Mast, mice and pine marten (*Martes martes*): the pine marten's reproductive response to wood mouse (*Apodemus sylvaticus*) fluctuations in the Netherlands

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Abstract: Mast production of beech (*Fagus sylvatica*) and common oak (*Quercus robur*) have been found to be synchronous, with annually alternating patterns of high and low production between 1993 and 2013. We found this to be the case in the Netherlands where the fluctuations in the Veluwe and the neighbouring central areas of the country were the same as in Drenthe, in the north of the country. Wood mice (*Apodemus sylvaticus*) show an immediate and high numerical winter response following an autumn of high mast production, and they are a main source of prey for pine marten. Our study, of a total of 372 litters of pine martens (*Martes martes*), found that pine martens responded to years of peak wood mouse abundance with significant larger litters, as a result of relatively higher numbers of litters with four and five kittens. Their litters were also born about one week later in years of low wood mouse numbers. The female pine marten seems to adapt different hunting behaviour during pre-weaning according to the density of wood mouse. In years of low wood mouse abundance the duration of females' hunting bouts are longer than in years of high wood mouse densities.

Keywords: pine marten, *Martes martes*, litter size, mast years, wood mouse dynamics.

Introduction

Fluctuations in mast production of deciduous trees seems to be coordinated in northwestern Europe (Övergaard 2007). In the central Netherlands the mast production of common oak (*Quercus robur*) and beech (*Fagus sylvatica*) dips every two or three years. This is followed by a decline in wood mouse (*Apodemus sylvaticus*) populations (Wijsman 2012). Interactions between mast production, small rodent abundance and the responses of their predators have been widely investigated (Ostfeld et al. 1996, McShea 2000, Zalewski 2004, Jensen et al. 2012, Selva et al. 2012, Wijsman 2012).

In a small country, such as the Netherlands, it can be assumed that fluctuations in mast production will follow a similar pattern nationwide. As such, this present paper investigates pine marten (*Martes martes*) data from the northern provinces of Friesland and Drenthe over the period 1993-2014. This data was collected by the first author and is combined with data from Wijsman (2012), the latter (from the central provinces) extended by three more seasons. The purpose of this study is to establish correlations and the strength of relations between wood mouse abundance (dependent on mast production) and the functional responses of pine marten, using a combined dataset of two geographically separate study areas in the Netherlands. On the supposition that low wood mouse abundance during the pine martens' lactating period might affect the female's hunting effort and possibly reduce the chances of kitten survival, the hunting response of lactating females at two levels of wood mouse abundance was also investigated.

Material and methods

Study area

Over the recent years the distribution of the pine marten in the Netherlands appears to have extended (Broekhuizen et al. 2015). Overall, however, the area mapped in Wijsman (2012) and the northern provinces are the core areas of Dutch pine marten presence (figure 1).

The study areas in the central part of the Netherlands are characterised by relatively poor and acidic sandy soils. Beech (*Fagus sylvatica*), common oaks (*Quercus robur*) and American oaks (*Quercus rubra*) are widespread, interspersed with coniferous plantations and heathland (Wijsman 2012). The northern study area the Drents-Friese Wold and its surroundings, on the border of Friesland and Groningen, consists of woodland that is about 60 years old on diluvial sands, again relatively poor in nutrients. Conifers abound, but deciduous trees, including beech and oak (*Quercus* sp.) also cover a considerable surface. These woodlands are widely spaced apart, separated by flat peat land and cultivated land (Kleef & Tydeman 2009).

Mast

Seed production of oaks and beeches in the Veluwe has been monitored by G.J. Spek of the *Vereniging Wildbeheer Veluwe* and in Drenthe by R.G. Bijlsma (figure 1). The Veluwe data cover the total mast production of beech and oak from 1990 to 2014, expressed in kilogrammes x 10^6 . Bijlsma's data are based on seed counts of beech and oak over the period 1993 to 2013, expressed in index classes of 1 to 5 for each species.

Figure 1. Core areas of pine marten presence in the Netherlands. A=Utrechtse Heuvelrug; B=Veluwe; C=Salland; D=Drenthe.

Wood mouse

Wood mouse abundance in Drenthe was sampled monthly by R.G. Bijlsma by counting active burrows in three plots of 10x10 m, data which was made available for the present study. Live trap sampling and nocturnal observations in the plots revealed bank voles (*Myodes glareolus*) to occur only occasionally. Accordingly these burrows are considered to be those of wood mice alone. Densities are expressed as the average number of active burrows per plot. We compare wood mouse abundance in winter to mast production from the preceding autumn.

Pine marten

Pine marten reproduction was assessed in

Table 1. Total mast production in the Veluwe (kg x 10^6), beech and oak mast production in Drenthe (index 0-10), wood mouse density (mean), pine marten litter size (mean) and date of birth (day number). Number of observations in brackets.

	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
Total mast*	9.2	3.6	7.8	5.0	2.8	4.3	1.9	6.0		
Beech / oak mast*	10	2	7	6	3	3	3	6	0	6
Wood mouse	5.8	0	1.6	2.7	0	4.6	0	3.6	0	3.1
Litter size	2.92 (37)	2.43 (30)	2.44 (32)	2.88 (43)	2.60 (40)	2.98 (46)	2.74 (35)	2.86 (36)	2.52 (42)	2.97 (31)
Date of birth				96.3 (24)	104.5 (32)	99.1 (37)	103.9 (29)	95.3 (31)	104.4 (40)	95.5 (28)

* preceding year

terms of litter size and the timing of litter production between 2005 and 2014 for nests in the Veluwe and 2008-2014 for those in the Drents-Friese Wold and surrounding woodlands. A total of 372 litters have been studied. Kittens were counted and aged, at an early stage whenever possible, to exclude early mortalities.

The age of kittens was estimated from overall habitus paying attention to their colour, the development of fur and throat patch and whether or not the eyes were open. The date of birth was expressed numerically as Julian date, accounting for leap years.

From the den activity patterns of the lactating female the average number of hours outside the natal den during the kitten's preweaning age (< 7 weeks), was calculated using Kleef & Tydeman's methodology (2009) of taking temperature recordings inside the den. The differences between years of high (group A: 1999, 2001, 2003, 2005, 2007) and low wood mouse abundance (group B: 1998, 2000, 2002 and 2006) were compared.

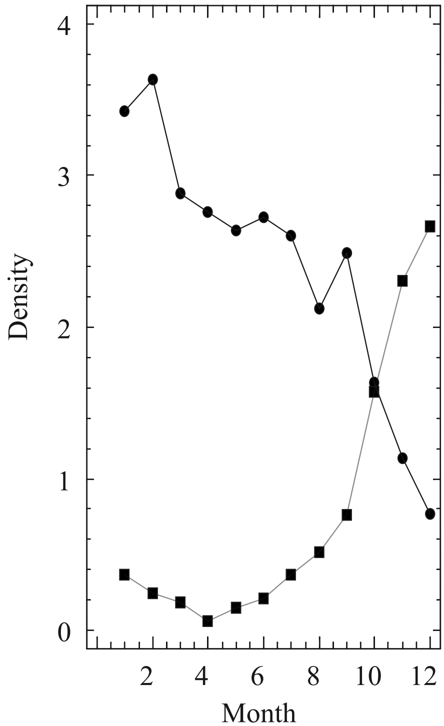

Figure 2. Seasonal variation of wood mouse density (mean) in 11 years of peak (circle) and 11 years of low density (square).

Statistical analyses

Relations between variables were tested by Pearson correlation and analysed by regression analysis when causality was suspected. Pearson correlation can be considered to be insensitive to non-normality and is to be preferred when using numeric variables (McDonald 2014).

The grouping of nominal variables was performed using Ward's method of cluster analysis and the results were subsequently tested for similarity using one-way analysis of variance (ANOVA) or two-sided *T*-tests when the

Table 2. Mean numbers and statistical differences for wood mouse density, pine marten litter size and date of birth in years of peak and low wood mouse density. Number of observations in brackets.

	Period	Peak	Low	*P*	Test
Wood mouse	1993-2014	2.21 (369)	0.78 (396)	0.0000	Mann-Whitney
Litter size	2005-2014	2.85 (225)	2.58 (147)	0.0054	ANOVA
Date of birth	2008-2014	96.7 (120)	104.3 (101)	0.0000	*T* - test

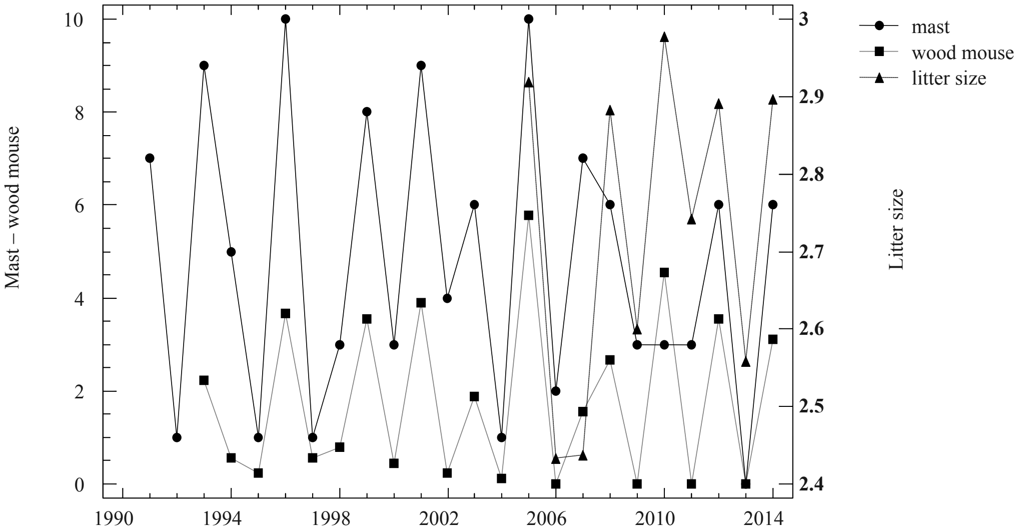

Figure 3. Beech/oak mast index (circle) in Drenthe, mean wood mouse density (square) and mean pine marten litter size (triangle) in the period 1991–2014. The mast index relates to the preceding year.

parametric conditions came close to normality and equality of variances. If far from these conditions a nonparametric Mann-Whitney signed rank test was used.

Results

The relationship between mast production and wood mouse abundance

Wood mouse densities increased throughout the year to reach a maximum number in winter and early spring. This increase was more pronounced in years of high numbers (see figure 2 and table 1). The abundance of wood mouse in late winter might be an important factor in the reproductive cycle of pine marten females because the blastocysts are on the verge of being implanted in the uterus wall. This process depends upon food availability and other factors such as photoperiod. According to Stubbe (1993, quoted in Stier 2012) the period of implantation ranges from mid-January to mid-March throughout the pine marten's geographical distribution. As such we chose to calculate annual densities of wood mouse for the period of January-March and compared these figures with the combined beech and oak mast production in Drenthe in the preceding autumn (see figure 3).

There was a significant correlation in beech and oak mast production in Veluwe and Drenthe (Pearson correlation R=0.6003, *P*=0.0051, resp. R=0.5725, *P*=0.0035). The total crop of beech and oak seeds was compared to the combined indices of beech and oak mast in the Drents-Friese Wold in order to look for spa-

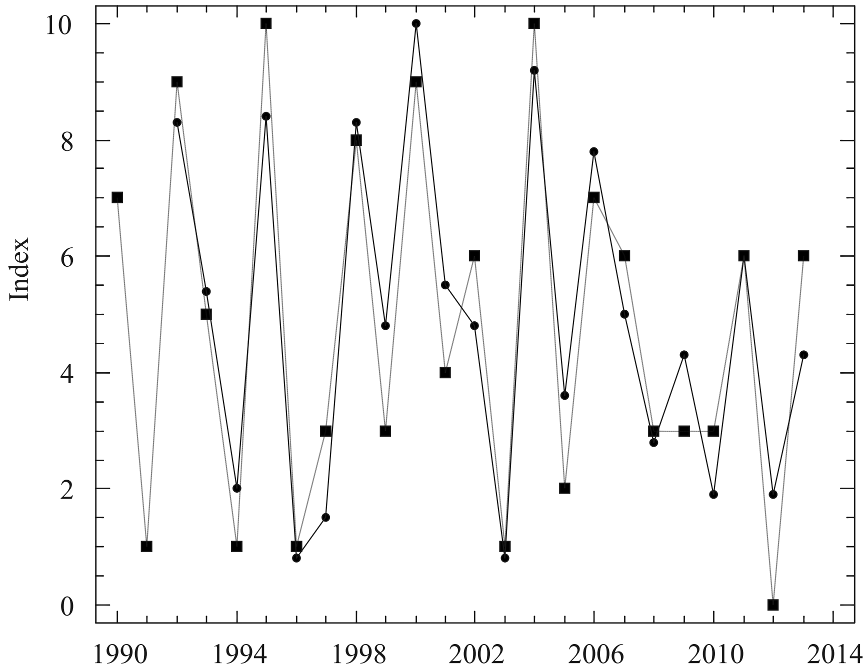

Figure 4. Total mast crop in the central area (circle) and beech/oak mast in the northern area of the Netherlands (square).

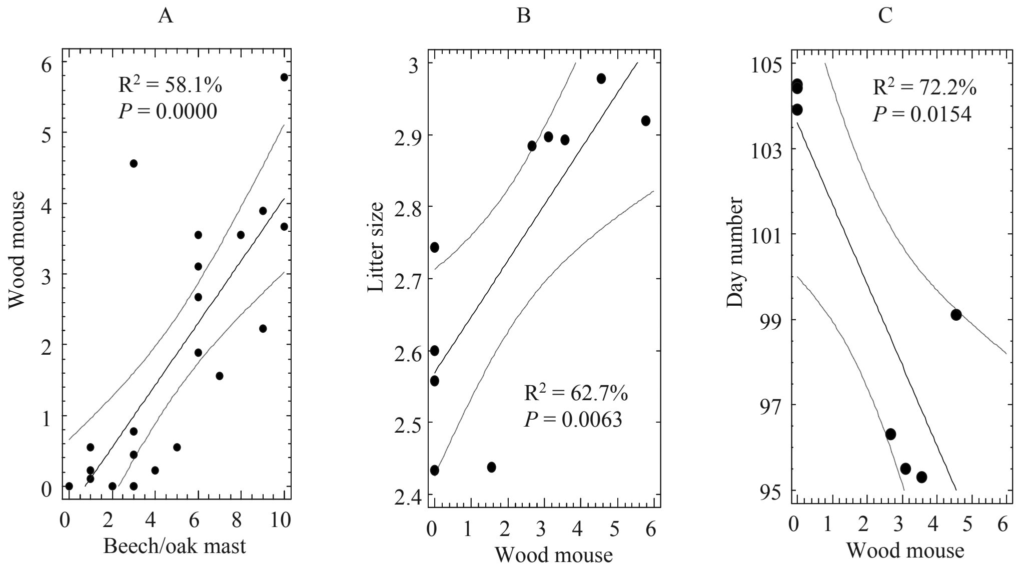

Figure 5. A: beech/oak mast (index) related to mean wood mouse density. B: mean wood mouse density related to mean pine marten litter size. C: mean wood mouse density related to pine marten mean date of birth, expressed as day numbers.

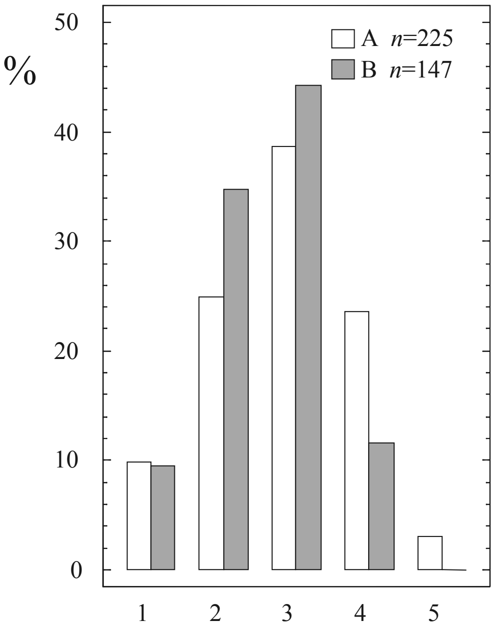

Figure 6. Relative distribution of pine marten litter size (%) in years of peak (A) and low (B) wood mouse density.

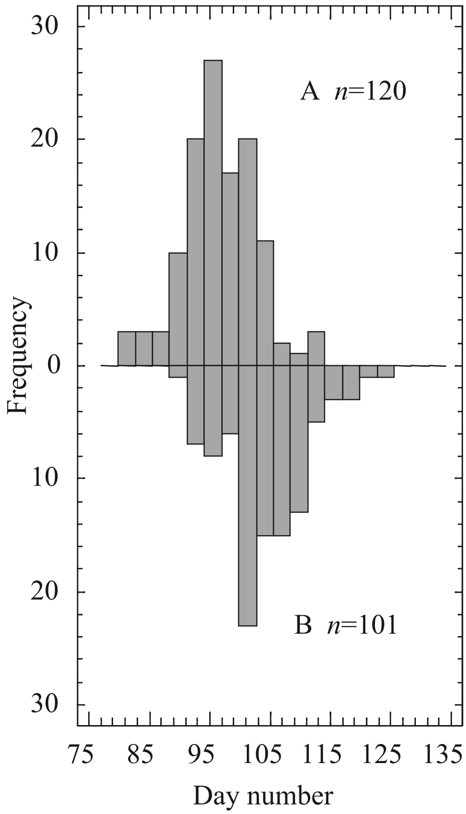

Figure 7. Frequency distribution of date of birth of pine marten litters (by day number) in years of peak (A) and low (B) wood mouse densities.

tial similarities in annual mast fluctuations. Masting in the two areas of the Netherlands was highly synchronised (Pearson correlation R=0.9259; *P*<0.0001) (see figure 4 and table 1).

The annual variations in masting and wood mouse abundance were also highly correlated (Pearson correlation R=0.7625; *P*<0.0001); 58% of the variation in wood mouse density was explained by mast variations (*P*<0.0001, figure 5A). Beech mast and oak mast were separately also significantly correlated with wood mouse numbers (Pearson correlation R=0.7931, *P*<0.0001 and R=0.5561, *P*=0.0072 respectively).

Wood mouse numbers and pine marten litter size

Apart from some minor deviations, wood mouse numbers showed a regular alternating pattern of high and low indices (figure 3). As such we grouped the years of high and low densities. The average index in wood mouse peak years (2.21 ± 0.10 SE) was almost three times higher than in low years (0.78 ± 0.07 SE), the difference being significant (Mann-Whitney, *P*<0.0001; table 2). The litter size of pine martens showed a similar pattern with larger litters in peak years of wood mouse (2.85 ± 0.07 SE) and smaller ones in years of low wood mouse abundance (2.58 ± 0.07 SE). Again, the difference is significant (ANOVA, *P*=0.0054; table 2). It was notable that litters of four and five kittens were more frequent in peak years of wood mouse (figure 6). Wood mouse abundance accounted for 63% of the variation in pine marten litter size (*P*=0.0063, figure 5B).

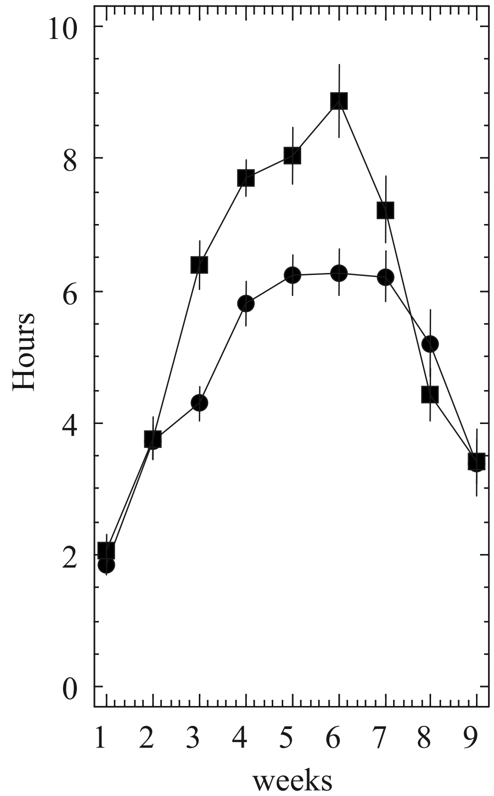

Figure 8. Time (hours) spent outside the natal den by the female pine marten related to the age (weeks) of the kittens in peak (circle) and low (square) wood mouse years.

The abundance of wood mouse and the date of birth of pine marten litters

The dates of birth of pine marten ranged between the second half of March and the first week of May, peaking in the second week of April. Birth dates in years of peak wood mouse numbers ranged from day 80 to day 112, but was later in years of low wood mouse numbers (days 91 to 125; figure 7). The average birth date in wood mouse peak years (day number 96.7 ± 0.55 SE) was about one week earlier than in years of low wood mouse numbers (day number 104.3 ± 0.68 SE) (*T*-test, $P<0.0001$, table 2). Wood mouse abundance accounted for 72% of the variation in these birth dates ($P=0.0154$, figure 5C).

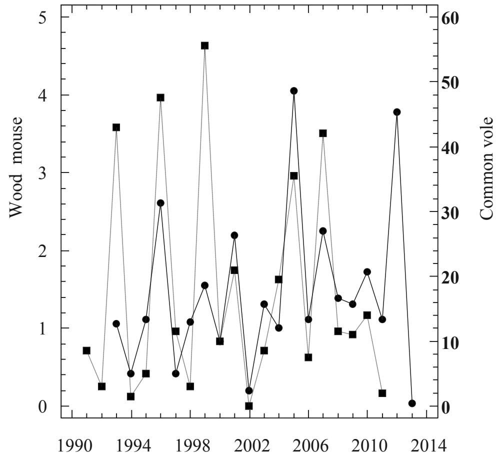

Figure 9. Mean densities of wood mouse (circle) and common vole (square) in the period 1991-2013.

The abundance of wood mouse and the activities of female pine martens

In years of low wood mouse densities the females' hunting time was on average one hour longer than in years of high wood mouse numbers (6.45 h ± 0.22 SE, resp. 4.99 h ± 0.14 SE) (*T*-test, $P<0.0001$). The time spent outside the den was strongly correlated with the kittens' age ($P=0.0033$; figure 8), increasing during lactation to about two and a half hours when the kittens reached 6 weeks of age, after which it declined towards the start of weaning.

Discussion and conclusions

Mast and mice

In a review of 15 studies on feeding ecology, Clevenger (1994) reported wood mice (*Apodemus* sp.), voles (*Microtus* sp.) and bank voles (*Myodes* sp.) to be the principal food of Eurasian pine martens. The representation of these species in the marten's diet varies with geographical region and prey density

(Jędrzejewski et al. 1993, Pucek et al. 1993, Helldin & Lindstrom 1995, Helldin 1999, Zalewski 2004, Rosellini et al. 2008). The densities of small rodents in winter and spring respond strongly to mast production (Jensen et al. 2012).

In the Netherlands bumper years of oak and beech are correlated but as oak trees are more common than beech trees, acorns account for the majority of the mast crop. The classic publication of the Białowieża Forest Group (Pucek et al. 1993) involves a 33-year long study of the population dynamics of small rodents. As there are no beech trees in Białowieża this may limit the relevance of this study to the Netherlands.

Data from Perdeck et al. (2000) and Hilton & Packham (2003) shows that the general biennial pattern of the fluctuation in beech mast production can be found in the Netherlands, England, Germany, Denmark and Sweden. A more or less synchronous production of beech mast production has also been observed over a wide area of northeastern Europe (Pucek et al. (1993) and the authors quoted by Perdeck et al. (2000)). In this light the correlation found in different parts of a small country such as the Netherlands is not surprising. Beech nuts are available as food for small mammals beyond the end of winter as witnessed by the many seedlings in May after a peak mast year (cf. Gurnell 1993).

The fluctuations in wood mouse numbers may be ascribed to fluctuations in mast production. Interestingly, although microtine species may occupy different habitats, their densities often show synchronous fluctuations. A study by Tkadlec et al. (2011) confirmed significant correlation in the annual fluctuations of common vole (*Microtus arvalis*) and wood mouse (figure 9, R=0,5966, P=0.0070). According to Zalewsky (2007), Elmeros et al. (2008) and Balestrieri (2011), bank voles are the more important prey item for pine martens. In general however the pine marten is an opportunistic feeder and can easily switch to different prey items according to the season, geographical range and abundance of prey (Jędrzejewski et al. 1993). Live trapping carried out around the 1st of March in 2013 (after a year of low mast production), caught 15 wood mice, while trapping the following year, at around the same time caught 115 wood mice, a factoral difference of 7.6 (Wijsman, unpublished results). Only a small fraction of the animals trapped in this study were voles. In another Dutch situation, the bank vole was also only occasionally found (Dijkstra 2013), indicating the wood mouse to be the main available prey item. In years with a high mast crop the wood mouse female produces about four litters with an average of five new born in each, which become reproductive after about 65 to 71 days (Bijlsma 2012). This high reproduction rate immediately after high autumn mast production results in peak wood mouse populations in winter and spring into the summer, producing a major food source that is easily available to the pine marten during a period that is of vital importance to successful reproduction.

Martens

Numerical responses of mustelids following cycles in microtine numbers have been documented in many studies (e.g. Erlinge 1981, Helldin 1999, Simon et al. 1999, Zalewski & Jędrzejewski 2006, Jensen et al. 2012). However these results do not always appear to be consistent and may sometimes reflect trap vulnerability more than actual numbers. Pine marten's longevity and territorial food behaviour result in a low potential increase rate and a slow numerical reaction to annual fluctuations in microtine numbers (Helldin & Lindstrom 1995, Helldin 1999). Our study has focused on the functional response of pine martens in terms of litter size, date of birth (Wijsman 2012), and the female's daily activity pattern. Pine martens in the Netherlands produce litters averaging 2.74 (this study). In years of peak abundance of wood mice more litters of 4-5 kittens were produced, increasing the average litter size compared to years of low wood mouse abundance, suggesting that reproduction might be influenced by food availability. Low populations of rodents result in smaller litters (Simon et al. 1999) possibly due to a higher mortality of embryos and nestlings (King et al. 2003 for the stoat, *Mustela erminea*, and Kirkpatrick 1988 (quoted by Frost & Krohn 1997) for the fisher, *Martes pennanti*). However, pine martens may compensate for there being fewer small rodents by switching to alternative prey, such as birds (Thompson & Colgan 1990, Jędrzejewski et al. 1993, Wijsman 2012). This might explain the small difference of litter sizes between years of peak and low wood mouse numbers. There is currently little data available on the survival and recruitment of young born pine martens in years with high and low mice numbers. Larger litters will only contribute to reproductive success if the kittens survive to be recruited into the population and to reach sexual maturity (Frost & Krohn 1997).

The date of birth was also influenced by wood mouse numbers. In peak wood mouse years the date of birth was about a week earlier, indicating advanced implantation. Early implantation may relate to the female pine marten being in good physical condition in years of food abundance during the relevant photoperiod. While the photoperiod lasts for a timescale of several months, the pine marten's body condition determines implantation on a timescale of days. Early birth gives the kittens longer to grow and to gain experience after reaching independence before winter starts as has been found among badgers (Woodroffe 2009).

Food availability may affect the female's hunting success and her capacity to meet the energetic demands of lactation, especially in the pre-weaning period when the kittens are less than seven weeks old. In years of low wood mouse availability, the average time females spent outside the den during the pre-weaning period was about 28% longer than in years of high abundance (Kleef & Tydeman 2009), increasing to 41% by the time kittens were near weaning. However the total proportion of time spent outside the natal den appears to be equal among years of peak and low wood mouse densities (about 29%), indicating that extended hunting bouts force the female to hunt less frequently.

Longer hunting bouts may provide a sufficient success rate under low food conditions as the pine marten hunts over a larger radius of action. Changing her hunting behaviour in this way especially during pre-weaning only stresses the high demand of sufficient food supply during lactation (Zielinski 2000, Kruuk 2002). A small litter may then be helpful.

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Samenvatting

Mast in relatie tot muizen en de voortplantingsrespons van de boommarter (*Martes martes*) op aantalsfluctuaties van de bosmuis (*Apodemus sylvaticus*) in Nederland

De mastdynamiek van eik en beuk vertoont niet alleen onderling een parallel verloop maar ook regionaal verlopen de fluctuaties synchroon. Jaren met een hoge productie van mast werden gevolgd door een hoge dichtheid van bosmuizen in de daaropvolgende winter en voorjaar. Bij 372 boommarternesten werd in de periode 2005 tot 2014 het aantal jongen geteld en het tijdstip van de geboorte werd geschat. In jaren met hoge bosmuisdichheid werden er bij de boommarter meer jongen geboren dan in jaren met lage dichtheid. In de jaren met lage dichtheid vond de geboorte ongeveer een week later plaats en het boommartermoertje moest langer op jacht gedurende de zoogperiode.

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