oude Kraan 8, NL-6811 LJ Arnhem, The Netherlands e-mail: lutra@vzz.nl
Website	Lutra abstracts are available from: http://www.vzz.nl
Subscription *Abonnement*	The annual fee for a subscription to Lutra is € 17.50. The annual fee for a Lutra subscription and VZZ-membership is € 25. This also includes a subscription to *Zoogdier*, a journal that publishes in Dutch only. Students are entitled to a discount of € 4.50 for the first two years of their VZZ-membership. Outside The Netherlands or Belgium: add € 3.50 to all prices. Send payment to one of the following accounts: The Netherlands: account 203737 of the ‘Postbank’, addressed to VZZ, Arnhem, Netherlands (IBAN: NL75PSTB0000203737; BIC: PSTBNL21). Belgium: account 000-1486269-35 of the ‘Bank van de Post’, addressed to VZZ, Arnhem, The Netherlands.
Stichting Publicatiefonds Lutra	Rob C. van Apeldoorn, Edgar A. van der Grift & Bauke Hoekstra Information: Bornsestraat 118, NL-7601 GK Almelo, The Netherlands

SOCIETY FOR THE STUDY AND CONSERVATION OF MAMMALS

Information *Secretariaat*	VZZ, Oude Kraan 8, NL-6811 LJ Arnhem, The Netherlands tel. +31 (0)26 37 05 318; fax +31 (0)26 37 04 038 e-mail: zoogdier@vzz.nl website: http://www.vzz.nl
Photograph cover by:	Edgar A. van der Grift
Art:	Froukje Rienks (page 100), Ed Hazebroek (page 112,142), Elias Nauta (pag. 126)

ISSN 0024-7634

Instructions to authors

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.
9. In general, refer to tables, figures and photographs at the end of a sentence between brackets: (figure 1) or (table 1) or (photo 1). With maps use a scale bar to depict the units of measurement or distance. For figures use simple symbols or patterns, all in black and white. Contact the editorial board if you need to have a figure printed in colour. When you construct a table use tabs or the table function and use only horizontal lines.
10. Tables, figures and photographs are either one or two columns wide. Please prepare your tables and figures in such a way that the axis titles remain readable. Use the “times new roman” font for the axis titles, legend and possible footnote. Axis titles start with a capital letter and have no point at the end.
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.

    Barrett, G.W. & J.D. Peles (eds.) 1999. Landscape ecology of small mammals. Springer, New York, USA.

    Bergers, P.J.M. 1997. Versnippering door railinfrastructuur. 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 landscapes in the Negev Desert, and the implications on military activity. Nature Reserves Authority, Jerusalem, Israel. (In Hebrew with English summary).
13. Use the entire width of the page; do not prepare your manuscript in two columns. Do not hyphenate words at the right margin and use only left justified text. Prepare your manuscript on A4 sized pages with 2.5 cm margins and double space between the lines.
14. The first page should show the title, authors and authors’ addresses. The page that follows starts with the abstract, immediately followed by the key words and the body of the manuscript. Tables and accompanying text should be placed at the end of the manuscript, followed by the text accompanying figures and photographs. The figures and photographs should be on separate pages that also show the figure number and the name of the first author.
15. Book reviews of Dutch publications may be written in either Dutch or English. Reviews of publications in any other language should be written in English.
16. We encourage you to submit your manuscript digitally (3.5’’ diskette or cd rom, preferably in Word97) and through e-mail as this speeds up the reviewing process. If you submit your manuscript on paper please include a total of three copies (laser printer, figures with 600 x 600 dpi). Please include the telephone number, fax number and e-mail address of the corresponding author.
17. There are no page charges for Lutra, but contact the corresponding editor for information concerning the costs of colour illustrations.
18. Manuscripts should be sent to the editorial board: Vereniging voor Zoogdierkunde en Zoogdierbescherming (VZZ), Redactie Lutra, Oude Kraan 8, NL-6811 LJ Arnhem, The Netherlands. The e-mail address of the editorial board is: lutra@vzz.nl. Close to or shortly after publication you will receive 25 reprints free of charge.
19. The editorial board strongly advises you to have your manuscript critically reviewed by colleagues before you submit your manuscript.

Sousliks

It is no easy task to understand fluctuations in population density and the mechanisms underlying the disappearance, (re)colonization and successful dispersal of species. Often tremendous efforts are necessary in order to gain insight in these processes, they include sampling many variables, radio tracking numerous individual animals, or the patience to wait for the outcome of observations consistently collected over a long time span. Insight into such ecological mechanisms is, however, indispensable to draw conclusions about population viability and the possibilities for the survival of a species.

In recent times our knowledge about the distribution of most species has improved considerably. However, all efforts to further improve our knowledge about species distribution remain highly relevant, especially in the case of rare or little known species. The collection of data on the distribution of the European mink in northwestern Spain by Zabala et al. is a good example. Keeping track of the distribution and density of the species will be the next step. Ideally, when monitoring a species, different and consistent sources of information can be drawn on. Such possibilities are well utilized by Camphuysen, who discusses the situation of the harbour porpoise in Dutch coastal waters, based on data of stranded animals, recordings from birdwatchers and at-sea observations.

Insights into the level and success of dispersion are of equal importance. Some species can experience great difficulty in their attempts to reoccupy suitable habitat patches. Reintroduction may be an option, however, it should only be considered if spontaneous recolonization can be excluded for the near future. It is highly relevant to extensively discuss prerequisites for the reintroduction of a species, and to judge whether they meet international standards, as is done by Van ’t Hof & Van Langevelde in the case of the release of otters in Overijssel (The Netherlands). However, such conditions are difficult to quantify, and only time will tell whether a reintroduction will be really successful or not.

In this issue, we are happy to host three articles, Millesi et al., Hoffmann et al. and Spoelstra et al., that result from a meeting on the ecology and conservation of the European souslik, that was organized in Madzharovo, Bulgaria, by BirdLife Bulgaria, October 25–28, 2002. The conference was held in response to the dramatic decline in European sousliks, an important food source for birds of prey in the Eastern Rhodope Mountains (southeast Bulgaria) during the summer season. Although much information concerning measures for habitat improvement was already available, the meeting was an excellent initiative, which was very productive in the establishing of contacts for future cooperation. The souslik papers that are included in this issue all originate from studies on a population in the municipal park of Langenzersdorf near Vienna, Austria. This area has a history as important resource for research on sousliks, but now apparently turns

Photograph: Edgar van der Grift

out to be an important sink for the species itself. Please get to know about these fascinating mammals: their mating behaviour in high and low population densities, the factors that determine the (minimal) chances for successful dispersion and the fine tuning of their daily activity patterns.

Together with Bauke Hoekstra, the editorial board has decided that, in the future, the list of Dutch publications on mammal research should be made available in a different format. The list of such publications from 2003 in this issue will be the last one. The tradition of annually printing such an overview in Lutra goes back to 1983, and the first list ran back to 1974! The annual publication of a similar list of Belgian papers on mammal research, assembled by Erik Van der Straeten, came to an end some years ago. A printed version in Lutra is, in our opinion no longer appropriate, since a printed list lacks the possibility to do, say, keyword searches. The editorial board is very grateful to Bauke Hoekstra and his co-workers for generating bibliographies for so many years. The Society for the Study and Conservation of Mammals intends to continue to work together and to make the list available soon, in a in a more dynamic and interactive format.

We are pleased to announce that with this issue Goedele Verbeylen has joined the Lutra editorial board. Actually, she has worked with the board before as a guest editor for issue 45(2), helping us with the special issue on rodents that resulted from a symposium in Antwerp in 2002. Goedele works with mammals in her profession as a scientific officer at the Flemish Institute for Forestry and Game Management. In addition, she has close ties with the Flemish Natuurpunt movement (especially the Mammal Working Group). The editorial board surely will benefit from her knowledge on rodents, as well as her contacts with Flemish mammal researchers.

Reproductive strategies of male European sousliks (*Spermophilus citellus*) at high and low population density

Eva Millesi[1], **Ilse E. Hoffmann**[1] **& Susanne Huber**[2]

[1] Department of Neurobiology and Behavioural Sciences, University of Vienna, Althanstrasse 14,
A-1090 Vienna, Austria, e-mail: eva.millesi@univie.ac.at
[2] Research Institute of Wildlife Ecology, University of Veterinary Medicine Vienna, Savoyenstrasse 1,
A-1160 Vienna, Austria

Abstract: The spring population density of European sousliks (*Spermophilus citellus*) in a suburban area near Vienna, Austria, changed from 60 to 6 individuals/ha from 1991 to 1998. The decline occurred during the active seasons of 1994 and 1995. In order to investigate effects of population density on reproduction we examined male mating effort and success. Male home-range size, intrasexual aggression, mass loss during the mating period, and individual reproductive success changed with population density. Home-range size increased with density decline, whereas aggression and mass loss decreased. High densities were characterized by more intense male-male competition and a skewed distribution of mates per male. Mate numbers in low-density situations were normally distributed and all males were able to acquire at least one mate. At low density, all yearling males were reproductively active compared to only 13% in the high-density years. Mature yearlings had lower growth rates than non-reproductive ones. Analyses of cortisol secretion indicated high stress levels at low density throughout the season. These changes could be viewed as a facultative response to changes in mate availability and the distribution of reproductive success. On the other hand, the costs of reproduction could be amplified by precociousness associated with population density changes.

Keywords: population dynamics, mating effort, cortisol, growth patterns, *Spermophilus.*

Introduction

In seasonal-breeding animals, reproduction is limited by energetic and temporal constraints. These constraints are even more pronounced in hibernating species (Heaney 1984). As a result, in many of these species mating is restricted to a short period in spring and females produce only one litter per year (Michener 1984). These patterns of reproduction are part of an animal's life-history strategy, which arises from trade-offs in time and energy allocation for different seasonal processes. Energetic demands of developmental processes like structural growth or prehibernatory fattening often compete with those associated with reproduction (Emlen & Oring 1977, Clutton-Brock 1988). Environmental bottlenecks associated with seasonal activity in hibernators intensify the effects of these interactions. Patterns of reproduction must then be adapted to environmental and social circumstances. However, these parameters may exhibit spatio-temporal variations within the same species. Selection should favour strategies, which specifically regulate the allocation patterns while adapting to changing demands of an animal's environment. In small mammals, density changes can result in populations, which remain stable or fluctuate to only a minor degree for long periods while others show marked fluctuations, which may occur as regular cycles of growth and decline (Feldhamer et al. 1999). Population density can affect different aspects of an individual's life history, such as intrasexual competition, reproductive effort and success, or even survival.

Age at the onset of sexual maturity is an im-

---

portant life-history trait, which can reflect this adaptability (Daan & Tinbergen 1997). Precociousness shortens the latency to reproduce and thereby can prolong the overall time span for reproduction. On the other hand, individual mating success, which may interact with age, is highly dependent on mating effort (Emlen & Oring 1977). This in turn is directly related to mate availability and factors like the operational sex ratio (Emlen & Oring 1977). High intrasexual competition and/or low female availability have been proposed to delay puberty in males (Clutton-Brock 1988). Deferred maturity allows males to allocate more energy to growth and thereby increase their competitive ability (Kenagy et al. 1989). Longevity plays an important role here, in that this strategy necessitates survival over a number of breeding periods. These trade-offs can be extremely complex. Nevertheless, they have been documented in a number of species (Emlen & Oring 1977, Clutton-Brock 1988, Daan & Tinbergen 1997). We have been able to study these trade-offs over the course of a long-term field study (1991-1998) on European sousliks (*Spermophilus citellus*) (Millesi et al. 1998, Millesi et al. 1999, Hoffmann et al. 2003). During 1991-1993 population density in the study area was high (57 animals/ha) and remained quite constant until 1994 (Hoffmann et al. 2003). The numbers of sousliks decreased during 1994 and 1995 in a stepwise manner. This drop seemed to be mainly caused by a lack of immigration probably due to the loss of dispersal corridors and low local survival rates (Hoffmann et al. 2003). The density decrease was even more pronounced in males compared to females. Thereafter, the number of individuals in the area was much lower (about 8 individuals/ha) but remained stable during 1996-1998. This situation enabled us to compare male reproductive strategies at high population density with those in a low-density situation. In this report we analyzed effects of population density on male reproductive effort, age at puberty and subsequent individual consequences. Endocrine parameters, testosterone and cortisol were measured to gain information on gonadal and adrenal activity in both situations. In addition, behavioural observations enabled us to compare intrasexual aggression, home-range size and foraging at high and low density.

Materials and methods

Study area and trapping techniques

The study was carried out in a recreation area in Langenzersdorf (48°18’ N, 16°22’ E), near Vienna, Austria from 1991-1998. The area was characterized by 8 ha meadowland with scattered trees, mainly robinia (*Robinia pseudoacacia*), alder (*Alnus glutinosa*) and ash-tree (*Fraxinus excelsior*). Human residences surrounded the study area, offering small patches of suitable habitat for sousliks. In the analyses of behavioural and physiological parameters only data from 1991-1993 (high density) and 1996-1998 (low density) were used. The years 1994 and 1995 were excluded from this report because population density appeared to be very unstable and none of the juveniles born in 1994 could be recaptured in 1995. Individuals were delegated to three age classes: juveniles (<1 year), yearlings (1 year, juveniles of the preceding year), and adults (≥2 years). For comparisons only individuals with known age and reproductive status were used. Sousliks were observed and captured from spring emergence until the last individual had immerged into hibernation. Live trapping was conducted with Tomahawk traps baited with peanut butter on five days per week for 4-8 hours depending on weather conditions and seasonal activity changes of the squirrels. Trapping techniques and frequency as well as observation methods did not differ among the years included in this study. For permanent identification of the animals a transponder chip (PIT tag, Indexel or Data Mars) was subcutaneously injected in the neck. In addition, the fur was painted with a commercial hair dye in an individually recognizable pattern. Females were marked with brownish-red colour and males with black. The sousliks were weighed (±0.5 g, Sartorius laboratory scale) and head length was measured using a calliper (maximal length of skull) at each capture.

The area was scanned at periodic intervals on a daily basis. In earlier studies we have shown that by scanning 1 ha five times per day, >90% of marked individuals could be identified (Millesi et al. 1999). Checklists that were maintained daily from the beginning until the end of surface activity expanded the scan data. In these checklists all sightings of marked individuals (during scans, captures or from other observations) were registered. Population density was defined as the number of individuals present during the mating period. The premating phase was defined as the period between the first male and the first female emergence. The mating phase started with female emergence and ended one week after the last female had emerged. Thereafter, all females showed signs of gestation or lactation and no male sexual behaviour was observed (S. Steurer, unpublished data). Postmating was defined as the period from the end of the mating phase until the onset of moult.

Behavioural parameters

To determine the reproductive success of individual males, male-female interactions were observed from the onset of the mating period until all females had signs of gestation and male testes regression started. When females went into oestrus interactions like genital inspection, grooming and spatial cohesion were observed. Earlier studies had shown that spatial proximity with a male and a decrease in female aggression towards males occurred simultaneously and preceded mating. Non-oestrous females do not tolerate male proximity (Millesi et al. 1998). Copulation occurred underground, in the female's burrow. Therefore, mating was defined as synchronous burrow use by a male and a female in bouts longer than 5 minutes. Positions of males and females above ground were recorded using scan sampling every 30 minutes. Whenever a male and female were seen together (within one body length distance) the observation of the interaction continued and burrow use was registered. We had previously noted that synchronous burrow use with a male was very limited during the mating phase and hence can be taken as a marker for receptivity and copulation (Millesi et al. 1998). As shown earlier, common use of the female's burrow was only seen with one individual male/female (Millesi et al. 1998). Comparable behavioural data sets were available for 1992 and 1993 for high density, and for 1996 and 1998 for low density. Individuals were repeatedly observed 2-10 times per phase. Focal protocols were done in periods where the animals were most active (morning and afternoon). Aggressive interactions (spatial displacements of other individuals, chases and fights) between the focals and other individuals were counted and recorded as units/30 s-interval. At the same time, individuals within 15 m of the focal were noted at 30 s-intervals. This distance was used because observations had shown that animals at larger distances were never attacked. For analysis the number of interactions/focal protocol was divided by the average number of close individuals (within 15 m from the focal animal) /protocol (Smith & Dobson 1994). This method was used to correct conflict frequencies for individual density. During protocols, locations of focal individuals were recorded every 30 s in a 3.75 m sector network. From these point locations, movement (locomotion) was quantified and range size determined using the method of outer polygonal analysis (Kenward 1990). The range was summed over each phase. Foraging behaviour was expressed as a binary variable (1 = yes, 0 = no) per time unit.

Physiological parameters

Emergence body mass was measured in animals captured within three days after their emergence from hibernation. Mass loss during mating (mean g/day) was determined in males, which were captured at least at the beginning, in the middle, and at the end of the mating period.

The reproductive condition of individual males was determined at capture by measuring testis width externally with a calliper (Millesi et al. 1998). Reproductively active males had descended testes and scrotal pigmentation at emergence from hibernation. Testis regression started at the end of the mating period but scrotal pigmentation was evident until moult had been completed in late June (Millesi et al. 1998).

At capture, 100 µl blood was taken from the femoral vein. The blood samples were collected in heparinized capillaries, centrifuged in the field, and plasma was stored at –20°C until analysis. Plasma testosterone levels were analyzed in duplicate after a diethylether extraction (85% recovery rates) using a biotin-streptavidin enzyme-immuno-assay according to Palme & Möstl (1993). Testosterone was used as standard, the assay showed cross-reactions with testosterone (100%), 5α-androstane-17ß-ol-3-one (23%) and 5ß-androstane-17ß-ol-3-one (12%). Inter- and intra-assay variation was less than 10%. Adrenal activity was determined by measuring cortisol metabolites in faecal samples collected during captures. For each sample 0.5 g faeces were used; extraction was done in 4 ml of 90% methanol. Analysis was done using standard biotin-streptavidin enzyme-immuno-assays (Palme & Möstl 1997). Inter- and intra-assay variation was less than 12%.

Results

Density changes

Population density changed from 1991-1998. From spring 1991-1993 densities were high and quite stable (table 1). In the years 1996-1998 population density was significantly lower than in the first three years (Chi-square test, $P<0.001$) but stabilized at this level (table 1). No significant differences in spring density were found within high and low-density years. Adult sex ratio changed with animal numbers. Sex ratios of reproductive individuals were female biased in all years but decreased from 37% males on average at high densities to 15% at low density (t-test, $P<0.01$, table 1).

Table 1. Numbers of reproductive animals/ha and sex ratio. Individuals present in the study area during the mating period were the basis for comparisons. Sex ratio is expressed as proportion of males in the breeding population.

	Males	Females	Sex ratio
High density			
1991	19	39	0.32
1992	22	34	0.39
1993	24	36	0.40
mean	22	36	0.37
Low density			
1996	1	8	0.11
1997	1	7	0.12
1998	2	7	0.22
mean	1	7	0.15

Sexual maturity and mate numbers

At high density, most yearling males (82.6%, $n=34$) were reproductively immature. Only a small number of yearlings had descended testes (1991: 12.5%, $n=8$; 1992: 7.7%, $n=13$; 1993: 30.8%, $n=13$). This proportion changed at low density where all male yearlings trapped in the study area during the mating period were sexually mature. Scrotal pigmentation was present in all reproductively active males and remained until even after complete testis regression. Developmental processes in yearling males differed between the two situations. We had shown earlier that non-reproductive yearling males continued growth in their second season (Millesi et al. 1999). Precocious yearlings terminated growth after their first hibernation. We compared head length of reproductive and non-reproductive yearlings at the end of the active season. The latter were significantly larger than the precocious males (means ± SD; 52.6 mm ± 2.0, $n=12$ versus 49.4 mm ± 61.8, $n=8$; t-test, $P<0.05$). Non-reproductive males entered hibernation with a significantly higher body mass than mature yearlings (388.2 g ± 34.5, $n=10$ versus 297.6 g ± 31.2, $n=7$; t-test, $P<0.001$).

We compared numbers of mates acquired by males at high and low density to determine whether the increased female availability at low density affected individual reproductive success in males (figure 1). At high density the distribution was skewed (Wilk-Shapiro test, $P<0.04$). A high percentage of the males in the focal area had only one or even no mate. Some males were quite successful and had up to four mates. The few reproductive yearlings in high-density years were never observed to acquire a mate. At low density all males were able to acquire at least one female (figure 1) and mate numbers/male were normally distributed (Wilk-Shapiro test, $P>0.3$).

We examined some behavioural parameters, which have been shown in previous studies to be related to reproductive effort and success (Millesi et al. 1998; table 2). Aggression among males was an important parameter to investigate. We found that more aggressive encounters occurred during the mating period at high densities even when corrected for potential recipients. Aggression in the premating and postmating period did not differ significantly between the two density situations. It was consistently low. Agonistic interactions during mating often resulted in injuries. We correspondingly found differences in the proportion of males that had been injured during this period. Most of the high-density males (90.7%, $n=65$) trapped during mating or shortly thereafter had injuries, in the low-density years only 25% of the males had been injured ($n=12$). Home-range size increased significantly during mating in both situations but in line with the spatial distribution of individual females, males had larger ranges at low than at high density (table 2). Another important parameter was the time an individual spent foraging especially during the mating phase. Males in a situation with high competition spent less time feeding during the mating period than those at low densities (table 2).

Physiological parameters

An important parameter of reproductive effort was body mass loss during the mating period. At high density mass loss during mating was higher than at low density (t-test, $t=2.97$, $P<0.01$), and was positively correlated with mate number ($r_P=0.84$, $P<0.01$, figure 2). This significant relationship was not found in the low-density situation ($r_P=0.21$, $P=0.52$).

We compared endocrine parameters associated with gonadal and adrenal activity before, dur-

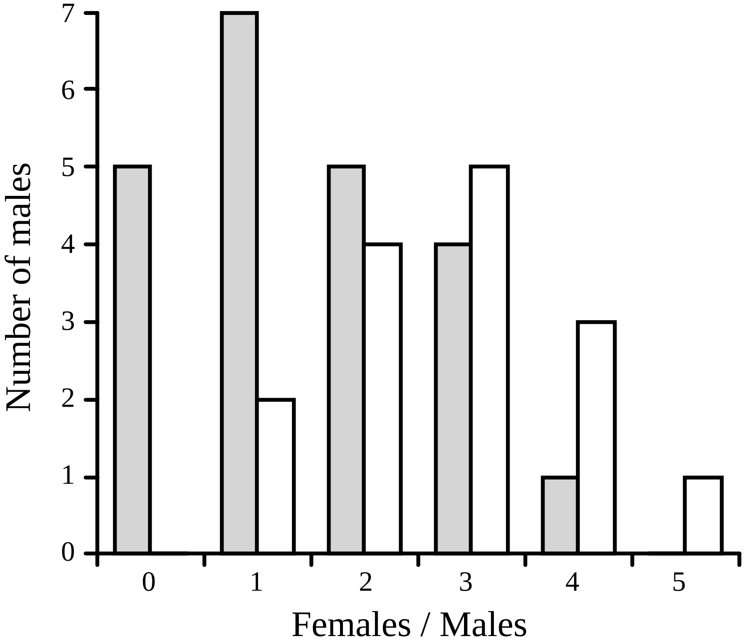


Figure 1. Distribution of acquired mate numbers of focal males at high (1992-1993; hatched bars) and low density (1996-1998; open bars).

Table 2. Seasonal changes in behavioral parameters of focal males at high and low population density. Male aggression is expressed as frequency/protocol, range size (ha) and foraging as percentage of time units/protocol in which the animal showed feeding behaviour. Medians and quartiles are shown, sample sizes per phase are 8/12/7 at high density and 6/6/5 at low density; (Mann-Withney *U*-tests, ** $P<0.05$, ns: not significant).

	High density	Low density	Significance
Male aggression			
Premating	0.0 (0.0, 0.2)	0.0 (0.0, 0.1)	ns
Mating	0.8 (0.6, 1.2)	0.5 (0.3, 0.6)	**
Postmating	0.4 (0.3, 0.6)	0.3 (0.3, 0.5)	ns
Range size			
Premating	0.05 (0.03, 0.08)	0.07 (0.06, 0.11)	ns
Mating	0.16 (0.12, 0.29)	0.38 (0.33, 0.48)	*
Postmating	0.06 (0.03, 0.09)	0.13 (0.08, 0.21)	ns
Foraging			
Premating	82.8 (66.2, 91.0)	67.3 (61.3, 79.7)	ns
Mating	17.7 (16.8, 33.1)	40.2 (38.2, 48.9)	*
Postmating	55.9 (51.6, 66.5)	47.5 (37.4, 63.8)	ns

ing and after the mating period. Patterns of testosterone secretion in plasma did not differ between high and low densities (figure 3). Males emerged from hibernation with elevated androgen levels independent of age and density. Levels decreased significantly after mating when males started testes regression (Mann-Whitney *U*-test, mating versus postmating, $P<0.001$ in both situations). Adrenal activity was monitored by documenting contents of cortisol metabolites in faecal samples (figure 4). The analyses showed that low-density males had higher cortisol levels in all three phases (high versus low density, Mann-Whitney *U*-test, premating: $P<0.01$, mating: $P<0.05$, postmating: $P<0.05$).

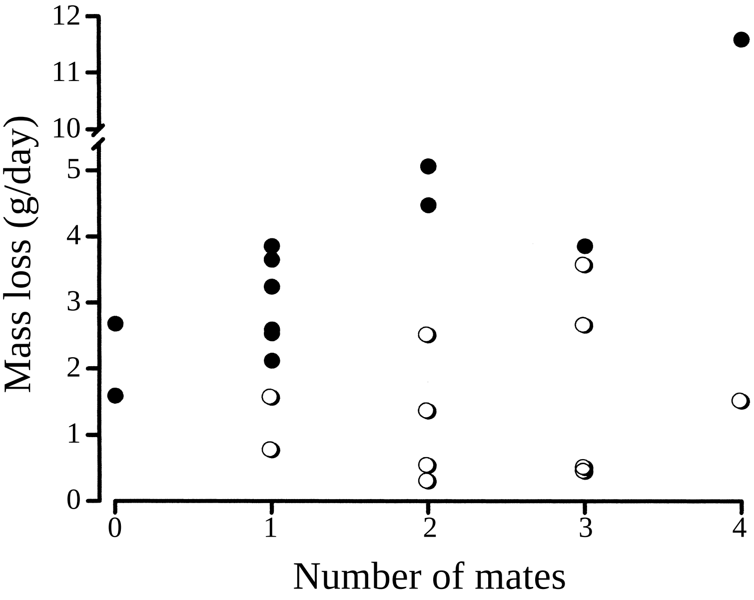


Figure 2. Mass loss and mating success of focal males at high (closed symbols) and low density (open symbols) during the mating period (high density: $n=15$, low density: $n=10$).

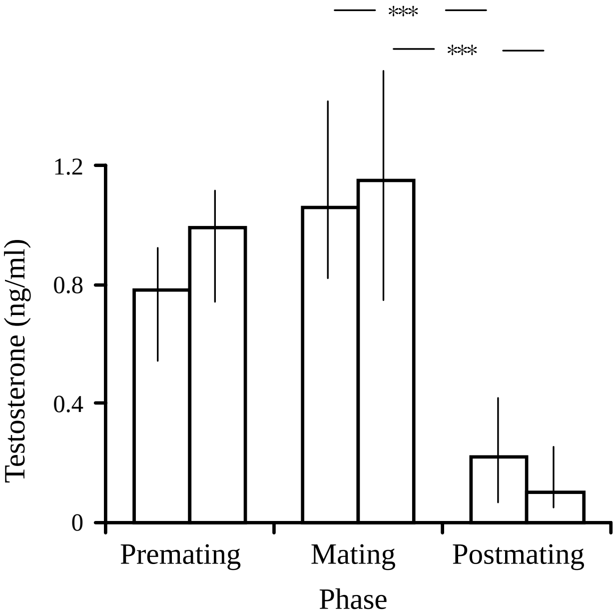


Figure 3. Patterns of androgen secretion in focal males during the premating, mating and postmating period at high (hatched bars) and low density (open bars). Medians and quartiles are plotted; sample sizes per phase are 11/16/8 at high density and 8/12/7 at low density. Significant differences are labelled ***.

Discussion

The comparison of male mating strategies, reproductive effort and success demonstrated differences between high and low population densities. In the high-density situation, intrasexual competition was high and evident in frequent displacements and fights. The sparse reproductive yearlings captured during the high-density years were not able to compete with older and heavier males. None of them was observed to acquire a mate and most disappeared at the end of the mating period. Non-reproductive yearlings were not attacked by older males (Millesi et al. 1998). They were able then to dedicate one complete active season to growth and preparation for hibernation. At high density with high frequencies of intra-male aggression an appropriate body condition may be considered as a pre-requisite to successfully compete for females. Mass-dependent delayed maturity among males of the genus *Spermophilus* has been described or proposed for a number of species including *Spermophilus beldingi*, *armatus* and *townsendii* (review in Michener 1984). As in *Spermophilus citellus*, the sexual maturation processes have been shown to be affected by trade-offs with growth patterns (*Spermophilus saturatus*, Kenagy et al. 1989) and potential mating success (*Spermophilus beecheyi*, Boellstorff et al. 1994). Kenagy et al. (1989) postulated that deferred maturity in yearling males is facultative in that some males forego testicular development and reproductive chances in one year to allocate more energy to growth. This kind of trade-off has been documented in *Spermophilus citellus* under certain circumstances (Millesi et al. 1999, Hoffmann et al. 2003).

In the low-density years, age at puberty in males changed (Hoffmann et al. 2003). All yearling males that emerged in the study area were reproductively mature. In contrast to the high-density situation, even yearlings with relatively low emergence body mass (<180 g) went through puberty in their first hibernation. Due to the wider distribution of females and strongly female-biased sex ratio, intra-sexual aggression was lower and locating oestrous females seemed to be more important for reproductive success than mate guarding. Therefore, mature yearlings had larger home-ranges and fewer agonistic encounters. All low-density males could acquire at least one mate and in contrast to high-density years, mate numbers were normally distributed among males. The

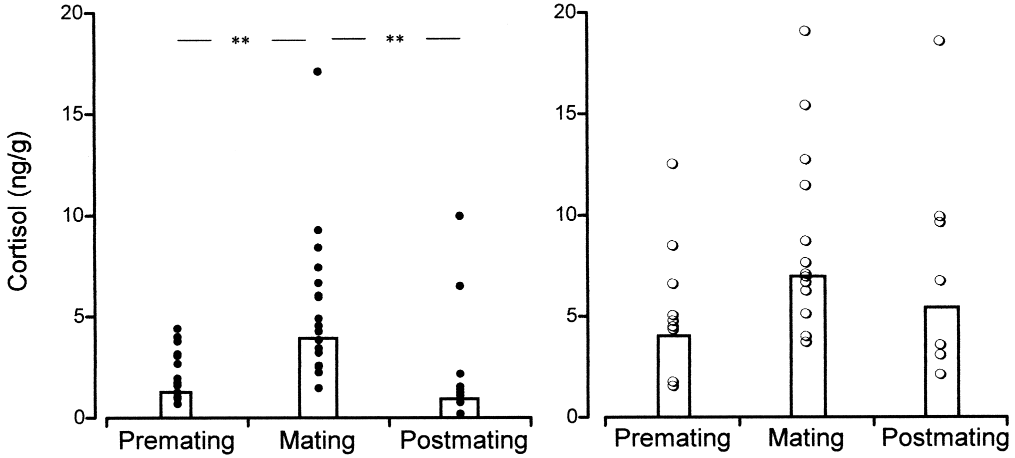


Figure 4. Cortisol metabolites in focal males during the premating, mating and postmating period at high (closed symbols) and low density (open symbols). Medians and individual values are plotted; sample sizes per phase are 11/16/8 at high density and 8/12/7 at low density. Significant differences are labelled ***.

behavioural results indicate that the energetic costs of mating were lower at low density. This is also reflected in the higher amount of time the animals could spend foraging and the lower proportion of mass loss during mating.

Adult male European sousliks immerge into hibernation with regressed gonads and emerge from their hibernacula with fully developed testes and elevated plasma testosterone levels in spring (Millesi et al. 1998). Testes growth and the onset of spermatogenesis hence occur in the burrow, during periodic arousals and/or after termination of torpor before vernal emergence, as has been shown for other *Spermophilus* species (Barnes 1986). Body condition before hibernation has been shown to be an important factor determining puberty in young males. Nonetheless, low density with high female availability was associated with precociousness in yearlings, apparently circumventing the body-mass constraint. Causes and effects here are still hypothetical. Different factors like the access to specific nutritional resources, suitable hibernacula and social interactions are affected by density and may have been critical in causing the changes (Florant 1998, Millesi et al. 1999, Bruns et al. 2000).

Mating is energetically costly with subsequent consequences for males. Body-mass loss, feeding decreases and perhaps stress effects of conflict and locomotion combined to initiate an earlier gonadal regression in highly successful males at high density (Millesi et al. 1998). High investment coupled with elevated adrenal activity can undermine maintenance levels of gonadal steroids via negative impacts on the pituitary. This explanation fits with the elevated cortisol levels during the mating period in both situations and the increase of agonistic interactions. High mating effort apparently can have carry-over effects, which are evident in the patterns of subsequent seasonal processes (Millesi et al. 1998). Early maturation, nonetheless, appears to create further difficulties for the males. Here one could assume disadvantageous metabolic and immune changes on the basis of adrenal activity. Negative metabolic effects of mating effort have been reported for some mammal species (Sapolsky 1987, Deutsch et al. 1990, Bronson & Heideman 1994). The results on adrenal activity at low density indicate high stress levels in spite of the apparently low frequencies of aggressive interactions. We propose that these findings might be related to a previously neglected aspect of early sexual maturity. One scenario would be that precocious individuals are more affected by mating effort than older males, producing elevated stress responses (Millesi et al. 2002). This in turn could result in lower survival rates due to decreased immuno-competency or susceptibility to predators. Survival seemed to be affected since at high population density males survived up to four breeding periods compared to a maximum of two seasons at low density. In a situation with high mortality rates especially among young males, selection should favour precocious males because the chance to survive to the next season might be very low.

High predation pressure on the other hand, could lead to increased adrenal activity throughout the season. Although first analyses indicate that the number of observed kills per year did not differ significantly between the two density situations, the individual risk of predation was certainly higher at low density producing higher stress levels for the males (I.E. Hoffmann, unpublished data). This effect would be reflected in elevated cortisol levels of all age and sex groups at low density. The samples analysed do not support this explanation (Millesi et al., unpublished data). We plan further investigations in semi-natural enclosures, which would provide the opportunity of manipulating specific environmental factors while monitoring changes in the males' physiology and behaviour.

Acknowledgements: The study was supported by the Austrian Science Foundation (FWF, Project P8337-BIO) and the Austrian National Bank (Project 6264). We thank Stefan Hanslik, Katharin Pieta and Sabine Steurer for their help in fieldwork and John P. Dittami for helpful comments on the manuscript.

References

Barnes, B.M. 1986. Annual cycles of gonadotropins and androgens in the hibernating golden-mantled ground squirrel. General and Comparative Endocrinology 62: 13-22.

Boellstorff, D.E., D.H Owings, M.C.T. Penedo & M.J. Hersek 1994. Reproductive behaviour and multiple paternity of California ground squirrels. Animal Behaviour 47: 1057-1064.

Bronson, F.H. & P.D. Heideman 1994. Seasonal regulation of reproduction in mammals. In: E. Knobil & J. D Niell (eds.). The physiology of reproduction, Volume 2.: 541-583. Raven Press, New York, USA.

Bruns, U., F. Frey-Roos, S. Pudritz, F. Tataruch, T. Ruf & W. Arnold 2000. Essential fatty acids: their impact on free-living alpine marmots (*Marmota marmota*). In: G. Heldmaier & M. Klingenspor (eds.). Life in the Cold, Volume 4: 215-222. Springer Verlag, Berlin, Germany.

Clutton-Brock, T.H. (ed.) 1988. Reproductive success. University of Chicago Press, Chicago, USA.

Daan, S. & J.M. Tinbergen 1997. Adaptation of life histories. In: J.R. Krebs & N.B. Davies (eds.). Behavioural ecology: An evolutionary approach: 311-333. Blackwell Science Ltd., Oxford, UK.

Deutsch, C.J., M.P. Haley & B.J. LeBoeuf 1990. Reproductive effort of male northern elephant seals: Estimates from mass loss. Canadian Journal of Zoology 68: 2580-2593.

Emlen S.T. & L.W. Oring 1977. Ecology, sexual selection and the evolution of mating systems. Science 197: 215-223.

Feldhamer, G.A., L.C. Drickamer, S.H Vessey & J. F. Merrit (eds.) 1999. Mammalogy: Adaptation, diversity and ecology. McGraw-Hill Company, Boston, USA.

Florant, G. 1998. Lipid metabolism in hibernators: the importance of essentially fatty acids. American Zoologist 38: 331-340.

Heaney, L.R. 1984. Climatic influences on life-history tactics and behavior of North American tree squirrels. In: J. O. Murie & G. R. Michener (eds.). The biology of ground-dwelling squirrels: 43-78. University of Nebraska Press, Lincoln, USA.

Hoffmann, I.E., E. Millesi, L.G. Everts, S. Huber & J.P. Dittami 2003. Population dynamics of European ground squirrels (*Spermophilus citellus*) in a suburban area. Journal of Mammalogy 84: 615-626.

Kenagy, G.J., S.M. Sharbaugh & K.A. Nagy 1989. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. Oecologia 78: 269-282.

Kenward, R. 1990. "Ranges V", Software for analysing animal location data. Institute of Terrestrial Ecology, Wareham, UK.

Michener, G.R. 1984. Age, sex and species differences in the annual cycles of ground-dwelling sciurids: implications for sociality. In: J.O. Murie & G.R. Michener (eds.). The biology of ground-dwelling squirrels: 81-107. University of Nebraska Press, Lincoln, USA.

Millesi, E., S. Huber, J.P. Dittami, I.E. Hoffmann & S. Daan 1998. Parameters of mating effort and success in male European ground squirrels, *Spermophilus citellus*. Ethology 104: 298-313.

Millesi, E., A.M. Strijkstra, I.E. Hoffmann, J.P. Dittami & S. Daan 1999. Sex and age differences in mass, morphology and annual cycle in European ground squirrels, *Spermophilus citellus*. Journal of Mammalogy 80: 218-231.

Millesi, E., I.E. Hoffmann, S. Steurer, M. Metvaly & J.P. Dittami 2002. Vernal changes in the behavioral and endocrine responses to GnRH-application in male European ground squirrels. Hormones and Behavior 41: 51-58.

Palme, R. & E. Möstl 1993. Biotin-streptavidin enzyme immunoassay for the determination of oestrogens and androgens in boar faeces. In: S. Görög (ed.). Advances of steroid analysis '93: 111–117. Akadeniai Kiado, Budapest, Hungary.

Palme, R. & E. Möstl 1997. Measurement of cortisol metabolites in faeces of sheep as a parameter of cortisol concentration in blood. Zeitschrift für Säugetierkunde 62: 192-197.

Sapolsky, R.M. 1987. Stress, social status and reproductive physiology in free living baboons. In: D. Crews (ed.). Psychobiology of reproductive behavior: 291-322. Englewood Cliffs, New York, USA.

Smith, A.T. & F.S. Dobson 1994. A technique for evaluation of spatial data using asymmetrical weighed overlap values. Animal Behaviour 48: 1285-1292.

Samenvatting

Reproduktiestrategieën van mannelijke siesels (*Spermophilus citellus*) bij hoge en lage populatiedichtheid

De voorjaarsdichtheid van een populatie siesels (*Spermophilus citellus*) in een suburbaan gebied bij Wenen, Oostenrijk, veranderde van 60 naar 6 individuen/ha tussen 1991 en 1998. De afname trad op tijdens de seizoenen dat de dieren actief zijn in 1994 en 1995. Om de effecten van populatiedichtheid op de reproduktie vast te stellen onderzochten we de reproduktie-inspanning en het reproduktiesucces van de mannelijke siesels. Homerange-grootte van de mannen, intrasexuele agressie, verlies aan lichaamsgewicht tijdens de voortplantingsperiode, en individueel reproduktief succes veranderde met de populatiedichtheid. Homerange-grootte nam toe met een afname in dichtheid, terwijl agressie en verlies aan lichaamsgewicht afnamen. Hoge dichtheden werden gekenmerkt door een sterkere man-man competitie en een ongelijke verdeling van vrouwtjes over de mannen. Het aantal vrouwtjes per man tijdens perioden met lage dichtheden was normaal verdeeld en alle mannen waren in staat om minstens één vrouw te verkrijgen. Tijdens lage dichtheden namen alle eenjarige mannen deel aan de reproduktie, vergeleken met slechts 13% van de eenjarige mannen in jaren met hoge dichtheden. Volwassen eenjarigen hadden een lagere groeisnelheid dan niet-reproduktieve eenjarigen. Analyses van cortisol secreties wezen op hoge stress niveaus gedurende het hele seizoen tijdens perioden met lage dichtheden. Deze veranderingen kunnen gezien worden als een facultatieve reactie op veranderingen in het aantal beschikbare vrouwtjes en de verdeling van reproduktief succes. Daarentegen kunnen de kosten van reproduktie verveelvoudigd worden door het vroeg tot volwassenheid komen, wat is gerelateerd aan veranderingen in populatiedichtheden.

Received: 15 October 2004
Accepted: 19 February 2005

Why males incur a greater predation risk than females in juvenile European sousliks (*Spermophilus citellus*)

Ilse E. Hoffmann, Ernst Muck & Eva Millesi

Department of Neurobiology and Behavioural Sciences, University of Vienna, Althanstrasse 14,
A-1090 Vienna, Austria, email: ilse.hoffmann@univie.ac.at

Abstract: Leaving a familiar area is assumed to involve an increased vulnerability to predation, yet rarely are movement patterns and mortality monitored directly. For this reason we examined the locomotor patterns and activity of 41 juvenile European sousliks (*Spermophilus citellus)* in relation to their individual fates. We investigated whether mortality risk increases with distance from the natal burrow, and we also attempted to distinguish sex-differential locomotor and anti-predator behaviours explaining the female-biased sex ratio among non-juveniles. During three years, weaned juveniles inhabiting a 4 ha plot in a recreation area north of Vienna, Austria, were equipped with radio collars. Nearly 76% of the tagged juveniles were killed by cats or disappeared with unknown fates. Only 5% (two females) permanently departed from their natal area and survived, that is to say, dispersed successfully. Survival of females more than doubled the male percentage and was independent from distance from the natal burrow, whereas most of the surviving males were philopatric. The major finding of this study was that nonsurviving juveniles had moved faster than survivors, with individual speed resulting in sex-differential mortality. Males tended to move faster than females, incurring a greater risk of predation when remote from their natal burrows. Further analyses of behaviour provided evidences that male-biased mortality could arise from sexually different patterns of time allocation to predator avoidance and vigilance. We conclude that among juvenile *Spermophilus citellus,* males perform an unfavourable trade-off in surface activity allocated to locomotion and vigilance.

Keywords: European souslik, *Spermophilus citellus*, ground squirrel, Austria, radio telemetry, natal dispersal, predation risk, survival, sex difference, locomotion.

Introduction

It is a common demographic trait of ground-dwelling squirrel populations that sex ratio is balanced among juveniles at emergence from their natal burrows, but female-biased among older animals (Boag & Murie 1981, Sherman & Morton 1984, Sauer & Slade 1987, Michener 1998). The proximate causes of this phenomenon are not as well documented. Although a wealth of information exists on sex-differential locomotor and exploratory activities (Holekamp 1984a, Holekamp 1984b, Michener 1989, Wiggett & Boag 1989, Shriner & Stacey 1991, Waterman 1995, Olson & Van Horne 1998, Byrom & Krebs 1999), virtually no explanation is given why these behaviours should be risky (Schmutz et al. 1979).

Similar to North American *Spermophilus*, sex ratios of European sousliks *(Spermophilus citellus)* are balanced at litter emergence and develop a skew towards females until the subsequent season (Hoffmann et al. 2003a). European sousliks are obligate hibernators with a pronounced endogenous annual cycle (Hoffmann 2002). The active season sets off with the emergence of reproductive males in early March and ends in late September, when the last juveniles immerge into hibernation (Millesi et al. 1999b). Mating is restricted to early spring, and females give birth 27–31 days later (Huber et al. 2001). Juveniles emerge from their natal burrows between the end of May and the beginning of July (Millesi et al. 1999b), 30–34 days after parturition, and are weaned at four to nine weeks of age (Millesi et al. 1999a, Huber et al. 2001). Fewer males than females are recruited into the yearling age class (Hoffmann 2003a), with most losses having occurred during the juvenile summer (Millesi et al.

1999b). To date, information on behaviour of juvenile European sousliks is sparse (Hoffmann 1995, Hoffmann 2002), and virtually nothing is known about behavioural sex differences in spacing and vigilance. We thus projected a detailed examination of movement patterns and concurrent activities during the juvenile summer as a first step to elucidate the origins of the skewed sex ratio among non-juveniles.

The purpose of our study was to track juvenile fates, and to detect sex-specific differences and possible risks associated with movement patterns, as has been described for North American members of the genus *Spermophilus* (Dobson 1981, Holekamp & Sherman 1989, Wiggett & Boag 1993). To this end, we radio-tracked locomotor behaviour of juvenile European sousliks in the field and investigated possible behavioural interactions with sex and mortality.

Materials and methods

Radio collars

We developed small-sized radio transmitters and collars for European sousliks, adapting circuit diagrams as described in Kenward (1987) and Naef-Daenzer (1993). Technical details appeared in Hoffmann (2002). The tag was shaped to fit a ground squirrel neck and was embedded in a latex collar with Velcro fasteners (figure 1). The collar could be adjusted to neck sizes between 8 and 10 cm and hence be suitable for juvenile and older sousliks. Compared to conventional radio collars, this design had several advantageous features: 1. the species-specific shape of the tag, 2. a total mass of maximum 4 g (<4% body mass of a weaned juvenile), 3. the elastic latex collar did not cut into the neck, and to a certain degree, expanded with juvenile growth, 4. the risk of strangling was minimised, because the animal was able to slip out and/or the Velcro fastener opened, 5. latex disintegrates and, in case the animal was not recaptured, the collar fell off.

Transmitter life was 15–30 days, after which the power cell could be replaced, enabling the reutilisation of the transmitter. The relatively small signal range (400 m) was compensated for by mobile bearing, that is, following weak signals or searching lost signals on foot. The range and life span of the transmitters proved workable in the field and enabled us to track sousliks virtually without disturbing their natural patterns of behaviour.

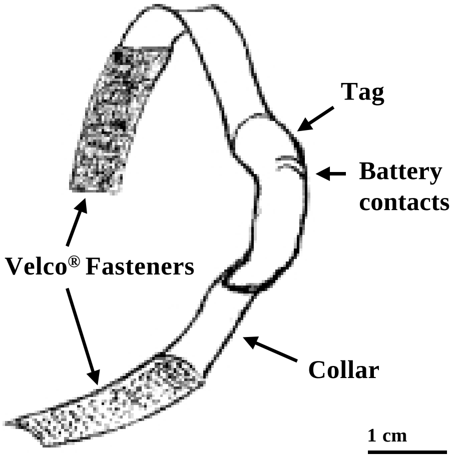


Figure 1. Radio collar for European sousliks (simplified representation).

Field study

We investigated European sousliks dwelling on a 4 ha plot in a recreation area (48°31’ N, 16°36’ E) north of Vienna, Austria. Detailed descriptions of the capture technique appear in Hoffmann et al. (2003a, b) and Millesi et al. (1999a, b). From 1996–1998, we consecutively equipped 41 weaned juveniles (29 males, 12 females) with radio collars. Between 25 June and 21 August, we followed each of the tagged individuals for a minimum of 5 days, unless its fate was known before. A programmable receiver (Telonics TR2+TS1) connected to a hand-held H-antenna and earphones was used to locate each tagged squirrel in 30-minute intervals daily between 8 a.m. and 2 p.m. At the same time we recorded whether the animal was seen aboveground. In 15 of the tagged animals (8 males, 7 females), we additionally monitored vigilance behaviour (bipedal postures). Locations were determined either visually by scanning the area with binoculars in the direction of the strongest signal, or acoustically by reference to the animal's preceding position. The individual bearings were transformed into x-y coordinates of a 15-m grid overlaying a 1:2000 field map. When a signal was received from outside the study site, it was followed on foot to check the location and state of the tagged animal. Kills were observed either directly during radio-tracking sessions or indirectly, when we recovered the radio collar and found evidence for predation (carcass, intestines, blood, etc.). Juveniles that disappeared after their radio collars had been removed had left the field site undetected, either actively as emigrants or passively as prey. Kills and disappearances were combined to nonsurvivors, if not mentioned otherwise. We used two estimates of survival: 1. until hibernation: juveniles known to be alive after 31 August (Millesi et al. 1999a), or 2. until the following year: individuals recaptured after hibernation.

We applied RANGES-V Software (Kenward & Hodder 1996) to analyse locations and to calculate locomotor attributes. We computed length of line between an animal's natal burrow and its location at specified times, and used this linear distance in meters (m) as an estimate of ranging behaviour. We related linear distances between locations to the time span within they had been covered, and thus calculated speed in meters per hour (m/h), which served as an approximation of mobility. As an average measure, its magnitude was influenced by both continuous running (temporal acceleration) and intermittent behaviour (deceleration). To examine developmental variations in movement patterns and their interactions with sex-specific survival and behaviour, we pooled individual data over 10-day periods (decades) post emergence from the natal burrow. Retreat into a burrow lowers predation risk even if not intended as anti-predator behaviour. Hence we regarded underground activity as predator avoidance and quantified it with the number of tracking intervals a focal individual was seen aboveground. Vigilance was measured with the number of observation intervals a focal animal spent in bipedal postures. Data sets were analyzed with non-parametric and parametric statistics, respectively, after performing Shapiro-Wilk tests for data distributions. *P*-values are outcomes of two-tailed tests.

Results

Most of the tagged juveniles were killed by house cats, and less than a third survived their first summer. The remainders' fate was unknown because their radio collars had been removed before they disappeared. Local survival of females more than doubled the male percentage, and >75% of the males were killed or disappeared with unknown fate, but only half of the females (table 1). Considering only juveniles with a known fate, 67% of the males died compared to 45% of the females (χ^2=9.1, df=1, P<0.01).

At nine weeks of age (during decade 4 after litter emergence), juveniles started to depart from their birth sites, travelling significantly farther distances than before (figure 2). Subsequently they either kept on with forays or shifted their home ranges. The period following the logistic incline (figure 2) coincided with the time of monitored predations. All kills involved juveniles during decades 4–7 after natal emergence at 9–14.5 weeks of age.

Table 1. Fates of radio-tagged juvenile European sousliks until hibernation. A significantly higher percentage of females than of males survived (χ^2 =14.4, df=1, P<0.001).

	Sample	% survived (n)	% killed (n)	% disappeared (n)
Males	29	24.1 (7)	48.3 (14)	27.6 (8)
Females	12	50.0 (6)	41.7 (5)	8.3 (1)
Total	41	31.7 (13)	46.3 (19)	22.0 (9)

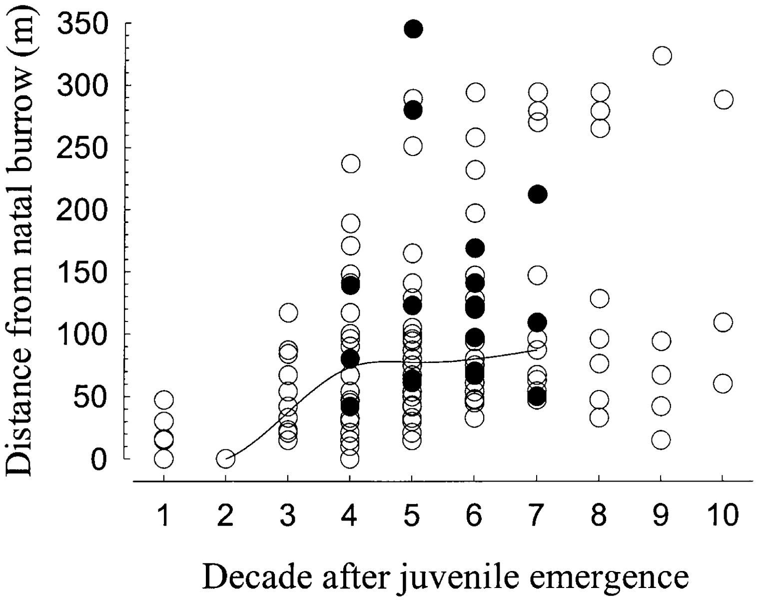


Figure 2. Association between age (10-day intervals post emergence) of juvenile European sousliks and maximum distance from their natal burrows. Distances in decade 3 were shorter than in decades 4 (n=11, P=0.005, Wilcoxon Z=-2.8), 5 (n=8, P=0.028, Z=-2.2) and 6 (n=7, P=0.028, Z=-2.2). During decade 7, juveniles travelled farther than during decade 4 (n=8, P=0.025, Z=-2.2). Median (*mdn*) ranging behaviour as a function of time (decades 1–7) is best fitted with a logistic regression (r^2>0.99). Black symbols indicate the timing of kills and the preceding maximum distance. Data points from decades 1, 2 and 10 are derived from visual localisations.

The six directly observed predation incidents occurred at a median (*mdn*) distance of 110 m from the natal burrow. This was significantly farther than the average movements of eight juveniles during decades 4–7 (*mdn*=38 m) that survived to the following year (P=0.028, Mann-Whitney U=7.0). Five of the six directly observed kills involved males. We therefore could not test statistically for sex-differential distances of fatal encounters; the female victim, however, was less remote from the natal burrow (97 m) than the males (*mdn*=123 m).

When we compared ranging behaviour of nonsurvivors and survivors (last distance recorded before predation, before transmitter removal or in decade 7), we found sex-dependent differences (figure 3a). Males that survived had remained more philopatric than nonsurviving males, and marginally nearer to their natal burrow than nonsurviving females. There were no other group differences in distances travelled (each P>0.11), in other words, survivorship among females was independent of travel distance.

None of the tagged males departed from his birthplace successfully to establish a new home range. Two females, however, dispersed and survived, one even to reproductive maturity. For a further investigation of the possible causes of such sex-dependent vulnerability to predation, we analysed speed, as it is the second dimension of locomotion. The ontogenetic development of mobility was comparable to that of ranging behaviour, but slightly less of the variation was explained by time (logistic regression: r^2<0.93), and hence, temporal effects were not as pronounced (Friedman ANOVA: ns). The logistic incline occurred from decades 2 (*mdn*=0.0) to 3 ($\bar{x}$=20.0 m/h), implying that average running speed increased earlier than travel distance and remained on similar levels thereafter (=20.3–32.6 m/h). In contrast to ranging behaviour, we

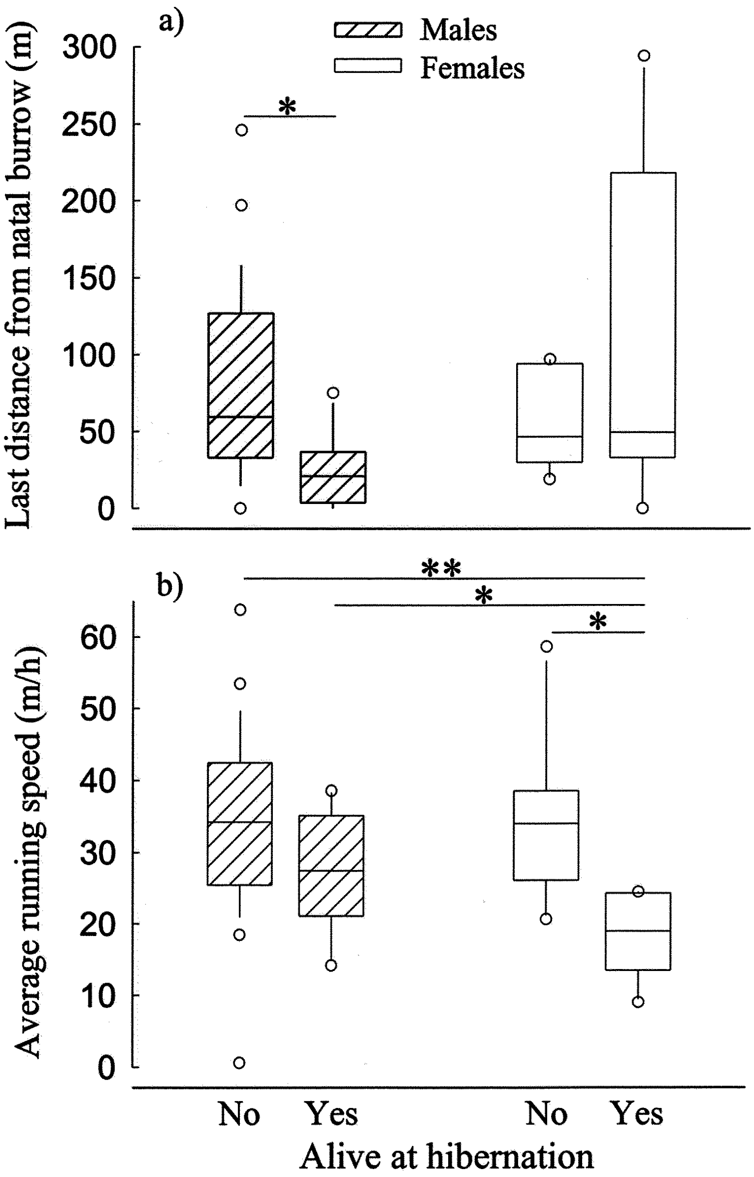


Figure 3. Sex-differential effects of distance from the natal burrow (a) and travel speed (b) on survival of juvenile European sousliks until hibernation. a. Surviving males had remained nearer to their natal burrows than nonsurvivors (males: *P*=0.014, Mann-Whitney *U*=29; females: *P*<0.1, *t*=1.8). b. Surviving females had moved slower than surviving males (*P*<0.05, *U*=7) and nonsurvivors (males: *P*=0.005, *U*=16; females: *P*=0.018, *t*=2.8). Each box-plot represents the median, quartiles, 5% and 95% percentiles, and outliers; see table 1 for sample sizes. Differences between samples indicated by horizontal lines and marked with * *P*<0.05, ** *P*<0.01.

found sex differences in two stages: males moved faster than females in decades 5 (20 males, x̄=37.3 m/h versus nine females, x̄=22.2 m/h; *P*=0.011, *t*=-2.7) and 7 (nine males, x̄=25.4 m/h versus six females, x̄=12.7 m/h; *P*=0.014, *t*=-2.8).

Maximal travel speeds of juvenile European sousliks during decades 4–7 after natal emergence exceeded 500 m/h. Juveniles that were directly observed to be killed had moved significantly faster (x̄=262.4 m/h) than year-to-year survivors in the critical time span x̄=115.8 m/h; post-hoc LSD, *P*=0.009). The killed males had travelled with an average maximum of 287.0 m/h, which was more than twice the maximal speed of the female victim (134.2 m/h). Analyses of average mobility revealed consistent results: during the critical time span (decade 4–7), killed and/or disappeared juveniles had been significantly faster ($\bar{x}$=34.3 m/h) than summer survivors ($\bar{x}$=23.2 m/h; P=0.008, t=2.8). When we took into account the sex (figure 3b), it turned out that surviving females had moved the slowest. No speed difference was found among the three rapid groups.

Note that results are somewhat reversed compared to ranging behaviour (figure 3a), where survival of males, but not of females was affected. In other words, surviving males had remained philopatric, despite of moving faster than surviving females, some of which dispersed. Females with male-like mobility were killed or disappeared, just like the males that departed from their natal burrows. Consistent with these sex-differential effects, we found no significant correlations between our measures of distance and speed (each P>0.14, each Spearman r_s<0.21), except in nonsurviving males. This group moderately decelerated with increasing distance from the natal burrow (r_s=-0.475, P=0.025, n=22).

Anti-predator behaviour may influence both vulnerability to predation and locomotion. We therefore analysed surface activity and vigilance, assuming that survivors allocated a greater portion of their aboveground activity to bipedal postures than nonsurvivors. Of the 15 focal juveniles (eight males, seven females), seven were killed (four males, three females), two disappeared (two males), and six survived until hibernation (two males, four females). Vigilance behaviour of survival- and sex groups was not significantly different. However, a correlative approach revealed that the number of bipedal postures increased with time allocated to surface activity (figure 4; r_s>0.89, P<0.0001). Correlations were stronger among females (r_s>0.90, P=0.005) than among males (r_s=0.83, P=0.011), and slightly weaker in survivors (r_s>0.81, P=0.050) than in nonsurvivors (r_s>0.84, P=0.004). Linear regressions of bipedal vigilance against surface activity (log scale) clarified variations between two groups (figure 4): The essential difference between nonsurviving males and surviving females is reflected not in the slopes, but in the intercepts, which are closer to 0 in the female (-1.16) than in the male (-3.42) group. The regression line of male nonsurvivors thus intersects the abscissa at a higher x-value (more surface activity) than that of female survivors, corresponding to a smaller number of bipedal postures in the male group. That is to say, compared to nonsurviving males, surviving females spent less time aboveground or allocated more time to vigilance behaviour, both resulting in lower travel speed when covering a given distance.

Discussion

European sousliks started to expand or shift their home ranges 30–40 days post natal emergence at about nine weeks of age. This timing coincides with the definitive end of weaning (Huber et al. 2001), and matches the onset of natal dispersal (the permanent departure of prereproductive individuals from their place of birth, Lidicker 1975) in many North American ground squirrel species (Holekamp 1984a). Our results indicate that the departure of juveniles from their natal burrows involved an increased risk of predation (figure 2), which depended on behaviour associated with locomotion (figure 3). It is evident that males were more vulnerable than females (table 1), which is also supported by sex differences in year-to-year survival of juveniles (Hoffmann et al. 2003a). The relatively high proportion of unknown fates (22.0%) might partly have been due to undetected dispersal, but the fact that virtually no immigration occurred during this study (Hoffmann et al. 2003a) suggests that most of the potential dispersers (88.9% male) were killed. Increased male vulnerability to predation is also reflected in sex differences in year-to-year survival of juveniles (Hoffmann et al. 2003a). Sex-specific comparisons of distance and speed were significant on a higher level when based on year-to-year instead of summer survival, indicating continued male-biased mortality after the onset of hibernation. Sex-differential predation pressure is also supported by findings on adrenal activity of yearling males, which suggest an in-

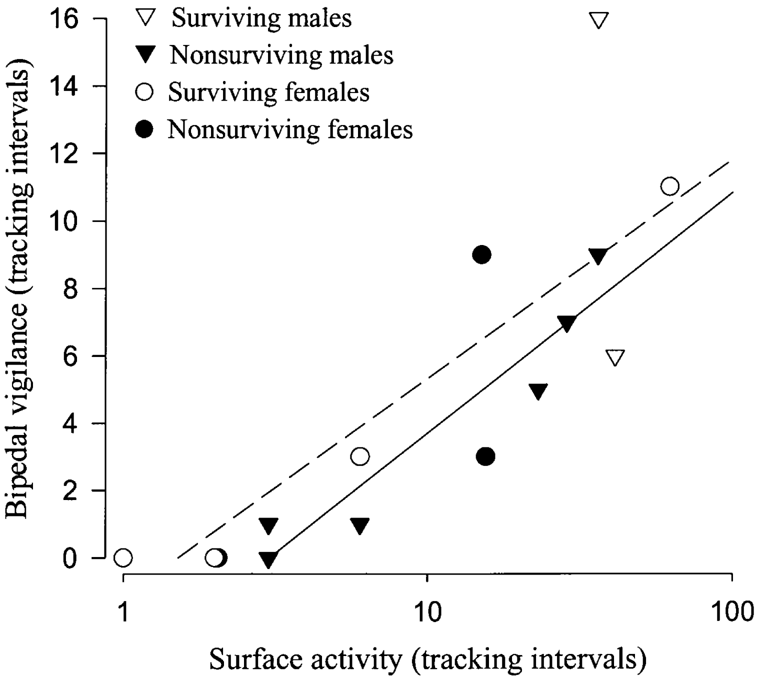


Figure 4. Association between surface activity (sum of tracking intervals each individual was observed aboveground) and vigilance (sum of tracking intervals with bipedal postures). Regression lines are shown for nonsurviving males (solid; $y = -3.42 + 7.13x$; $r^2>0.91$, $n=6$) and for females known to be alive shortly before hibernation (dashed; $y = -1.16 + 6.49x$; $r^2>0.96$, $n=4$). Because of small sample sizes, no regressions were performed for surviving males and killed females.

creased stress response (Millesi et al. 2005), maybe due to both carryover effects from the preceding year and current hazards. Consistently, juvenile male arctic ground squirrels (*Spermophilus parryii plesius*) showed endocrine characteristics indicative of a prolonged period of stress in mid-August (Boonstra et al. 2001).

Surprisingly, distance from the natal burrow did not depend on sex (figure 3a). This finding is in contrast to North American ground squirrels (Dobson 1981, Waterman 1986, Holekamp & Sherman 1989, Byrom & Krebs 1999). The magnitude of the observed ranges (figure 2, figure 3a) was smaller than those reported for dispersing juvenile *Spermophilus columbianus* (Wiggett & Boag 1989, Wiggett & Boag 1993). No tagged squirrel, including individuals that departed from the central study site, actively left the 8-ha recreation area, which is surrounded by suburban terrace houses. We propose that dispersal beyond the monitored distances was inhibited by extrinsic factors like predation (this study) and landscape fragmentation (Hoffmann et al. 2003b). Thus potential sex differences in dispersal distance might have been concealed.

Our results indicate that the sex-differential mortality (table 1) and hence, the female bias among yearlings (Millesi et al. 1999a, Hoffmann et al. 2003a) were mediated by concurrent behaviour interacting with locomotion. Kenagy & Hoyt (1989) suggested that golden-mantled ground squirrels (*Spermophilus saturatus*) run fast to reduce exposure to predation. In European sousliks, surviving males were faster than surviving females, but nonetheless both moved slower than nonsurvivors. The maximum speed recorded in our study (553 m/h, equivalent to 9.2 m/s) was higher than what has been reported for nonjuvenile members of European souslik and other *Spermophilus* species except *Spermophilus leptodactylus* (Trombulak 1989). In *Spermophilus beldingi*, natal dispersal was temporally correlated with high levels of locomotor and exploratory activity, and after having escaped into a burrow, males reappeared more rapidly than did females at four to ten weeks of age (Holekamp 1984a). Time allocated to antipredator behaviour (bipedal postures and/or retreat into a burrow) instead of locomotion evidently affects mobility and hence, running speed is accelerated when vigilance and predator avoidance are reduced (cf. Ydenberg & Dill 1986). Male European sousliks were less vigilant than females while spending the same or even more time aboveground, indicating an unfavourable trade-off in surface activity allocated to vigilance and locomotion. Only two of the focal males were known to be alive shortly before hibernation, one of which had been extremely vigilant. Females apparently pursued one of two different strategies: they either minimised surface activity, vigilance thus becoming negligible, or when aboveground more often, they allocated a considerable amount of time to bipedal postures, resulting in low travel speed. Among the killed females, one behaved male-like in allocating too little time to bipedal postures, the other two died despite of following each of the female strategies. The second strategy could explain the difference between surviving and nonsurviving females in proportional surface activity as an observation bias: among the total of tagged females, survivors supposedly were bipedal more often, resulting in better visibility than nonsurvivors. Philopatric male European sousliks were familiar with the burrow systems in their surroundings and presumably still associated with some of their kin. Due to the dilution effect (Dehn 1990) and nepotistic vigilance of their kinship group (Desportes et al. 1991, Hoffmann 1995), reduced anti-predator behaviour was not as detrimental as for males departing from their birth site. Nonsurviving females had apparently behaved like males, moving as fast as the dispersers and marginally farther than the philopatrics. It is probable that they reduced vigilance in favour of speed while leaving their natal site. Fifty percent of the females obviously accomplished a beneficial trade-off in time allocation between locomotor activity and anti-predator behaviour, and survived even when dispersing.

We conclude that in European sousliks, like in many other small mammal species, sexually dimorphic losses can be associated differentially with time allocation to conflicting behaviours during aboveground activity (Holekamp 1984b, Wiggett & Boag 1989). Why males tend to perform an unfavourable trade-off between vigilance and mobility remains to be investigated. A hormonal approach might help to settle this issue: during this study all yearling males were reproductively mature (Hoffmann et al. 2003a). Thus it is likely that the onset of male puberty is already initiated during the juvenile summer, coinciding with elevated testosterone levels. These in turn might both mediate dispersal (Nunes et al. 1999) and stimulate quick and unwary locomotion. Further analyses of endocrine aspects are required to elucidate the proximate causes of the sex difference in juvenile mortality.

Acknowledgements: We are grateful to K. Pieta, S. Huber and S. Steurer, who helped to trap and monitor European sousliks over the years. We thank J. Dittami and two anonymous reviewers for constructive comments on a former version of the manuscript. Funding for this study was provided by the University of Vienna (Research Grant GZ. 89/2) and the Austrian National Bank Fund (OeNB, No. 6590). The competent authorities issued a license to capture sousliks (Local Authority Korneuburg: 9-N-90). As radio tagging was possible without anaesthetisation, and the attachment of collars is not considered an animal experiment in Austria, no additional licence was required.

References

Boag, D.A. & J.O. Murie 1981. Population ecology of Columbian ground squirrels in southwestern Alberta. Canadian Journal of Zoology 59: 2230–2240.

Boonstra, R., C.J. McColl & T.J. Karels 2001. Reproduction at all costs: The adaptive stress response of male arctic ground squirrels. Ecology 82: 1930-1946.

Byrom, A.E. & J.C. Krebs 1999. Natal dispersal of juvenile arctic ground squirrels in the boreal forest. Canadian Journal of Zoology 77: 1048-1059.

Dehn, M.M. 1990. Vigilance for predators: detection and dilution effects. Behavioral Ecology and Sociobiology 26: 337-342.

Desportes, J.-P., F. Cézilly & A. Gallo 1991. Modelling and analysing vigilance behaviour. Acta Oecologica 12: 227-236.

Dobson, F.S. 1981. An experimental examination of an artificial dispersal sink. Journal of Mammalogy 62: 74-81.

Hoffmann, I.E. 1995. Raubdruck, Warnrufe und Wachsamkeit bei Europäischen Zieseln (*Spermophilus citellus citellus*). MSc thesis. University of Vienna, Vienna, Austria.

Hoffmann, I.E. 2002. The case of the European ground squirrel. Population dynamics and plasticity of life-history traits in a suburban environment. PhD thesis. University of Vienna, Vienna, Austria.

Hoffmann, I.E., E. Millesi, S. Huber, L.G. Everts & J.P. Dittami 2003a. Population dynamics of European ground squirrels (*Spermophilus citellus*) in a suburban area. Journal of Mammalogy 84: 615–626.

Hoffmann, I.E., E. Millesi, K. Pieta & J.P. Dittami 2003b. Anthropogenic effects on the population ecology of European ground squirrels (*Spermophilus citellus*) at the periphery of their geographic range. Mammalian Biology – Zeitschrift für Säugetierkunde 68: 205–213.

Holekamp, K.E. 1984a. Dispersal in ground-dwelling Sciurids. In: J.O. Murie & G.R. Michener (eds.). The biology of ground-dwelling squirrels: 297–320. University of Nebraska Press, Lincoln, USA.

Holekamp, K.E. 1984b. Natal dispersal in Belding's ground squirrels (*Spermophilus beldingi*). Behavioral Ecology and Sociobiology 15: 293-301.

Holekamp, K.E. & P.W. Sherman 1989. Why male Ground squirrels disperse. American Scientist 77: 232-239.

Huber, S., I.E. Hoffmann, E. Millesi, J. Dittami & W. Arnold 2001. Explaining the seasonal decline in litter size in European ground squirrels. Ecography 23: 205-211.

Kenagy G.J. & D.F. Hoyt 1989. Speed and time-energy budget for locomotion in golden-mantled ground squirrels. Ecology 70: 1834-1839.

Kenward, R. 1987. Wildlife radio tagging. Equipment, field techniques and data analysis. Academic Press, London, UK.

Kenward, R.E. & K.H. Hodder 1996. Ranges V: An analysis system for biological location data. Institute of Terrestrial Ecology, Wareham, UK.

Lidicker, W.Z. Jr. 1975. The role of dispersal in the demography of small mammal populations. In: F.B. Golley, K. Petrusewicz & L. Ryszkowski (eds.). Small mammals: their productivity and population dynamics. Cambridge University Press, Cambridge, UK.

Michener, G.R. 1989. Sexual differences in inter-year survival and life span of Richardson's ground squirrels. Canadian Journal of Zoology 67: 1827-1831.

Michener, G.R. 1998. Sexual differences in reproductive effort of Richardson's ground squirrels. Journal of Mammalogy 79: 1–19.

Millesi, E., I.E. Hoffmann & S. Huber, 2005. Reproductive strategies of male European sousliks at high and low population density. Lutra, this issue.

Millesi, E., S. Huber, L.G. Everts & J.P. Dittami 1999a. Reproductive decisions in female European ground squirrels: factors affecting reproductive output and maternal investment. Ethology 105: 163-175.

Millesi, E., A.M. Strijkstra, I.E. Hoffmann, J.P. Dittami & S. Daan 1999b. Sex and age differences in mass, morphology and annual cycle in European ground squirrels, *Spermophilus citellus*. Journal of Mammalogy 80: 218-231.

Naef-Daenzer, B. 1993. A new transmitter for small animals and enhanced methods of home-range analysis. Journal of Wildlife Management 57: 680-689.

Nunes, S., T.R. Duniec, S.A. Schweppe & K.E. Holekamp 1999. Energetic and endocrine mediation of natal dispersal in Belding's ground squirrels. Hormones and Behavior 35: 113-124.

Olson, G.S. & B. Van Horne 1998. Dispersal patterns of juvenile Townsend's ground squirrels in southwestern Idaho. Canadian Journal of Zoology 76: 2084-2089.

Sauer, J.R. & N.A. Slade 1987. Uinta ground squirrel demography: is body mass a better categorical variable than age? Ecology 68: 642–650.

Schmutz, S.M., D.A. Boag & J.K. Schmutz 1979. Causes of the unequal sex ratio in populations of adult Richardson's ground squirrels. Canadian Journal of Zoology 57: 1845–1859.

Sherman, P.W. & M.L. Morton 1984. Demography of Belding's ground squirrels. Ecology 65: 1617-1628.

Shriner, W.M. & P.B. Stacey 1991. Spatial relationships and dispersal patterns in the rock squirrel, *Spermophilus variegatus*. Journal of Mammalogy 72: 601–606.

Trombulak, S.C. 1989. Running speed and body mass in Belding's ground squirrels. Journal of Mammalogy 70: 194-197.

Waterman, J.M. 1986. Behaviour and use of space by juvenile Columbian ground squirrels (*Spermophilus columbianus*). Canadian Journal of Zoology 64: 1121-1127.

Waterman, J.M. 1995. The social organization of the cape ground squirrel (*Xerus inauris*; Rodentia:

Sciuridae). Ethology 101: 130-147.
Wiggett, D.R. & D.A. Boag 1989. Intercolony natal dispersal in the Columbian ground squirrel. Canadian Journal of Zoology 67: 42-50.
Wiggett, D.R. & D.A. Boag 1993. The proximate causes of male-biased emigration in Columbian ground squirrels. Canadian Journal of Zoology 71: 204- 218.
Ydenberg, R.C. & L.M. Dill 1986. The economics of fleeing from predators. Advances in the Study of Behaviour 16: 229-249.

Samenvatting

Waarom lopen bij juveniele siesels (*Spermophilus citellus*) mannetjes een groter predatie-risico dan vrouwtjes?

Het verlaten van bekend terrein leidt, naar men aanneemt, tot een verhoogde kans op predatie. Toch worden bewegingspatronen en mortaliteit zelden direct waargenomen. Om die reden onderzochten we de bewegingen en de activiteit van 41 juveniele siesels (*Spermophilus citellus)* in relatie tot hun individuele lot. We onderzochten of het mortaliteitsrisico toenam met de afstand tot het geboorteburcht, en we probeerden ook sekse-specifieke verschillen in de bewegingspatronen en het anti-predatiegedrag te vinden die zouden kunnen verklaren waarom er een sexe-ratio ten gunste van de vrouwtjes bestaat bij niet-juveniele dieren. In een 4 ha groot recreatiegebied ten noorden van Wenen (Oostenrijk) werden gedurende drie jaar gespeende juvenielen voorzien van radiozenders. Bijna 76% van de gemerkte dieren werd gedood door katten of verdween met onbekend lot. Slechts twee vrouwtjes (5%) overleefden de natale dispersie van hun geboortegrond met succes. Het overlevingspercentage van vrouwtjes was meer dan twee keer zo hoog als dat van de mannetjes en was onafhankelijk van de afstand tot de geboorteburcht, terwijl de meeste overlevende mannetjes hun geboortegrond trouw bleven. De belangrijkste vondst van dit onderzoek was dat niet-overlevende juveniele dieren zich sneller hadden verplaatst dan overlevende dieren, met snelheden die resulteerden in een per sekse verschillende mortaliteit. Mannetjes neigen zich sneller te verplaatsen dan vrouwtjes en daarmee een groter risico te lopen op predatie wanneer ze zich op afstand van hun geboorteburcht bevinden. Verdere analyse van gedrag leverde sterke aanwijzingen dat de grotere sterfte onder mannetjes veroorzaakt zou kunnen zijn door een per sekse verschillende tijdsbesteding in het vermijden van predatoren en waakzaamheid. Wij concluderen dat onder jonge siesels, mannetjes een ongunstige balans kiezen tussen verplaatsing en waakzaamheid bij activiteit aan de oppervlakte.

Received: 15 October 2004
Accepted: 25 January 2005

The European souslik in the natural light-dark cycle: what is the signal for afternoon retreat?

Kamiel Spoelstra, Roelof A. Hut, Arjen M. Strijkstra & Serge Daan

Department of Animal Behaviour, University of Groningen, P.O. Box 14, NL-9751 NN Haren,
The Netherlands, e-mail: K.Spoelstra@rug.nl

Abstract: European sousliks (*Spermophilus citellus*) are strictly diurnal with a very precise daily activity rhythm in field conditions. This activity rhythm is regulated by the internal biological clock which in turn is synchronized by the natural light/dark cycle (entrainment). Due to their regular retreats into the darkness of their burrows, fast light intensity changes in natural light cannot be used for resetting of their biological clock. Careful analysis of retreat behaviour at the end of the day shows that neither a specific light intensity level nor a specific light intensity decrease can explain the day-to-day variations in the timing of retreat. If a general decrease in light intensity is a signal indeed, its effect must be phase dependent since a light intensity decrease by the solar eclipse on August 11, 1999, in the middle of the day failed to induce retreat behaviour.

Keywords: *Spermophilus citellus*, European souslik, entrainment, behaviour, solar eclipse, light intensity, telemetry.

Introduction

European sousliks (*Spermophilus citellus*) in their natural habitat emerge from their burrows around four hours after twilight at dawn and disappear around three hours before twilight at dusk (Everts et al. 2004). This poses a problem for circadian entrainment. They might see the dusk and dawn transitions if they would observe the outside light from the entrance of their burrows. This is, however, prevented by the complete blocks the sousliks make in their entrance tunnels after their last afternoon retreat (Hut & Scharff 1998). Entrainment to daily temperature fluctuations can be excluded since they are absent in the burrows underground (Hut et al. 1999a). The largest temperature changes are induced by emergence and retreat itself. In addition, temperature cycles have shown to be unreliable as a Zeitgeber for squirrels (Pohl 1998, Rajaratnam & Redman 1998) and for sousliks (Hut et al. 1999a).

Due to late emergence and early retreat, the most precise signals indicating the time of day, the fast changes in light intensity during dawn and dusk twilight, are not available for synchronization of their circadian system. Sousliks might, however, respond to the very slow afternoon decrease in light intensity related to the gradual decrease in the sun's azimuth above the horizon rather than its disappearance under the horizon. If they would respond to this decrease by retreating into the darkness underground (Hut et al. 1999b), they would generate a secondary lights-off signal, to be used for entrainment of their endogenous circadian clock. In this study we closely studied properties in the afternoon light decrease and phase dependent sensitivity for natural light decrease.

Methods

Afternoon light decrease

Four male and five female sousliks were maintained in an outdoor enclosure in Haren, The Netherlands (53°10' N, 6°36' E). They were equipped with light sensitive radio-transmitter collars (Televilt, International AB, Lindesberg,

---

Lutra abstracts on the internet: http://www.vzz.nl

Sweden; see Hut et al. 1999b) from March 16 to October 29, 1996. The presence above ground was indicated by the pulse interval of the transmitter signals. The transmitter generated a radio-pulse signal of 1 Hz when the collar sensor was exposed to a light intensity of more than 0.03 Lux, and a pulse signal of 2 Hz when the collar sensor received less than 0.03 Lux. Signals of individual sousliks could be identified by frequency. All transmitter signals were received and stored in 2-minute intervals by a receiver (Televilt, RX900-C). From the entire course of these recordings, all individual retreats (66 in total) on precipitation-free days were selected. Concurrent light intensity measurements in 60-minute intervals were obtained from Groningen airport Eelde, at 6-km distance. We determined daily light intensity ($W*m^{-2}$) and rate of change in light intensity ($W*m^{-2}*s^{-1}$) at the precise time of each souslik's final afternoon retreat in its burrow.

Solar eclipse

We exploited the solar eclipse of August 11, 1999, to test whether sousliks respond to a decrease in light intensity independently of circadian phase. This was done in a field population of European sousliks near Vienna, Austria (48°18' N, 16°22' E) (Millesi et al. 1999). At this location the moon covered 99% of the sun's disk at 12:46 h local time. On August 10, 11 and 12, we recorded the number of sousliks above ground every 5 minutes in a 1-ha focal area, from circa 06:00 h until circa 20:00 h. Light intensity was measured every 10 minutes, around the partial solar eclipse data were recorded every single minute. To validate visual observations, on August 9 five sousliks were equipped with light-sensitive radio-transmitter collars as described above. Their presence above ground during August 10-12 was recorded every 10 minutes, and every single minute around the time of the eclipse. The results of the solar eclipse study have been published elsewhere (Spoelstra et al. 2000).

Results

Afternoon light decrease

Figure 1 shows the timing of all 66 retreats recorded and the corresponding curves of declining light intensity in the afternoon. For all animals, retreat occurred within a range of 2 log units. This does not impress as a constant light intensity. However, if one looks at

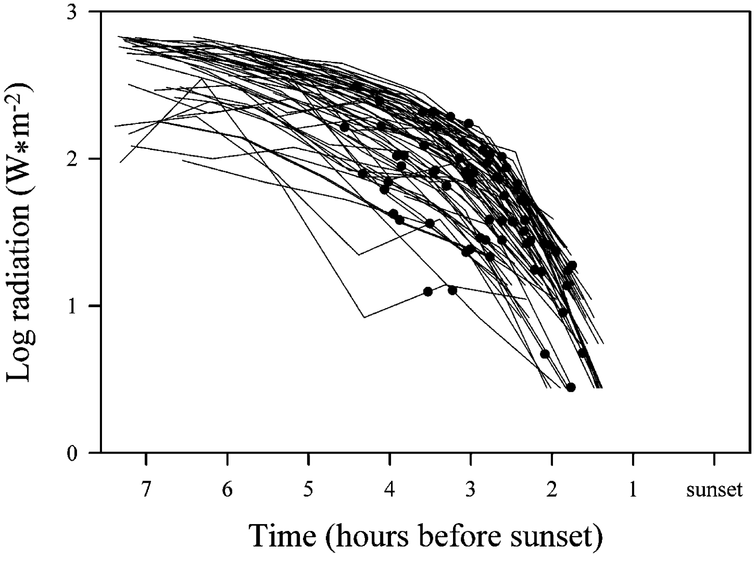


Figure 1. Daily curves describing radiation and the times of souslik afternoon retreat in their burrows (dots).

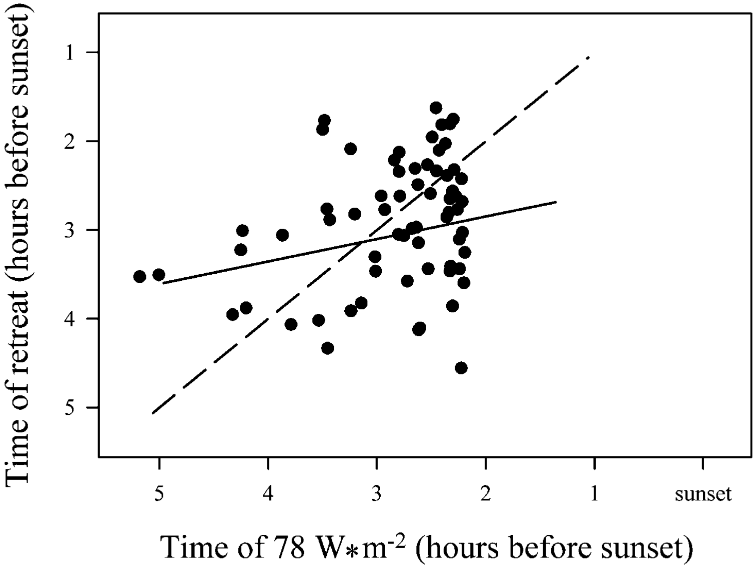


Figure 2. Occurrence of average retreat light intensity (78 W∗m^{-2}) and average retreat time (in hours before sunset) for each subjective day. Dashed line: y = x (if animals on average would retreat exactly at average retreat light intensity).

figure 1 in more detail, it appears as though the earliest retreats occurred at light intensities that were at least sub-maximal, while the latest retreats tend to be seen on the brightest days.

We further analysed this by first calculating the average light intensity at the time of afternoon retreat (78 W∗m^{-2}). Then we plotted retreat time against the time at which this light intensity was reached on the same day (figure 2). Although the timing of 78 W∗m^{-2} is not the only determinant of retreat, the later this intensity occurs the later the animals retreat into their burrows (P=0.017).

It might also be that the sousliks wait for a particular rate of change of the light intensity to make their final afternoon retreat. To determine whether there is such a specific decline in light intensity that triggers the afternoon retreat,

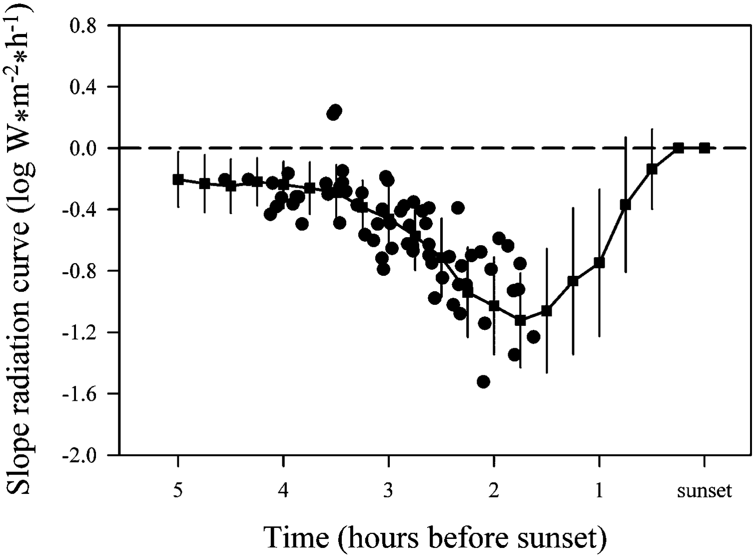
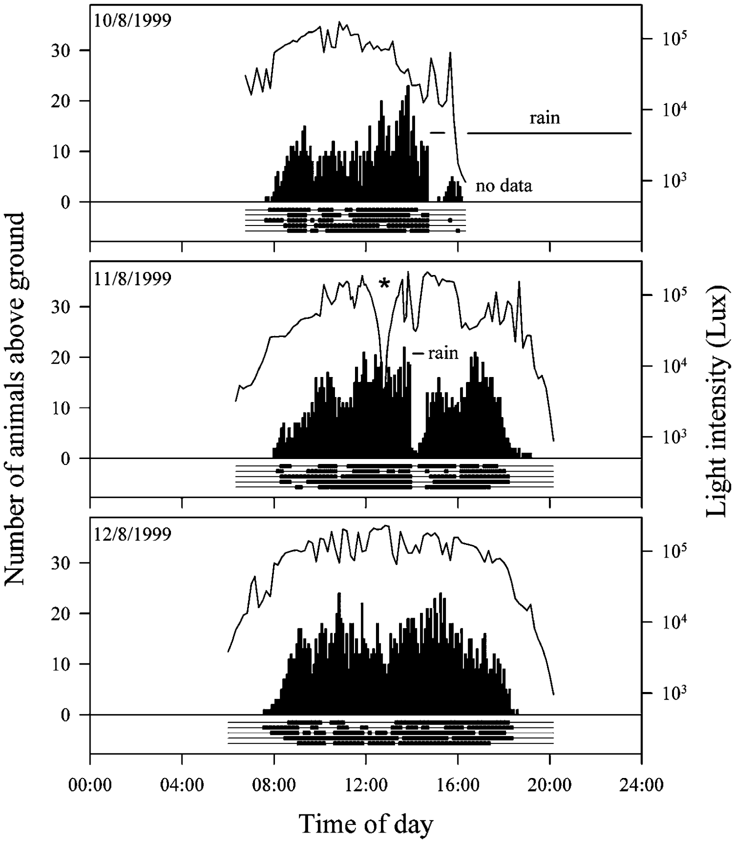


Figure 3. Average decline in light intensity of all subjective days (±SD, solid line) and moments of retreat (dots) with corresponding momentary decline in light intensity.

Figure 4. Number of sousliks active above ground (grey bars) and concurrent light intensity (thin black line), observed in a 1-ha focal area in a population near Vienna, Austria. Thick horizontal lines indicate presence of five animals with radio transmitters above ground. Asterisk denotes timing of the partial (99 %) solar eclipse at 12:46 h local time, on August 11, 1999 (civil twilight dawn 5:07 h; civil twilight dusk 20:51 h). (Spoelstra et al. 2000).



we plotted the actual times of retreat along with the light intensity decrease (figure 3, which also shows the average values for the rate of decrease starting five hours before sunset). We conclude from figure 3 that there is no association of the final retreat with light intensity decline, since afternoon retreats are distributed between intensity decreases ranging from 0.2 to 1.1 $W*m^{-2}*h^{-1}$.

Solar eclipse

During the three observation days, light intensity was $24*10^3$-$37*10^3$ Lux at the appearance of the first souslik above ground, and $20*10^3$-$27*10^3$ Lux when the last animal retreated, as reported by Spoelstra et al. (2000) (figure 4). Rain always suppressed aboveground activity, and persistent rain on August 10 precluded data acquisition from 16:20 h onwards. The sky was clear during the partial solar eclipse. Light intensity before the eclipse (11:16 h-11:46 h) was circa $110*10^3$ Lux and dropped more than 2 log units to 1039 Lux at 12:46 h. From 12:16 h to 13:16 h on average 16.3 animals were active above ground. This number was similar to either the hour before (15.4) or the hour after the eclipse (16.4).

Four of the sousliks equipped with radio-transmitters were above ground for most (156-160 minutes, 20 minutes absence by rain) of a three-hour period around the eclipse. The remaining animal was underground for two brief episodes of 21 and 12 minutes, i.e., it behaved indistinguishably from its activity pattern during the other days.

Conclusion

The afternoon retreat data indicate that neither a specific light intensity nor a specific rate of light

A European souslik *(Spermophilus citellus)* collects nest material. Langenzersdorf, Vienna, August 1999. *Photograph: Kamiel Spoelstra.*

intensity decrease solely determine the timing of the sousliks' afternoon retreat in their burrows. If a combination of both is responsible for the timing of the afternoon retreat, the response to this signal is apparently circadian phase dependent. This conclusion is based on an experiment under natural conditions with a solar eclipse around the middle of the day, where low levels of light intensity (well below levels normally perceived at the end of activity) and sharp rates of light intensity decrease failed to induce retreat behaviour.

Acknowledgements: We thank Ilse Hoffmann, Gerard Overkamp, Froukje Rienks, Thomas Ruf and Alois Smalwieser for their practical and logistic support.

References

Everts, L.G., A.M. Strijkstra, R.A. Hut, I.E. Hoffmann & E. Millesi 2004. Seasonal variation in daily activity patterns of free-ranging European ground squirrels. Chronobiology International 21: 39-53.

Hut, R.A. & A. Scharff 1998. Endoscopic observations on tunnel blocking behaviour in the European ground squirrel (*Spermophilus citellus*). Zeitschrift für Säugetierkunde 63: 377-380.

Hut, R.A., S. Daan & N. Mrosovsky 1999a. Nonphotic entrainment in a diurnal mammal, the European ground squirrel (*Spermophilus citellus*). Journal of Biological Rhythms 14: 409-419

Hut, R.A., B.E.H. van Oort & S. Daan 1999b. Natural entrainment without dawn and dusk: the case of the European ground squirrel (*Spermophilus citellus*). Journal of Biological Rhythms 14: 290-299.

Millesi, E., A.M. Strijkstra, I.E. Hoffmann, J.P. Dittami & S. Daan 1999. Sex and age differences in mass, morphology and annual cycle in European ground squirrels, *Spermophilus citellus*. Journal of Mammalogy 80: 218-231.

Pohl, H. 1998. Temperature cycles as Zeitgeber for the circadian clock of two burrowing rodents, the normothermic antelope ground squirrel and the heterothermic Syrian hamster. Biological Rhythms Research 29: 311-325.

Rajaratnam, S.M.W. & J.R. Redman 1998. Entrainment of activity rhythms to temperature cycles in diurnal palm squirrels. Physiology & Behavior 63: 271-277.

Spoelstra, K., A.M. Strijkstra & S. Daan 2000. Ground squirrel activity during the solar eclipse of August

11, 1999. Zeitschrift für Säugetierkunde 65: 307-308.

Samenvatting

De Europese siesel in de natuurlijke licht-donkercylcus: wat is het signaal voor terugtrekking in de middag?

Siesels *(Spermophilus citellus)* zijn uitsluitend dagactief en hebben een zeer precieze timing van hun gedrag. Dit wordt geregeld door de interne circadiane pacemaker die wordt gesynchroniseerd door de natuurlijke licht-donkercyclus (‘entrainment’). Deze synchronisatie kan niet plaatsvinden aan de hand van snelle veranderingen in lichtintensiteit, omdat deze onregelmatig voorkomen doordat siesels zich overdag vaak terugtrekken in de duisternis van het ondergrondse hol.

Deze studie analyseert de lichtcondities op het moment dat de siesels stopten met hun dagelijkse activiteit en tot de volgende ochtend onder de grond bleven. Een specifieke lichtintensiteit noch een specifieke snelheid in afname van deze lichtintensiteit blijkt hiervoor het signaal te zijn. Als het zo is dat een afname van lichtintensiteit in het algemeen een signaal is om voor de rest van de dag te stoppen met bovengrondse activiteit, dan is deze bovendien afhankelijk van de circadiane fase.
De sterke afname van het daglicht door de zonsverduistering van 11 augustus 1999 midden in de activiteitsperiode had geen effect op het activiteitspatroon en het circadiane ritme van de siesels.

Received: 20 October 2004
Accepted: 4 February 2005

The historical and current distribution of the Iberian population of the European mink (*Mustela lutreola*)

Jabi Zabala[1,*], Iñigo Zuberogoitia[1] & Jose Antonio Martinez-Climent[2]

[1] Department of Zoology and Animal Cellular Dynamics, Euskal Herriko
Unibertsitatea, E-48080 Bilbo, P.O. Box 644, Basque Country
[2] C. Juan de la Cierva 43 (S.T. 100), El Campello, E-03560 Alicante, Spain

Abstract: As most records of the European mink (*Mustela lutreola*) in the Iberian Peninsula have been published in local papers or remain as unpublished reports, it is difficult to determine its current distribution and to assess historical changes in its distribution. In this paper, we analyse data on the distribution of the European mink in the Iberian Peninsula. We conclude that the European mink most probably colonised the Iberian Peninsula in the late 1940's. Since it was first reported, the European mink has been slowly but steadily expanding its range across the northern Iberian Peninsula, mainly southwards but recently also eastwards and, possibly, westwards. Possible explanations for the assumed expansion are briefly discussed.

Keywords: European mink, *Mustela lutreola*, changes in distribution, Iberian Peninsula.

Introduction

The European mink (*Mustela lutreola*) is a riparian mustelid native to the European continent that once inhabited a large part of Europe (Youngman 1982). During the second half of the 20th century its distribution range shrank severely, and minks disappeared from most of their range (Youngman 1982, Maran & Henttonen 1985, Romanowsky 1990, Maran et al. 1998b, Sidorovich 2000). As a result of this decline, there are three major population nuclei nowadays: one in the north (Maran & Henttonen 1985, Tumanov 1992), one in the east (Kranz et al. 2003), and one in the west.

In the northern and eastern parts of their range minks have disappeared from most countries over the last decades, and populations continue to decline in areas where they are still present (Maran & Henttonen 1985, Maran et al. 1998b). Even if no single factor has been identified as responsible for the decline, recent studies point to competition from the American mink *(Mustela vison)* as responsible for the decline of its European counterpart, at least in some regions (Maran et al. 1998a, Maran et al. 1998b, Sidorovich 2000, Sidorovich et al. 2000).

The situation is quite different for the western population. Minks disappeared from Brittany and Pays de Loire (France) in the 20 years to 1997 (Lodé et al. 2001). Nowadays, the European mink still occupies the south of the country, approximately half of the area occupied previously. The underlying cause of the decline seems to be anthropic pressure upon the species (Maizeret et al. 1998, Lodé et al. 2001). The situation of the southwestern population is interesting, because the species seems to be expanding southwards, although data are inconclusive (Maran & Henttonen 1985, Palazón & Ruiz-Olmo 1992, Torres & Zuberogoitia 1997, Macdonald et al. 2002). Most studies on the status and distribution of the European mink in the Iberian Peninsula focus on small regions, are published in local journals or remain as unpublished reports. Therefore, the current distribution, status and trends are difficult to assess. This has led to confusion, and in some cases to misunderstandings

Lutra abstracts on the internet: http://www.vzz.nl

---

[*] *Present address:* Sebero Otxoa 45, 5 B. 48480 Arrigorriaga, Basque Country, e-mail: jzabalaalbizua@yahoo.com

both in local and international publications, with some papers presenting incorrect data.

In this paper we review the available information on the European mink in the Iberian Peninsula. The aim of the paper is to assess distributional changes, population trends, and the origin of the European mink in the Iberian Peninsula. Two alternative hypotheses are considered: 1. the European mink reached the Iberian Peninsula in the 20th century, and 2. it has always been part of the Iberian fauna, but went unnoticed until the last century, when increased interest among researchers prompted the collection of new records.

Materials and methods

This study draws on data from the northern Iberian Peninsula (figure 1). In the regions of Biscay, Gipuzkoa, Cantabria and northwestern Navarre, the climate is oceanic. Annual rainfall ranges between 1200 and 2200 mm, winters are mild and there is no aestival drought. In these regions streams are short, small and fast flowing, running into the Bay of Biscay (Flores 1989, Walter 1997).

The climate of the more southern regions (Soria, Rioja and Southern Navarre, and Burgos) is Mediterranean. Winters are rainy and summers dry, and there is a marked contrast between winter and summer temperatures. In this area streams run towards two majors rivers: the Ebro, which flows eastwards to the Mediterranean Sea, and the Duero, which flows westwards to the Atlantic Ocean. Some small streams may disappear due to the summer drought (Walter 1997).

We consulted a total of 22 works dealing with the distribution of European mink in the Iberian Peninsula, mostly international and local papers or books not widely available. Consulted works were: Rodríguez de Ondarra (1955), Puente (1956), Rodríguez de Ondarra (1963), Blas Aritio (1970), Senosiain & Donazar (1983), Castién & Mendiola (1985), Ruiz-Olmo & Palazón (1990), Palazón & Ruiz-Olmo (1992), Palazón

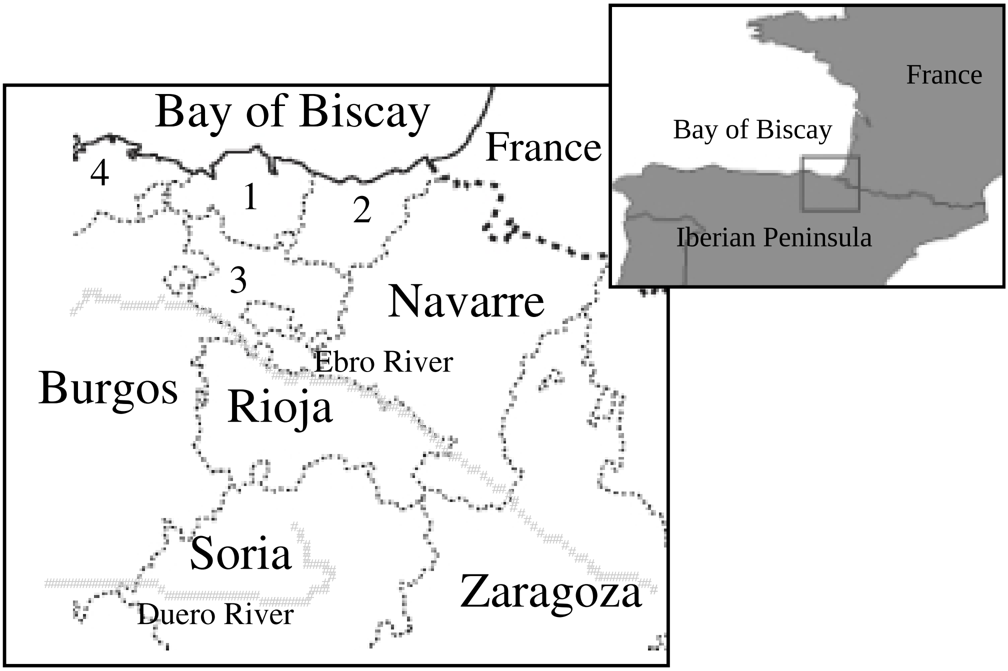


Figure 1. Map of the study area including the major rivers. 1 Biscay, 2 Gipuzkoa, 3 Araba and 4 Cantabria.

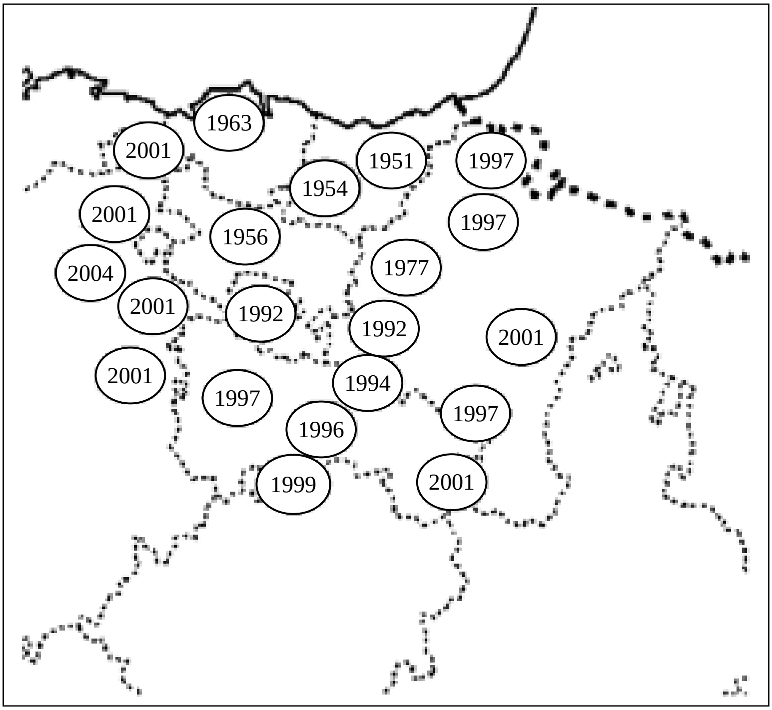


Figure 2. First record dates of European mink in different areas of the northern Iberian Peninsula.

(1993), Illana (1994), Torres & Zuberogoitia (1996), Arambarri et al. (1997), Palazón & Ruiz-Olmo (1997), Torres & Zuberogoitia (1997), Ahiartza et al. (1999), Belamendia (2001), Ceña et al. (2001), Gonzalez-Estaeban et al. (2001), Zabala et al. (2001), Zuberogoitia et al. (2001), Palazón et al. (2002), Zabala & Zuberogoitia (2003a).

These papers deal with different areas, focus at different scales, and often use different methods. Therefore, the discussion is coarse-grained in order to provide a general overview. We evaluated the reliability of each paper in relation to the methods used and the effort made to detect the species (table 1). Works were thoroughly reviewed and only those based on live-trapping data, road kills, triggered cameras or techniques that involve the handling of the animal, or provide secure proof of its presence were considered. Works based on observations were only considered when made by professional researchers or well known naturalists. A few other works not considered reliable, are discussed separately.

Results

The first data on European minks in the Iberian Peninsula date back to 1951 (Rodríguez de Ondarra 1955). The author provides data about three European minks captured in 1951 and 1952 at two locations in Gipuzkoa (figure 2). Puente (1956) subsequently reports on the presence of the species in the nearby region of Araba. In

Table 1. Reliability of different types of data.

Data source	Reliability
Trapping data	Reliable
Photographic data	Reliable
Road kills, hunted or stuffed animals	Reliable
Observations and presence reports	Depending on source: Scientists / renowned naturalists: reliable Others: not reliable
Inquests	Not reliable
Indirect reports (not from the author)	Not reliable

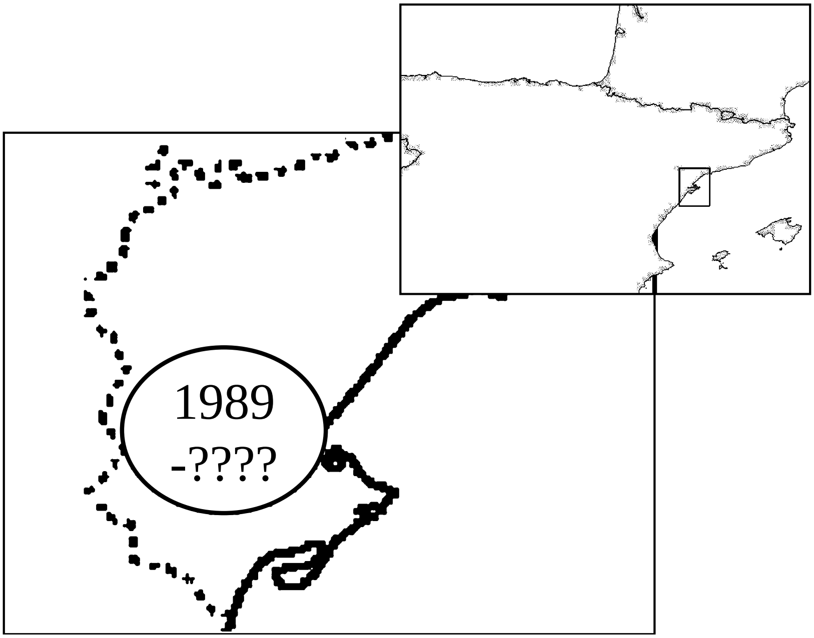


Figure 3. Location of the data provided by Ruiz-Olmo & Palazón (1990) and Palazón & Ruiz-Olmo (1992) for Catalonia.

1963, new locations in Gipuzkoa and Araba are identified, as well as the first data from two other locations in Biscay and one in Navarre, near the border with Gipuzkoa (Rodríguez de Ondarra 1963). Senosiain and Donazar (1983) confirm the southerly spread of the species into Navarre, based on road-kills between 1977 and 1982. Castién and Mendiola (1985) report the presence of the populations in Gipuzkoa, eastern Biscay and central Araba. The presence of European minks in these areas has been subsequently confirmed by several authors (Palazón & Ruiz-Olmo 1992, Palazón 1993, Illana 1994, Arambarri et al. 1997, Aihartza et al. 1999, Ceña et al. 2001, González-Esteban et al. 2001, Zabala et al. 2001, Zuberogoitia et al. 2001, Zabala & Zuberogoitia 2003a). Blas Aritio (1970) reports European minks in western Cantabria, based on indirect data from trappers.

In the 1990s, Palazón and Ruiz-Olmo (1992) report new European mink locations in Navarre, indicating a southerly range expansion, towards the Ebro River. Palazón (1993) shows similar results for the mink population in central Araba. By 1997, the presence of European mink in large areas of the Ebro River and La Rioja is documented (Torres & Zuberogoitia 1996, Arambarri et al. 1997, Palazón & Ruiz-Olmo 1997). Before 1994 the species was unknown in La Rioja, but during this year a trapping study revealed the presence of the species in the area (Torres & Zuberogoitia 1996). A few years later, road kills and illegally shot individuals were also reported (Torres & Zuberogoitia 1996). The latest results show higher densities at those sites where the minks were first trapped (Ceña 2003).

At the same time, in 1990 there is a single record of minks in Catalonia in the Ebro Delta (Ruiz-Olmo & Palazón 1990) (figure 3), and in 1992 there were another two possible records from that area, one of which is doubtful (Palazón & Ruiz-Olmo 1992). This record is located far from the European mink's distribution area and has not been explained or subsequently confirmed. The authors speculate about a possible long distance migration of a single mink or of some individuals (Ruiz-Olmo & Palazón 1990).

Finally, by 1999 the presence of the European mink in Burgos and northern Soria as well as the first data from the catchment of the Duero river were reported (Palazón et al. 2002).

Discussion

Did European mink colonise the Iberian Peninsula?

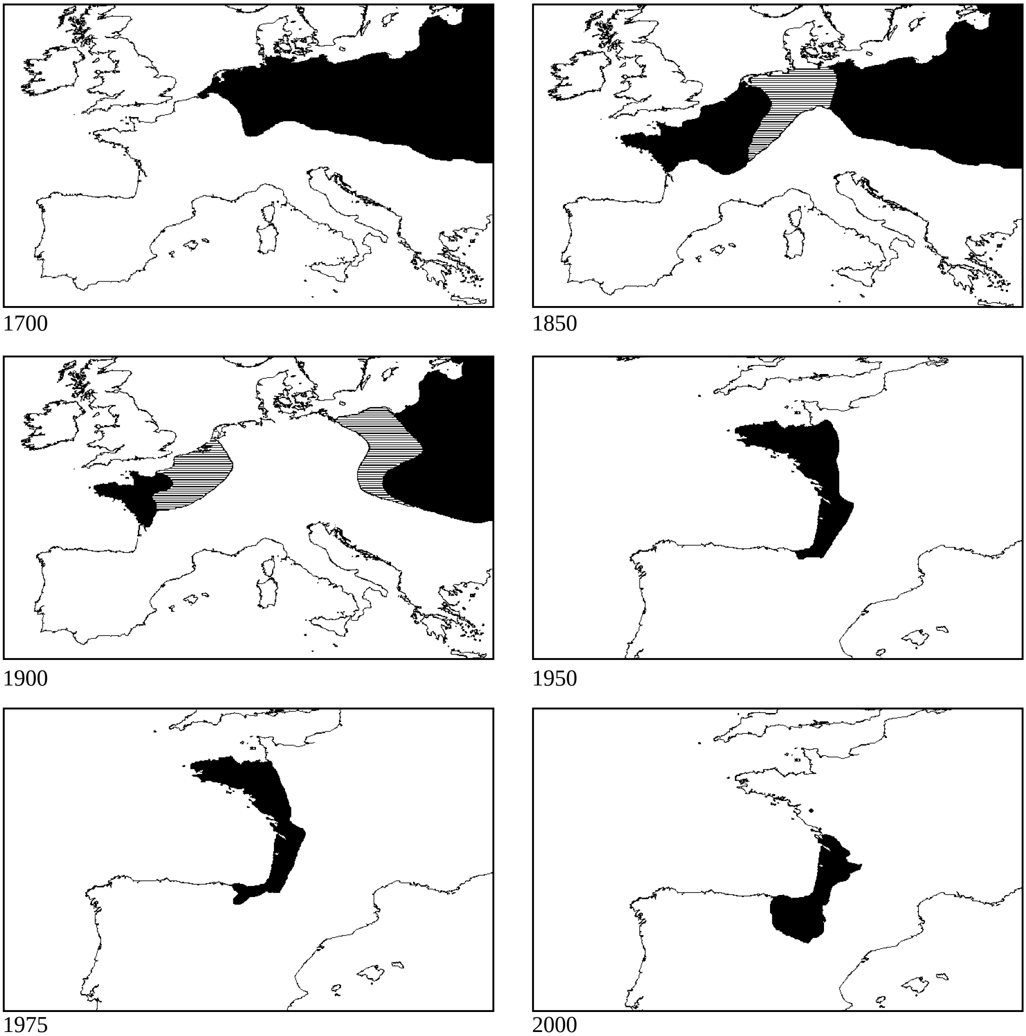
Although there is no scientific basis to reject either of our hypotheses on the historical distribution of European mink in the Iberian Peninsula, the information available suggests that the species first reached the Iberian Peninsula around 1950.

There are no records of European minks in the area before 1951, even though commercially valuable furbearers are among the first species to be recognised by local hunters, trappers and naturalists (Youngman 1982). Although there are no statistics available on the intensity of trapping in the past, it is known that it was quite common, practised not only by trappers but also by farmers, who regard most mustelids as pests. Indeed, the first European mink found in the study area was captured by a fur trapper who, not recognising the species, submitted it to naturalists for identification. It turned out to be unknown to naturalists as well (J. Elosegi, personal communication). Subsequent reports of European minks are based on trapped and hunted individuals (Rodríguez de Ondarra 1955, Rodríguez de Ondarra 1963, Puente 1956, Blas Aritio 1970, Senosiain & Donazar 1983). In this way, Rodríguez de Ondarra (1963) gathered data on more than 35 minks captured between 1951 and 1958 in the Basque Country, although this probably accounts for only a small part of the total number of animals caught.

Nowadays, road kills are a major source of information (see Belamendia 2001, Maizeret et al. 2002, Zabala & Zuberogoitia 2003a). There are, however, no records on road kills from the study area before 1951, nor are there any known fur or cranial samples of European mink from that period. Moreover, during the late 19th and the early 20th centuries the Iberian fauna attracted the attention of several naturalists who described many subspecies for the Iberian Peninsula, including subspecies of stoats *(Mustela erminea)* (two), weasels *(Mustela nivalis)* (two), polecat *(Mustela putorius)* (one), stone marten *(Martes foina)* (one), and several small mammals (see Garcia-Perea & Gisbert 1997). Thus, it is unlikely that the European mink went unnoticed. Besides, changes in the knowledge of the distribution of the species show a consistent pattern of south-westerly expansion accompanied by an extinction front to the east and north (see figure 4). Therefore, we support the contention of most authors that the European mink reached the Iberian Peninsula in the late 1940s (Rodríguez de Ondarra 1955, Youngman 1982, Senosiain & Donazar 1983, Aihartza et al. 1999, Zabala & Zuberogoitia 2003b). In addition, based on the same reasons and given the increased fieldwork effort from the 1990s onwards, we assume that the first records of the species, approximately, coincide with the colonisation of new areas.

Indications of an expanding population

The European mink has been slowly but steadily expanding southwards from the time that it was first identified in Spain in 1951 (Rodríguez de Ondarra 1955) (figure 2). There is also evidence of an eastward expansion through the colonisation of the Ebro River tributaries (Senosiain & Donazar 1983, Palazón & Ruiz-Olmo 1992, Palazón & Ruiz-Olmo 1997). The European mink initially seemed to have reached its western distribution limit by 1963 (Rodríguez de Ondarra 1963), but more recently there are indications of a further westward expansion (Zuberogoitia et al. 2001, Zabala & Zuberogoitia 2003a). Despite the introgression of some American mink populations (Ceña et al. 2001, Zuberogoitia et al. 2001, Palazón et al. 2002), the presence of European minks has been confirmed at large spatial scales. Interestingly, the authors found a road killed European mink at Burgos in the summer



1700

1850

1900

1950

1975

2000

Figure 4. Distributional changes of European mink. Black areas indicate the known European mink presence, shaded areas indicate where mink was recorded as rare or disappearing at that time. Maps have been built after Youngman (1982), Saint-Girons (1994), Lodé et al. (2001), Maizeret et al. (2002), Palazón et al. (2002), and Zabala & Zuberogoitia (2003a).

of 2004 (figure 2), in an area where the species had not been previously detected, despite trapping having been conducted there (for the latest map on the species' distribution see Palazón et al. 2002).

The only outlier in this distributional pattern is the record from Catalonia reported by Ruiz-Olmo & Palazón (1990), which is some 400 km away from the current known distribution area. Bowman et al. (2002) suggest that the dispersal distance of mammals is isometric to the linear dimension of their home range multiplied by a constant that ranges from 7 to 40. The home ranges of male European minks in the study area are about 13 km long (Garin et al. 2002), which would, according to the model of Bowman et al. (2002), enable dispersion distances of 91–520 km. This model does provide an explanation of the seemingly large gap between the main areas and the Catalonian observation, a possibility that is noted by Ruiz-Olmo and Palazón (1990) and Palazón and Ruiz-Olmo (1997).

Another problem regarding the distribution is the presence of European minks in Cantabria reported by Blas Aritio (1970). Trappers from that area recorded two types of polecat. One of these, was considered by Blas Aritio (1970) to be a European mink, had a darker coat. However, since the presence of minks there has not been confirmed by captures, road kills or examination of old material, and since the author based his conclusions on indirect reports of trappers, we do not consider these records as reliable. Polecats are known to have a dark phenotype, that is often confused with that of the European mink (Lodé et al. 2001) and which seems to be common in the north of the Iberian Peninsula (Zuberogoitia et al. 2001).

Recent genetic research, which included populations from Southwestern Europe, found very low intra-specific genetic variability in mtDNA for European minks, which is consistent with the hypothesis of an expanding population (Michaux et al. 2004). Moreover, there is hardly any genetic variation between European minks from France and Spain, suggesting that the population was established by a few individuals, and possibly even by a single female (Michaux et al. 2004). However, an early Holocene origin is also possible, with some long distance migrants from a refugium establishing the population (Michaux et al. 2004). Studies based on mtDNA and microsatellites also show that the genetic variability between the European mink populations from France and Spain is negligible, the most probable explanation being a severe bottleneck, or the consequence of a founder effect. This is consistent with the probable absence of minks in the area before the 19th century (Cabria et al. 2003, Gómez-Moliner et al. 2003).

The colonisation of the Iberian Peninsula in the late 1940s would also coincide with, and possibly be a consequence of, a period of high population density in neighbouring France, judging from the large number of specimens deposited in museums in France during that time (Youngman 1982).

Possible explanations

How can we explain the recorded population expansion in the Iberian Peninsula? Factors limiting a species' distribution may be abiotic or biotic. It is difficult to identify one single abiotic factor responsible for the distribution, current or past, or for any changes in distribution. Indeed, the European mink is currently distributed across the Eurosiberian and Mediterranean biogeographical areas of Europe, areas with very different climate conditions (Walter 1997, Palazón et al. 2002).

Biotic factors also vary. Competition with the American mink is suggested as the cause for the decline in Eastern Europe (Macdonald et al. 2002), yet the most likely underlying cause in France seems to be anthropic pressure upon the species, specifically, the conjunction of intensive trapping, alteration of water quality, and habitat modification (Lodé et al. 2001, Lodé 2002). In addition interspecific relationships with polecat have been proposed, based on experiments conducted in captivity (Schröpfer et al. 2001). We will discuss the possible role of these factors for the distributional changes in our study area here.

Water quality. Data on water quality are scarce in the study area. It seems that there has been a slight improvement over the last few years, at least in some areas, and there are some policies favouring the use of natural fertilisers and regulating the use of pesticides, which could favour the presence of minks in some rivers. Since these have only been implemented just recently, it is unlikely that they could had a significant bearing in explaining the apparent recent expansion of minks (Anonymous 2000, Anonymous 2001, Arluziaga 2002, Anonymous 2003).

Habitat modification due to land use changes. Changes in landscape and land use are known to influence the distribution of predators, especially of habitat specialists like the European mink, and intensification of agricultural practices is supposed to be one of the reasons for its historic and current decline (Lodé et al. 2001, Macdonald et al 2002, Robinson & Sutherland 2002, Schadt et al. 2002). In the Basque Country, agricultural practices have experienced a severe regression, especially during the 1980s and 1990s, in favour of forest cultures that currently occupy 54% of the area (Anonymous 2001). However, in a study on the habitat selection of the European mink conducted in the Basque Country, minks were found to avoid forests and forest cultures, preferring meadows and small orchards (Zabala et al. 2003). In La Rioja, trends in land use changes over the past decade are less clear-cut. There has been an expansion of agricultural lands and forest cultures since 1996 (by 2% and 16% respectively), while meadows have declined by 23% of their previous area (Anonymous 2000). In Navarre, only minor changes took place. From 1991 to 2000, agricultural areas have been reduced by 4%, meadows and pastures experienced a decline of 9%, and forest cultures expanded by 1% (Anonymous 2003). The overall pattern in land use varies among areas (table 2), and its possible influence in the assumed expansion of minks is difficult to assess. However, in areas where expansion seems to have occurred over the last decade, like Navarre and La Rioja, changes in land use are relatively insignificant. The only exception could be the reduction of pastures and meadows in La Rioja area (Anonymous 2000), but no study has pointed out possible benefits of the reduction of this habitat for the European mink. The few studies conducted hitherto on the habitat selection of the European mink stress the importance of riverbank structures such as bramble thickets (Zabala et al. 2003, Zabala & Zuberogoitia 2003c). Some changes in agricultural practices and intensity as a result of the abandonment of rural areas over the last decades, may be an important factor favouring the expansion of the European minks in the Iberian Peninsula. Moreover, riverbank protection policies have been developed, with different intensity in different areas, which could also affect the expansion of European minks. Another practice the importance of which is difficult to assess, but which undoubtedly has had an effect, is a reduction in the indiscriminate use of poisons, which was also common in the past. This has also been pointed out as an important factor influencing the current distribution of some carnivores in the area (Aihartza et al. 1999). The law 4/1989 of the 27th of March of 1989 forbade these practices, and it is noticeable that, for instance in Araba, since 1988 there are no records of kill-trapped individuals (Arambarri et al. 1997). Even if this last factor is not sufficient to explain an expansion, it is likely, to have had some beneficial effects for the species.

Interspecific relations. Last, but not least, intragild effects should be considered. There are some American mink populations in the Iberian Peninsula, the oldest of them dating back to the late 1950s or the early 1960s. By the 1990s American minks were present in several areas of the Iberian Peninsula, especially in the north, including areas already occupied by the European mink (Bravo & Bueno 1999, Zuberogoitia et al. 2001). The expansion of both species is therefore synchronic and, since there are relatively well preserved areas where both species are absent, the observed pattern can not be a consequence of the presence or absence of the American mink. Moreover, the westernmost distribution area of the European mink in Biscay lies besides the well preserved streams of Cantabria were both species of mink are unknown, whilst both species are present in the less well preserved rivers of Biscay (Bravo 2002, Zabala & Zuberogoitia 2003a, Zuberogoitia & Zabala 2003). On the other hand, it is important to recognise that in

Table 2. Land of use (in %) in the Basque Country, Navarre, and la Rioja (adapted from Anonymous 2000, Anonymous 2001, Anonymous 2003).

Land use	Agriculture	Pastures & meadows	Forests & forest cultures	Other
Basque Country	14	19	54	13
Navarre	34	25	30	11
La Rioja	32	22	27	19

some areas occupied by both mink species, local extinctions of European mink have occurred (Ceña et al. 2001, Zuberogoitia et al. 2001, Palazón et al. 2002).

Little is known about the ecology of polecats in the Iberian Peninsula. However, they are distributed across most of the European mink area and may locally reach fair densities (Virgós 2002). Some studies point out that this mustelid may not show semi-aquatic behaviour in the area (Zuberogoitia et al. 2000, Virgós 2002). Moreover, the polecat is common in the neighbouring French area, where it is regarded as a pest, but not as a cause for the decline of the European mink (Lodé et al. 2001).

Conclusions

In conclusion, even if we cannot definitively reject the hypothesis that the European mink is an old part of the Iberian fauna, there are strong indications that the species is a recent arrival to the Iberian Peninsula. We can not currently present a conclusive explanation for this phenomenon as none of the proposed causes for the decline of European mink in its neighbouring distribution area in France has changed significantly among the areas where it is present or absent. Furthermore, the influence of American mink on its European counterpart in the area, is as yet unclear. Zabala & Zuberogoitia (2003a) state that the European mink recently extended its distribution westwards in Biscay, therefore the expansion could still be an ongoing process and this could be one reason for the absence of explanatory variables.

Future research

Further research is needed in order to check for a possible expansion of European mink into nearby areas and to determine those causes that may have favoured changes in its distribution. Genetic research might play an important role by determining the origin of the western population in space and time, and by confirming or rejecting the model of expansion proposed in this paper. Research on those land uses and policies that influence the presence of European minks at landscape scale would also help increase understanding of distributional changes. It would also be interesting to determine the potential distribution area of the species, by identifying areas suitable for colonization, and then periodically checking these, especially at the borders of known distribution areas, in order to find out if expansion is still happening. Finally, studies on mink pathologies could help understand the decline or the absence of European mink in some historically occupied areas in Europe, which are nowadays apparently suitable but remain unoccupied.

Acknowledgements: We wish to thank the Junta de Castilla y León, Delgación Territorial de Soria, J. M. Meneses, and S. Hornilla from the Deparatamento de Medio Ambiente y Ordenación del Territorio of the Basque Government for their help, and especially to Drs. T. Lodé, T. Maran, two anonymous referees, and the editors of Lutra for their comments and suggestions on a previous draft. We also thank A. Secilla for his help with the maps. A. Albizua improved the English of the original manuscript.

References

Aihartza, J.R., I. Zuberogoitia, E. Camacho-Verdejo & J.J. Torres 1999. Status of carnivores in Biscay (N. Iberian Peninsula). Miscelanea Zoologica 22: 41-52.

Anonymous 2000. Estadística agraria regional. Government of La Rioja, Logroño, Spain.

Anonymous 2001. Medio Ambiente en la Comunidad Autónoma del País Vasco. Basque Government, Vitoria-Gasteiz, Spain.

Anonymous 2003. Manual de estadística agraria. Navarra y comarcas. Año 2000. Government od Navarre, Pamplona-Iruña, Spain.

Arambarri, R., A. Rodríguez & G. Belamendía 1997. Selección de hábitat, mortalidad y nueva aportación a la distribución del Visón Europeo (*Mustela lutreola*) en Alava. Estudios del Museo de Ciencias Naturales de Alava 12: 217-225.

Arluziaga, I. 2002. Variación de la calidad de las aguas en los ríos gipuzkoanos al cabo de veinte años (1981-2001). Munibe 53: 39-56.

Blas Aritio, L. 1970. Estudio bioecológico de la familia Mustelidae. SPCN, Madrid, Spain.

Belamendia, G. 2001. Mamíferos carnívoros inventariados en la colección Zoología Vertebrados del Museo de Ciencias Naturales de Álava. Estudios del Museo de Ciencias Naturales de Alava 16: 221-226.

Bowman, J., J.A.G. Jaeger & L. Fahrig 2002. Dispersal distance of mammals is proportional to home range size. Ecology 83: 2049-2055.

Bravo, C. 2002. *Mustela vison* Schreber, 1777. In: L.J. Palomo & J. Gisbert (eds.). Atlas de los mamíferos terrestres de España: 258-261. Dirección General de Conservación de Naturaleza – SECEM – SECEMU, Madrid, Spain.

Bravo, C. & F. Bueno 1999. Visón americano, *Mustela vison* SCHREBER, 1977 (Mamíferos de España). Galemys 11: 3-16.

Cabria, M.T., J. Rubines, R. Zardoya & B.J. Gómez-Moliner 2003. Genetic variability of the west population of European mink (*Mustela lutreola*) based on mtDNA control region sequence data. Abstracts of the 'International Conference on the Conservation of the European mink': 35-36. Logroño, Spain.

Castién, E., & I. Mendiola 1985. Mamíferos. In: Viceconsejería de Medio Ambiente. Vertebrados de la Comunidad Autónoma del País Vasco. Eusko Jaurlaritza-Gobierno Vasco, Vitoria-Gasteiz, Spain.

Ceña, A., J.C. Ceña & L. Lobo 2001. Desplazamiento del visón europeo (*Mustela lutreola*) por el visón americano (*Mustela vison*) en el municipio de Vitoria-Gasteizt. Abstracts of the 'V Jornadas de la Sociedad Española de Conservación y Estudio de Mamíferos': 55. Vitoria-Gasteiz, Spain.

Ceña, J.C. 2003 The European Mink in Spain: Ecology, population locations, and aspects of conservation. Abstracts of the 'International Conference on the Conservation of the European Mink': 17-21. Logroño, Spain.

Flores, A.M. 1989. Kartografía. In: Viceconsejería de Medio Ambiente. Euskal Autonomi Elkarteko ornodunak: 21-51. Eusko Jaurlaritza, Vitoria-Gasteiz, Spain.

Garin, I., I. Zuberogoitia, J. Zabala, J., Aihartza, A. Clevenger & A. Rallo 2002. Home range of European mink (*Mustela lutreola* L.) in Southwestern Europe. Acta Theriologica 47: 55-62.

Gómez-Moliner, B., M.T. Cabria, J. Rubines, E.G. González & R. Zardoya 2003. Development of molecular markers to the study of the conservation, management and action plans for the endangered European mink. Abstracts of the 'International Conference on the Conservation of the European mink': 56-57. Logroño, Spain.

González-Esteban, J., I. Villate & I. Irizar 2001. Área de distribución y valoración del estado de las poblaciones del visón europeo en la Comunidad Autónoma del País Vasco. Unpublished report.

Illana, A. 1994. El visón europeo (*Mustela lutreola*), distribución y conservación en Alava. Unpublished report.

Kranz, A., A. Toman & J. Botond Kiss 2003. The European mink in the Danube Delta; distribution-habitats-threats. Abstracts of the 'International Conference on the Conservation of the European Mink': 24-25. Logroño, Spain.

Lodé, T 2002. An endangered species as indicator of freshwater quality: fractal diagnosis of fragmentation within a European mink, *Mustela lutreola*, population. Archives Hydrobiology 156: 163-176.

Lodé, T., J.P. Cornier & D. Le Jacques 2001. Decline in endangered species as an indication of anthropic pressures: the case of European mink *Mustela lutreola* western population. Environmental management 28: 221-227.

Macdonald, D.W., V.E. Sidorovich, T. Maran & H. Kruuk 2002. European mink, *Mustela lutreola*: analyses for conservation. Wildlife Conservation Research Unit, Oxford, UK.

Maizeret, C, P. Migot, H. Galineau, P. Grisser & T. Lodé 1998. Répartition et habitats du Visond'Europe (*Mustela lutreola*) en France. Arvicola, Actes "Amiens 97": 67-72.

Maizeret, C., P. Migot, R. Rosoux, J.P. Chusseau, T. Gatelier, H. Maurin & C. Fournier-Chambrillon. 2002. The distribution of the European mink (*Mustela lutreola*) in France: towards a short term extinction? Mammalia 66: 525-532.

Maran, T., & H. Henttonen 1985. Why is the European mink (*Mustela lutreola*) disappearing? A review of the process and hypotheses. Annales Zoologici Fennici 34: 47-54.

Maran, T., H. Kruuk, D.W. Macdonald & M. Polma 1998a. Diet of two species of mink in Estonia: displacement of *Mustela lutreola* by *M. vison*. Journal of Zoology, London 245: 218-222.

Maran, T., D.W. Macdonald, H. Kruuk, V. Sidorovich & V.V. Rozhnov 1998b. The continuing decline of the European mink *Mustela lutreola*: evidence for the intraguild aggression hypothesis. In: N. Dunstone & M.L. Gorman (eds). Behaviour and Ecology of Riparian Mammals: 297-324. Cambridge University Press, Cambridge, UK.

Michaux, J.R., R. Libois, A. Davison, P. Chevret & R. Rosoux 2004. Is the western population of European mink, (*Mustela lutreola*) a distinct management unit for conservation? Biological Conservation 115: 357-367.

Palazón, S. 1993. Situación del visón Europeo (*Mustela lutreola*) en Alava. Estudios del Museo de Ciencias Naturales de Alava 8: 237-240.

Palazón, S. & J. Rúiz-Olmo 1992. Status of European mink (*Mustela lutreola*) in Spain. Semiaquatische Säugetiere 1992: 337-340.

Palazón, S. & J. Ruiz-Olmo (eds.) 1997. El visón europeo (*Mustela lutreola*) y el visón americano (*Mustela vison*) en España. Ministerio de Medio Ambiente, Madrid, Spain.

Palazón, S., J.C. Ceña, S. Mañas, A. Ceña & J. Ruiz-Olmo 2002. Current distribution and status of the European mink (*Mustela lutreola* L., 1761) in Spain. Small Carnivore Conservation 26: 9-11.

Puente, F. 1956. El visón en Alava. Munibe 8: 24-27.

Robinson, R.A. & W.J. Sutherland 2002. Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology 39: 157-176.

Rodríguez de Ondarra, P. 1955. Hallazgo en Guipúzcoa de un mamífero no citado en la “Fauna Ibérica” de Cabrera. Munibe 4: 201-207.

Rodríguez de Ondarra, P. 1963. Nuevos datos sobre el visón en España. Munibe 15: 103-110.

Ruiz-Olmo, J. & S. Palazón 1990. Occurrence of European mink (*Mustela lutreola*) in Catalonia. Miscelanea Zoologica 14: 249-253.

Saint-Girons, M.C. 1994. Wild mink (*Mustela lutreola*) in Europe. Nature and environment 54. Council of Europe press, Strassbourg, France.

Schadt, E., E. Revilla, T. Wiegand, F. Knauer, P. Kaczensky, U. Breitenmoser, L. Bufka, J. Cerveny, P. Koubek, T. Huber, C. Stnisa & L. Trepl 2002. Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. Journal of Applied Ecology 39: 189-203.

Schröpfer, R., C. Bodenstein, C. Seebass, K. Recker & M. Jordan 2001. Niche analysis of the Mustela species *lutreola*, *putorius* and *vison* by craniometry and behavioural observations. Säugetierkundliche informationen 25: 121-132.

Senosiain, A. & J.A. Donazar 1983. Nuevos datos sobre la presencia del visón europeo (*Mustela lutreola* L.) en Navarra. Doñana, Acta Vertebrata 10: 219-221.

Sidorovich, V. 2000. The on-going decline of riparian mustelids (European mink, *Mustela lutreola*, polecat, *Mustela putorius*, and stoat, *Mustela erminea*) in eastern Europe: a review of the results to date and an hypothesis. In: H.I. Griffiths (ed). Mustelids in a modern world. Management and conservation aspects of small carnivore: human interactions: 295-319. Backhuys Publishers, Leiden, The Netherlands.

Sidorovich, V.E., D.W. MacDonald, H. Kruuk & A. Krasko 2000. Behavioural interactions between the naturalised American mink *Mustela vison* and the native riparian mustelids, NE Belarus, with implications for population changes. Small Carnivore Conservation 22: 1-5.

Torres, J.J. & I. Zuberogoitia 1996. El visón europeo. In: Ceña, A. (ed.) Mamíferos: 102-107. Caja Rioja, Logroño, Spain.

Torres, J.J. & I. Zuberogoitia 1997. Distribución de lo mesocarnívoros en el río Ebro a su paso por la Comnidad Autónoma de La Rioja. Aegypius 14: 31-34.

Tumanov, I.L. 1992. The number of European mink (*Mustela lutreola* L.) in the eastern area and its relation to American mink. Semiaquatische Säugetiere 1992: 329-335.

Virgós, E. 2002. *Mustela putorius* Linnaeus, 1758. In: L.J. Palomo & J. Gisbert (eds.). Atlas de los mamíferos terrestres de España: 262-265. Dirección General de Conservación de Naturaleza – SECEM – SECEMU, Madrid, Spain.

Walter, H. 1997. Zonas de Vegetación y Clima. Omega, Barcelona, Spain.

Youngman, P.M. 1982. Distribution and systematics of the European Mink *Mustela lutreola* Linnaeus 1761. Acta Zoologica Fennica 166: 1-48.

Zabala, J. & I. Zuberogoitia 2003a. Current and historical distribution of European mink (*Mustela luteola*) in Biscay. Evolution and comments of the results. Small Carnivore Conservation 28: 4-6.

Zabala, J. & I. Zuberogoitia 2003b. Is the European mink (*Mustela lutreola*) old part of the Iberian fauna or it reached in the XX century? Small Carnivore Conservation 24: 8-9.

Zabala, J. & I. Zuberogoitia 2003c. Habitat use of male European mink (*Mustela lutreola*) during the activity period in Southwestern Europe. Zeitschrift für Jagdwissenschaft 49: 77-81.

Zabala, J., I. Zuberogoitia, I. Garin & J.R. Aihartza 2001. Small carnivore trappability: seasonal changes and mortality. A case study on European mink *Mustela lutreola* and spotted genet *Genetta genetta.* Small Carnivore Conservation 25: 9-11.

Zabala, J., I. Zuberogoitia, I. Garin & J.R. Aihartza 2003. Landscape features in the habitat selection of European mink (*Mustela lutreola*) in Southwestern Europe. Journal of Zoology, London 260: 415-421.

Zuberogoitia, I. & J. Zabala 2003. Data on the distribution of the American mink in Biscay. Galemys 15: 31-37.

Zuberogoitia, I., J.J. Torres, J. Zabala & M.A. Campos 2001. Carnívoros de Bizkaia. Bilbao Bizkaia Kutxa, Bilbao, Spain.

Samenvatting

De historische en huidige verspreiding van de Europese nerts (*Mustela lutreola*) op het Iberisch Schiereiland.

De meeste meldingen van de Europese nerts (*Mustela lutreola*) op het Iberisch Schiereiland zijn niet vastgelegd in internationale of nationale literatuur. De verspreiding van de soort is daarom niet precies bekend en ook moeilijk te bepalen. In dit artikel wordt aan de hand van onder meer ongepubliceerde rapporten en moeilijk toegankelijke artikels met een lokale verspreiding, een beeld gegeven van de historische en huidige verspreiding van de Europese nerts op het Iberisch Schiereiland. Geconcludeerd wordt dat de soort het noorden van Iberië waarschijnlijk aan het eind van de jaren ‘40 van de vorige eeuw heeft bereikt. Sindsdien lijkt de soort zich langzaam maar gestaag uit te breiden, vooral in zuidelijke richting, maar meer recentelijk ook oostwaarts en, waarschijnlijk, westwaarts. Mogelijke verklaringen voor deze vermoedelijke uitbreiding worden kort besproken.

Received: 7 September 2004
Accepted: 2 November 2004

The return of the harbour porpoise (*Phocoena phocoena*) in Dutch coastal waters

Kees C.J. Camphuysen[1,2]

[1] Koninklijk Nederlands Instituut voor Onderzoek der Zee,
P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands, e-mail: camphuys@nioz.nl
[2] Nederlandse Zeevogelgroep, Marine Mammal Database,
Ankerstraat 20, 1794 BJ Oosterend, Texel, The Netherlands, e-mail: kees.camphuysen@wxs.nl

Abstract: The harbour porpoise (*Phocoena phocoena*) became virtually extinct in Dutch coastal waters in the early 1960s. A systematic method to record seabird passage along the coast became established in the early 1970s and was used ever since. These observations allowed a reconstruction of the return of the elusive harbour porpoise in Dutch coastal waters. A small, but gradually increasing number of sightings in the mid-1980s to early 1990s was followed by a proportional rate of increase of 41% per annum over the last 15 years. At first, only full-grown animals were seen and the occurrence was virtually restricted to mid-winter. In later years, numbers sharply increased in winter, and more and more animals were seen also in summer and autumn, including mother-calf combinations. Both the historic decline and the recent increase are concurrent with similar trends in strandings and at-sea survey data. Unambiguous explanations for the initial decline have never been given and it is equally difficult to fully understand the come-back. There is evidence, however, that distributional shifts rather than population fluctuations underlie the trends observed. The re-distribution of harbour porpoises in the North Sea may have been triggered by local reductions or shifts in principal prey availability.

Keywords: harbour porpoise, *Phocoena phocoena,* sightings, The Netherlands, population trends, historical decline, distribution shift.

Introduction

In the 1950s, or even in the 1940s, a decline in sightings of the harbour porpoise (*Phocoena phocoena*) in Dutch coastal waters occurred. The first reports indicating fewer sightings date back to 1939 (Viergever 1955), but it was immediately after the Second World War that the decline became more obvious (Verwey 1975). Not everyone was immediately convinced that harbour porpoises had declined (van Deinse 1952, Vader 1956, van Deinse 1959), since numerous corpses of porpoises littered the Dutch beaches. When a general consensus was reached that porpoises were less common than they used to be, the animal had become a rarity. Unfortunately, from reported sightings, the decline is poorly documented. Smeenk (1987) and Addink & Smeenk (1999) reconstructed the decline from strandings records and encountered a similar problem. At first, porpoises were so abundant that corpses on the beach were not systematically recorded (van Deinse 1925, van Deinse 1931, van Deinse 1946). Only since 1951 porpoises were included in a recording scheme of beached marine mammals, a scheme that collapsed in the early 1960s as a consequence of the death of its organiser in 1964. Hence, strandings were recorded when the decline was already prominent and the final phase, when the animals became rare, was not documented. Very few harbour porpoises were seen in The Netherlands in the 1960s, 1970s, and early 1980s and strandings were at a very low level compared to the first half of that century (Camphuysen 1982, Smeenk 1987). The harbour porpoise, once a very common cetacean in Dutch coastal waters and “a typical summer animal” (Viergever 1955) had gone.

Amateur ornithologists developed an interest in seabirds somewhere in the late 1960s and early 1970s. High powered, but relatively cheap binoculars became available in these years and with those mounted on a tripod, a revolution in bird recording took place. Many more true seabirds could be seen than anyone had realised before, and violent autumn storms attracted crowds of observers at strategic lookouts to witness the spectacle (Camphuysen & van Dijk 1983, Camphuysen 1985). Spring migration turned out to be equally spectacular and not before long, "seawatchers" were observing seabirds almost every day, throughout the year, at the more popular sites. The establishment of the "Club van Zeetrekwaarnemers" in 1972 formalised seawatching and the development of a standard record card was the foundation of a highly successful scheme for the years to come, until the present day. Although seabirds formed the motivation for these coastal observations, marine mammals were also recorded and included as "highlights" in bi-annual, reports. The seawatching scheme became established when marine mammals were extremely rare in Dutch coastal waters and very few were recorded in the first ten years (Camphuysen 1982).

In the mid-1980s, the number of harbour porpoise sightings gradually increased. While only 20 harbour porpoises were recorded between 1972 and 1985, during 39,704 hours of observation (one every 2000 hours), 75 porpoises were observed between 1986 and 1990 during a further 14,565 hours of observation (one every 190 hours; a tenfold increase). Between 1991 and 1995, 222 porpoises were recorded during 17,732 hours of observation (one every 80 hours), or another 2.5 fold increase compared to the preceding years. Camphuysen & Leopold (1993) and Camphuysen (1994) published early accounts of what they thought might be a comeback of the harbour porpoise in Dutch coastal waters. These reviews were largely based on seawatching data from the Dutch coast, but with additional information on the distribution of porpoises from ship-based and aerial surveys in the Dutch sector of the North Sea. This paper, ten years later, intends to be an update based largely on the continuing seawatching results.

Methods

Harbour porpoise abundance was analysed by extracting sightings from the seawatching database of the Nederlandse Zeevogelgroep (NZG/CVZ database; 1972-2004). A second dataset used is a series of incidental sightings obtained directly from the observers or extracted from numerous smaller publications in local, regional or even national journals and, more recently, from websites. Both data sets are restricted to sightings from coastal sites; records (even incidental sightings) from ships and aircraft have been excluded. The seawatching data set is the more important collection of sightings, because the observer effort is known. Observers record the date, the duration (start- and end-time), and weather characteristics for each set of data and usually record their sightings per hour of observation. Equally important, the observers were considered trained and experienced in cetacean identification. It is from these data that reliable long-term trends can be calculated and the seasonal patterns analysed. Incidental sightings come from a variety of sources and outliers have been checked individually in order to exclude erroneous sighting reports. The identification of cetaceans, including porpoises, is not easy (Camphuysen 1987, Camphuysen 1991) and people who rarely see them have a tendency to just guess what it might have been. The greatest additional value of the data presented here is above all the contribution to our knowledge of the geographical distribution: seawatchers work from a small number of sites, while porpoises are much more widespread.

The effort-corrected data from systematic seawatches in this paper are expressed as "number per hour of observation" (n h^{-1}). Considering the observer effort, some assumptions had to be made, for not all data have yet fully been submitted (and there will always be a backlog in that). Sightings of porpoises during seawatching have been promptly reported by nearly all observers *before* all observational and effort data are logged on record cards and subsequently entered into the database. With only part of the record cards being processed and, hence, observer effort in 2001-2004 not (yet) completely known, this has been assumed to be similar as in the preceding five-year period (table 1). Future reports using the same source, but with an updated database, may therefore report slightly different levels of abundance for the most recent years. However, with the activity of most observers currently well known (e.g. reported at www.trektellen.nl), it is unlikely that later adjustments will lead to substantial changes in the results.

Results

Between 1970 and 2004, 3024 harbour porpoises have been reported; 626 as ‘incidental reports’ and 2398 during systematic seawatching (table 2). The results show that the animals were near-absent between 1970 and 1985, that their numbers slowly increased in the late 1980s and that an exponential increase occurred in the 1990s and early 21st century (figure 1). Over the last 15 years, the numbers of harbour porpoises seen during systematic seawatching have increased significantly at a proportional rate of 41% per annum ($\ln(n\ h^{-1}) = 0.3438x - 6.054$, $r^2 = 0.91$).

Initially, during 1970-1985, when porpoises were still rare, they could be seen in any month (table 2). Of 34 recorded individuals, twelve were recorded in winter (Dec-Feb, 35%), nine in spring (Mar-May, 26%), six in summer (Jun-Aug, 18%), and seven in autumn (Sep-Nov, 21%). During 1986-1990, when the frequency of sightings increased, 67% were observed in winter, and another 26% in spring (n=84 animals recorded). Since then, harbour porpoises became winter/early spring visitors, arriving around October and disappearing around April with a peak from December through March (table 2, figure 2). The largest numbers were seen in March 1997 (108 individuals), February-March 2001 (137, 160), March 2002 (141), March 2003 (123), March 2004 (147), and December 2004 (297).

In June harbour porpoises were seldom reported, indicating a near-complete contraction away from the Dutch coast in early summer. In the most recent years, increasing numbers were seen in late summer/early autumn (Jul-Sep). Apparently, we are currently witnessing the development of a (late) summer population along the coast. Harbour porpoises can now be seen virtually everywhere along the coast.

Discussion

Harbour porpoises in the past: seasonal pattern and decline

Harbour porpoises have historically been described as ‘summer visitors’ in The Netherlands (van Deinse 1925, van Deinse 1931, IJsseling & Scheijgrond 1943, Viergever 1955, Verwey 1975). According to Verwey (1975), who recorded sightings of harbour porpoises in the western Wadden Sea during 1931-1945, a *“striking scarcity or even complete absence”* in March-April occurred, followed by a marked increase in “*May and (or) June*”. Verwey (1975) explained this ‘spring dip’ (Mar-Apr) by a contraction of the wintering population away from the coast. Despite published claims that porpoises were

Table 1. Observer effort during seawatching from Dutch coastal sites, 1972-2004 (hours of observation; all sites combined). The amount of effort for the last period (2001-2004) is not exactly known due to a backlog in data processing, but is assumed to be similar as in the preceding five years (see text).

	J	F	M	A	M	J	J	A	S	O	N	D	total
1972-1985	1533	1355	2536	4541	3881	2024	2660	5020	5775	5646	2967	1764	39704
1986-1990	725	712	886	1582	1394	536	911	1634	1929	1915	1368	973	14565
1991-1995	1156	1012	1482	1837	1675	936	1238	2177	2069	1845	1334	971	17732
1996-2000	739	761	1226	1549	1309	751	825	1220	1245	1355	788	664	12432
2001-2004	740	760	1225	1550	1300	750	835	1220	1245	1350	790	665	12420

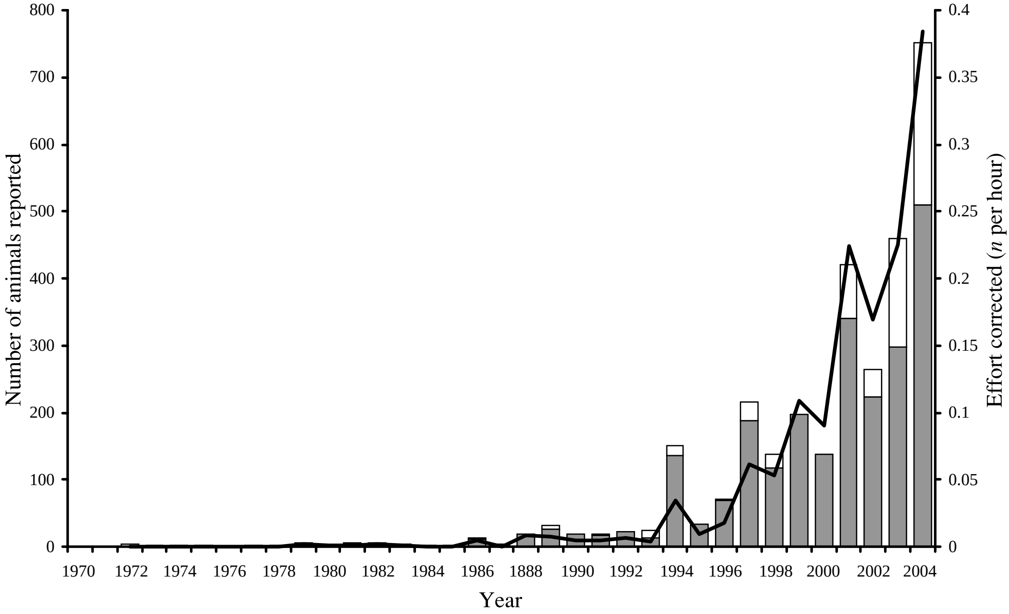


Figure 1. Numbers of harbour porpoises observed in Dutch coastal waters since 1970 from incidental sightings (white bars) and systematic seawatching results (grey bars), and long-term trend (*n* h^{-1}) based on seawatching results (black line).

normally seen on warm summer days, they could be numerous in autumn and winter too, perhaps with the exception of very cold seasons (with ice cover in the Wadden Sea; Verwey 1975). The increase in summer was explained by *“the fact”* that the animals were seeking the coast at that time and it coincided with an increase in newly born young. IJsseling & Scheygrond (1943), actually citing Van Deinse (1931), highlighted the summer as the period of highest abundance and claimed that pregnant female porpoises entered river mouths in summer, apparently attracted by salmon (*Salmo salar*). The annual return of harbour porpoises in early summer in the western Waddensea coincided with the arrival of herring (*Clupea harengus*), entering the Wadden Sea and Zuiderzee (currently the IJsselmeer, and now a fresh water lake) through the Marsdiep area. Heinsius (1914), observed numerous harbour porpoises in summer in the Zuiderzee targeting shoals of anchovy (*Engraulis encrasicolus*) and garfish (*Belone belone*).

There was considerable debate in the 1950s if a decline had taken place (Vader 1956). Sightings reports in the late 1950s were rather confusing, with for example ‘high numbers’ in summer and autumn 1957, and Jan-Feb 1958 in the western Wadden Sea (van Deinse 1959). A keen observer, F.J. Appelman, recorded porpoises during 10 out of 15 beach visits at Loosduinen (The Hague) in summer 1958 (van Deinse 1959), while numerous visits by the same observer in 1959-1962 did not produce a single sighting (van Deinse 1964). From the data collected by Verwey (1975) after the war (1945-1961) around Den Helder (circa 121 animals), some 49% were seen in January, 8% in February, 4% in March, 14% in April, 17% in November (remarkably, none in December) and only 8% in summer and early autumn (May-Oct). There was no evidence for a summer influx of pregnant females in coastal waters. Viergever (1955), in the Delta area, observed that harbour porpoises had become very scarce immediately after the Second World War and had his opinion confirmed by “field experiences” of local skippers and fishermen. Harbour

Table 2. Harbour porpoises per month in Dutch coastal waters, 1970-2004. (A) Incidental sightings (number of individuals), (B) sightings during systematic seawatching (number of individuals) and (C) relative abundance from seawatching results (number per observation hour).

	J	F	M	A	M	J	J	A	S	O	N	D	total
(A) Incidental sightings (*n*)													
1970-1985	3	1	2	2	1	1	1	0	1	0	0	2	14
1986-1990	0	0	4	0	1	0	0	0	0	0	0	4	9
1991-1995	2	0	10	1	12	0	0	0	0	0	0	4	29
1996-2000	3	3	37	3	0	0	1	1	0	0	0	2	50
2001-2004	27	91	150	54	4	1	14	12	28	25	17	101	524
													626
(B) Systematic observations (*n*)													
1972-1985	0	4	2	2	0	1	3	0	4	2	0	2	20
1986-1990	34	5	10	7	0	0	5	1	0	0	0	13	75
1991-1995	27	19	65	55	6	0	0	0	1	12	18	19	222
1996-2000	69	160	293	59	6	1	4	0	7	11	36	63	709
2001-2004	162	206	421	59	16	3	18	48	30	58	70	281	1372
													2398
	J	F	M	A	M	J	J	A	S	O	N	D	mean
(C) Effort corrected systematic sightings ($n\ h^{-1}$)													
1972-1985	0	0.00	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
1986-1990	0.05	0.01	0.01	0.00	0	0	0.01	0.00	0	0	0	0.01	0.01
1991-1995	0.02	0.02	0.04	0.03	0.00	0	0	0	0.00	0.01	0.01	0.02	0.01
1996-2000	0.09	0.21	0.24	0.04	0.00	0.00	0.00	0	0.01	0.01	0.05	0.09	0.06
2001-2004	0.22	0.27	0.34	0.04	0.01	0	0.02	0.04	0.02	0.04	0.09	0.42	0.11

porpoises were distinctly less abundant than they had been prior to the war, but it was the scarcity of porpoises in summer immediately after the war that may well have been the first signal of an overall decline. In the 1960's and 1970's, it was highly unusual to see a porpoise alive in The Netherlands anywhere and at any time of year.

Harbour porpoises in recent years: a recent come-back

We are very lucky to have been able to document the return of the harbour porpoise, as a side-product of a scheme that aimed at recording seabird migration. Certainly in the 1970s and early 1980s, it would have made no sense to set up a porpoise monitoring system, when waiting for a single sighting required on average 2000 hours of watch on a wind-swept look-out. Today, harbour porpoises are winter visitors in the Southern Bight (i.e. the North Sea between the French Channel in the south and 53°30'N in the north), and only the last few years can they be seen virtually year-round, but still with low numbers in June. Harbour porpoises can now be so numerous and close to the coast that a keen observer can spot some even during a winter walk along the beach. It is only because these elusive animals are so notoriously difficult to detect that relatively few 'incidental sightings' occur. Mother-calf combinations have been reported and are seemingly increasingly common (difficult to quantify, for most sightings are of unaged animals). From ship-based surveys in recent years, we have evidence that in peak periods (winter), thousands of porpoises may occur within the 20 m depth contour along the mainland coast of Noord-Holland alone (circa 3000 were estimated to occur between IJmuiden and Texel, winter 2003/2004; Leopold et al. 2004).

When studying the recent sightings data in more detail, the occurrence of harbour porpoises is highly irregular, with influxes at times

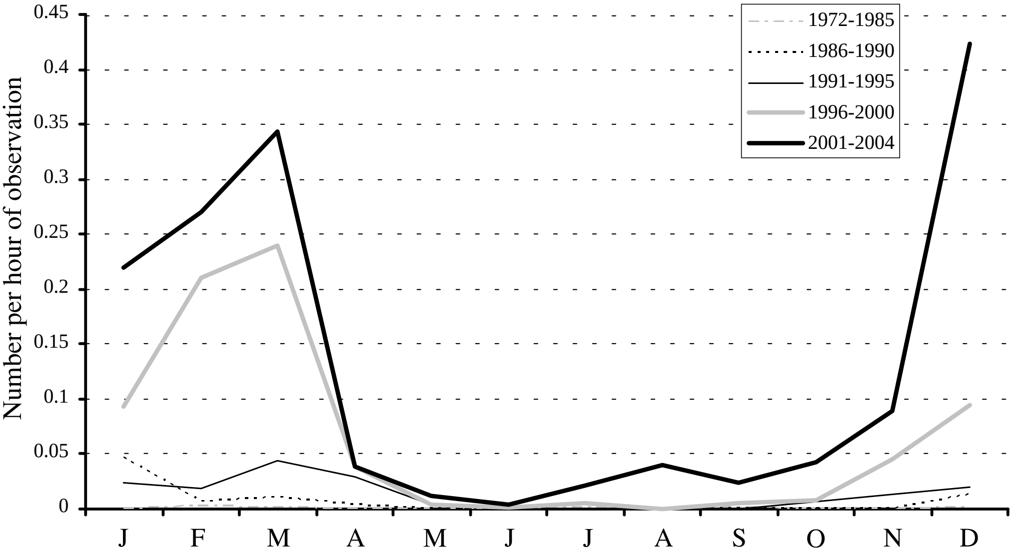


Figure 2. Numbers of harbour porpoises per hour per month observed in Dutch coastal waters since 1972 from systematic seawatching results. At this scale, the seasonal pattern in the earliest sightings (1972-1985) is hardly visible, but porpoises could be seen in virtually every month, if recorded at all. In recent years, the U-shape curve developed more and more strongly, while a mid-summer peak in occurrence is in fact from a very recent date, i.e. 2003-2004.

(recorded everywhere along the Dutch coast, but of a few days or weeks duration at most) followed by periods of absence. Movements to and from the coast are the most likely explanation for the variability in abundance between seasons and between months. We have no evidence for regular north-south or vice versa movements along the Dutch coast; the animals tended to arrive and disappear everywhere simultaneously at times. Possible reasons for inter-annual and within-season differences in abundance and distribution may include changes in availability of primary prey species, or movements among population units with the North Sea at large.

So what happened?

Is this a return to the 'original' situation (whatever that might have been), is this a population recovery following the near-extinction of a local stock, or are we receiving animals from abroad that are for example seeking alternative foraging areas? These questions are easier asked than answered. We have very few empirical data on demography, foraging ecology, migration routes and (offshore) population fluctuations of porpoises in the southern North Sea. Both the historical decline and the recent increase are therefore subject to major speculation. Some remarks can be made, however.

Woodley & Read (1991) estimated the natural rate of increase of harbour porpoises at 4% or less per annum. Barlow & Boveng (1991), using demographic models, produced an estimate of 9.4% for the maximum potential rate of increase of these animals. Caswell et al. (1998) used a series of rescaled mortality schedules and a Monte Carlo sampling procedure to estimate the potential rates of increase for harbour porpoise. Their distribution of potential rates of increase had a median of about 4%, and it was concluded that a rate of more than 10% per year would be highly unlikely. So, even when the reproductive success of harbour porpoises in the southern North Sea has been exceptionally high in the past decades, it could not have accounted for the 41% increase per annum as currently ob-

Harbour porpoises, Eemshaven, 21 February 2004. *Photograph: Klaas Kreuijer.*

served in Dutch coastal waters. Shifts in distribution, or immigration, must therefore have been underlying the observed trend.

In order to try and understand why harbour porpoises would have returned to Dutch coastal waters during the last 15 to 20 years, it is essential to know something of their spatial distribution patterns and feeding ecology. A North Sea wide census in 1994 resulted in an estimated 263,000 harbour porpoises (Hammond et al. 2002), 70% of which were found in the northwest North Sea and around Orkney and Shetland. Few porpoises were found in the Channel area, while they were locally abundant in the German Bight. These patterns are similar to those described by Reid et al. (2003). In a recent comparative study of harbour porpoise diets, based on stranded or drowned individuals collected in Scotland, Denmark, and The Netherlands, principal prey and the dietary diversity differed significantly between areas (Santos 1998). In Scotland, whiting (*Merlangius merlangus*) and sandeels (Ammodytidae) were the most important prey categories, making up >84% of prey mass. In Denmark, cod (*Gadus morhua*), viviparous blenny (*Zoarces viviparus*) and whiting made up almost two thirds of the total prey mass. In porpoises stranded in The Netherlands, whiting made up more than 75% of the total estimated prey mass, and other important species were sandeels and gobies (Gobiidae).

In the northern North Sea, starting in Shetland, several piscivorous seabirds have had highly variable reproductive success since a major crisis in seabird breeding occurred in the late 1980s as a result of failed sandeel recruitment (Monaghan et al. 1992, Wright & Bailey 1993). Breeding success of seabirds during 2002, 2003, and 2004 were the worst on record, apparently as a result of declines of northwest North Sea sandeel stocks. Food shortages resulting from sandeel recruitment failures have been reported from an growing part of the northwest North Sea, including the Orkneys and Scottish east coast in 2003 and 2004. Based on the most recent estimates, the International Council for the Exploration of the Seas (ICES, Copenhagen) classified the North Sea sandeel stock as having reduced reproductive capacity and for 2004 the population was estimated to be at a historic low value (325,000 ton) due to a historic low recruitment in 2002.

Low recruitment and reduced stocks of planktivorous fish have been linked with climate change, found to cause a drop in the quality and quantity of plankton in the North Sea (Beaugrand et al. 2003). This decline in plankton has been attributed to a rise in surface water temperatures causing warm-water plankton species to move north, displacing cold-water species. That reduced the number and size of the plankton and it also caused major plankton blooms to be out of synchrony with the larval stage development of fish, meaning fewer fish larvae were reaching adulthood. The decoupling of phenological relationships will have important ramifications for trophic interactions, altering food-web structures and leading to eventual ecosystem-level changes (Edwards & Richardson 2004). Sandeel recruitment was found to be reduced in warm winters, and Frederiksen et al. (2004) proposed that this explains the temperature effects on breeding success of some Scottish seabirds.

It is currently unclear what is going on in the northern North Sea, but the summering humpback whales (*Megaptera novaeangliae*) in Shetland disappeared and minke whales (*Balaenoptera acutorostrata*) were found to concentrate in summer feeding areas further to the south and in larger numbers than previously (Camphuysen et al., in press). Apparent redistributions of large cetaceans and poor breeding of piscivorous seabirds may be interpreted as signals of shifts in prey availability in the affected area. Declines in prey availability in the northwest North Sea may have triggered distribution shifts even in species with a mixed diet, such as harbour porpoises.

Conclusions

We have witnessed a return of an animal that had nearly completely disappeared from the Dutch coastal waters after the Second World War. The return cannot be interpreted as a population recovery, but rather as a shift in distribution. The Netherlands have been avoided during several decades for reasons we don’t quite understand, but are increasingly used by porpoises in recent years, at first mainly during winter and at present during most of the year. The reason for the re-appearance is possibly a reduction in principal prey stocks further north in the North Sea. There are no signs as yet that the increase in sightings is levelling off and we should therefore continue monitoring, by using the same methods, in the years to come. Meanwhile, if we are to gain understanding of the foraging and breeding opportunities for porpoises in the Dutch waters, or if we simply wish to monitor their well-being in the southern North Sea, it is time to set up dedicated research programmes. The animals are numerous enough by now to make them attractive study objects.

Acknowledgements: This study would not have been possible without the numerous volunteers participating in the seawatching scheme of the “Club van Zeetrekwaarnemers”, a working group of the Nederlandse Zeevogelgroep (NZG). It is impossible to name them all, but substantial contributions have been made by J. van Dijk, A. Dwarshuis, S. Geelhoed, F. Geldermans, C.J. de Graaf, N.F. van der Ham, N.C. Hoogendoorn, J.-N. IJnsen, M. de Lange, C. Rebel, P. Thomas, C. van der Vliet, R. Westerduijn and J. Wierda. Important contributions to the ‘incidental sightings’ part of the database come from J. van der Hiele. Marine mammal sightings from this scheme, plus incidental reports, have been collected by the author and stored into a separate database, the *Marine Mammal Database*, as part of the NZG activities. This database is freely accessible for interested researchers, updated on a daily basis, and recent data are accessible online via http://home.planet.nl/~camphuys/Cetacea.html. Mardik Leopold and two anonymous referees kindly commented on drafts of this contribution and the first mentoined also assisted with both the literature search and the trend analysis.

References

Addink, M.J. & C. Smeenk 1999. The harbour porpoise *Phocoena phocoena* in Dutch coastal waters: analysis of stranding records for the period 1920-1994. Lutra 41 (1-2): 55-80.

Barlow, J.P. & P. Boveng 1991. Modeling age-specific mortality for marine mammal populations. Marine Mammal Science 7: 50-65.

Beaugrand, G., K.M. Brander, J.A. Lindley, S. Souissi & P.C. Reid 2003. Plankton effect on cod recruitment in the North Sea. Nature 426: 661-664.

Camphuysen, C.J. 1982. Zeezoogdieren langs de Nederlandse kust. Mededelingen Club van Zeetrekwaarnemers 5 (2): 6-8.

Camphuysen, C.J. 1985. Zeetrektellingen. In: M.F.H Hustings, R.G.M. Kwak, P.F.M. Opdam & M.J.S.M. Reijnen (eds.). Vogelinventarisatie: 215-219. Pudoc, Wageningen, The Netherlands.

Camphuysen, C.J. 1987. Het ontdekken en herkennen van Bruinvissen *Phocoena phocoena* op zee. Sula 1 (3): 66-72.

Camphuysen, C.J. 1991. Het herkennen van de Bruinvis *Phocoena phocoena* op zee. Huid & Haar 10 (1): 31-37.

Camphuysen, C.J. 1994. The harbour porpoise *Phocoena phocoena* in the southern North Sea, II: a come-back in Dutch coastal waters? Lutra 37 (1): 54-61.

Camphuysen, C.J. & J. van Dijk 1983. Zee- en kustvogels langs de Nederlandse kust, 1974-79. Limosa 56 (3): 81-230.

Camphuysen, C.J. & M.F. Leopold 1993. The harbour porpoise *Phocoena phocoena* in the southern North Sea, particularly the Dutch sector. Lutra 36 (1): 1-24.

Camphuysen, C.J., B. Scott & S. Wanless, in press. Distribution and foraging interactions of seabirds and marine mammals in the North Sea: multi-species foraging assemblages and habitat-specific feeding strategies. In: I.J. Boyd, S. Wanless & C.J. Camphuysen (eds.). Management of Marine Ecosystems: monitoring change in upper trophic levels. Blackwell Science, London, UK.

Caswell H., S. Brault, A.J. Read & T.D. Smith 1998. Harbor porpoise and fisheries: an uncertainty analysis of incidental mortality. Ecological Applications 8: 1226-1238.

Deinse, A.B. van 1925. De bruinvisch. De Levende Natuur 29: 195-203.

Deinse, A.B. van 1931. De fossiele en recente Cetacea van Nederland. PhD thesis. Universiteit van Utrecht, Utrecht, The Netherlands.

Deinse, A.B. van 1946. De recente Cetacea van Nederland van 1931 tot en met 1944. Zoölogische Mededelingen Leiden 26 (1-4): 139-210.

Deinse, A.B. van 1952. De walvisachtige dieren in Nederland waargenomen in 1951, alsmede bijzonderheden omtrent onze oude en moderne walvisvaart. Zeepaard 12: 19-29.

Deinse, A.B. van 1959. Walvisnieuws 1958. Mededelingenblad van de Vereniging voor Zoogdierkunde 20 (= Lutra 1 (20)): 205-208.

Deinse, A.B. van 1964. Walvisnieuws over 1963. Lutra 6 (3): 61-66.

Edwards, M. & A.J. Richardson 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430: 881-884.

Frederiksen, M., S. Wanless, M.P. Harris, P. Rothery & L.J. Wilson 2004. The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. Journal of Applied Ecology 41: 1129-1139.

Hammond, P., P. Berggren, H. Benke, D.L. Borchers, A. Collet, M.P. Heide-Jørgensen, S. Heimlich, A.R. Hiby, M.F. Leopold & N. øien 2002. Abundance of harbour porpoises and other cetaceans in the North Sea and adjacent waters. Journal of Applied Ecology 39: 361-376.

Heinsius, H.W. 1914. Langs de Zuiderzee. De Levende Natuur 18: 282-286.

IJsseling, M.A. & A. Scheygrond 1943. De Zoogdieren van Nederland II. Thieme, Zutphen, The Netherlands.

Leopold, M.F., C.J. Camphuysen, C.J.F. ter Braak, E.M. Dijkman, K. Kersting & S.M.J. van Lieshout 2004. Baseline studies North Sea wind farms: lot 5 Marine Birds in and around the future sites Nearshore Windfarm (NSW) and Q7. Alterra Report 1048. Alterra, Wageningen, The Netherlands.

Monaghan, P., J.D. Uttley & M.D. Burns 1992. Effect of changes in food availability on reproductive effort in Arctic Terns *Sterna paradisaea*. Ardea 80: 71-81.

Reid, J.B., P.G.H. Evans & S.P. Northridge (eds.) 2003. Atlas of cetacean distribution in north-west European waters. Joint Nature Conservation Committee, Peterborough, UK.

Santos, M.B. 1998. Feeding ecology of harbour porpoises, common and bottlenose dolphins and sperm whales in the North East Atlantic. PhD thesis. University of Aberdeen, Aberdeen, UK.

Smeenk, C. 1987. The Harbour Porpoise *Phocoena phocoena* (L., 1758) in The Netherlands: stranding records and decline. Lutra 30 (1): 77-90.

Vader, W. 1956. Reuzen van de vloedlijn. Amoeba 32 (6-7): 101-103.

Verwey, J. 1975. The cetaceans *Phocoena phocoena* and *Tursiops truncatus* in the Marsdiep area (Dutch Wadden Sea) in the years 1931-1973, part 1 and 2. Publicaties & Verslagen Nederlands Instituut voor Onderzoek der Zee 17a: 1-98; 17b: 99-153.

Viergever, J. 1955. Hoe staat het met de bruinvis? Het Zeepaard 15: 90-91.

Woodley, T.H. & A.J. Read 1991. Potential rates of increase of a Harbour Porpoise (*Phocoena phocoena*) population subjected to incidental mortality in commercial fisheries. Canadian Journal of Fisheries and Aquatatic Sciences 48: 2429-2435.

Wright, P.J. & M.C. Bailey 1993. Biology of sandeels in the vicinity of seabird colonies at Shetland. Fisheries Research Report 15/93. Marine Laboratory, Aberdeen, UK.

Samenvatting

De terugkeer van de bruinvis (*Phocoena phocoena*) in de Nederlandse kustwateren

De bruinvis (*Phocoena phocoena*) was zo goed als uitgestorven in de Nederlandse kustwateren in de jaren zestig van de vorige eeuw. Sinds het begin van de jaren zeventig wordt een systematische methode toegepast om verplaatsingen van kust- en zeevogels langs de Nederlandse kust te registreren. Aanvankelijk werden daarbij gedurende 40.000 waarnemingsuren vrijwel geen zeezoogdieren gezien. In de loop van de jaren tachtig werd door deze 'zeetrekwaarnemers' in winter en voorjaar steeds vaker melding gemaakt van bruinvissen voor de kust. Een geleidelijk toenemend aantal waarnemingen in de tweede helft van de jaren tachtig werd gevolgd door een toename met gemiddeld 41% per jaar tot aan 2004. Aanvankelijk werden uitsluitend volgroeide bruinvissen gezien, maar tegenwoordig komen hier ook veel moeder-kalf stelletjes voor. Werden aanvankelijk vooral veel bruinvissen gezien van oktober tot en met april, de laatste jaren worden daarnaast ook in de nazomer en vroege herfst en steeds regelmatiger groepjes opgemerkt. Zowel de historische afname, als de recente toename wordt weerspiegeld in de gegevens van gestrande bruinvissen op de Nederlandse kust. Voor de afname is nooit een ondubbelzinnige verklaring gevonden en ook de recente terugkeer is niet eenvoudig te begrijpen. De gegevens laten zien dat er sprake moet zijn geweest van een verschuivende populatie, omdat de toename veel te snel is gegaan om alleen door reproductief succes te kunnen worden verklaard. Het is mogelijk dat een afnemend voedselaanbod in het noorden van de Noordzee deze verplaatsing heeft veroorzaakt, waardoor bruinvissen in toenemende mate tot in de Zuidelijke Bocht van de Noordzee zijn doorgedrongen.

Received: 17 December 2004
Accepted: 3 February 2005

Short Note

Morula's van een otter (*Lutra lutra*): een toevallige waarneming

Sim Broekhuizen, Hugh Jansman* & Gerard J.D.M. Müskens

Alterra, Centrum voor Ecosystemen,
Droevendaalsesteeg 3, Postbus 47, NL-6700 AA Wageningen, e-mail: hugh.jansman@wur.nl

Op 4 juni 2004 werd een ottervrouwtje (*Lutra lutra*) doodgereden op de Heuvenweg in het Nationaal Park De Weerribben (Amersfoort-coördinaten 194-532). Het dier was naar schatting 1,5 à 2 jaar oud toen ze een jaar eerder, op 7 juli 2002, in De Weerribben werd uitgezet, afkomstig uit een otteropvangcentrum in Tsjechië (Niewold et al. 2003). Het zal dus globaal in het najaar van 2000 zijn geboren.

Het verongelukte dier werd één dag in een donkere, koele kelder bewaard en daarna in een vrieskast bij -20 °C opgeslagen. Bij de autopsie op 24 juni waren in de baarmoeder littekens van drie placenta's zichtbaar, waaruit geconcludeerd werd dat dit vrouwtje drie jongen had geworpen. Geschat werd dat de geboorte voor de jaarwisseling 2003/2004 had plaatsgevonden. Bij een draagtijd van twee maanden zal het vrouwtje in het najaar van 2003 bevrucht zijn, toen het circa drie jaar oud was. Het nageslacht zou dan op de dag van het verongelukken van de moeder ongeveer zeven maanden oud zijn geweest. Het was de vraag of de jongen ten tijde van het ongeluk al zo groot waren, dat ze zich zelf net konden redden. Chanin (1991) geeft aan dat de jongen 7-12 maanden bij de moeder blijven, Reuter (1993) noemt perioden van 9-14 maanden en Kruuk (1995) vond dat jonge otters vanaf acht maanden zelfstandig kunnen leven.

Uit analyse van DNA uit mest (spraints) die in het vroege voorjaar van 2004 in het uitzetgebied werd verzameld, bleek dat van het verongelukte wijfje in ieder geval een dochter de winter had overleefd. In de winter 2004/2005 werden in De Weerribben wederom spraints verzameld, waarvan enkele ook weer afkomstig waren van deze dochter. Dit dier had het verlies van haar moeder dus overleefd en was in 2004 in De Weerribben gebleven. Ook werden in het noordelijke deel van De Wieden, ten zuidwesten van De Weerribben, enkele spraints verzameld. Deze bleken afkomstig te zijn van een zoon van het verongelukte wijfje, zodat tenminste twee van de drie foeten zelfstandig waren geworden.

Bij autopsies van dood gevonden vrouwelijke dassen (*Meles meles*) en boom- en steenmarters (*Martes martes, Martes foina*) is het de laatste jaren gewoonte de baarmoeder te onderzoeken op de aanwezigheid van blastocysten. De blastocyste is het ontwikkelingsstadium van het bevruchte ei, waarbij binnen de door deling ontstane klont cellen een zo grote holte is ontstaan, dat het geheel een doorzichtig blaasje is geworden. De wand van dit blaasje wordt gevormd door één laag cellen, die men de trophoblast noemt. De binnenste cellen van de oorspronkelijke klont cellen komen op een hoopje aan de binnenkant van de trophoblast terecht en vormen de embryonaalknop of blastofoor, waaruit zich later het embryo vormt.

In het algemeen hechten de blastocysten zich binnen enkele dagen vast aan de baarmoeder-

---

* *Corresponding author*

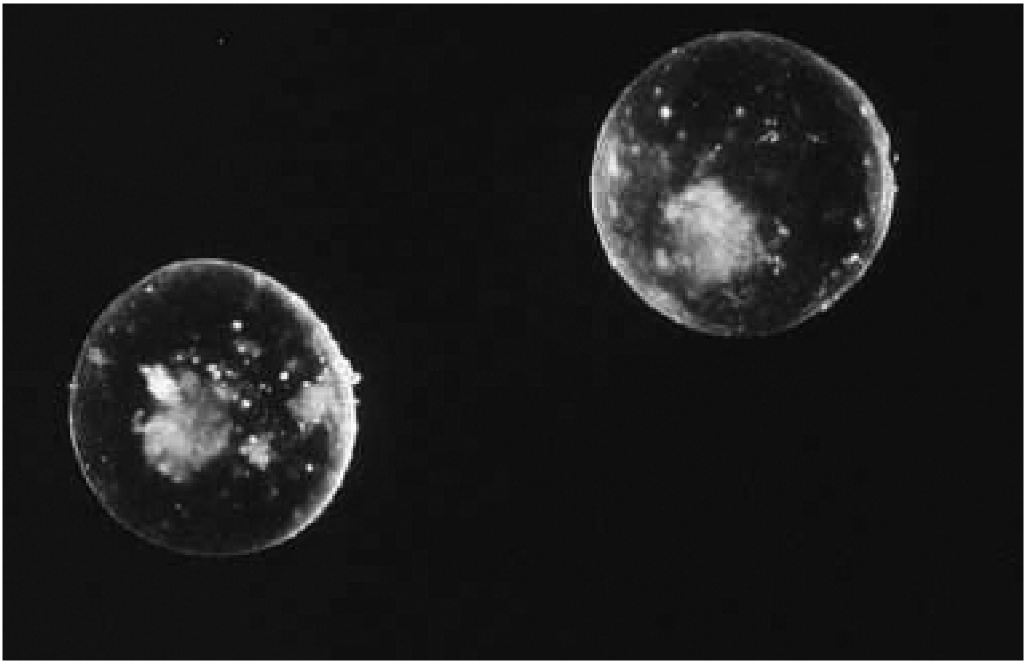


Foto 1. Blastocysten, gespoeld uit de baarmoeder van een steenmarter (*Martes foina*). *Foto: Wim Dimmers.*

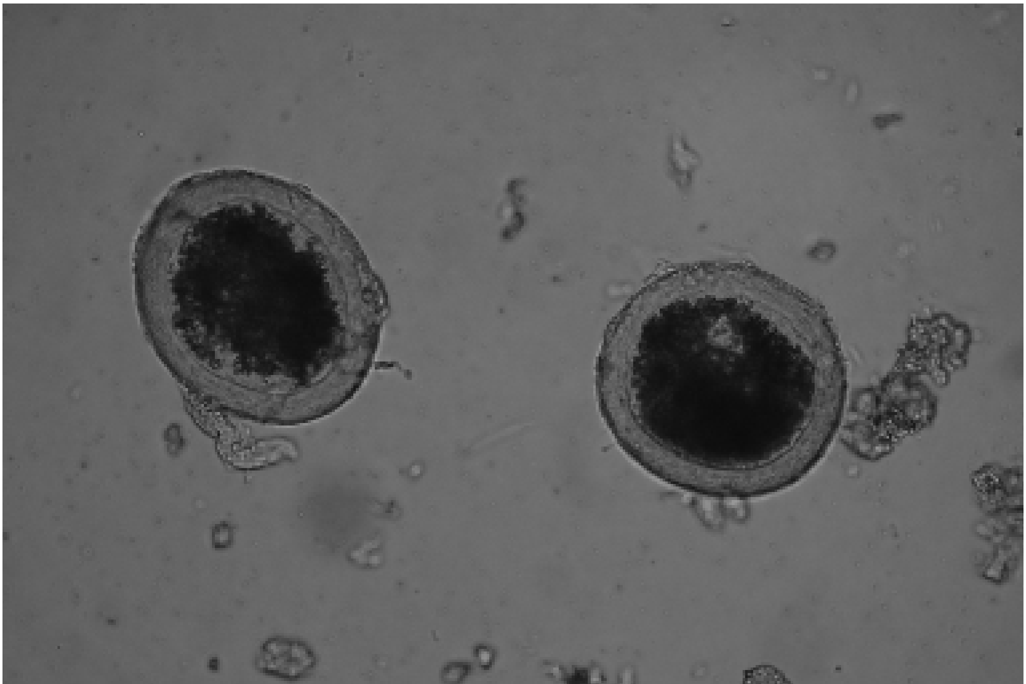


Foto 2. Morula’s, gespoeld uit de baarmoeder van het otterwijfje (*Lutra lutra*). *Foto: Wim Dimmers.*

wand, doordat cellen van de trophoblast ingroeien in het baarmoederslijmvlies. Bij dassen en marters hechten de blastocysten zich echter pas na verloop van maanden vast aan de baarmoederwand, waarna de verdere ontwikkeling van de vrucht wordt voortgezet. Door de afgeknipte baarmoeder met behulp van een injectiespuit met water door te spoelen, kunnen eventueel aanwezige blastocysten in een horlogeglas worden opgevangen en onder een binoculair worden geteld, zodat in de periode van uitgestelde implantatie toch een beeld kan worden gekregen van de worpgrootte. Foto 1 toont enkele blastocysten van een steenmarter.

Een uitgestelde vasthechting van blastocysten aan de baarmoederwand komt weliswaar ook bij andere zoogdiersoorten voor, zoals bij reeën *(Capreolus capreolus)* en sommige muizensoorten, maar het is zeker niet het algemene patroon bij zoogdieren. Bij dieren zonder uitgestelde implantatie, waartoe ook de otter hoort, heeft het dan ook weinig zin om naar vrije blastocysten te zoeken. Het was dan ook meer uit de macht der gewoonte, dat de baarmoeder van het verongelukte otterwijfje toch op blastocysten werd onderzocht. Hoewel de onlogica van de handeling al was onderkend, leverde het toch even dóórkijken een verrassing op: drie ‘rijpe’ morula’s. Helaas is één daarvan tijdens het manipuleren verloren gegaan, maar van de twee andere konden foto’s worden gemaakt (foto 2). De diameter van de meest ronde morula was 0,23 mm, de langste diameter van de meer ovaal geworden morula was 0,26 mm. De vervorming is wellicht het gevolg van het feit dat het dier ingevroren was geweest.

De morula is het ontwikkelingsstadium vóór de blastocyste, waarbij uit de eicel door een aantal delingen een trosje van 12-16 cellen is ontstaan. Aanvankelijk is de buitenkant van de morula ongelijkmatig en doet ze eventueel denken aan een moerbei, waarnaar het Latijnse morula verwijst. Bij verdere deling, waarbij de cellen steeds kleiner worden, wordt die buitenkant gladder. Wanneer er 50-60 cellen zijn gevormd begint zich tussen de cellen een holte te vormen, waardoor de morula overgaat in de blastocyste.

Bij veel diersoorten wordt de morula nog omgeven door een dikke transparante gelatineachtige membraan: de zona pellucida. Dit omhulsel is al in de eierstok gevormd door cellen die de eicel omgaven en heeft een beschermende functie tegen ongeschikt sperma. Bij het groeien van de blastocyste gaat de zona pellucida verloren. Bij de blastocysten die we bij dassen en marters vonden werden tot nu toe geen resten van de zona pellucida meer aangetroffen.

In welk stadium de zich ontwikkelende bevruchte eicel bij de otter na de passage van de eileiders in de baarmoeder komt, is ons niet bekend. Bij fretten (*Mustela furo*) duurt de reis van de eicel door de eileider tot in de baarmoeder ruim vijf dagen, waarin een pril morula-stadium wordt bereikt van 32 cellen (Biggers 1979). Hoe snel de morula zich bij de otter in de baarmoeder ontwikkelt tot een blastocyste die zich in het slijmvlies van de baarmoeder vasthecht, is ons ook onbekend. Bij de mens is dat ongeveer drie dagen (Moore 1988). De kans dat bij een otter een vrij-zwevende morula in de baarmoeder aangetroffen wordt is dus klein, gesteld dat er al naar wordt gezocht.

De macht der gewoonte heeft in dit geval dus tot een bijzondere waarneming geleid. Het is echter wel sneu dat dit productieve wijfje niet aan haar tweede worp is toegekomen. Ze heeft wel aangetoond dat het voor de uitgezette otters in De Weerribben mogelijk is met succes te paren en jongen voort te brengen.

Literatuur

Biggers, J.D. 1979. Fertilization and blastocyst formation. In: N.J. Alexander (red.). Animal models for research on contraception and fertility: 223-237. Harper & Row Publishers, Hagerstown, Maryland, USA.

Chanin, P. 1991. Subfamily Lutrinae, Genus *Lutra*. In: G.B. Corbet & S. Harris (red.). The handbook of British mammals, 3rd edition: 423-431. Blackwell Scientific Publications, Oxford, UK.

Kruuk, H. 1995. Wild otters, predation and population. Oxford University Press, Oxford, UK.

Moore, K. 1988. The developing human, clinical oriented embryology, 4th edition. W.B. Saunders Company, Philadelphia, USA.

Niewold, F.J.J., D.R. Lammertsma, H.A.H. Jansman & A.T. Kuiters 2003. De otter terug in Nederland. Eerste fase van de herintroductie in Nationaal Park De Weerribben in 2002. Alterra - Research Instituut voor de Groene Ruimte, Wageningen, Nederland.

Reuter, C. 1993. *Lutra lutra* (Linnaeus, 1758) – Fischotter. In: M. Stubbe & F. Krapp (red.). Handbuch der Säugetiere Europas, Band 5, Teil II: 907-961. Aula-Verlag, Wiesbaden, Duitsland.

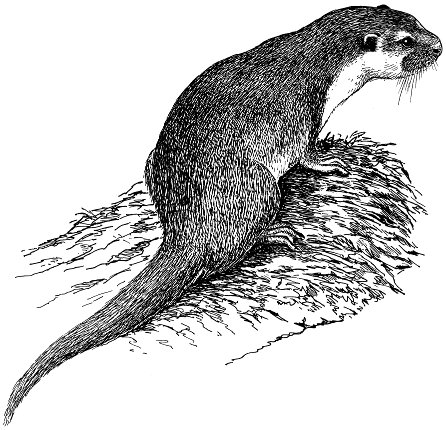
Summary

The accidental discovery of a morula in an otter (*Lutra lutra)*

On the 24th of June, 2004, a four year old female otter (*Lutra lutra*) was killed by a car in the reintroduction area National Park De Weerribben (province of Overijssel, The Netherlands). She originated from a rehabilitation centre in the Czech Republic and was reintroduced in De Weerribben early July 2002. During post-mortem examination three placenta scars were noticed. In January 2004 a spraint of a newborn otter was found that genetically matched to this female and a male otter that originated from Belarus. In the winter of 2004/2005 again spraints of this cub were found as well as spraints of a second cub that was missed the winter before. The cubs were probably born in the autumn of 2003, meaning they were approximately seven months old when the mother died. We assume these cubs were on the brink of independency.

Most mustelid species we receive for post-mortem examination are pine marten (*Martes martes*), stone marten (*Martes foina*), and badger (*Meles meles*). Those mustelids have a delayed implantation of the blastocysts in the uterus. For measuring the reproductive status we routinely inject water through the uterus horns and collect the follow-through. This we check under a binocular for blastocysts. During post-mortem examination of this female otter we didn’t deviate from our protocol, although we knew it would be very exceptional to find a fertilized egg not yet attached in the uterus, since otters don’t have a delayed implantation. To our great surprise we did find three morula’s with a well developed zona pellucida, but no signs of formation of the cavity (blastula). We do not know what the duration is of the journey of a fertilized egg through the oviduct before nestling in the uterus. In ferrets (*Mustela furo*) it takes five days and in humans approximately three days. We think that the chance of finding this early stage of pregnancy is extremely small in European otters. Therefore we were very lucky, apart form the death of this reproductive otter female.

Ontvangen: 11 februari 2005
Geaccepteerd: 8 april 2005



Reintroduction of the otter (*Lutra lutra*) in the Netherlands meets international guidelines

Pieter van ’t Hof & Frank van Langevelde

Resource Ecology Group, Wageningen University, Bornsesteeg 69, NL-6708 PD Wageningen,
The Netherlands, e-mail: Pieter.van’thof@wur.nl

Abstract: In the past, the otter (*Lutra lutra)* was a predator in Dutch freshwater ecosystems. Due to hunting, fishing, destruction and fragmentation of its habitat, pollution, traffic mortality and disturbances due to recreation, the otter became extinct. Fourteen years after extinction, the otter has been reintroduced in the Weerribben, an area in the northwest of Overijssel province. There was much discussion about releasing otters in the Netherlands. This paper discusses the reintroduction project in the light of the IUCN (International Union for Conservation of Nature and Natural Resources) guidelines, which are internationally recognized and applied in many reintroduction projects. The IUCN guidelines stress the importance of biodiversity and public nature conservation awareness (important in a highly populated country as the Netherlands). The guidelines stipulate that the former causes of death should have been removed or minimised in the release area and that the chances of a spontaneous recolonisation by otters, sufficient to establish a viable population, should be small. Capturing otters for reintroduction should not have negative effects, the released otters should be genetically similar to the extinct otter population and the project has to be monitored. Assessment of the project to reintroduce otters into the Netherlands shows that that the IUCN guidelines were followed.

Keywords: otter, *Lutra lutra*, reintroduction, IUCN guidelines, Weerribben, The Netherlands, nature conservation, biodiversity.

Introduction

The otter (*Lutra lutra*) was a common predator in the Netherlands, but has been persecuted for over a century (Broekhuizen et al. 1992). After legal protection in 1942, hunting was no longer the main cause of death, but mortalities increased as wet ecosystems were reclaimed for agriculture or built upon. Eutrophication and pollution were responsible for bad water quality. The road infrastructure expanded very rapidly and became an important cause of mortality. Roads became more dangerous to cross and also fragmented the remaining small patches of habitat. This decreased exchange between isolated local populations and was one of the major reasons for the extinction of the otter in the Netherlands (Broekhuizen et al. 1992). In addition, illegal hunting and drowning in fykes, further contributed to the decline of the population. Despite increased efforts in nature conservation, the otter became extinct in 1988.

The Ministry of Agriculture, Nature management and Fisheries started efforts to retrieve the otter population, by setting up a working group It mainly addressed the quality of the freshwater ecosystem that the otter used to inhabit. For fourteen years, it has been worked on improving freshwater quality, which is now deemed suitable for otters (Jansman et al. 2003). In July 2002, seven otters were released in the Weerribben, followed by a second group of eight individuals at the end of 2002. Not everybody was pleased with the reintroduction plan. Its advantages and drawbacks were extensively discussed and this discussion has continued after the rein-

---

Lutra abstracts on the internet: http://www.vzz.nl troduction. This discussion has motivated this evaluation of the reintroduction project against the internationally accepted guidelines of the International Union for Conservation of Nature and Natural Resources (IUCN).

IUCN guidelines

The IUCN tries to protect the integrity and diversity of nature worldwide and the sustainability and preservation of natural resources. To carry out this vision, the IUCN has drawn up guidelines (IUCN 1995), which are internationally recognised. Reintroduction is defined by the IUCN as “an attempt to establish a species in an area, which was once part of its historical range, but from which it has been extirpated or become extinct”. From this perspective, releasing otters in the Netherlands is a reintroduction. Under IUCN guidelines, a basic reintroduction programme should involve a study to investigate the opportunities for reintroduction and a preparation phase. Monitoring should always follow the actual releasing phase. IUCN states that the main aim of a reintroduction project should be the re-establishment of a viable, free-ranging population of a species, subspecies or race, which has become locally extinct or naturally extinct in the past. These guidelines cover several issues which will be discussed in the context of the Dutch otter project.

IUCN aims for reintroductions

One IUCN aim of a reintroduction is to enhance the long-term survival of an endangered species. In the last century, and especially over recent decades, otter numbers have been in constant decline in Europe. However, as the area of distribution of the otter stretches from Ireland to Japan (Broekhuizen et al. 1992) the otter as a species is not globally endangered. Some populations on the Iberian Peninsula and in Eastern Europe have been expanding, due to improving environmental conditions and successful reintroductions (Sjöåsen 1996, Ruiz Olmo 2002). A sustainable local population in the Netherlands could function in a future network of local populations within Europe and contribute to the sustainability of these populations.

Another aim is the re-establishment of a “keystone species” in the ecological sense. According to the IUCN, a keystone species represents an indispensable species, whose extinction may cause a structural change of an ecosystem. However, a structural change of the freshwater ecosystem is not expected, because of their small impact on the ecosystem as top predator (H. Jansman, personal communication). So, the otter is not a keystone species in the ecological sense.

As the top predator of freshwater ecosystems, otters could accumulate heavy metals and PCBs in their fatty tissue. The absence of otters, or their decreased fitness, could also indicate poor water quality. Good water quality is a prerequisite for their reintroduction. Reintroducing otters in the Netherlands means that freshwater ecosystems might be more complete as the conditions should be suitable for other species as well.

The third IUCN aim, preservation or restoration of natural biodiversity, also fits the Dutch situation, as otters used to be an integral part of Dutch biodiversity (Broekhuizen et al. 1992). Historically, the Netherlands was a marshland with characteristic peat bog areas and lakes, but reclamation and urbanisation resulted in a drastic decrease of these areas. Establishing and restoring nature conservation areas is important to preserve these (future) animal habitats. Other characteristic marshland species already profit from measures included in the otter reintroduction programme.

The fourth aim covered by the IUCN is the expected long-term economic benefit to the local or national economy. More visitors could be expected in the release areas, but this effect might be quite minimal as otter sightings are rare. Realisation of this aim might thus be difficult.

The last aim for reintroduction, according to the IUCN, can be to enlarge public nature awareness. This public awareness is especially important for densely populated countries such as the

Netherlands. The Netherlands have an average of over 450 inhabitants per square kilometre. Over the last twenty years, an area with the size of the province of Utrecht has been turned into farmland, roads and cities (Statistics Netherlands 2003). While urbanisation was only permitted on formerly agricultural land, claims for land will increase in the future as the Dutch population grows further: Statistics Netherlands (2003) predicts 17 million inhabitants in 2015. Nature and biodiversity need social protection against ongoing human pressure. Otters easily attract attention (Mulder 2002) and public opinion puts them high on the list of favourite animals such as koalas, pandas and elephants (Rientjens 2000). By using the otter as a symbol to stimulate nature awareness, the last aim for reintroduction from the IUCN guidelines can be met.

IUCN criteria for reintroduction

Besides these aims for reintroduction, the IUCN has developed a list of criteria, which should be taken into consideration before starting a reintroduction programme. This list includes pre-project biological activities such as conducting a feasibility study, background research and thorough research into previous reintroductions. Preliminary research into previous otter reintroductions, such as in Spain and Sweden, are important, as they provide crucial information on the chances of success (Sjöåsen 1996, Ruiz Olmo 2002). Other biological criteria are related to the choice of the release site and type, evaluation of the reintroduction site, the availability of suitable release stock and the release of captive stock. Besides biological criteria, also socio-economic and legal requirements are distinguished (IUCN 1995).

The following criteria from the IUCN list for reintroductions will be discussed in the following paragraphs: preliminary research, elimination of previous causes of decline, feasibility study, chances of spontaneous recolonisation, release of captive or captured wild otters and possible negative effects on wild host populations, genetic relations with original native stock, local human attitude assessment and a post-project monitoring stage. These criteria cover most of the IUCN reintroduction guidelines and we focus on these topics as they also formed the basis of the discussion around the reintroduction project.

One of the first prerequisites for any species reintroduction is that the conditions that caused the extinction in the past should no longer be present. After a feasibility study, carried out initiated by the Dutch government, a cooperative effort of several organisations (Ministerie van Landbouw, Natuurbeheer en Visserij, Stichting Otterstation Nederland, Staatsbosbeheer, Vereniging Natuurmonumenten, It Fryske Gea, Natuur en Milieu Overijssel, Provincie Overijssel, Provincie Friesland, Waterschap Reest en Wieden, Waterschap Friesland, Rijkswaterstaat, Alterra, Technische Commissie Muskusrattenbestrijding) selected five wetland areas in the northeast of the province of Overijssel and in the southwest of the province of Friesland as potential reintroduction areas. These were Lindevallei, Rottige Meenthe, National Park de Weerribben, Wieden and Oldematen. Although these areas were already well-connected special devices, such as otter-friendly tunnels and ledges under bridges, were established to increase exchange. This created a 12,000 ha marsh and bog area, where the shores provide otter habitat and places where otters can easily get out of the water (Jansman et al. 2003). To reduce traffic mortality passages under fenced roads have been built in and around the release area. Water quality had improved since the otter extinction (Stichting Otterstation Nederland 1998), while fishermen and muskrat catchers in the reintroduction area use different fykes and cages from the ones that are normally used in the Netherlands (Faber 2002). Adult otters are not able to swim into these adapted fykes.

Hunting (forbidden in the Netherlands since 1941) was assumed to be of no significance for this reintroduction project and disturbance from recreation to have a minimal impact because of the existence of many restricted access areas in the reintroduction area.

The IUCN guidelines also specify that the chances of spontaneous colonisation from neighbouring populations should be minimal. The closest viable otter populations are found in Eastern Germany. Specialists are convinced of the possibility of otters returning by themselves, but the time needed establish a viable otter population by spontaneous colonisation is a matter of debate. Some claim that German otters move rapidly in western direction and will reach the eastern provinces of the Netherlands within ten years (Reuther 1998). Otter footprints and spraints are occasionally found in the Southern province of Limburg, near the German and Belgian border (Smit 1991, Winter 1993, Backbier & Jansen 2002). Others predict that a spontaneous establishment of a viable population cannot be expected within fifty years (De Jongh 1998). Human population growth and land use will continue to put pressure on, or even destroy, potential habitats and nature conservation areas will become islands in a sea of urban or agricultural areas.

The IUCN criteria recommend the release of captured wild otters, because of their higher ability to adapt to natural situations. Wild caught otters in a Swedish reintroduction project showed higher survival rates than those released from captivity. One year after release, 79% of the captured wild otters had survived, against 42% of former captive ones (Sjöåsen 1996). Also the age of the released animals is important. The survival rate of introduced captive otters increases when young otters are reintroduced that were taken from their mother at a low age. Captured wild animals of two years or more should not be released, as they are likely to try to leave the release areas in an attempt to return to their original source areas.

Capturing wild animals in their original habitat should not have a negative impact on the source populations. For this project the original intention was to reintroduce 12 wild caught otters in 2002, but due to delays and capture problems, only three wild otters and four otters out of zoos were reintroduced in the Weerribben. (This after a short quarantine time, and with a thorough veterinary screening). With the release of previously captive individuals the project did not fully follow the suggestions of the IUCN guidelines. This first group was followed a few months later by a second group of eight wild caught otters. In all, the project involved the capture of 40 otters in Belarus and Latvia, which would not effect the large and stable populations in these countries (about 5,000 otters in Latvia, Jansman et al. 2003). However, four otters died during the capture process, and as a result the Dutch Minister of Agriculture, Nature Management and Fisheries immediately and indefinitely halted the capture in Eastern Europe, because of animal welfare concerns (Veerman 2002).

Another IUCN criterion is that reintroduced otters should be genetically similar to the former Dutch otters. Some have disapproved of the reintroduction of Eastern European otters in the Netherlands, because they believe that otter populations in Eastern Europe possess genetic differences (Anonymous 2002). These newly established Dutch otters could mix with German ones, causing a loss of genetic variation and a higher susceptibility to diseases. Recent research rejected this hypothesis: DNA from different otter populations in eastern Europe was compared with DNA belonging to historic Dutch individuals out of museums, and minimal genetic differences were found between these samples (Mulder 2002).

The IUCN states that a thorough assessment of attitudes of local people to the proposed project is necessary to ensure the long-term protection of the reintroduced population. This reintroduction project partly fulfilled this aim by educating local people through special newspapers, lectures and excursions into the release area, as well as television and radio programmes to inform citizens about the project.

Another IUCN criterion for reintroduction is that the newly established population is monitored. The well-being of the reintroduced otters should be followed for at least two or three years, so conclusions can be made about the success of the project. An intensive monitoring programme, of at least four years, was set up to follow the released animals (H. Jansman, personal communication). Such monitoring requires the use of radio transmitters and telemetric methods (Sjöåsen 1996). Without using these methods, it is not possible to track otters (Niewold et al. 2002); other reintroduction projects, have found that otter sightings are very rare, owing to the shy nature of the animal (Sjöåsen 1996).

Besides these IUCN guidelines, there has been a specific debate in the Netherlands about why the reintroduced otters were captured in Latvia and Belarus, as opposed to populations from countries closer to the Netherlands. There would have been less debate if, for example, German or Polish otters had been released.

Conclusion

Looking at the IUCN guidelines and their meaning for the reintroduction of the otter in the Netherlands, it can be stated that the main aims are the enhancement of a top predator endangered in Western Europe, preservation or restoration of the Dutch biodiversity and stimulating the nature awareness of the Dutch inhabitants. The majority of the IUCN reintroduction criteria appear to have been followed by this otter reintroduction project: the causes of death in the past have been largely eliminated and, although a spontaneous colonisation of German otters within a short time span can not fully be excluded, it is not widely accepted that this will happen. Capturing wild otters in Eastern Europe will not have a negative impact on the source populations and minimal genetic differences have been found between different local otter populations in Eastern Europe and the former Dutch otters. A monitoring stage after release is being undertaken.

We conclude that the reintroduction project of the otter in the Netherlands has followed the IUCN guidelines, which are designed to promote the restoration of plant and animal populations, based on best available practice.

Acknowledgements: We would like to thank Hugh Jansman of the Department of Ecology and the Environment at Alterra Wageningen, for all his help during the project.

References

Anonymous 2002. Deskundigen: Zet otter niet in het wild uit. Friesch Dagblad, 28 March 2002. Available from the internet, accessed 15 November 2004. URL: http://www.frieschdagblad.nl/artikel.asp?artID=3840

Backbier, L. & S. Jansen 2002. Zum vorkommen des Fischotters (*Lutra lutra*) in Limburg von 1990 bis 2000. Saügetierkundliche Informationen, Jena 5, H. 26: 210-209.

Broekhuizen, S., B. Hoekstra, V. van Laar, C. Smeenk & J.B.M. Thissen 1992. Atlas van de Nederlandse zoogdieren. Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht, The Netherlands.

De Jongh, A.W.J.J. 1998. Re-introduction of otters-support or risk for otter conservation. IUCN Otter Specialist Group Bulletin 15 (2): 80-84.

Faber, G. 2002. Regeling eenmalig project herintroductie otters. Staatscourant, 5 juli 2002.

IUCN 1995. IUCN/SCC guidelines for reintroductions. IUCN/SCC re-introduction specialist group. The World Conservation Union, Gland, Switzerland, 10 pages. Available from the internet, accessed 21 July 2003. URL: http://www.iucn.org/themes/ssc/pubs/policy/reinte.htm

Jansman, H., A. de Jongh & L. Zandbergen 2003. De otter is terug in Nederland. Available from the internet, accessed 21 July 2003. URL: http://www.terugkeer.nl

Mulder, D. 2002. Uitzetten van otters blijft kansspel. Grasduinen 7: 12-17.

Niewold, F.J.J., Lammertsma, D.R., Jansman, H.A.H & Kuiters, A.T, 2003. De otter terug in Nederland. Eerste fase van de herintroductie in Nationaal Park De Weerribben in 2002. Report 852. Alterra, Wageningen, The Netherlands.

Reuther, C. 1998. Re-introduction of otters: support or risk for otter conservation? IUCN Otter Specialist Group Bulletin 15 (2): 71-78.

Rientjens, S. (ed.) 2000. Getting support for otter action plans - what the mass media can - and cannot - do. European Centre for Nature Conservation, Tilburg, The Netherlands.

Ruiz Olmo, J. 2002. The influence of resource seasonality on the breeding patterns of the Eurasian otter (*Lutra lutra*) in Mediterranean habitats. Canadian Journal of Zoology 80 (12): 2178-2189.

Sjöåsen, T. 1996. Survivorship of captive-bred and wild-caught reintroduced European otters (*Lutra lutra*) in Sweden. Biological Conservation 76: 161-165.

Smit, M. 1991. Otterinventarisatie Limburg, februari/maart 1991. Stichting Otterstation Nederland, Leeuwarden / Zoogdieren Werkgroep Natuurhistorisch Genootschap Limburg, Maastricht, The Netherlands.

Statistics Netherlands 2003. Available from the internet, accessed 21 July 2003. URL: http://www.cbs.nl

Stichting Otterstation Nederland 1998. Onderzoeksrapport herintroductie otter. Stichting Otterstation Nederland, Leeuwarden, The Netherlands.

Veerman, C. 2002. Correspondentie met het parlement: 29 October 2002.

Winter, L., 1993. De otter in Limburg. Natuurhistorisch Genootschap, Maastricht, The Netherlands.

Samenvatting

Herintroductie van de otter (*Lutra lutra*) in Nederland is in overeenstemming met internationale richtlijnen

De otter (*Lutra lutra*) vervulde in de Nederlandse zoetwaterecosystemen een rol als predator, maar bejaging, vernietiging en verkleining van zijn habitat, verontreiniging, verkeer en verstoringen door recreatie hebben geleid tot het uitsterven van de otter. Veertien jaar na zijn uitsterven is de otter opnieuw door herintroductie uitgezet in de Weerribben, een laagveengebied in noordwest Overijssel. Er is veel discussie geweest over het uitzetten van otters in Nederland. In dit artikel wordt het herintroductieproject besproken aan de hand van de richtlijnen van de International Union for Conservation of Nature and Natural Resources (IUCN), die internationaal herkend worden en door veel herintroductieprojecten worden nageleefd. De IUCN-richtlijnen benadrukken dat biodiversiteit en natuurbewustzijn belangrijk zijn (zeker belangrijk in een dichtbevolkt land als Nederland). De IUCN beschrijft in de richtlijnen dat de oorzaken die in het verleden als oorzaak werden gezien voor het uitsterven van een diersoort afwezig zijn in het uitzetgebied voordat er tot herintroductie overgegaan dient te worden en dat kans op een spontane herkolonisatie van een duurzame populatie van otters afkomstig uit het buitenland klein dient te zijn. De bronpopulaties dienen geen negatieve gevolgen te ondervinden van het vangen van otters voor een herintroductie. Verder moeten uitgezette otters genetisch identiek zijn aan de otters vóór het uitsterven. Monitoring na uitzetting is gewenst. Na toetsing van het herintroductieproject aan deze richtlijnen, concluderen we dat de IUCN-richtlijnen door het Nederlandse herintroductieproject worden opgevolgd.

Received: 21 July 2003
Accepted: 10 August 2004

Publicaties over recente zoogdieren van Nederland, verschenen in 2003

Bauke Hoekstra

Bornsestraat 118, NL-7601 GK Almelo, The Netherlands, e-mail: b.hoekstra@home.nl

Abbing, L. Terugkeer van de bever. Rondom het Leudal 28: 239-240.

Achterberg, C. & M. van der Horst. Het voorkomen van boommarters in de Zuidwestpoort van Apeldoorn. Rapport 2003.07. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Achterberg, C. Boommarters in de omgeving van het Landal Greenpark Coldenhove [bij Eerbeek]. Rapport 2003.48. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Achterberg**,** B. De marters van Broekhuizen [Utrecht]. Marterpassen 9: 16-20.

Achterkamp, G. Vleermuisonderzoek langs de “IJzeren Rijn” door Midden-Limburg. Vleermuiswerkgroep VZZ, Nieuwsbrief 15 (3): 3-4.

Aelberts, F. Middagvleermuizen in Heusden en Helmond. ’t Grootoortje 10 (2): 25-26.

Akker, P van den. Voedsel en territoriumgebruik van overwinterende klapeksters in de Engbertsdijksvenen [met lijst prooidieren, 11 soorten]. Vogels in Overijssel 2003: 68-79.

Anonymus. Tien jaar vleermuistellingen in winterverblijfplaatsen op het Eiland van Dordrecht. Veldwerk 4 (7): 1-3.

Baarle, R. van. Ontsnapte sikaherten gevaar voor Veluws hert? Het Edelhert 38 (1): 25-26.

Backbier, L. De otter en het oeverloze gestuntel met natuurwaarden. Limburgs Milieu 17 (1): 11-13.

Bakker, E.S. Herbivores as mediators of their environment. The impact of large and small species on vegetation dynamics. Proefschrift Wageningen Universiteit, Wageningen, Nederland. Zie ook Lutra 47 (1): 65-68.

Bankert, D. & K. in ’t Groen. Konijnen tellen in de duinen van Meijendel. Duin 26 (1): 10-11.

Bankert, D. & K. in ’t Groen. Konijnen in de duinen van Meyendel [vier telmethoden]. Hollands Duinen 42: 5- 11.

Bankert, D., K.C.G. in ’t Groen & S.E. van Wieren. A review of the transect method by comparing it with three other counting methods to estimate rabbit (*Oryctolagus cuniculus*) density. Lutra 46: 27-34.

Barends, F. Cyclische bewegingen in de dichtheid van muskusratpopulaties. Muskusrat en Beheer 23 (1): 19-23, 23 (2): 14-16.

Barends, F.K.N. Bestrijding van muskusrat en beverrat in Nederland: 159-170. In: E.C. de Bordes & E. Evertsen (red.). Handhaving wetgeving dierenwelzijn. Koninklijke Vermande, SDU Uitgevers, Den Haag, Nederland.

Barends, F. Het voorkomen van de beverrat in Nederland tussen 1935 en 2003. Nieuwsbrief Beverratbestrijding 1 (3): 2-9.

Bekker, D. Eikelmuis in Sprundel. Zoogdier 14 (2): 25-26.

Bekker, D. Wintertellingen vleermuizen [2002-2003]. De Telganger 2003 (3): 1-3

Bekker, D. Verspreidingsonderzoek muizen en spitsmuizen 2003. Rapport 2003.43. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Bekker, J.P. Zoogdierinventarisatie Sint Philipsland en Tholen. Mededeling 68. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Bekker, J.P. Vleermuizeninventarisatie Molendreef te Hoek (Zeeland). Rapport 2003.020. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Bekker, J.P. Verdrongen naar de marge?: verkennend onderzoek naar het voorkomen van de noordse woelmuis (*Microtus oeconomus*) in deelgebieden aan de zuidkant van Schouwen. Rapport. Eigen uitgave, Veere, Nederland.

Bekker, J.P. Kleine zoogdieren in akkerranden in Zeeuws-Vlaanderen: een tussenrapportage van een zoogdierinventarisatie op vijf locaties in 2002.

Eigen uitgave, Veere, Nederland.

Bekker, J.P. Vleermuizen in de polder Welzinge en Schorerpolder. Eigen uitgave, Veere, Nederland.

Bekker, J.P. Lokbuizen voor eikelmuizen in Zeeuws-Vlaanderen, een tussenbalans. Eigen uitgave, Veere, Nederland.

Bestman, M. Boommartervriendelijk beheren. Marterpassen 9: 52-54.

Bijtel, H.J. van den & J. Vink. De das *Meles meles* in Zuidoost-Utrecht: populatieontwikkeling, knelpunten en voorstellen voor gerichte maatregelen. Intern rapport. Bureau H.J.V. van den Bijtel, Driebergen-Rijsenburg, Nederland.

Bleeker, T., M. Moonen & F. Leereveld. Eindverslag van het monitoringsproject “De das in Zuidoost-Fryslân”, periode januari 2002 tot eind juni 2003 inclusief evaluatie van de periode 1999-2003. Intern rapport. Staatsbosbeheer, Leeuwarden / Vereniging Das en Boom, Beek-Ubbergen, Nederland.

Bode, A.D. & A.E. Brink. De zwarte rat en zijn klimcapaciteiten. Zoogdier 14 (2): 3-6.

Boer, E.P. de. Bruinvissen langs de Friese kust. Twirre 14: 128.

Boerrigter, T. Sociale rangorde van het ree in Europa (1). Capreolus 11 (37): 10-12.

Bongers, F. Vleermuizen op defensieterreinen. Zoogdier 14 (1): 16-19.

Boo, M. de. Het dubieuze succes van het duinhert. Landschap Noord-Holland 2003 (4): 4-7.

Boonman, M. De noordse woelmuis in noordwest Utrecht en het Noorderpark. Rapport 2003.06. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Boonman, M. De noordse woelmuis in natte duinvalleien op Texel. Rapport 2003.36. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem/ Bureau Natuurbalans – Limes Divergens BV, Nijmegen, Nederland.

Boonman, M., R. Foppen & L. Verheggen. Hazelmuizen in de peiling. Zoogdier 14 (1): 14-15.

Bosch, A. Seal management polices around the entire Wadden Sea: 39-41. In: B. Reineking (red.). Management of North Sea harbour and grey seal populations. Proceedings of the International Symposium at EcoMare, Texel, The Netherlands, November 29-30, 2002. Wadden Sea Ecosystem no. 17. Wadden Sea Secretariat, Wilhelmshaven, Germany.

Bosch, F. Duikvluchten van gewone dwergvleermuizen. Vleermuiswerkgroep VZZ, Nieuwsbrief 15 (3): 11.

Bosveld, A.T.C., P.A.F. de Bie & T. Hamers. Bodemverontreiniging in de Biesbosch en doorvergiftiging naar kleine zoogdieren. Rapport 654. Alterra - Research Instituut voor de Groene Ruimte, Wageningen, Nederland.

Boudewijn, T.J., N.W. van den Brink, C. Klok & B. van Hatttum. Pollution in the floodplains of the Meuse: exposure and contamination of badgers. Rapport. Ministerie van Verkeer en Waterstaat, Directie Limburg, Maastricht/Rijksinstituut voor Zuivering Afvalwater, Lelystad, Nederland.

Brandsma, O. Vos decimeert weidevogelstand in weidevogelgebied Giethoorn-Wanneperveen. De Noordwesthoek 30 (1): 24-35.

Brasseur, S.M.J.M. & M. Fedak. Habitat use of harbour seals in relation to recreation, fisheries and large infra structural works: 27-31. In: B. Reineking (red.). Management of North Sea harbour and grey seal populations. Proceedings of the International Symposium at EcoMare, Texel, The Netherlands, November 29-30, 2002. Wadden Sea Ecosystem no. 17. Wadden Sea Secretariat, Wilhelmhaven, Germany.

Breukelen, L. van & R. Schoon. Beëindiging van de beheersjacht op reeën in de Amsterdamse Waterleidingduinen. Effecten op de populatie. Rapport Gemeentewaterleidingen, Amsterdam, Nederland.

Broekhuizen, S. Wat zijn de karakteristieken van een boommarternest? Marterpassen 9: 29-34.

Broekhuizen, S. Wezel en hermelijn. Twee niet-alledaagse “muizensperen”. Gelders Landschap 25 (3): 14-15.

Bruijn, Z. Binding tussen moeder en jong bij dwergvleermuizen. Zoogdier 14 (3): 25.

Bruijn, Z. Het gedrag van hondsdolle vleermuizen. Zoogdier 14 (3): 27-28.

Buys, J. Kerkzolders en vleermuizen. Zoogdier 14 (1): 10-13.

Buys, J. Hoeveel hazen zitten er op een hectare? Zoogdier 14 (3): 18-21.

Casteren, J. van. Zeulen met otters. Vrij Nederland 10 mei 2003: 50-55.

Coenen, A. Het walvisboek. Walvissen en andere zeewezens beschreven door Adriaen Coenen. Walburg Pers, Zutphen, Nederland. Zie ook Lutra 47 (1): 68-71.

Colpa, H. Resultaten vleermuistellingen Drenthe 2002/2003. Vleermuiswerkgroep VZZ, Nieuwsbrief 15 (2): 22-23.

Das & Boom. Onderzoek naar de dassen op Keent en de effecten van de natuurontwikkeling (fase 1) op de dassenpopulatie. Rapport. Vereniging Das en Boom, Beek-Ubbergen, Nederland.

Delden, C.J. van. Populatieontwikkeling reeën en de gevolgen voor het beheer. Capreolus 11: 4-7.

Delden, C.J. van. Uitgangspunten voor modern reeënbeheer. Capreolus 11: 13-14.

Densen, W.L.T. van. Variabilities and the perception of time trends in Dutch whaling in the 17th and 18th century: 215-259, 293-294. In: W.L.T. van Densen (red.). On the perception of time trends in resource outcome. Its importance in fisheries co-management agriculture and whaling. Proefschrift. Universiteit Twente, Enschede. Eigen uitgave, Wageningen, Nederland.

Dijkstra, V. Vallende boommarters, niet kapot te krijgen. Zoogdier 14 (1): 20.

Dijkstra, V. Vallende boommarters, niet kapot te krijgen. Marterpassen 9: 15-16.

Dijkstra, V. De aantalsontwikkeling van de rode eekhoorn in de periode 1995-2002. De Telganger 2003 (2): 1-4.

Dijkstra, V. Bevers in Limburg. Castor 2003 (12): [3].

Dijkstra, V. Onderzoek op de Veluwezoom, meer boommarters in 2002? Marterpassen 9: 39-42.

Dijkstra, V. Monitoring van de bever in Limburg 2002/2003. Eerste tussenrapport. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Dijkstra, V. & M. Zijlstra. De rode eekhoorn in de periode 1995-2002. Twirre 14: 116-118.

Dorenbosch, M. & L. Verheggen. Vleermuizen op kerkzolders in het zuidelijk Peelgebied en Midden-Limburg West. Voorstellen voor aanpassingen van kerken. Rapport 2003.018. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Driessen, J.J.H.& B.P.M. van Noorden. Hamsterinventarisatie Mergelland-West, najaar 2003. Rapport. Provincie Limburg, Maastricht, Nederland.

Egmond, F., P. Mason & K. Lankester (red.). Het walvisboek. Walvissen en andere zeewezens beschreven door Adriaan Coenen in 1585. Walburg Pers, Zutphen, Nederland.

Ellenbroek, F. Muizen die geen muizen zijn [spitsmuizen]. Zoogdier 14 (2): 7-10.

Epe, M.J., F.L.A. Brekelmans & R.W.G. Andeweg. Flora en Fauna van het Kralingse Bos. Rapport 16. Bureau Stadsnatuur Rotterdam, Rotterdam, Nederland. Zie ook: Natuurlijk Rotterdam 4 (2): 5-6.

Geraeds, R. , T. Sijstermans & E. van Veldhuizen. Dás pas leven in Cuijk. Integrale dassennota. Gemeente Cuijk, Nederland.

Giessen, J.W.B. van der & F.H.M. Borgsteede. *Echinococcus multilocularis*: De kleine lintworm van de vos met mogelijk grote gevolgen voor de mens. Muskusrat en Beheer 23 (2): 1-4.

Glatson, A. & S. de Vries. Experiences with breeding common hamsters in the Netherlands. In: R.C. van Apeldoorn & M. Stubbe. Protection of the common hamster. Publicaties van het Natuurhistorisch Genootschap in Limburg. Reeks XLIII (1): 29-32. Natuurhistorisch Genootschap in Limburg, Maastricht, Nederland.

Glas, G. Een steenoven [bij Vuren, Gelderland] vol dwergen. Vleermuiswerkgroep VZZ, Nieuwsbrief 15 (1): 10-11, (2): 21.

Graaff, A. van de. Dassen in de dijk netjes weggepest. H2O 2003 (14): 41

Gresnigt, M.C. & R.A. Vermeulen. Ontwikkeling van vlier (*Sambucus nigra* L.) en wilg (*Salix* spp) onder invloed van grote herbivoren in de Oostvaardersplassen. Wageningen Universiteit, Wageningen, Nederland.

Gronouwe, J. & F. Barends. Gebruik van live-traps in de muskusratbestrijding. Literatuuronderzoek en onderzoeksvoorstel. Rapport. Landelijke Coördinatiecommisse Muskusrattenbestrijding, provincie Noord-Brabant, Den Bosch, Nederland.

Haarsma, A-J. Meervleermuizen ringen en dan terugvinden! Zoogdier 14 (2): 26-27.

Haarsma, A-J. Resultaten van transponderwaarnemingen. Vleermuiswerkgroep VZZ, Nieuwsbrief 15 (3): 6-8.

Haarsma, A-J. Vleermuizen nemen heel Zuid-Holland over. Resultaten van een tweede jaar telemetrie onderzoek aan vleermuizen in Nederland. Zoogdier 14 (4): 18-21.

Haarsma, A-J., R. van der Kuil, J. van Vliet, F. van der Vliet, R. Vermeulen, F. Bongers, H. Limpens & G. Achterkamp. Vleermuizen, Bomen en Bos. De betekenis van bomen en bos voor vleermuizen. Brochure. Stichting Vleermuis Bureau / Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Haeck, J. Mollen. Een halve eeuw wroeten. Zoogdier 14 (3): 3-8.

Halley, D.J. & F. Rosell. Population and distribution of European beavers (*Castor fiber*). Lutra 46: 91-101.

Härkönen, T. Development of populations of harbour seals and grey seals in the Wadden sea and the North Sea since 1988: 13-18. In: B. Reineking (red.). Management of North Sea harbour and grey seal populations. Proceedings of the International symposium at EcoMare, Texel, The Netherlands, November 29-30, 2002. Wadden Sea Ecosystem no. 17. Wadden Sea Secretariat, Wilhelmshaven, Germany.

Helm, F. van der. Getalenteerde bouwmeester [bever]. Natuurbehoud 34 (2): 36-38.

Helm, F. van der. Das woont op stand. Natuurbehoud

34 (3): 22-25.

Hidding, A. Drentse reinaerts's weer onder vuur. Argus 28 (1): 17-18.

Hoeksteen, M., S.J. Lilipaly & P.L. Meininger. Vliegtuigtellingen van watervogels en zeezoogdieren in de Voordelta 2000/2001 (met gegevens van zeehonden in de Oosterschelde en Westerschelde. Rapport 2003.046. Rijksinstituut voor Kust en Zee, Middelburg, Nederland.

Honing, T. van der. De noordse woelmuis in Skarsterlân. Vanellus 56: 155-156.

Hoorn, D. van den. Dammen op de Veluwe. Het Edelhert 38 (1): 18-19.

Hoorn, D. van den. De eerste dagen van een nieuw gewei. Het Edelhert 38 (1): 20-24.

Hoorn, D. van den. Zijn edelherten zwervers? Het Edelhert 38 (3): 19-23.

Horn, B. van den. Onderzoek in 2002 op Den Treek-Henschoten en Austerlitz. Marterpassen 9: 43-46.

Horst, M. van der. Onze "eerste" [boommarter]. Marterpassen 9: 49-50.

Huitema, H. Vleermuizen in de schijnwerpers [Kernhem, Ede]. Zoogdier 14 (4): 27-28.

Jansen, R. Zoogdiereninventarisatie Ede-Veenendaal in 2003. Rapport 2003.14. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Jansen, W. Een gouden mol uit Noord-Limburg. Natuurhistorisch Maandblad 92: 228.

Jansen, E.A. The occurrence of the parti-coloured bat *Vespertilio murinus* in the Netherlands, a change of status. Abstract IXth European Bat Research Symposium 7. Le Havre 26-30 August 2002.

Jansen, E.A. Het gebruik van het MOB complex Groenekam en het voormalige sportterrein te De Bilt door vleermuizen. Rapport 2003.024. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Jansen, E.A. Het huidige gebruik van de Wageningse Berg door vleermuizen. Rapport 2003.031. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Armhem, Nederland.

Jansen, E.A. & E. Korsten. Vleermuisleefgebieden aan de noord en oostkant van Baarle-Nassau (NL) en Baarle-Hertog (B). Analyse van het gebruik van het gebied door vleermuizen en knelpunten in het ontwerptracé van de omlegging. Rapport 2003.05. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Jansman, H.A.H., J. Dekker, B. van Hattum, P.E.G. Leonards & S. Broekhuizen. Using molecular markers and PCB analysis to infer the origin of the otter (*Lutra lutra*) found on the Knardijk, The Netherlands, in 1998. Lutra 46: 3-12.

Jansman, H.A.H., D.R. Lammertsma & T.J.L. Niewold . Monitoring the re-introduction of the otter in the Netherlands: telemetry versus genetical and hormonal analysis: 125. In: M. Machlán, J. Bryja & J. Zima (red.). European Mammalogy 2003; 4th European Congress of Mammalogy, Brno, Czech Republic, July 27- August 1, 2003; program & abstracts & list of participants. Institute of Vertebrate Zoology, Brno, Czech Republic**.**

Jansman, H.A.H., G.J.D.M. Müskens, K. Neumann & S. Broekhuizen. Breeding and re-introduction of the hamster in the Netherlands: 126. In: M. Machlán, J. Bryja & J. Zima (red). 4th European Congress of Mammalogy, Brno, Czech Republic, July 27-August 1, 2003; program & abstracts & list of participants. Institute of Vertebrate Zoology, Brno, Czech Republic.

Jansman, H.A.H., L. van de Zande & K. Bijlsma. Reintroduction of the otter in the Netherlands: the genetical study: 126. In: M. Machlán, J. Bryja & J. Zima (eds). European Mammalogy 2003; 4th European Congress of Mammalogy, Brno, Czech Republic, July 27-August 1, 2003; program & abstracts & list of participants. Institute of Vertebrate Zoology, Brno, Czech Republic.

Jong, J. de. Eerste veldmuizen op Schiermonnikoog. Vanellus 2003 (6): 138-139.

Jong, M. de. Albinohaard [egel]. Grasduinen 2003 (3): 12.

Jong, M. de. Verstekeling [Kuhl's dwergvleermuis]. Grasduinen 2003 (4): 8.

Jong, M. de. Parasieten op zeldzame bultrug. Grasduinen 2003 (12): 7.

Jong, P. de. De vos weer vogelvrij. Argus 28 (1): 4-7.

Jonge, J. de. De beverrat in Zeeland. Nieuwsbrief Beverratbestrijding 1 (2): 5-8.

Jordan, M. Reintroduction and restocking protocols for the common hamster (*Cricetus cricetus*). In: R.C. van Apeldoorn & M. Stubbe (red.). Protection of the common hamster. Publicaties van het Natuurhistorisch Genootschap in Limburg. Reeks XLIII(1): 24-28. Natuurhistorisch Genootschap in Limburg, Maastricht, Nederland.

Kastelein, R.A., M. Hagedoorn, W.W.L. Au & D. de Haan. Audiogram of a striped dolphin (*Stenella coeruleoalba*). Journal of the Acoustical Society of America 113: 1130-1137.

Kerssen, H. Dassen inventarisatie Nunspeet. Rapport. Stichting Behoud Dierenwereld Veluwe, Apeldoorn, Nederland.

Keulen, A. Mogelijke waarneming van de kleine dwergvleermuis. Vleermuiswerkgroep VZZ, Nieuwsbrief 15 (1): 8-9.

Keusterman. J. Nerts vangt beverrat? Nieuwsbrief Beverratbestrijding 1 (3): 1.

Kip, B. Leeftijdsbepaling bij reeën, subjectief en objectief. Capreolus 11 (37): 12-14.

Koelman, R. Natuurtoets HOV-as Peizerweg te Groningen – vleermuizen. Rapport 2003.10. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Koelman, R. Vleermuizeninventarisatie Winschoter Driehoek (Groningen). Rapport 2003.15. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Koelman, R. Natuurtoets Oostindië-Leek. Vleermuizen en waterspitsmuis. Rapport 2003.16. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Koelman, R. Vleermuizeninventarisatie Coendersborg (Groningen-Stad). Rapport 2003.17. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Koelman, R. Natuurtoets Europapark Groningen Zoogdieren. Rapport 2003.44. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Koelman, R. Natuurtoets Schildwolde-Schatterswold Zoogdieren. Rapport 2003.45. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Koelman, R. Meervleermuizen in Groningen. Vleermuiswerkgroep VZZ, Nieuwsbrief 15 (3): 10.

Koelman, R. & D. Bekker. Zoogdierinventarisatie Honswijkerwaarden [Vianen] 2003: terrestrische zoogdieren. Rapport 2003.32. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Koelman, R. & H.J.G.A. Limpens. Vleermuisonderzoek slooppanden Hindeloopen. Rapport 2003.38. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Koning, F.J. Voedsel van de ransuil (*Asio otus*) en de kerkuil (*Tyto alba*) in het Zwanenwater. Periode 1996-2002. [huisspitsmuis stapelvoedsel van kerkuil]. De Tringiaan 26: 72.

Korsten, E. Oude vondst van een bosvleermuis *Nyctalus leisleri* (Kuhl, 1817) in Noord-Brabant. Lutra 46: 35-38.

Korsten, E. Inzwermende gewone dwergvleermuis bij zonsondergang. ’t Grootoortje 10 (2): 28.

Korsten, E. Verslag wintertelling de Mattenburgh 18-1-2003. ’t Grootoortje 10 (3): 7-9.

Korsten, E. Vleermuizen bij “De Wandeling” van Omroep Brabant. ’t Grootoortje 10 (3): 20-23.

Kuiken, T. Infectieuze en niet-infectieuze ziekten [bij zeehonden]: 34-41. In: D. Hayder (red.). Compilatie van gegevens over zeehonden en zeehondenopvang in de Nederlandse Waddenzee. Groningen, september 2002. Eindrapport. Ministerie van Landbouw, Natuur en Voedselkwaliteit, Den Haag, Nederland.

Kuiken, T. & J. Kuiper. Strandingen van gewone- en grijze zeehonden in Nederland. 1989-2000: 3-14. In: D. Hayder (red.). Compilatie van gegevens over zeehonden en zeehondenopvang in de Nederlandse Waddenzee. Eindrapport. Wetenschappelijk Platform Zeehonden Waddenzee, Groningen, september 2002. Ministerie van Landbouw, Natuur en Voedselkwaliteit, Den Haag, Nederland.

Kuil, R. van der. Zoogdieren in de Zuidpolder van Delfgauw. Rapport 2003.11. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Kuil, R. van der. Zoogdieren in de Oosttak van de N470. Rapport 2003.12. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Kuil, R. van der. Zoogdieren in de Zuidtak van de N470. Rapport 2003.13. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Kuil, R. van der. Meervleermuistellingen 2002. Vleermuiswerkgroep VZZ, Nieuwsbrief 15 (2): 8.

Kuil, R. van der & B. Noort. De betekenis van Heijplaat [Rotterdam] voor vleermuizen. Rapport 2003.37. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Kurstjens, G. Veldinventarisaties Flora en fauna NVO Keent in 2003. Rapport. Kurstjens Ecologisch Adviesbureau, Beek-Ubbergen, Nederland.

Kurstjens, G. & J. Bekhuis. Adaptation of beavers (*Castor fiber*) to extreme water level fluctuations and ecological implications. Lutra 42: 147-151.

La Haye, M., M. Cox & A. Damen Hoe zeldzaam is de waterspitsmuis? Honderd jaar braakballen onderzocht. Zoogdier 14 (1): 7-9.

La Haye, M. & J. de Jong. De veldmuis nu ook op Schiermonnikoog. Texel in de gevarenzone?! Zoogdier 14 (4): 22-24,

Lammertsma, D.R., F.J.J. Niewold, H.A.H. Jansman & A.T. Kuiters. Otters opsporen: ervaringen in het eerste jaar van uitzetten. Zoogdier 14 (4): 13-17.

Langeveld, M. Discussie rond de vos. De Steltkluut 33 (2): 17-21.

Leuven, J. van. Ree; kleurrijk zwart. [fotoboek albinisme/melanisme]. GMB Uitgeverij, Haarlem, Nederland.

Leuven, J. van. Zwarte en witte reeën. Grasduinen 2003 (10): 38-39.

Limpens, H. De boer op voor de franjestaart. Zoogdier 14 (2): 21-24.

Limpens, H. Nog kleiner dan de dwergvleermuis, en toch te vinden? Zoogdier 14 (1): 32-33.

Limpens, H. Vleermuissteentjes…en of vleermuizen wel tandpijn krijgen van steentjes??? Vleermuiswerkgroep VZZ, Nieuwsbrief 15 (3): 13.

Limpens, H.J.G.A., L. Bach, E.A. Jansen & H. Mellema. Vleermuizen rond de A74/BAB61; een veldinventarisatie ter beoordeling van de effecten van de aan te leggen A74/BAB61 op de vleermuizen, en ten behoeve van aanbevelingen voor mitigatie en compensatie. Rapport 2003.01. Eco Consult en Management, Wageningen, Nederland.

Limpens, H.J.G.A. & D. Bekker. Zoogdierinventarisatie Ede-Veenendaal in 2003. Rapport 2003.14. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Limpens, H.J.G.A. & P.H.C. Lina. Status and distribution of the barbastelle (*Barbastella barbastellus*) in the Netherlands. Nyctalus 8: 608-610.

Maanen, E. & D. van Dullemen. Flora en fauna in het openbaar groen in Zeewolde in 2002. Rapport 370. Altenburg & Wymenga Ecologisch Onderzoek bv., Veenwouden, Nederland.

Margry, K. & I. Margry. Gezien in de omgeving. Witsnuitdolfijn. De Groene Dolphijn 2003 (10): 4-5.

Meer, H.P. van der. Reeën in Meijendel en Berkheide, monitoringverslag 1999-2002. Duinwaterleidingbedrijf Zuid-Holland. Voorburg, Nederland.

Meininger, P.L., R.H. Witte & J. Graveland. Zeezoogdieren in de Westerschelde: knelpunten en kansen. Rapport 2003.041. Rijksinstituut voor Kust en Zee, Middelburg, Nederland.

Melchers, M. De zoogdieren: 133-135. In: D. de Jonge (red.). Het Amsterdamse Bos. Natuur dichtbij de stad. Schuyt & Co, Utrecht, Nederland

Mil, J. van. Shaping coexistence: Twenty years of population interactions between roe deer (*Capreolus capreolus* L.) and red deer (*Cervus elaphus* L.). Wageningen Universiteit, Wageningen, Nederland.

Molenaar, J.G. de, R.J.H.G. Henkens, C. ter Braak, C. van Duyne, G. Hoefsloot & D.A. Jonkers. Wegverlichting en Natuur IV. Effecten van wegverlichting op het ruimtelijk gedrag van zoogdieren. DWW-rapport 2003-012. Rijkswaterstaat, Dienst Weg- en Waterbouwkunde, Delft/Rapport 648. Alterra - Research Instituut voor de Groene Ruimte, Wageningen, Nederland.

Mostert, K. Muizen van de Reeuwijksche Plassen. Zoogdier 14 (4): 39.

Mulder, J. De vos is weer de gebeten hond. Zoogdier 14 (1): 30-31.

Mulder, J. Hoe is de vossenpopulatie in Noord-Holland te monitoren? Rapport 2003.02. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Müskens, G. Gestaag vooruit, hamsters vinden hun plek. Limburgs Landschap 30 (4): 16-17.

Müskens, G. & S. Broekhuizen. Boommarterwaarnemingen in 2002. Marterpassen 9: 11-15.

Müskens, G.J.D.M., R.M.A. Wegman & C.J.F. ter Braak. Boommarters en wegen; een eerste analyse van de relatie “wegbermen – verkeersslachtoffers”. Rapport 849. Alterra - Research Instituut voor de Groene Ruimte, Wageningen, Nederland.

Neumann, K. & H. Jansman. Genetical status of the common hamster in The Netherlands and other European countries. Consequences for conservation in the Netherlands and Belgium. In: S. Mercelis, A. Kayser & G. Verbeylen (red.). Proceedings of the 10th meeting of the International Hamster Workgroup, 12-14 October 2002, Tongeren, Belgium: 90.

Neumann, K., A. Kayser, R. Gattermann, S. Maak, R.C. van Apeldoorn & H. Jansman. The genetic situation of Dutch common hamsters assessed with microsatellite markers. In: R.C. van Apeldoorn & M. Stubbe (red.). Protection of the common hamster. Publicaties van het Natuurhistorisch Genootschap in Limburg. Reeks XLIII (1): 8-11. Maastricht, Nederland.

Niewold, F. Nieuwere ontwikkelingen in de Gelderse Poort. Castor 2003 (12): [2-3].

Nijland, M. De gebeten hond. Nieuwe Wildernis. 2003 (27/28): 13-18.

Nijssen, A. Vleermuiswandeling in Uden op 20 juni 2003. ’t Grootoortje 10 (3): 11.

Nooren, M. J. Jonge dassen gered. De Levende Natuur 104: 64.

Nusselein, J. Vleermuiskasten regio Dongen. ’t Grootoortje 10 (1): 27-29.

Nusselein, J. Overzicht wintertellingen 2002-2003 [Noord-Brabant]. ’t Grootoortje 10 (2): 4-7.

Nusselein, J. Vleermuisinventarisatie Spinolaschans 2002. [Noord-Brabant]. Rapport 2003-09. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Osterhaus, A.D.M.E. Virusinfecties van Pinnipeden. In: D. Hayder (red.). Compilatie van gegevens over zeehonden en zeehondenopvang in de Nederlandse Waddenzee. Groningen, september 2002. Eindrapport: 27-33. Ministerie van Landbouw, Natuur en Voedselkwaliteit, Den Haag, Nederland.

Osterhaus, A. & T. Kuiken. Re-emergence of phocine distemper in the harbour seal population of Western Europe. In: B. Reineking (red.). Management of North Sea harbour and grey seal populations: 37-38. Proceedings of the international symposium at EcoMare, Texel, The Netherlands, November 19-20, 2002. Wadden Sea Ecosystem no. 17: 37-38. Wadden Sea Secretariat, Wilhelmshaven, Germany.

Pouwels, R, G.W.T.A. Groot Bruinderink & H. Kuipers. Ecologisch rendement van ontsnippering : de casestudie edelhert en wild zwijn Veluwe. Rapport 533. Alterra, Research Instituut voor de Groene Ruimte, Wageningen, Nederland.

Reineking, B. Phocine distemper epidemic amongst seals in 2002. In: B. Reineking (red.). Management of North Sea harbour and grey seal populations: 57-63. Proceedings of the International Symposium at EcoMare, Texel, The Netherlands, November 19-20, 2002. Wadden Sea Ecosystem no 17. Wadden Sea Secretariat, Wilhelmshaven, Germany.

Reid, J.B., P.G.H. Evans & S.P. Northridge (red.). Atlas of Cetacean distribution in north-west European waters. Joint Nature Conservation Council Committee. Peterborough, United Kingdom.

Reijnders, P.J.H. Effecten van hormoonverstorende stoffen op reproductie en ontwikkeling van zeezoogdieren. In: D. Hayder (red.). Compilatie van gegevens over zeehonden en zeehondenopvang in de Nederlandse Waddenzee: 52-60. Eindrapport. Wetenschappelijk Platform Zeehonden Waddenzee. Groningen, september 2002. Ministerie van Landbouw, Natuur en Voedselkwaliteit, Den Haag, Nederland.

Reijnders, P.J.H. Zeehonden en menselijke activiteiten. In: D. Hayder (red.). Compilatie van gegevens over zeehonden en zeehondenopvang in de Nederlandse Waddenzee: 70-73. Eindrapport. Wetenschappelijk Platform Zeehonden Waddenzee. Groningen, september 2002. Ministerie van Landbouw, Natuur en Voedselkwaliteit, Den Haag, Nederland.

Reijnders, P.J.H. Reproductive and developmental effects of environmental organochlorines on marine mammals. In: J.G. Vos, G.D. Bossart, M. Fournier & T. O'Shea (red.). Toxicology of marine mammals: 55-66. Taylor & Francis, London, UK.

Reijnders, P.J.H. & S.M.J.M. Brasseur. Vreemde snuiters aan de Nederlandse kust. Zoogdier 14 (4): 5-10.

Reijnders, P.J.H., K. Abt, S. Brasseur, S. Tougaard, U. Siebert & E. Vareschi. Sense and sensibility in evaluating aerial counts of harbour seals in the Wadden Sea. Wadden Sea Newsletter 28: 9-12.

Reijnders, P.J.H. & S.M.J.M. Brasseur. Veränderungen in Vorkommen und Status der Bestände von Seehunden und Kegelrobben in der Nordsee - mit Anmerkungen zum Robbensterben in 2002. In: J.L. Lozán, E. Rachor, K. Reise, J. Sündermann & H. von Westerhagen (red.). Warnsignale aus Nordsee und Wattenmeer, eine aktuelle Umweltbilanz: 330-339. Wissenschaftliche Auswertungen. Hamburg, Deutschland.

Reijnders, P.J.H. & S.M.J.M. Brasseur. Populatieontwikkelingen van zeehonden in de Nederlandse Waddenzee. In: D. Hayder (red.). Compilatie van gegevens over zeehonden en zeehondenopvang in de Nederlandse Waddenzee: 3-14. Eindrapport. Wetenschappelijk Platform Zeehonden Waddenzee. Groningen, september 2002. Ministerie van Landbouw, Natuur en Voedselkwaliteit, Den Haag, Nederland.

Reijnders, P.J.H., S.M.J.M. Brasseur, K.F. Abt, U. Siebert, M. Stede & S. Tougaard. The harbour seal population in the Wadden Sea as revealed by the aerial surveys in 2003. Wadden Sea Newsletter 29: 11-12.

Reijnders, P.J.H., S.M.J.M. Brasseur & A.G. Brinkman. The phocine distemper virus outbreak of 2002 amongst harbour seals in the North Sea and Baltic Sea: spatial and temporal development, and predicted population consequences. In: B. Reineking (red.). Management of North Sea harbour and grey seal populations: 19-25. Proceedings of the international symposium at EcoMare, Texel, The Netherlands, November 29-30, 2002. Wadden Sea Ecosytem no. 17. Wadden Sea Secretariat, Wilhelmshaven, Germany.

Reijnders, P.J.H. & M.P. Simmonds. Global temporal trends of organochlorines and heavy metals in pinnepeds. In: J.G. Vos, G.D. Bossart, M. Fournier & T. O'Shea (red.). Toxicology of marine mammals: 491-506. Taylor & Francis, London, UK.

Reineking, B.(red.). Management of North Sea harbour and grey seal populations. Proceedings of the international symposium at Ecomare, Texel, The Netherlands, November 29-30, 2002. Wadden Sea Ecosystem No 17. Wadden Sea Secretariat, Wilhelmhaven, Germany.

Reinhold, J. [Bever]Tellingen in Flevoland. Castor 2003 (12): [2].

Reinhold, J. Boommarterkast in gebruik. Zoogdier 14 (4): 23.

Reinwold, J. & A. Wolfs. Een kast voor een boommarter in Flevoland. Marterpassen 9: 54-56.

Reinhold, J. The beaver (*Castor fiber*) in Flevoland, The Netherlands. Lutra 42: 135-138.

Revier, H.M. & P.J.H. Reijnders. Visie op de natuur van de Waddenzee en op het beheer van zeehonden in de Waddenzee. In: D. Hayder (red.). Compilatie van gegevens over zeehonden en zeehondenopvang in de Nederlandse Waddenzee: 85-90. Eindrapport. Wetenschappelijk Platform Zeehonden Wadenzee. Groningen, september 2002. Ministerie van Landbouw, Natuur en Voedselkwaliteit, Den Haag, Nederland.

Rienks, F. & P. Twisk. Ingekorven vleermuis terug in Noord-Brabant. Zoogdier 14 (4): 34.

Rintjema, S. 25 jaar reeëntellingen in de Alde Feanen. Twirre 14 : 66-67.

Roosendaal, A. van. Boommarter in focus, boommarter (onder- of over-)belicht. Marterpassen 9: 57-59.

Rouwenhorst, J. Kannibalisme bij wilde zwijnen. Zoogdier 14 (3): 26.

Rouwenhorst, J. Das en bronst. Zoogdier 14 (3): 26-27.

Selten, B. Overdag jagende vleermuis. Zoogdier 14 (1): 20.

Siebenga, S. Beheer van vossen, tips uit de praktijk. De Nederlandse Jager 108 (7): 11-14.

Sluijs, A.M. van der. Bever-Transect -Tellingen in de Biesbosch in 2003. Rapport 2003.42. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Sluiter, H. The reintroduction and the present status of the beaver (*Castor fiber*) in the Netherlands: an overview. Lutra 42: 129-133.

Smeenk, C. Strandingen van Cetacea op de Nederlandse kust in 1993-1997. Lutra 46: 45-64.

Smeenk, C., M. Addink & K. Camphuysen. De eerste bultrug voor Nederland. Zoogdier 14 (4): 3-4.

Smulders, M.J.M., L.B. Snoek, G. Booy & B. Vosman. Complete loss of MHC genetic diversity in the common hamster (*Cricetus cricetus*) population in The Netherlands. Consequences for conservation strategies. Conservation Genetics 4: 441-451.

Sneep, J-W. National report on the implementation of the agreement on the conservation of bats in Europe. The Kingdom of the Netherlands. Internetsite Eurobats. Secretariat Bonn, Germany.

Stafleu, F., B. Bovenkerk, R. Tramper, J. Vorstenbosch & F.W.A. Brom. The public debate in the Netherlands – The ethics of seal population management. In: B. Reineking (red.). Management of North Sea harbour and grey seal populations: 43-50. Proceedings of the International Symposium at EcoMare, Texel, The Netherlands, November 29-30, 2002. Wadden Sea Ecosystems no 17. Wadden Sea Secretariat, Wilhelmshaven, Germany.

Stege, H. ter. De betekenis van de Nederlandse namen van zoogdieren, reptielen en amfibieën. Eigen uitgave, Wageningen.

Stempher, W. & E. Timmerman. Eerste resultaten en opzet monitoring gericht op veldsporen. Rapport Internationale Agrarische Hogeschool Larenstein, Velp/Alterra - Research Instituut voor de Groene Ruimte, Wageningen, Nederland.

Stichting Instandhouding Kleine Landschapselementen in Limburg. Jaarverslag Vleermuisbescherming in Limburg 2002. Roermond, Nederland.

Thissen, J.B.M. & M. Stubbe. The situation of the common hamster (*Cricetus cricetus*) in Europe and European law. In: R.C. van Apeldoorn & M. Stubbe (red.). Protection of the common hamster. Publicaties van het Natuurhistorisch Genootschap in Limburg. Reeks XLIII (1): 8-11. Maastricht, Nederland.

Tuitert, D., R. Janssen & K. Spoelstra. Bechsteins vleermuis in Overijssel. Zoogdier 14 (4): 25-26. Zie ook: Rectificatie. Zoogdier 15: 5

Twisk, P. Zoogdiereninventarisatie Maliskamp in 2002. Rapport 2003.04. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Twisk, P. Vleermuizeninventarisatie Oude Buisse Heide in 2002. Rapport 2003.08. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Twisk, P. Vleermuizeninventarisatie Vrachelen – Oosterhout. Rapport 2003. 021. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Twisk, P. Vleermuizeninventarisatie Bosje bij Liessel. Rapport 2003.023. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Twisk, P. Vleermuizen rond Koningshof te Veldhoven Rapport 2003.030. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Twisk, P. Resultaten vleermuiskasten Groote Wiel ‘00-’03. ’t Grootoortje 10 (1): 11-14.

Twisk, P. Verslag inventarisatie de Vughtse Hoeven 18, 21, 22 en 23 juni ’02. ’t Grootoortje 10 (1): 17-22.

Twisk, P. Vleermuisinventarisatie Groote Slink en Beestenveld [Noord– Brabant] 14-16 juni 2002. ’t Grootoortje 10 (2): 11-23.

Twisk, P. Vleermuisbescherming …. vanuit een ivoren toren. Zoogdier 14 (1): 27-29.

Twisk, P. Jaarverslag 2001 Vleermuiswerkgroep

Noord-Brabant. Vleermuiswerkgroep VZZ, Nieuwsbrief 15 (1): 5-7.

Twisk, P. & A. Nijssen. Grootoren in Zundert. ’t Grootoortje 10 (1): 22-25.

Van Den Bogaert, J. Bevers in België [en Nederland, Limburg]. Zoogdier 14 (3): 9-14.

Verheggen, L. Hazelmuisinventerisatie 2002. Aanvulling verspreidingsonderzoek Gulpdal, Westelijk Geuldal en Plateau van de Bahnerheide. Rapport 2003.19. Verening voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Verwoerd, G.W.H. & G.J. Spek. Staken van registratie doet gewond wild ellendig lijden. Het Edelhert 38 (3): 10--14.

Visscher, G. Boommarter op de kast. Marterpassen 9: 22-23.

Vlaming, P. Reddingsactie voor vleermuizen in de kerk. Vleermuiswerkgroep VZZ, Nieuwsbrief 15 (3): 12.

Vlaming, P. Vleermuizen overleven houtwormbestrijding in kerk. Tussen Duin en Dijk 2 (4): 9.

Vliet, F. van der, S. Bouma & H.W. Waardenburg. Muskusrattenbestrijding in Nederland. Een onderzoek naar optimalisatie van het gebruik van vangmiddelen en van vangststrategieën. Rapport 2003-017. Bureau Waardenburg, Culemborg, Nederland.

Vliet, F. van der. Nieuwe [vleermuis]winterverblijven in Amsterdam. Vleermuiswerkgroep VZZ, Nieuwsbrief 15 (1): 2-3.

Vliet, F. van der. Vleermuizen. In: D. de Jong (red.). Het Amsterdamse Bos. Natuur dichtbij de stad: 136-139. Schuyt en Co, Utrecht, Nederland.

Vuure, C. van. De oeros. Het spoor terug. Rapport 186. Wetenschapswinkel, Wageningen, Nederland.

Wansink, D. Vleermuizen in bomen langs de Koningsweg te Arnhem. Rapport 2003.040. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Wassink, G. Eerste broedgeval van oehoe *Bubo bubo* in de Achterhoek [predatie op egel]. Limosa 76: 1-10.

Werkgroep Boommarter Nederland. [Boommarter]onderzoek in 2002 op de terreinen “Natuurmonumenten”. Marterpassen 9: 34-39.

Westerlaak, I. van & G. Stooker. 10 jaar dassen-monitoring in beheerseenheid Maasdal. Staatsbosbeheer, Roermond, Nederland.

Wijsman, H. Veldwaarnemingen in 2002 van de boommarter. Marterpassen 9: 24-29.

Wijsman, H. Individueel herkenbare boommarters. Marterpassen 9: 46-48.

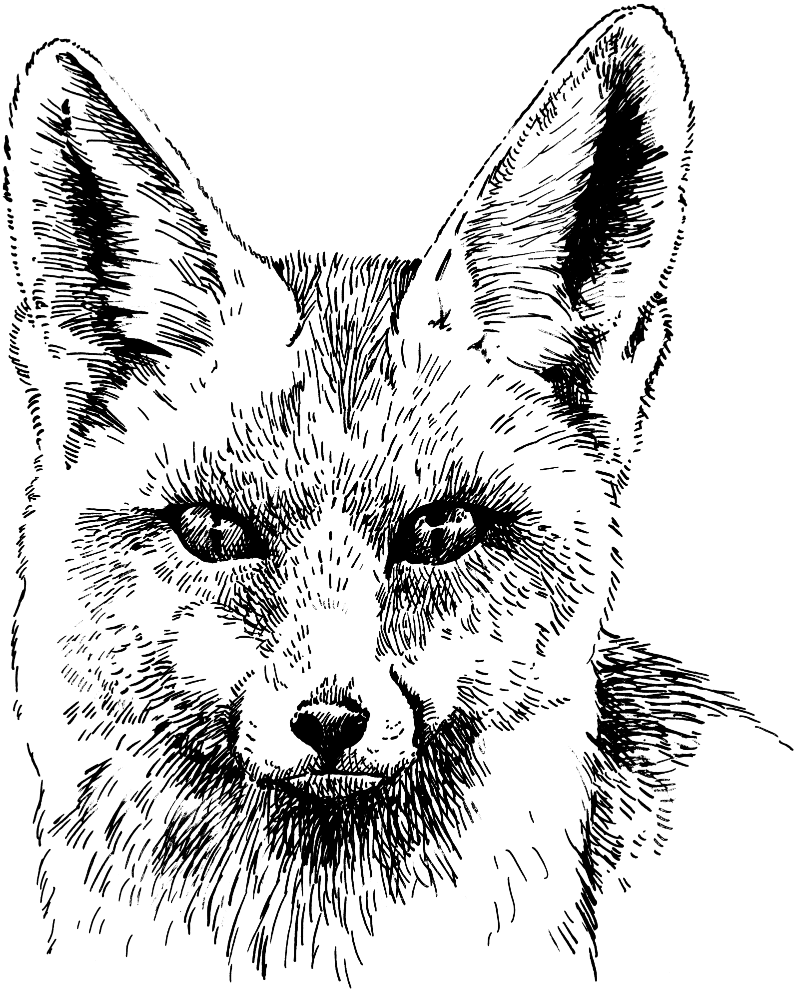
Wijsman, H. & J. Reinhold. De boommarter in Flevoland. De Grauwe Gans 19 (1): 17-19, (3): 6-8.

Wilgen, A. van. Paargedrag dwergvleermuis in de badkamer. ’t Grootoortje 10 (1): 29-30.

Zelfde, R. van ‘t. Zichtbaarheid van boommarters. Marterpassen 9: 20-22.

Zoon, C.P.M. Onderzoek naar de waterspitsmuis in het gebied Stadshagen II (Zwolle). Rapport 2003.25. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.

Zoon, C.P.M. Onderzoek naar de waterspitsmuis rond bedrijventerrein Hessenpoort (Zwolle). Rapport 2003.26. Vereniging voor Zoogdierkunde en Zoogdierbescherming, Arnhem, Nederland.



ED.

Index

Contents of Volume 47 (2004)

Research Papers

Short Notes

Opinion

Recent Publications

Book Reviews