Highlights

1) Most conservation projects failed so far in conserving the Common hamster Cricetus cricetus

2 The effects of litter size and timing of harvest on population growth and persistence were evaluated.

3) Farming practices have been intensified and have become an important threat to this species.

4) The timing of harvest determines the total reproductive output of a population.

5) Conservation projects should focus on delaying harvest of cereals until September.

Modelling population dynamics of the Common hamster (*Cricetus cricetus*): timing of harvest as a critical aspect in the conservation of a highly endangered rodent.

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Abstract

The Common hamster *Cricetus cricetus* was an agricultural pest in large parts of Europe less than 50 years ago. Currently the species is highly threatened or locally extinct and acknowledged as an important and even iconic species for nature conservation in farmland areas in Western Europe. The species was listed in the European Habitats Directive in 1992 to prevent a further decline, but the Common hamster is still declining in most parts of its European range despite large conservation efforts. Only a few local conservation successes have been reported so far. These disappointing conservation results raise the question: why is it so difficult to conserve this former pest species?

Farming practices have been intensified in Europe and this has resulted in a more efficient way of harvesting cereals in combination with a strong reduction of spring sown cereals in favour of winter sown cereals. It is possible that these changes have become an important threat for survival of populations of this species. We developed both a deterministic and a stochastic population model for a better understanding of the current way of harvesting on the population ecology of this species and evaluated the effects of using different litter sizes on population growth and persistence. Our results suggest that under the current efficient harvest of cereals in Europe, it is highly unlikely that females of the Common hamster produce enough offspring for a sustainable population. Conservation projects for this species should focus on creating cereal fields which are not harvested until the end of August, as lack of cover is a major cause of high predation rates.

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1. Introduction

The Common hamster *Cricetus cricetus*, a medium sized rodent, inhabits agricultural landscapes throughout Europe and was considered to be a pest by the farming community for generations. However, the species has declined dramatically in range and numbers during the second half of the 20th century and is nearly extinct in several Western European countries as a result of changes in the agriculture landscape and farming practices (Nechay 2000; Weinhold 2013; Meinig *et al.* 2014). Nowadays the species is the subject of many national agri-environmental schemes and nature conservation projects (Orbicon 2008). Surprisingly, most of these initiatives have not stopped the decline of Common hamster populations in Europe (Weinhold 2013), although a reintroduction project in the Netherlands has reported short-term successes when having large areas with adaptive agricultural management (La Haye *et al.* 2010; Kuiters *et al. 2010*). These overall results suggest that, despite more than twenty years of Common hamster conservation and research, we are not able to pinpoint the cause of this decline so far and act accordingly. One of the reasons is that the basic population ecology of the species is not fully understood (Leirs 2003) causing current conservation measures to be inadequate (La Haye *et al.* 2011a).

The Common hamster originally inhabited steppe-like habitats, but the species has adapted to a life in agricultural landscapes in the past (Nechay 2000). Common hamsters prefer arable fields on loess and loamy soils with crops like cereals (with the exception of maize) and alfalfa, which provide food, cover (protection against detection by predators) and an opportunity to construct a burrow. Today, the adaptive capacity of the Common hamster to cope with modern agriculture seems to have become insufficient and the species is rapidly declining (Nechay 2000; Weinhold 2013). As cereals are the most important crop for Common hamsters in Europe (Nechay 2000), our study has focused on the changes in cereals, although cultivation of other suitable crops as alfalfa may have changed as well. In the last decades, farming practices have been intensified in Europe (Brickle & Harper 2002) and this has, for example, resulted in a strong reduction of spring sown cereals in favour of winter sown cereals

(Butler *et al.* 2007) and in a more efficient way of harvesting cereals by using combine harvesters (Hartmann – local farmer- pers. comm.; Bieleman 1992). Several studies have shown the detrimental effect of harvest on the faith of individual Common hamsters by increasing their chance of getting predated (Müskens *et al.* 2005; Kupfernagel 2007; Villemey *et al.* 2013). It is possible that the proportional decrease of spring sown cereals and the introduction of combine harvesters has become an important threat for populations of Common hamsters as both changes limit the period of cover during the breeding season, increasing the risk of predation and therefore limit the possibility for a successful reproduction during an important part of the breeding season (Kayser 2002; Kupfernagel 2007; Out *et al.* 2011a). Winter sown cereals are harvested a few weeks earlier than spring sown cereals (Brickle & Harper 2002) and combine harvesters substantially limit the period of harvest in large areas to a few days, whereas manual harvest takes several weeks (Bieleman 1992). However, the negative effect of a shortened breeding period on populations and population sustainability is underexposed in Common hamster studies (Ulbrich & Kayser 2004; La Haye *et al.* 2011a).

We designed both a deterministic and a stochastic population model for the Common hamster and analysed the effects of different moments of cereal harvest, differences in litter size and the occurrence of occasional "optimal" years (with an earlier start of the reproductive season) on the population dynamics of the species. Litter size was varied for several reasons. The study of La Haye *et al.* (2012) has shown that genetic deterioration in fragmented populations of the Common hamster can result in a 30% reduction of mean litter sizes (from 7 to 5). Second, agricultural intensification might have caused a deterioration of the habitat quality, which can result in a reduction of mean litter sizes. By increasing the knowledge of the population ecology of the Common hamster we hope to contribute to the improvement and effectiveness of Common hamster conservation projects and measures..

2 Material and method

2.1 Common hamster life-cycle

Common hamsters are nocturnal, solitary living rodents, which have an underground hibernation period from the end of October until the beginning of April (Nechay 2000; Schmelzer & Millesi 2008). The species is polygamous and litters are born after a pregnancy of ca. 19 days (Nechay 2000). The first litters are observed from the end of May until the end of June and are typically followed by a second wave of litters later in mid-summer, in July-August (Franceschini-Zink & Millesi 2008). Reproduction earlier in the season, from March onwards, has been reported during a period of mass-outbreaks in 1971-1973 in the Czech republic and Slovakia, but seems exceptional (Grulich 1986). Common hamsters start their preparation for hibernation from the end of August, by terminating further reproduction and by hoarding food (seeds, rhizomes) in their burrow (Monecke & Wollnik 2005; Hufnagl, Franceschini-Zink & Millesi 2011). Depending on the agricultural environment the hamster occupies, harvest will interrupt the reproduction or the preparation for hibernation, causing an increased mortality (as a result of the reduction of cover) and forcing the hamster to move or to start hibernation earlier (La Haye 2008; La Haye *et al.* 2011b). Only few individuals live more than 1 year, with females having a better yearly survival (30%) than males (<10%) (Losík *et al.* 2007; Kuiters *et al.* 2010). Figure 1 shows a simplified life cycle of the Common hamster.

2.2 Model construction

We constructed time-based numerical population models, using the software STELLA 9.0.1.V (isee Systems, inc.), to simulate Common hamster population dynamics, using the survival and reproduction parameters described below (also see appendix 1). Every simulation starts with 50 adult females on day 1 (1st of January of Year 1). This cohort 'flows' through the model with time steps of 1 day. Each day, the individuals in a cohort are exposed to 'a daily mortality rate'. On specific days, the cohort can be exposed to 'produced births' and 'harvest'. In the case of births, a certain number of juveniles was added to the model as a new cohort at a specific time. Harvest was modelled as an extra 40% mortality (La Haye *et al.* 2011b) of adult females on top of the daily survival (Table 1) and prevented further litters by females exposed to harvest. Model scenarios were run for 50 years and model output was the daily population size throughout this period.

Only the number of females was calculated in the model as adult males have no distinct impact on population development in this polygamous species. Obviously, this is only true if the number of males is large enough to fertilise all sexually mature females present, which we assumed to be the case. Each day, a given cohort is assigned to one of three age classes (juveniles, sub-adults, adults) depending on their age with different values of demographic parameters applicable to each class. Juveniles become sub-adults and are able to reproduce 42 days after their day of birth. Sub-adults become adults on 1st of January of the subsequent year. Both sub-adults and adults can reproduce but only the adults experience additional mortality at the time of harvest, as the effect of harvest on the survival of sub-adults is already incorporated in the 40% chance of becoming sub-adult after the juvenile phase (Gorecki 1977 and see below). The number of living sub-adult and adult females at the end of a year, after 365 days, is used as the input of the population size for the next year.

At first, a deterministic model was developed allowing to simulate the main population trends with different litter sizes of 5, 6 or 7 and different harvest data. We used the minimum number of adults alive per year for calculating annual growth rates ($\lambda = N_{t+1}/N_t$ with N_t = minimum number of hamsters in year t), Graphs representing population development using different harvest data were constructed. The annual minimum number of adults is relevant as it represents a population during its most critical period. Populations went extinct, by definition, when the number of adult females was smaller than one.

The deterministic model was expanded by adding two stochastic components in the model: variation in litter size and inter-annual variation in the start of the reproductive period. Litter size is influenced by genetics and possibly by habitat quality and therefore mean litter size was drawn from a normal distribution with an average of 5, 6 or 7 and a standard deviation of 1.25 (La Haye *et al.* 2012). The start of the reproductive period is influenced by weather conditions (Grulich 1986; Hufnagl *et al.* 2011) and we allowed reproduction to start 30 days earlier in on average one out of 10 years, thus allowing females to produce an additional litter in the same season (depending on the timing of harvest). Such ‘optimal years’ also occur in reality with an average frequency of once every 10 years (Nechay 2008). Including more stochastic parameters was not feasible in our opinion, because of the lack of reliable data. Including more stochastic parameters would also have made it more difficult to analyse the effects of harvest and litter size on the population ecology of this species, while the importance of these parameters for population persistence and development had been shown in earlier studies (Out *et al.* 2011a; Harpenslager *et al.* 2011; La Haye *et al.* 2012). The output of the stochastic model analysis was the percentage of populations that went extinct within 50 years based on 500 runs.

2.3 Parameterisation

In the model we used parameter values from wild populations as much as possible. An overview of all parameter values and their references is presented in Appendix 1. Other important data were collected in the period 2002-2012 in a large research and reintroduction project in the Netherlands (Harpenslager *et al.* 2011; Kuiters *et al.* 2010; La Haye *et al.* 2010; Müskens *et al.* 2005; Müskens *et al.* 2011; Out *et al*. 2011a; van Wijk *et al.* 2011), however, only data from wild-born individuals were used as released captive-bred individuals show different behaviour and survival rates (Kuiters *et al.* 2010; Harpenslager *et al.* 2011). The data from the Dutch reintroduction project were collected in areas with a combination of regular and hamster-friendly managed agricultural plots, but (values of) population parameters did not differ among these plots in the period before harvest. The timing of harvest is the crucial difference between plots with or without hamster-friendly management (La Haye *et al.* 2010; Kuiters *et al.* 2010; Out *et al.* 2011a).

The timing of births of litters from adult and sub-adult females of the 1st litter were fixed in the model (given that there was no harvest before these birth dates), although it is known that there is variation in timing of births (Albert 2013). However, detailed data on variation in timing of births under natural conditions is very limited because births take place in underground burrows (Out *et al.* 2011b; Albert 2013). Birth of litters by adult females was set to occur at two moments in normal years: on 14th of June and on the 27th of July and at three moments in 'optimal' years (16 May, 27 June and 10 August) (see appendix 1). Litters by sub-adult females, born in the 1st litter of adults, occurred in normal years on 27th of July and in optimal years on 27th of June and 10th of August. In all scenarios, we assumed that all living adults and sub-adults of the 1st adult litter reproduced. The possibility of reproduction by sub-adults in their year of birth has been debated in the past (Saint Girons *et al.* 1968; Gorecki 1977), but several studies have clearly shown that reproduction by early-born sub-adult, sexual mature, Common hamsters is the rule (Grulich 1986; La Haye & Müskens 2004; Franceschini-Zink & Millesi 2008). We therefore assumed that all living sub-adults females born in the 1st adult litter reproduced in their natal year, because their weight is high enough for giving birth on the 27th of July (La Haye & Müskens 2004; Müskens *et al.* 2011).

Survival of litters in the first three weeks after birth was set on 100%, unless the mother died. To our knowledge no data exist on survival of litters in the wild and the survival rate of litters must be seen as an 'assumed' survival of litters resulting in a certain litter size of 5, 6 or 7: the number of juveniles alive three weeks after birth as derived from La Haye *et al.* (2012). To simulate female numbers in the model, the number of juveniles 5, 6 or 7 was divided by two as there are no indications of a bias in sex ratio in litters of Common hamsters (Gorecki 1977; Grulich 1986). If the mother died in the first three weeks as a result of harvest or by another cause, the complete litter died as well.

Survival rates of adults depend on the season (Losík *et al.* 2007; Kuiters *et al.* 2010). We therefore used different daily survival rates between months, but constant daily survival rates within each month (Table 1). We supposed that juveniles are also affected by harvest since they are unexperienced and therefore more likely to be predated on an arable field without cover (Villemey *et al*. 2013). We modelled survival of juveniles after harvest depending on their age: no survival for juveniles of an age of ≤20 days since they are not yet weaned and thus will die when their mother dies or was forced to emigrate (Müskens *et al.* 2005). Juveniles of 21-31 days experienced a mortality of 50%, juveniles of 32-42 days experienced a mortality of 25% (see Table 2). The survival rates of juveniles were chosen to simulate differences in the impact of harvest on juveniles, as we expect that survival of juveniles after harvest increases at they are older. On the 42th day of their life, surviving juveniles had a 40%

chance of becoming sub-adult in our model (based on Gorecki 1977 who reported an overall 40% rate of sub-adult recruitment). Reproduction by sub-adults was not possible after harvest, similar to adult females. No density-dependent effects were incorporated in the model since we did not aim to determine the maximum carrying capacity or how a hamster population behaves at high densities, we were mainly interested in the effects of different harvesting data. Including a maximum density would not, in our opinion, contribute to the understanding of the mechanisms influencing population development and persistence.

Table 1

Monthly survival rates of wild-born adult females in the Netherlands (data from Dutch reintroduction project, n=184, Kuiters et al. 2010).

Month	Nr of days (d)	Monthly survival rate (s)	Daily mortality rate (1-s^(1/d))
January	31	0.966	0.00112
February	28	0.960	0.00145
March	31	0.919	0.00272
April	30	0.953	0.00161
May	31	0.859	0.00487
June	30	0.827	0.00632
July	31	0.839	0.00562
August	31	0.838	0.00567
September	30	0.910	0.00315
October	31	0.897	0.00348
November	30	0.923	0.00266
December	31	0.972	0.00090

Table 2

Theoretical effects of the timing of harvest on the mortality of juveniles from a specific litter as used in the model. Depending on the age of the juveniles, harvest resulted in a mortality of 100% (age ≤ 20 days), 50% (age 21-31 days), 25% (age 32-42 days) or 0% (age > 42 days).

Timing of harvest	July 8th	July 23th	August 8th	August 23th	September 8th	No harvest
Normal year						
Juvenile mortality 1st adult litter (14 June)	50% (24 days)	25% (39 days)	0% (>42 days)	0% (>42 days)	0% (>42 days)	0% (>42 days)
Juvenile mortality 2nd adult litter & 1st litter sub-adults (27 July)			100% (12 days)	50% (27 days)	0% (>42 days)	0% (>42 days)
Optimal year						
Juvenile mortality 1st adult litter (16 May)	0% (>42 days)	0% (>42 days)	0% (>42 days)	0% (>42 days)	0% (>42 days)	0% (>42 days)

Juvenile mortality 2nd adult litter & 1st litter sub-adults (27 June)	100% (11 days)	50% (26 days)	25% (42 days)	0% (>42 days)	0% (>42 days)	0% (>42 days)
Juvenile mortality 3rd adult litter & 2nd litter sub-adults (10 August)				100% (13 days)	50% (29 days)	0% (>42 days)

2.4 Harvest scenarios

To investigate the effects of different harvesting data, six harvest scenarios were run ranging from an early harvest in July (early harvest), until postponed harvest in September and even a scenario without harvest (Figure 1). Harvest is defined as the moment where the last cereal is removed. Indicative harvest data from cereals in the Netherlands in the period 2010-2014 are presented in Table 3. The different scenarios comprise the variation shown in Table 3. Furthermore we included 2 scenarios 'postponed harvest' and 'no harvest' where agri-environmental schemes could be used in order to delay the harvest. At the same time, all these six scenarios represent historical changes. Because of mechanisation of agriculture, the same cereal varieties harvested under the same climatological circumstances in current times results in a nearly immediate loss of cover, while for example 50-60 years ago, the harvest of these varieties would take 2 to 3 weeks resulting in an extended breeding season, at least on some of the cereal fields. Furthermore, our scenarios also represent the change from summer to winter cereals, as winter cereals are harvested a few weeks earlier.

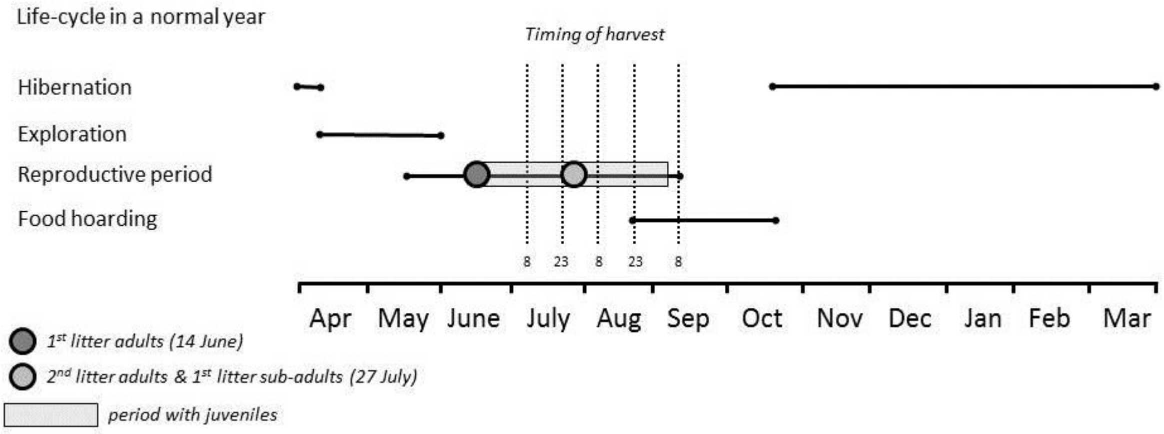

Figure 1a)

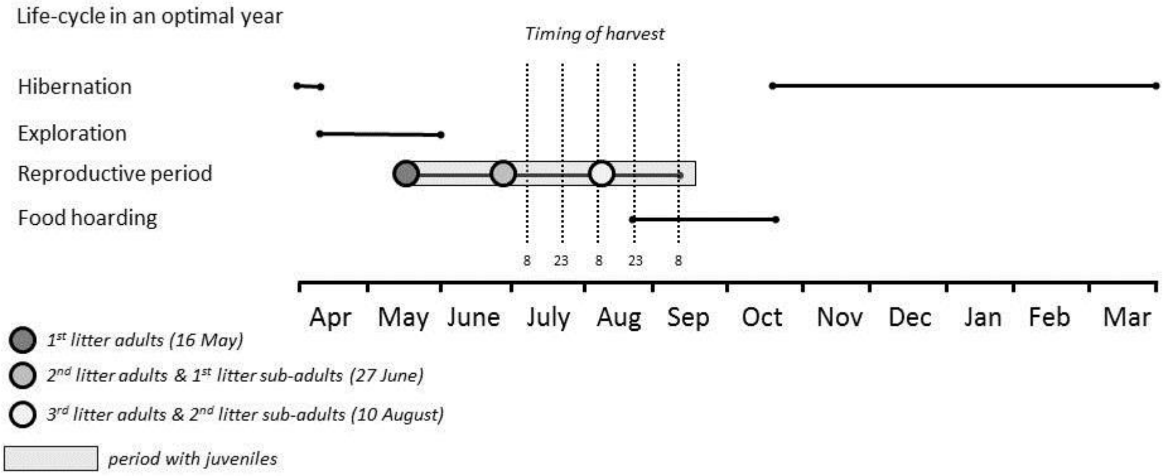

Figure 1b)

Figure 1. The different phases of the Common hamster's yearly life cycle in normal years (top) and "optimal" years (bottom). Harvest takes place on different dates: 8 July = early, 23 July = regular, 8 August = late, 23 August = very late, 8 September = postponed. (a) Adult females' first litter is born on 14 June, the second litter on 27 July. Litters produced by sub-adult, sexually mature, females (born in adult females' 1st litters) are born on the 27 July. (b) Adult females' litters are born at three moments instead of two, 16 May, 27 June and 10 August. Litters produced by sub-adult, sexually mature, females (born in the adult females' 1st litter) are born on 27 June and 10 August.

Table 3

Indicative harvest data of winter sown barley and wheat in the South of the Netherlands in 2010-2014 (data provided by local farmer H. Hartmann).

Year	Barley	Wheat
2010	14th of July	15th of August
2011	9th of August	27th of August
2012	24th of July	14th of August
2013	15th of July	12th of August
2014	4th of July	26th of July

Under all harvest scenarios it is possible for adult females to produce a first litter in June (Figure 1a). The second wave of litters born at the end of July, produced by adult females and sub-adult females (born in adult females' first litter), occurs only when harvest is delayed until August or when harvest is not allowed. The percentage of surviving juveniles depends on different harvest scenarios (see Table 2). Harvest in September and 'no harvest at all' do not affect survival of juveniles of adult females' first nor second litters.

The same six scenarios were also applied to the stochastic model. In optimal years litters are less affected by harvest, as juveniles are older at the moment of harvest (Figure 1b).

3 Results

3.1 Deterministic model

The output of the deterministic model is visualised in figure 2a-2c and summarised in Table 4 for all different harvest scenarios in combination with different litter sizes. The results show that a positive population growth rate is achieved in scenarios with a very late harvest (with litter sizes of 6 or 7), a postponed harvest (all litter sizes) or no harvest (all litter sizes). The populations show a strong decline under scenarios of an early, regular or late harvest. Such harvest regimes result in extinction of the population in just a few years.

An increased litter size had a positive effect on population growth, but this effect is small and timing of harvest is much more important as can be seen in figure 2a-2c: the overall picture is the same for all graphs with large differences between harvest scenarios, but only small differences between litter sizes (Table 4). The main difference between harvest scenarios, with a positive and a negative growth rate is the possibility of successfully raising the second wave of litters born at the end of July. The second wave of litters and juveniles is not, or only partially, affected by harvest under a scenario with a very late, a postponed or no harvest, whereas a successful second wave of litters is impossible under harvest scenarios with an early or regular timing of harvest. These results show that litter size is of less importance compared to the number of successful litters. The most effective way of increasing the number of successful litters in a population is by extending the breeding season through a late harvest, which result in more cover allowing sub-adults to successfully reproduce in their natal year and which increases the survival of second litters of adult females.

Table 4

Population growth rate (λ) and the number of years till extinction under different harvest scenarios and with different litter sizes in the deterministic model (det) and the percentage of surviving populations after 50 years (500 runs) in the stochastic model (sto).

	Litter size 5			Litter size 6			Litter size 7		
Harvest	λ det. model	No. years till extinction	No. pop. 50 years sto. model	λ det. model	No. years till extinction	No. pop. 50 years sto. model	λ det. model	No. years till extinction	No. pop. 50 years sto. model
Early, July 8th	0.35	3	0%	0.38	3	0%	0.41	3	0%
Regular, July 23th	0.43	3	0%	0.48	4	0%	0.53	4	0%
Late, August 8th	0.52	4	0%	0.58	5	0%	0.65	6	0%

Very late, August 23th	0.87	16	2%	1.05	-	99%	1.25	-	100%
Postponed, September 8th	1.22	-	100%	1.51	-	100%	1.84	-	100%
No harvest	1.33	-	100%	1.63	-	100%	1.96	-	100%

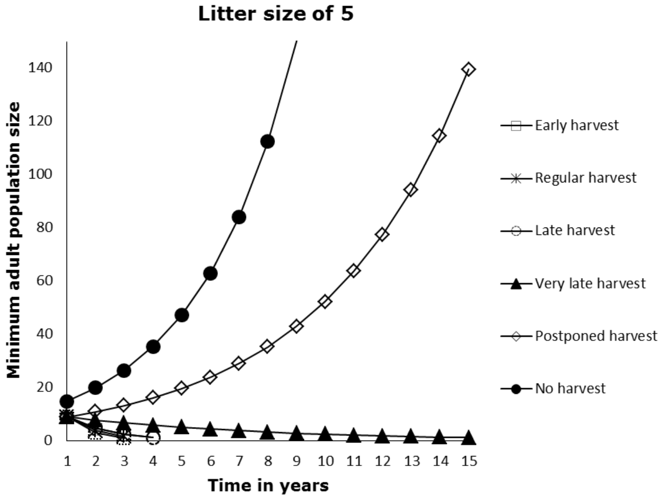

Figure 2a

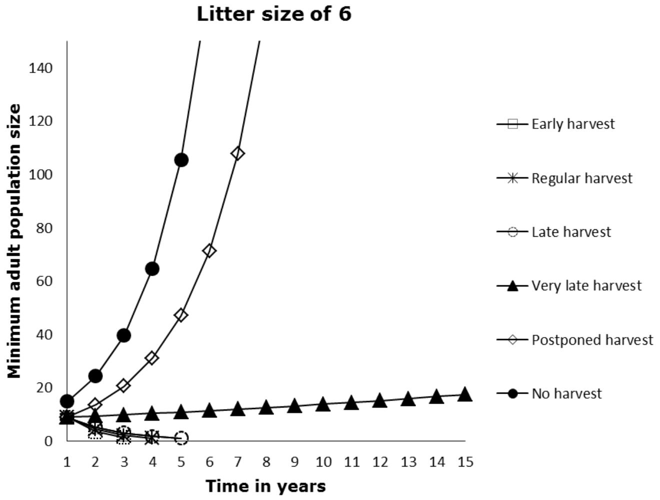

Figure 2b

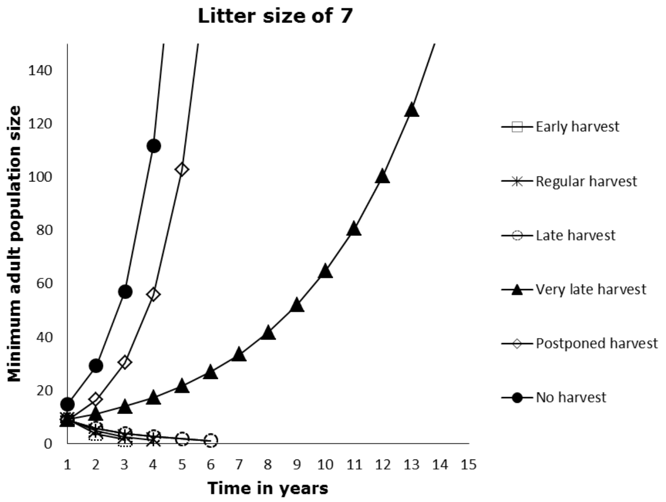

Figure 2c

Figure 2. The development of a Common hamster population based on the deterministic model with litter sizes of (a) 5, (b) 6 and (c) 7 over a period of 15 years under different harvest scenarios.

3.2 Stochastic model

The results of the stochastic model are in line with the results of the deterministic model (Figure 3a-c). An early harvest and a small litter size results in a rapid extinction of the population (Figure 3a-c), whereas a very late harvest and an increased litter size results in a persistent population. Hence, including stochasticity in the model results in a small chance of population survival in harvest scenarios with a negative growth rate compared to the deterministic model. On the other hand, stochasticity also results in extinction of a few populations when having a litter size of 6 and a very late harvest (Table 4).

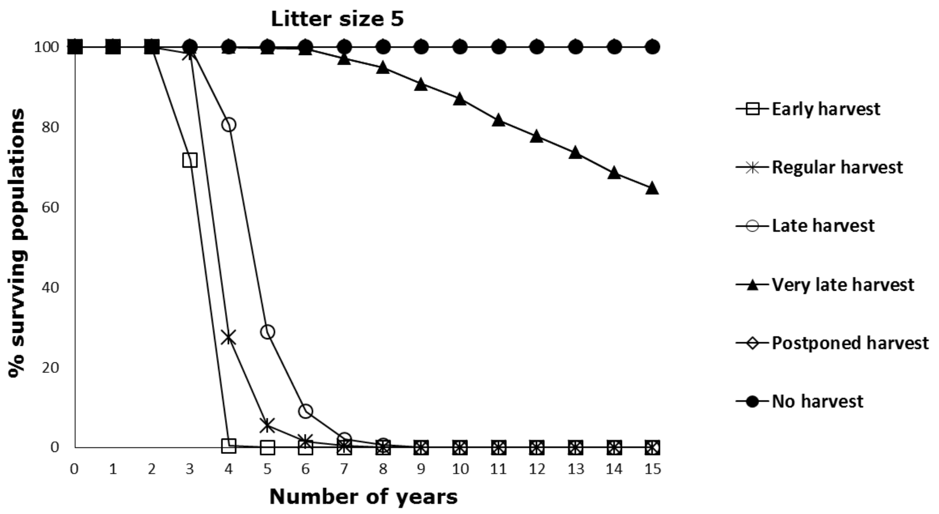

Figure 3a

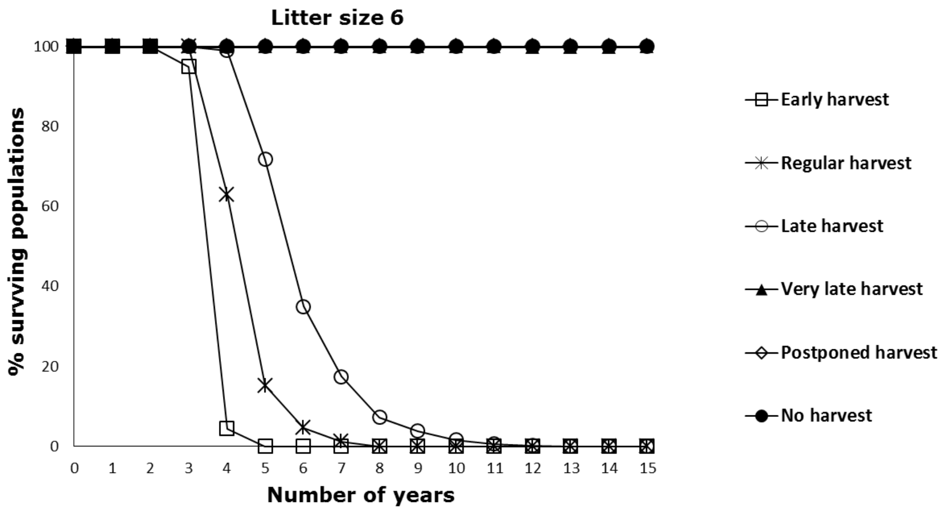

Figure 3b

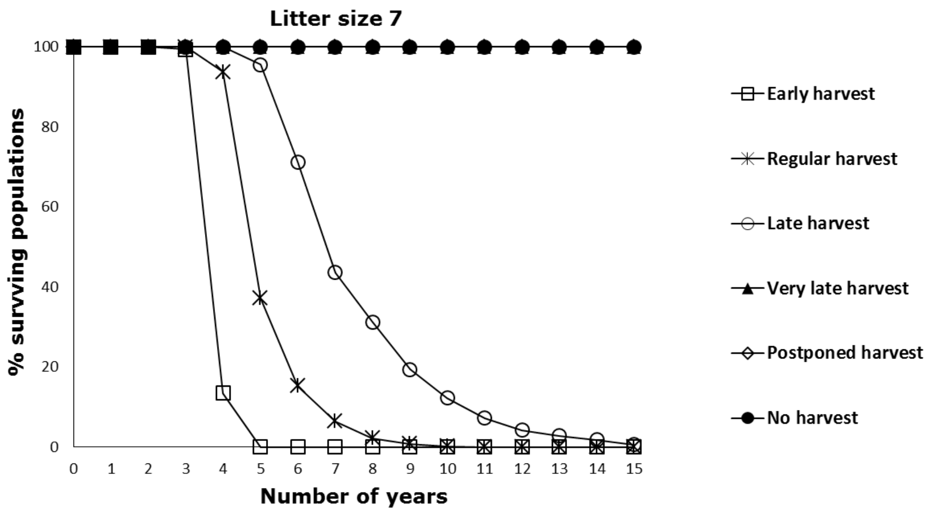

Figure 3c

Figure 3. Percentage of surviving populations based on the stochastic model-variant presented for the first 15 years of a total period of 50 years. Each harvest scenario was simulated 500 times. Per year, litter sizes were drawn from a normal distribution with an average of (a) 5, (b) 6 or (c) 7 juveniles, with a standard deviation of 1.25. Good years appeared on average once every 10 years.

3.3 Balance between growth and persistence

Both the deterministic and stochastic model show that the balance between population growth and population persistence mostly depends on the timing of harvest, with harvest scenarios allowing a successful second wave of litters having positive growth rates and more persistent populations. The limit for population persistence is formed by litter sizes of 5-6 combined with a very late harvest; the larger and the later, the better.

4 Discussion

The main focus of our model was to explore the sustainability and persistence of Common hamster populations with different timing of harvest, differences in litter size and the occurrence of “optimal” years. The results of our study show that timing of harvest, is crucial for the sustainability of Common hamster populations, whereas the other parameters had only minor effects. A change in litter size, regardless whether this is influenced by genetic deterioration or a loss of habitat quality, had only small effects. Hence, the timing of harvest determines the total reproductive output by influencing the number of successfully raised litters and especially the number of successful second or even third litters. Harvest activities before the first half of August, have a strong negative impact on the number of second litters, survival of juveniles and, furthermore, excludes a continued reproduction on harvested arable fields as cover is removed (Out *et al.* 2011a). A very late, postponed or no harvest at all gives adult females and sub-adults the possibility of producing a second litter, respectively, to produce a litter in the same breeding season (Hufnagl *et al.* 2011; Out *et al.* 2011a; Albert 2013). These second or late litters appear to be very important for population sustainability as survival of Common hamsters is quite low and population turn-over relative high (Gorecki 1977; Grulich 1986; Kuiters *et al.* 2010).

The intensification of agriculture in Europe, and especially the intensification of cereal management, negatively influence the population dynamics of the Common hamster in different ways. First, the area of spring sown cereals, has declined dramatically in the last decades in several European countries (Brickle & Harper 2002;

CBS *et al.* 2013; Villeymey *et al.* 2013). Spring sown cereals have the advantage of a postponed harvest compared to winter sown cereals, increasing the chance for females within a population to reproduce for a longer period during the breeding season. Second, besides the shift from spring sown cereals to winter sown cereals, the absolute area with cereals has declined as well (Donald *et al.* 2002) and it is expected to occur in Eastern Europe in the coming years (Nagy *et al.* 2009), a region where the Common hamster is still relative abundant (but see Weinhold 2013). Third, the introduction of combine harvesters in the second half of the last century has had a large effect on the length of the harvest period, whereas manual cereal harvest takes several weeks (Bieleman 1992), combine harvesters have the work done in just a few days (H. Hartmann pers. comm.). Currently, populations of Common hamsters have to deal with a reduced area of suitable habitat, which becomes hostile in just a few days in the middle of the breeding period (Figure 1a-b; Table 3) (Bieleman 1992; Harpenslager *et al.* 2011; Out *et al.* 2011a). Similar negative effects of an early harvest, even in otherwise good habitat, have been reported for other animals living in cereal fields like farmland birds (Peach *et al.* 2011; Perkins *et al.* 2013) and butterflies (Johst *et al.* 2006).This makes an appropriate management of the remaining cereals fields in suitable hamster regions very important. Furthermore, the absolute loss of cereal fields and the absence of alternative habitat probably results in more isolated and smaller populations of Common hamsters, with an increased probability of stochastic extinction (Fagan & Holmes 2006). Small populations can persist for some time due to landscape features (Fahrig & Merriam 1994) or due to the influx of occasional immigrants (Stacey & Taper 1992). However, in a short distance migrating species as the Common hamster (Van Wijk *et al*. 2011) it is highly unlikely that small and isolated populations can or will be saved by regular immigrants if source populations are too far away. Moreover, letting populations decline for too long has significant implications for the costs of conservation measures (Drechsler *et al.* 2011).

The finding that our population modelling results show large similarities with the individual-based model-study of Ulbrich & Kayser (2004), supports our confidence in our model and the used parameter values. However, the uncertainty in our study of some parameters as the percentage of juveniles becoming sub-adults, the rate of reproduction in sub-adults or the effect of harvest on survival of juveniles cannot be neglected as these parameters have potentially large effects on population development and persistence because of their effect on the number of successful litters. During this study, it became very clear that there is a lack of data for these parameters and that new studies addressing these issues are very important. Other parameters like variation in birth dates, variation of harvest data for different types or cereals or the start of the breeding season were simplified for modelling reasons and because of a lack of reliable data, but can easily be measured in the wild in future studies. Last, more attention for aspects as migration distances, effects of population densities and survival of juvenile and sub-adult hamsters after harvest would help to understand the population ecology of the species. Although, we had to make assumptions, we concluded that all parameter values used in our models were plausible and ecological feasible, but it is strongly recommended that new studies give more attention to these aspects and will try to determine the effect of hamster conservation measures on these parameters.

An appropriate conservation strategy for the Common hamster is to delay the harvest on the remaining cereals fields till September or to use cereals varieties that are not harvested before September without too much loss of yield quality. As applying conservation measures on all or most of the arable fields in hamster areas is impossible (Eppink & Wätzold 2009), it is recommended to initiate research to find out which percentage of all agriculture plots should be protected by agri-environmental schemes for sustainable populations of the Common hamster (Arroyo *et al.* 2002; La Haye *et al.* 2011a).

5 Conclusions

Our study shows that an early cereal harvest has a strong negative impact on population growth and persistence of Common hamsters, as a second wave of litters is impossible within the same breeding season. This second wave of litter is crucial for a sustainable and persistent population. Under the current regular and agri-environmental schemes it is impossible for females to produce enough off-spring for a sustainable population, even when they have large litters. An early harvest results in a rapid collapse of the population, whereas conditions related to late harvesting of cereals can result in a strong population increase. Existing agri-environmental schemes focusing on the Common hamster should be checked for timing of harvest and the reproductive output of females on fields with agri-environmental schemes. Conservation measures for this species should focus on a postponement of cereal harvest to create an optimal habitat which provides cover until September.

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Appendix 1

Population parameters as measured in the wild and as reported in review publications (Nechay 2000, Wencel *et al.* 2001).

Parameter	Value used in the models	Values in literature	References
Duration of pregnancy (days)	19	20	Mohr (1954)
		18-21	Nechay (2000)
		18-19	Kuiters *et al.* (2010)
Number of litters of adult females	Dependent on the harvest scenario. Maximum of 2 litters in normal years or 3 litters in optimal years if not interrupted by harvest	2-3	Mohr (1954)
		2-3	Nechay *et al.* (1977)
		2-3	Wencel (2001)
		0-3	Franceschini-Zink & Millesi (2008)
		1-3	Harpenslager *et al.* (2011)
Frequency of optimal years	Once every 10 years	Once every 10 years	Nechay (2008)
Timing of litters	Normal years: 14th of June, 27th of July Optimal years: 16th of May, 27th of June, 10th of August	April till September	Nechay *et al.* (1977)
		Beginning of May – beginning of September	Kayser (2002)
		End of May till middle of August	Kupfernagel (2007)
Litter size	5,6 or 7	5,15	Gorecki (1977)
		6	Gorlach (1984) in Wencel (2001)
		7	Wencel (2001)
		5-7	La Haye *et al.* (2012)
S.d. around litter size	1,25	This value was chosen, based on the published range in litter sizes	
Sex ratio	50% males, 50% females	50% males, 50% females (n=228)	Gorecki (1977)
		53,6% males, 46,4% females (n=2705)	Grulich (1986)
Reproduction by sub-adults in their natal year	Possible	Possible	Grulich (1986), La Haye & Müskens (2004), Losík *et al.* (2007), Franceschini-Zink & Millesi (2008)
Frequency of reproduction by sub-adults of the first litter in their natal year	As all sub-adult females from first litters are physiologically sexual mature, we assumed 100% reproduction.	At least the sub-adults females of the first litters have the weight to be sexual mature.	La Haye & Müskens (2004), Müskens *et al.* (2011), Out *et al.* (2011b)
Chance of becoming sub-adult	40%	Calculated from Gorecki (1977)	Gorecki (1977)
Survival rates adults & sub-adults	Table 1	Table 1	Kuiters *et al.* (2010)
Harvest data	8 July, 23 July, 8 August, 23 August, 8 September	Table 3, combined with scenarios for delayed harvest and no harvest	Bieleman (1992)
Harvest stops all further	Yes	Yes	Harpenslager *et al.*

reproduction		Yes	(2011) Albert (2013)
Mortality of juveniles (age ≤ 20 days) after harvest	100%	This value is an assumption	
Mortality of juveniles with an age of 21-31 days after harvest	50%	This value is an assumption.	
Mortality of juveniles with an age of 32-42 days after harvest	25%	This value is an assumption	
Mortality of sub-adults after harvest	0%	Harvest was modelled as having no effect on sub-adults, because the percentage of juveniles becoming sub-adults was collected in an area with harvest, which means that a mortality effect from harvest is already included	Gorecki (1977)
Mortality of adults after harvest	40%	40%	La Haye *et al.* (2011b)