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

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

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

Introduction

In central and western Europe, mice and voles (Muridae and Microtidae, hereafter referred to as small rodents) represent a substantial part of the diet of the pine marten (*Martes martes*) (Marchesi & Mermod 1989, Jędrzejewski et al. 1993, Nitze 1998). Small rodent populations fluctuate in size (Pucek et al. 1993, Zalewski et al. 1995, Helldin 1999) according to fluctuations in the mast production of deciduous trees, mainly common oak (*Quercus robur*) and beech (*Fagus sylvatica*). In the central Netherlands, the mast production of beech and oak dips every two to three years (Wildbeheer Veluwe, unpublished data). The following winter will then often see a reduction in the small rodent population (Jędrzejewski et al.1993); in times of rodent dearth, martens turn to alternative prey (Zalewski et al. 1995), such as birds or squirrels (the latter are seldom reported as prey in the Netherlands), so it is to be expected they will be indirectly affected by mast volume. In 2001, H. Kleef (personal communication) observed indolent pine marten females in and around their dens, easily satisfied by short bouts of hunting, this in contrast to the activity in many other years such as 2002, when small rodents were at a low. He provisionally concluded that the levels of marten activity depended on differences in the availability of small rodent prey.

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

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hunting for longer, and did so more frantically.

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

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

Material and methods

Study area

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

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

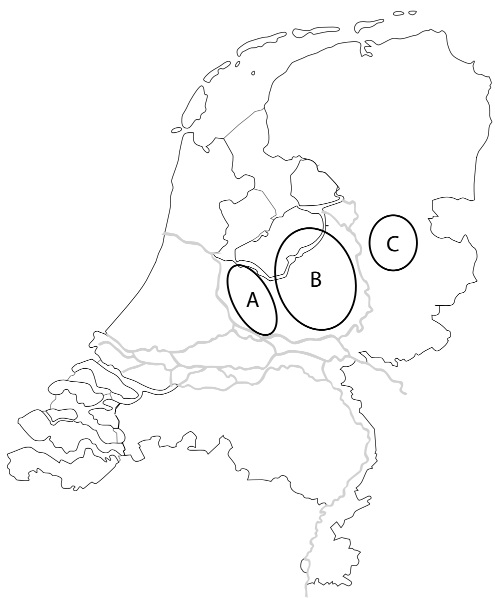

Figure 1. Map of the Netherlands showing the location of study areas. A=Utrechtse Heuvelrug; B=Veluwe; C=Salland.

Mast

Data on the production of mast have been kindly provided by Wildbeheer Veluwe (G.J. Spek); beech mast has been grouped into four classes: 3. mast plentiful, 2. mast normal, 1. mast locally, 0. no mast worth mentioning. Furthermore, Wildbeheer Veluwe produces a yearly assessment of the total seed production for beech, indigenous oak and American oak, by extrapolation expressed in kg for the Veluwe area, that is to say, around the area called Kroondomein (the area is dominated by "indigenous oak" with a great majority of *Quercus robur* interspersed with some *Q. petraea*). The Veluwe is located centrally in the study area, so it can be assumed that the data are more or less valid in the other provinces.

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

Abundance of small rodents

The relative abundance of wood mice (*Apodemus sylvaticus*) has been assessed by Bijlsma (2009, 2011) since 1993 on the basis of the frequency of holes per 10x10 m^2. For the present study, Bijlsma communicated his original data on the wood mouse in February, and also made additional data for 2011 available.

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

Litter size

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

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

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

Identification of individuals

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

Date of birth

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

Predation on nest boxes for passerines

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

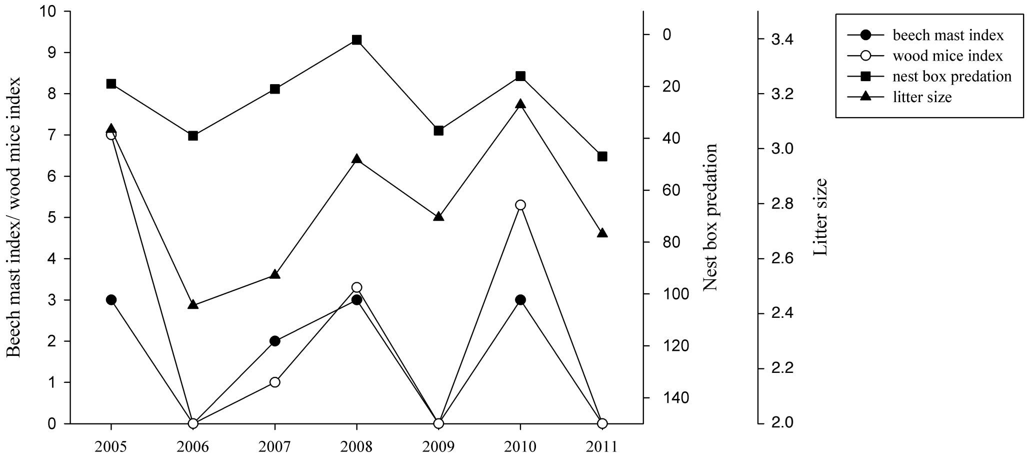

Figure 2. Beech mast (according to the index 0-3), wood mouse density in February (mean number of occupied holes per 10x10 m), mean pine marten litter size per year and nest box predation (percentage of young birds removed from nest boxes) in the Kootwijk area over 2005-2011. Note that the y-axis for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

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

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

Statistical analyses

Relations between litter size, mast, rodent abundance, and nest box predation were quantified using Spearman's rank correlation coefficients.

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

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

Results

Mast

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

Table 1. Total and oak mast (x 10,000 kg) in the Veluwe area, small rodent density (mean number of occupied holes per 10x10 m^2), number of young buzzards ringed in the Gooi area and number of young fledged tawny owls over 2005-2011. Spearman's correlation coefficient between beech mast index and tawny owl breeding success was ρ=0.77 (P=0.04). nd = no data available.

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

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

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

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

Abundance of small rodents

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

The numbers of ringed nestling buzzards in the Gooi area over the years 2005-2011 are shown in table 1, as well as the numbers of fledged tawny owls. G. de Graaff (in Wijsman et al. 2010) confirmed that 2005 was a productive year for tawny owls in the Veluwe area, while in 2006 only a few young owls left the nest. In the winter of 2008/2009 there were practically no acorns or beech nuts in the terrains he studies and this was followed by an unproductive owl year in 2009.

Litter size

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

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

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

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

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

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

*After correction for the leap year.

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

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

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

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

Date of birth

The mean date of birth, the spread in birth dates and the numbers of litters were assessed for the years 2008-2011, together with an indication of the abundance of small rodents in the relevant spring (table 4). In the poor rodent springs of 2009 and 2011, the birth of marten kittens was about one week later than in the peak rodent springs of 2008 and 2010. The two sets of birth dates differ significantly (figure 3; ANOVA, $F_{1,85} = 10.157$, $P<0.001$).

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

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

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

Change to passerine predation

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

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

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

Discussion

Mast production

Data of beech mast production, density of wood mouse holes, litter size and the (inverted) percentages of predated nest boxes in the forestry Kootwijk show that the fluctuations in pine marten litter size correlate closely to those of mast production in the area and wood mouse abundance (figure 2). This can be considered a causal relationship, stemming from periodicity in mast production. Oak mast was at its lowest in the years when beech mast was virtually absent (table 1). Studies in the Białowieża National Park, Poland, tend to stress the importance of acorns, but that is only because the beech does not occur in that area.

Small rodent abundance

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

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

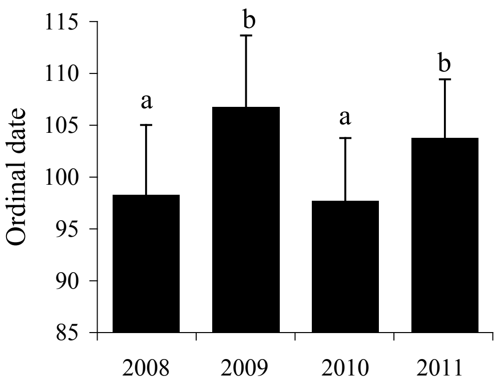

Figure 3. Date of birth (expressed as ordinal date) of pine martens in 2008-2011. Differences between 2008 + 2010 (a) and 2009 + 2011 (b) were tested using ANOVA, followed by Tukey's post hoc test ($F_{1,85}$=10.157, *P*<0.001).

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

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

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

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

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

Marten litter size

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

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

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

Mead (1994) only mentions the influence of a seasonal increase in the duration of daylight in spring as determining blastocyst implantation. However, Douglas & Strickland (1987), referring to the fisher (*Martes pennanti*), speak of successful reproduction depending upon the condition of the females. A poor food supply (of the main prey) may result in little or no production of young.

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

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

Date of birth

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

It is interesting that some individuals seem genetically determined to give birth earlier, or later, than others (table 5). This can be confirmed by Kleef's data. Kleef's date of birth has carefully been determined as the day on which the female remains in the nest hole for 24 hours or more (Kleef & Tydeman 2009), and is accordingly very precise. Our qualitative findings were that litters of five and births in March only occurred in rodent peak years. We only studied a small number of individual females, but our findings are supported by Kleef (unpublished results), who studied two females around Veenhuizen over five years. One was consistenly three weeks ahead of the other with the litter (with one case of a small overlap). Four others, in the same region in Drenthe, consistently gave birth over 3, 4, even 7 years in a middle period compared with the Veenhuizen situation. The consistent timing of parturition among individual females in consecutive years seems to point to the influence of the mother's condition at the time of the implantation process rather than on embryo development, in view of the latter's more complex, random traits.

Alternative prey

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

Conclusions

Autumnal shortage of mast leads to a collapse in small rodents in winter time, which weakens the condition of marten females in February, the season when the foetus starts to develop. When this occurs the foetus develops later than usual and with reduced effectiveness of implantation in the uterus. This causal sequence provides an explanation for the delayed implantation as it combines mating in an energetically favourable season (summer) with the opportunity of reproductive success more than a half year later, at least in favourable years. Finally, even late in spring the shortage of rodent food leads to more birds being taken as prey.

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

Acknowledgements: In relation to marten nests, I wish to thank all the colleagues observers who counted kittens: Bram Achterberg, Chris Achterberg, Ruud van den Akker, Harry van Diepen, Vilmar Dijkstra, Ben van den Horn, Robert Keizer, Olga van der Klis, Mark Ottens, Daniel Tuitert, for their diligent efforts and enthusiasm. Particular thanks go to Bram Achterberg who by now has obtained similar results in his own study terrain. Jan ten Böhmer, Wim Bomhof, Wilco Busstra, Margriet Hartman, Harry Hees, Tim Hofmeester, Rick van Kesteren, Dick Klees, Peter van der Leer, René van Lopik, Hans Teunissen, all assisted by finding nests. Special dispensation of the Flora and Fauna Law was kindly granted to the author by the Ministry of Agriculture, Nature Conservation and Food Quality, no. FF/75A/2009/013. All the owners of woodlands who were approached cooperated. For writing the paper, I am grateful in the first place to Rob Bijlsma for taking an interest and discussing data on mice and mast; next to Jacob van Olst for paving the way to cooperation and for moral support. Koen Van Den Berge, Sim Broekhuizen, Hans Kleef, Erwin van Maanen and Jasja Dekker gave helpful and expert comments on the paper. Furthermore I am indebted to Jasja Dekker for statistical advice and digital support; to Hans Kleef and Florian Bijmold for moral support as well as many a discussion and to Hans also for being the first to see the link between rodent periodicity and marten behaviour and providing data on individual females. I thank Wildbeheer Veluwe and G.J. Spek for the quantitive data on mast; Hanneke Sevink for data on ringed young buzzards in the Gooi area; Ronald Beskers for data on fledged owls, on tits in nest boxes in the Gooi area, and for technical advice; G. de Graaff for data on tawny owls around Kootwijk; Aart Mulder and Jim van Laar for data on nest success in nest boxes on the Veluwe; Johan Thissen for moral support.

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Samenvatting

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

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

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

Received: 11 January 2012
Accepted: 12 April 2012