Biological Conservation 158 (2013) 147–154

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Testing restocking methods for an endangered species: Effects of predator exclusion and vegetation cover on common hamster (*Cricetus cricetus*) survival and reproduction

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ARTICLE INFO

Article history:
Received 5 May 2012
Received in revised form 30 July 2012
Accepted 5 August 2012

Keywords:
Electric fences
Predation
Radio-tracking
Reintroduction
Vegetative cover

ABSTRACT

Animal restocking is a widely used conservation tool to restore relict populations of endangered species. However, success of such operations is often low due to poor short-term survival and experimental evidence is required to improve restocking results. We tested the impact of different release conditions on survival and reproduction of captive bred common hamsters (*Cricetus cricetus* L. 1758), a highly endangered species in Western Europe. As predation plays a determinant role for released hamsters, especially during the first days after restocking, we performed two release experiments intending to reduce mortality: we tested (1) the efficiency of terrestrial predator proof electric fences and (2) the impact of improved shelter availability. We assessed both survival rate and reproductive success by radiotracking 70 hamsters between release date and the end of their aboveground active period. Reducing contact between released animals and predators thanks to electric fences had a strong positive impact on hamsters' survival and allowed them to have enough time to reproduce. It also appeared that release of hamsters was more efficient in wheat crop than in alfalfa. As expected, wheat harvest, inducing a sudden lack of shelter, negatively impacted restocking success. Finally, lifetime after release affected the number of litters per female and varied with individual characteristics: it decreased with burrow change frequency and was slightly lower for males. We conclude that electric fences associated with permanent well-developed vegetative cover like unharvested wheat seem to be suitable for releasing hamsters.

1. Introduction

In the current context of biodiversity decline, reintroduction, translocation and restocking – i.e. supplementing a declining population with captive-bred animals – have become essential conservation tools for restoring relict populations of highly endangered species (IUCN, 1998). However, despite huge economic and research investments, a high proportion of restocking programs have failed at establishing viable populations mostly due to heavy short-term mortality (Armstrong and Seddon, 2008). This could be due to deficiencies in foraging capacities (Jule et al., 2008), unfamiliarity with local conditions (Calvete and Estrada, 2004) and predation (Griffin et al., 2000). As a result, for each restocking program, experiments and post-release monitoring are crucial to continuously assess and improve survival and reproductive success of released animals (Armstrong and Seddon, 2008; Sarrazin and Barbault, 1996).

The common hamster (*Cricetus cricetus* L. 1758) is a highly endangered species in Western Europe and has been the subject of several conservation schemes in the last decade to support the remaining populations. Actions have included habitat restoration, captive breeding and restocking programs (Weinhold, 2008). This medium-sized rodent, with a distribution ranging from Siberia to Western Europe, originally lived in natural or semi-natural steppe-like habitats but has adapted to agricultural fields (Nechay, 2000). However, recent landscape fragmentation (Ulbrich and Kayser, 2004), changes in agriculture (crops, mechanization, pesticides) and land use have led to a dramatic decrease in their numbers. In the last decades, the species declined dramatically throughout Europe (Weinhold, 2008), especially in the western part of its range (France, Belgium, the Netherlands, Western Germany) where only a few relict populations survive. In France, the common hamster was present in 329 municipalities in 1972, 56 in 2000 and only 19 in 2012. The common hamster is currently strictly protected and listed in Appendix II of the Bern

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http://dx.doi.org/10.1016/j.biocon.2012.08.007

Convention as well as Appendix IV of the European Habitats Directive.

In France, restoration of hamster habitats has been running since 2000. Along with this action and because the species is known to disperse over short distances even in unfragmented landscape, thereby limiting a natural expansion of its range (van Wijk et al., 2011), France began a breeding program in 2002 and a restocking program in 2003 to help relict hamster populations develop in restored areas. The first results of the French restocking program showed a very low survival rate due to high mortality in the days after release (Losinger and Petiteau, 2004). In the following years, other restocking operations were performed with low success: very few hamster burrows could be found in restocking areas in the year after release.

Despite some studies in other European countries (The Netherlands, Müskens et al., 2008; Germany, Sander and Weinhold, 2008; Belgium, Verbist, 2008), there is a huge lack of references for the conservation of this species and we are short of knowledge about how to improve these operations. Moreover, learning from the reintroduction of other species has limited value because in most cases they concerned large and long-lived animals (Sarrazin and Legendre, 2000) and success of such operations is highly species-specific.

It is assumed that predation is one of the major causes of mortality for a prey species such as the hamster (Kayser et al., 2003; La Haye et al., 2010) and captive bred animals are very vulnerable to predation due to unfamiliarity with the release habitat (Griffin et al., 2000; Müskens et al., 2008). In this study, we thus performed two distinct experiments to test different methods intending to mitigate this mortality factor.

During the first experiment, we reduced contacts with predators by installing electric fences (Calvete and Estrada, 2004) especially efficient against red foxes, *Vulpes vulpes*, known to be one of the main hamster predators (Kayser et al., 2003). We expected better survival rates and reproduction, and fewer mortality cases inside fenced enclosures than in unfenced areas. In the second experiment, we compared the impact of diverse agricultural covers, which are important shelter resources for rodents (Out et al., 2011), on released hamsters' survival probabilities and reproduction. More precisely, we compared the fate of hamsters released in wheat and alfalfa plots, two crops known to be suitable for the species (La Haye et al., 2010) and which differ in vegetation covers. Then, as cover removal due to harvest, a classic agricultural practice, seems to have a strong negative impact on hamster survival (Kayser et al., 2003), we hypothesized that harvest would reduce survival and reproduction of released animals. In addition, in the two experiments, we tried to detect periods of vulnerability after release and we tested for the influence of individual characteristics such as age, sex, and frequency of burrow change on post-release survival.

2. Methods

2.1. Study area

We carried out our restocking experiments in Blaesheim (Alsace, Eastern France) in 2010 and 2011. The Alsatian plain is the only region in France where common hamsters are present and constitutes one of the westernmost parts of their range (Nechay, 2000). The site of Blaesheim is located within the main historical distribution area of the species. However, in 2007, the hamster population of the district was nearly extinct (less than 10 active burrows in spring). Consequently, considerable conservation efforts were undertaken in this district, leading to a larger amount of favourable crops in 2008 (winter cereal, alfalfa), and a restocking program began the same year by releasing captive bred hamsters.

The release area is a 300 ha intensive agricultural landscape, composed of small fields (0.75 ha on average) of corn (49%), winter cereals (30%), cabbage (10%), alfalfa (8%) and potatoes (2%, field observations). In the release area, wheat strips (between 20 and 100 m wide) are left unharvested to increase hamster survival and to enhance pre-hibernation conditions after harvest time (La Haye et al., 2010; Kayser et al., 2003).

Some mammalian predators such as red fox, weasel (*Mustela nivalis*), polecat (*Mustela putorius putorius*), domestic dog and cat (*Canis familiaris, Felis catus*), and birds of prey: buzzard (*Buteo buteo*), kestrel (*Falco tinnunculus*) occurred in the area. No additional predator control was applied.

2.2. Field methods

Our two experiments benefited from restocking operations performed the third week of May in 2010 (178 released hamsters) and 2011 (141 hamsters). We monitored randomly chosen individuals among the released animals using a radiotracking system to know their fate. In the first experiment (in 2010), we compared the fate of hamsters released inside and outside electric fences: 14 hamsters (5 males, 9 females) were released in two batches inside electric fences, and 14 hamsters (5 males, 9 females) in two batches outside fences (Fig. 1A). In the second experiment (in 2011), we compared the fate of female hamsters released inside electric fences in three different agricultural environments: harvested wheat (14 hamsters), unharvested wheat (14 hamsters) and mown alfalfa plots (14 hamsters). Each treatment was tested with two replicates (Fig. 1B). Hamsters were released in batches of 5–30 animals (mean = 15.6) of both sexes (sex ratio between 1:1.4 and 1:1.7). Distances between batches were 300 m on average and less than 800 m to allow connections (van Wijk et al., 2011).

Hamsters were moved from the breeding units managed by the association "Sauvegarde Faune Sauvage" (Alsace) to the release area in individual wooden boxes. To favour the quick generation of a wild-born cohort (Sarrazin and Legendre, 2000), all released hamsters were sexually mature (>1 year). In the vegetative cover experiment, all animals were one year old. Because of logistic constraint, in the fence experiment hamsters aged one and two years were equivalently distributed between fenced and unfenced areas. Females were not pregnant to avoid additional costs due to maternal investment. Release operations were conducted in spring when all individuals had emerged from hibernation and were ready for reproduction (Jordan, 2002).

Animals were released in arable fields, on loess or loamy soil, on crops of winter cereals or alfalfa. Hamsters were released without human handling to prevent them from being stressed (Teixeira et al., 2007). Each hamster was put into an artificial burrow (two pipes: one vertical and one sloping, connecting each other at about one meter below ground; Müskens et al., 2008) closed with retention caps, kinds of stoppers made with grass. Artificial burrows provide temporal shelters in the first days after release and favour the acclimatization of ground dwelling species (Gedeon et al., 2011; Müskens et al., 2008). Burrows were dug every 20–40 m along parallel transects to maximize potential contacts between animals. Electric fences surrounding release plots were set up before release and removed after the end of the hamster aboveground active period (i.e. end of September; Weinhold, 2008). This predator exclusion device consisted in a net composed of nine electrified wires located at 10–100 cm above ground to prevent medium sized terrestrial predators like red foxes from getting through. We preferred predator exclusion to lethal techniques such as night shooting, because of ethical considerations and cost/benefit ratio. Indeed, regulating predators to protect prey species is often ineffective in the long-term and very expensive. Predator facilitation and influx of new individuals compromising regulation efforts were observed in several conservation programs (Maron et al., 2010).

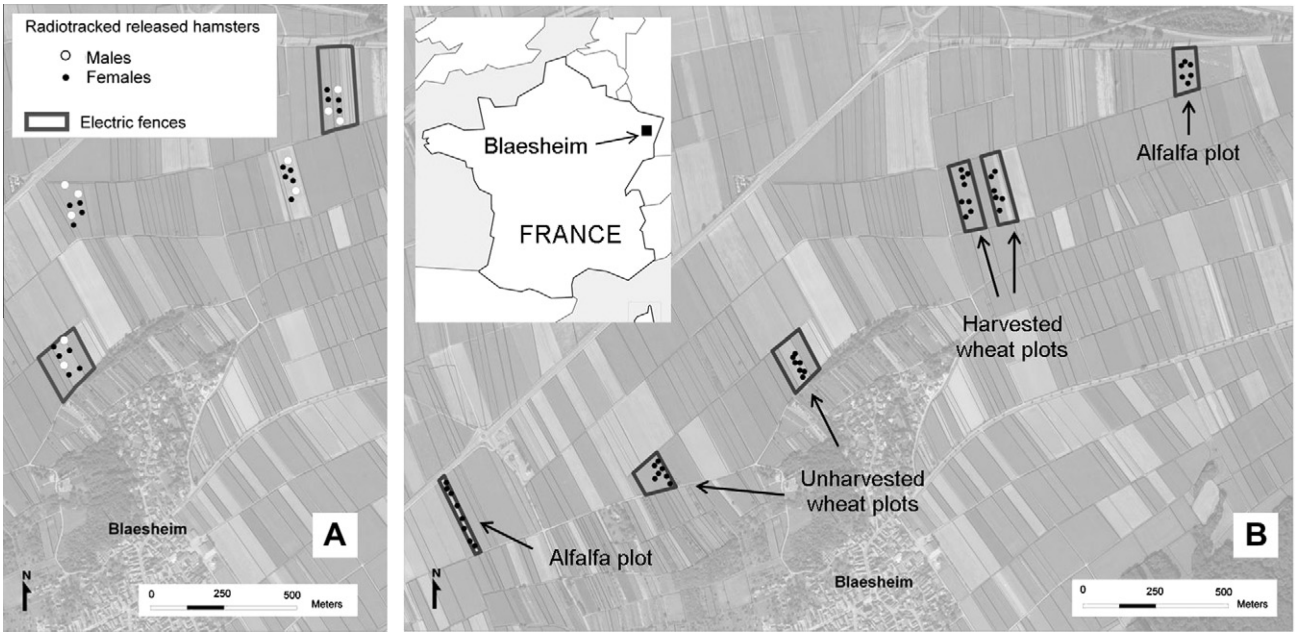

Fig. 1. Map of release sites and batches of radiotracked released hamsters for the fence experiment (A) and the vegetative cover one (B).

We radiotracked released hamsters using intra-abdominal thermo-sensitive radio transmitters (Microtes MTX3, 13×13 mm). Transmitters weighed 6.5 g, corresponding to 1.3–3.8% of hamster body mass (ranges from 170 to 500 g), below the recommendation threshold of 4% (Theuerkauf et al., 2007). Surgeries to implant transmitters (Capber, 2011) were performed at least a week before release dates. Transmitters' batteries lasted 6 months on average, allowing us to radiotrack released hamsters until the end of their aboveground active period. In the first experiment, we caught living animals before hibernation period to change transmitters but unfortunately, we faced batteries' deficiency during winter and it was not possible to relocate animals in spring 2011 nor to estimate winter survival.

Transmitter pulse can be located up to a distance of 150 m even when the animal is underground and provide information about hamster status (alive or dead, detected by changes in pulse frequency). Each marked hamster was radiotracked during daylight every 2–4 days between release date (mid May) and the end of the aboveground active period (end of September). We followed up any loss of signal by repeatedly searching over wide areas (>500 m from the last known location).

For each radiotracking session, hamsters were located by homing method using hand-held antenna (Microtes), portable receiver (Icom Inc, IC-R10) and GPS (Garmin, Etrex Legend HCX). Moving animals were not located to avoid disturbance and because, as crepuscular, secretive and fearful species, they are very difficult to visually locate aboveground. For this reason hamsters were only located during daytime when they were more likely to be in their burrows.

2.3. Biological parameters estimated

Classically, released animals have a lower survival probability in the wild than their wild-born counterparts because of captive experience (Jule et al., 2008). However, heavy mortality is not a major problem if it is balanced by a high reproduction, especially for a species such as the hamster with a short lifespan and a high investment in reproductive output (Weinhold, 2008). We thus focused on survival, death causes, and also on reproduction to assess restocking success.

When a dead hamster was detected, its carcass was examined and the cause of mortality determined thanks to clues left by predators on and around the carcass following Cuthbert (2003) categories: avian and mammalian predation. We considered two other categories: unknown predation (e.g. transmitters found alone without remains) and unknown death cause (no evidence). Intervals between radiotracking sessions were quite close but could not completely ensure that there were no scavenging, decay and bias in death cause identification (Kostecke et al., 2001).

The effectiveness of post' release reproduction was estimated by the number of litters per female. Successful litters, meaning pup(s) being detected when emerging from the maternal burrow, were confirmed by setting automatic cameras (Cam Trak South Inc. W-55 CB, Reconyx Inc. HC 600 Hyperfire) in front of burrows of females suspected to have given birth, to get pictures of emerging pups. This gave us the number of successful litters per female and an estimation of lifetime after release corresponding to the first and the second litter detection; but it could not provide information about litter failure, litter size, early mortality and survival of juveniles after weaning. A female was suspected to have given birth if lifetime after release exceeded 6 weeks (pregnancy: 18–20 days, weaning of young: 3–4 weeks; Franceschini-Zink and Millesi, 2008) and if females spent more than 4 weeks in the same burrow (burrow residence time; Harpenslager et al., 2011); additional litters were suspected every 4 weeks because hamsters can have a post-partum oestrus (Harpenslager et al., 2011).

Individual behaviour such as mobility can impact rodent survival. It could increase the chances of meeting a predator (Norrdahl and Korpimäki, 1998), but reduces the accumulation of visual and olfactory clues around burrows (Banks et al., 2000). Accordingly, in the vegetative cover experiment, we assessed the effect of frequency of burrow change on survival rates. For each radiotracking session, we located the burrow in which each hamster was. We considered that a hamster changed burrow in a time interval if it was located in another burrow the following session and so on. Individual mobility in a given time interval was estimated by dividing the number of burrow changes detected during this interval by the hamster lifetime during this period.

2.4. Statistics

Because of unequal radiotracking intervals, we considered our known-fate radiotelemetry data as ragged telemetry data (Rotella et al., 2004). So we used the Nest Survival model of Program MARK

(Dinsmore et al., 2002; Rotella et al., 2004; White and Burnham, 1999) to assess the daily survival rates of released hamsters. For each hamster, we coded encounter histories with five types of information: (1) the day of release (*k*), (2) the last day the hamster was known to be alive (*l*), (3) the last day the hamster was radiotracked (*m*), (4) the hamster fate: 0 = signal loss or hamster still alive, 1 = dead hamster (*f*), and (5) the number of hamsters with the encounter history (*n*). We numbered the days considering the days of release as a baseline (Day1 = 20th May in 2010, 18th May in 2011).

For the fence experiment, we divided monitored hamsters into four groups corresponding to the two batches of hamsters released inside electric fences and the two batches of hamsters outside fences. For the vegetative cover experiment, cover types and batches were combined and modelled as groups, resulting in six groups (two batches for each of the three cover types).

We used an information-theoric approach (Burnham and Anderson, 1998) to assess a set of candidate models. All models used a logit link function because it enforces parameter values in the [0, 1] interval (White and Burnham, 1999). We compared models using Akaike's Information Criterion corrected for small samples (AICc, Akaike, 1973), the best model having the lowest AICc value. We estimated daily survival rates by model averaging, weighting estimates from selected models according to their relative Akaike weight (Burnham and Anderson, 1998). We deducted weekly and monthly survival rates by multiplying daily survival rates on these periods. We used the delta method (Powell, 2007) to calculate standard errors for the model-averaged estimates.

For each experiment, our candidate-model set included the simplest possible model where daily survival rate was constant within time and between groups. Then, we tested a model where release treatments (two batches inside and outside fences in the fence experiment, two batches for each cover type in the second experiment) were included as groups. In a first step, we tried to group replicates of each treatment. Then, we looked for the best time effect for the remaining groups: we included a linear time trend based on the assumption that daily survival rate may change linearly over time after release, we also performed models with time after release divided in intervals in order to detect potential critical periods. In the last step, in the fence experiment, we added standardized individual covariates (age (1 or 2 years) and sex of hamsters) to find the model that explained the most variation in the data.

To test frequency of burrow change, we used the most parsimonious model for the complete vegetative cover experiment dataset as the base model on a subset of these data corresponding to hamsters known to be alive at the first radiotracking session. As a result, four females were excluded from these models: two females released inside an unharvested wheat plot, another in a harvested wheat plot and the last one in an alfalfa plot. We added to the base model individual standardized covariates related to hamsters' burrow changes during the first session, the 2, 4, 10 first sessions, and all radiotracking sessions.

We compared the relative importance of death causes on recovered animals between release conditions with exact Fisher tests.

In both experiments, we tested the effect of release treatments on the number of litters per female using a linear model (General Linear Model with Poisson distribution, R 2.14.1 software; R Development Core Team, 2011) and we compared the null model and the model with release treatments using an analysis of deviance (anodev, χ^2 test).

3. Results

3.1. Survival

In both experiments, except in harvested wheat plots, there was low support for a significant temporal variation in survival: in the fence experiment, the first model with time variation was 4-fold less supported than the best model (Table 1, models 1 and 4); in the vegetative cover experiment, models with time variation were not supported (Table 2a, model 4, AICc weight = 0.01). Whatever the release conditions, we could not highlight any critical period corresponding to the first weeks after release (Tables 1 and 2).

In the fence experiment, 3 hamsters were lost (two released inside fences, one outside), and one female inside fences was still alive at the end of the aboveground active period. As a result, they were included in the analyses and considered as censured data ($f = 0$ in their encounter history). Model selection clearly showed that daily survival rates differed inside and outside fences (Table 1, models 2 and 15, constant model AICc weight = 0, model with two groups: inside and outside fences, AICc weight = 0.12). In the best parsimonious model, weekly survival rates inside fences were about three to 4-times higher than outside, leading to weekly survival rates of 0.893 [0.831, 0.954] inside and 0.274 [0.055, 0.493] outside fences. The most-parsimonious model (Table 1, model 1) also included a sex-specific effect with lower survival in males than females (Table 3).

In the second experiment, the dataset included 4 lost hamsters (signals lost, three released in alfalfa plots, one in unharvested wheat plot), and three females released in unharvested wheat plots were still alive at the end of the aboveground active period. As a result, these animals were included in the analyses and considered as censured data. There was a batch effect for hamsters released in alfalfa and unharvested wheat plots (Table 2a, model 1). When pooled together, the difference between agricultural covers was slightly significant: monthly survival seemed lower in alfalfa ($S_{alfalfa}$: 0.345 [0.095, 0.595]) than in wheat (S_{wheat}: 0.609 [0.415, 0.804], unharvested and harvested plots pooled together before harvest). Model selection supported two distinct time intervals in harvested wheat plots corresponding to periods before and after harvest date (Table 2a, models 1 and 5, best model: AICc weight = 0.68, model without time effect: AICc weight = 0.01). Monthly survival rate was higher before harvest date than thereafter (Table 3, S_{before}: 0.612 [0.322, 0.901], S_{after}: 0.167 [0.000, 0.392]). Daily survival rates decreased with the frequency of burrow change estimated over the whole active period (Table 2b, model 1, $\beta = -0.554$ [−0.988, −1.010]). As an example, in the

Table 1
Survival (S, Nest Survival analysis) of released hamsters in the fence experiment ($N = 28$). The most parsimonious model is in bold. Models included in model averaging are indicated by *.

	Model	K[1]	AICc[2]	Δ AICc	W[3]	Dev[4]
1	**S (in out + sex)**	**3**	**149.04**	**0.00**	**0.30**	**143.00***
2	S (in out)	2	150.83	1.80	0.12	146.82*
3	S (in out + sex + age)	4	150.97	1.93	0.11	142.91*
4	S (in out + t (1–7–164))	3	151.61	2.57	0.08	145.57
5	S (out + T/in)	3	152.39	3.35	0.06	146.36
6	S (in out + T)	3	152.74	3.70	0.05	146.71
7	S (in out + t (1–14–164))	3	152.77	3.74	0.05	146.74
8	S (in + T / out)	3	152.78	3.74	0.05	146.74
9	S (in out 1–2)	3	152.78	3.75	0.05	146.75*
10	S (in out + t (1–21–164))	3	152.82	3.78	0.04	146.79
11	S (in out + t (1–28–164))	3	152.83	3.80	0.04	146.80
12	S (in out + T + T^2)	4	154.07	5.04	0.02	146.02
13	S (in 1–2 out 1–2)	4	154.39	5.35	0.02	146.33*
14	S (.)	1	180.73	31.70	0.00	178.73

S(.) = constant survival probability. Time effect: T = linear time trend, T + T^2 = quadratic time effect, t (*x*–*y*–*z*) = time divided in two periods: the first period between days *x* and *y* and the second between *y* + 1 and *z*. Groups: in out = fence effect, 1–2 = batch effect. "/" is added when groups do not have the same time effect. Individual covariates: sex, age.
1: Number of estimated parameters, 2: Akaike's information criterion corrected for small sample size, 3: Akaike weight, 4: deviance.

Table 2
Survival (S, Nest Survival analysis) of released animals in the vegetative cover experiment based on (a) all released hamsters (*N* = 42) and (b) on a subset of these data to test for the effect of frequency of burrows change (*N* = 38).

	Model	K	AICc	Δ AICc	W	Dev
(a) Survival						
1	**S (Unh 1–2 Alf 1–2/Har + t (be-af))**	**6**	**259.62**	**0.00**	**0.68**	**247.58***
2	S (Alf 1–2 Unh 1–2 + T/Har + t (be-af))	7	261.59	1.97	0.25	247.53*
3	S (Alf 1–2 Unh 1–2 Har + t (be-af))	6	266.06	6.44	0.03	254.02*
4	S (Alf 1–2 + T/Unh 1–2 Har + t (be-af))	7	267.66	8.04	0.01	253.60*
5	S (Unh 1–2 Har Alf 1–2)	5	269.13	9.51	0.01	259.10
6	S (Unh 1–2 Har Alf 1–2 + T)	6	269.52	9.90	0.00	257.48
7	S (Unh 1–2 Har Alf 1–2 + t (0–14-165))	6	270.16	10.54	0.00	258.12
8	S (Unh 1–2 Har Alf 1–2 + t (0–7-165))	6	270.44	10.82	0.00	258.40
9	S (Unh 1–2 Har Alf 1–2 + t (0–28-165))	6	271.08	11.46	0.00	259.04
10	S (Unh 1–2 Har 1–2 Alf 1–2)	6	271.09	11.47	0.00	259.05
11	S (Unh 1–2 Har Alf 1–2 + t (0–21-165))	6	271.14	11.52	0.00	259.10
12	S (Unh 1–2 Har 1–2 Alf)	5	272.17	12.55	0.00	262.14
13	S (Unh Har 1–2 Alf 1–2)	5	275.10	15.48	0.00	265.07
14	S (.)	1	275.95	16.33	0.00	273.94
(b) Survival with frequency of burrows change						
1	**S (Unh 1–2 Alf/Har + t (be-af) + mob39)**	**7**	**225.25**	**0.00**	**0.48**	**211.19***
2	S (Unh 1–2 Alf/Har + t (be-af) + mob39 + mob39^2)	8	226.26	1.01	0.29	210.18*
3	S (Unh 1–2 Alf/Har + t (be-af) + mob10)	7	228.64	3.39	0.09	214.58
4	S (Unh 1–2 Alf/Har + t (be-af) + mob10 + mob10^2)	8	229.81	4.56	0.05	213.74*
5	S (Unh 1–2 Alf/Har + t (be-af))	6	230.37	5.12	0.04	218.33*
6	S (Unh 1–2 Alf/Har + t (be-af) + mob4)	7	231.57	6.32	0.02	217.51*
7	S (Unh 1–2 Alf/Har + t (be-af) + mob2)	7	232.18	6.94	0.01	218.13
8	S (Unh 1–2 Alf/Har + t (be-af) + mob1)	7	232.37	7.12	0.01	218.32
9	S (Unh 1–2 Alf/Har + t (be-af) + mob3)	7	232.38	7.13	0.01	218.32

t (be-af) = 2 periods of time: before and after harvest date (58th day), Unh Har Alf = vegetative cover effect (Unh = unharvested wheat, Har = harvested wheat, Alf = Alfalfa), mobX = frequency of burrows change during the X first radiotracking sessions. See Table 1 for the others abbreviations.

Table 3
Daily, weekly and monthly survival estimates (S) and standard errors (SE) for hamsters released in both experiments, according to release conditions and hamsters' sex (in the fence experiment).

Survival rates		Fence experiment				Vegetative cover experiment					
		Inside fences		Outside fences		Unharvested Wheat		Harvested wheat		Alfalfa	
		Male	Female	Male	Female	Plot 1	Plot 2	Before harvest	After harvest	Plot 1	Plot 2
Daily	S	0.980	0.986	0.801	0.848	0.973	0.994	0.984	0.942	0.983	0.952
	(SE)	(0.006)	(0.005)	(0.053)	(0.048)	(0.012)	(0.003)	(0.008)	(0.022)	(0.009)	(0.019)
Weekly	S	0.871	0.905	0.212	0.315	0.824	0.960	0.892	0.658	0.888	0.707
	(SE)	(0.035)	(0.031)	(0.098)	(0.126)	(0.073)	(0.023)	(0.050)	(0.106)	(0.058)	(0.098)
Monthly	S	0.553	0.652	0.001	0.007	0.436	0.841	0.612	0.167	0.602	0.226
	(SE)	(0.095)	(0.097)	(0.003)	(0.012)	(0.166)	(0.086)	(0.148)	(0.115)	(0.167)	(0.135)

second unharvested plot, multiplied frequency of burrows change by five induced a survival rate 18% lower.

3.2. Death causes

In both experiments, eight hamsters were lost despite extended research; this could be due to transmitter failure, carcass carried far away by the predator or dispersal. Four hamsters were still alive at the end of the study period, and we could determine the death cause of 45 cases among the 58 animals found dead. Predation represented 76% of the death causes; the other death causes (24%) were unknown ones.

In the fence experiment, if we focused on terrestrial predation alone, despite a lower number of hamsters killed by terrestrial predators inside fences than outside (eight against five), the difference was not significant (Fisher test, $p > 0.05$).

In the second experiment, hamsters' causes of death differed between harvested wheat plots and the other crops (Fisher test, $p < 0.05$). Nevertheless, the only difference was in the number of unknown death cases: they were more numerous in harvested wheat plots than in other plots (Fisher test, $p < 0.05$).

3.3. Reproduction

In the fence experiment, all hamsters died within 2 weeks outside fences, so there was no successful litter detected. Inside fences, four females had a successful litter. AIC comparison showed that there was a difference inside and outside fences (General Linear Model, null model: AIC = 22.0, model outside/inside fences: AIC = 18.5, ANODEV $p(\chi^2) = 0.019$). The number of litters per female was estimated at 0.44 (±0.22) inside fences and 0 (±0.00) in control plots.

In the vegetative cover experiment, seven females raised a first litter and five of them had a second one in unharvested wheat plots; six females raised a first litter and one of them had a second one in harvested wheat plots; whereas in alfalfa plots, only two first litters were detected. Release treatments had an impact on the number of litters detected per female (General Linear Model, null model: AIC = 82.7, model unharvested wheat/harvested wheat/alfalfa: AIC = 78.8, ANODEV: $p(\chi^2) = 0.018$). Number of litters per female was estimated at: 0.86 ± (0.25) in unharvested wheat plots, 0.57 (±0.20) in harvested ones and 0.14 (±0.10) in alfalfa. For the vegetative cover experiment, pups emerging from females' burrows were detected 66.3 (±2.6) days after release for the first litter and 102.0 (±3.2) days after release for the second one. All females that survived more than 66 days had a first litter, and four among the five females that survived more than 100 days had a second litter.

4. Discussion

The main objective of this study was to compare release treatments to improve hamsters' short-term survival and reproductive success. We confirmed the hypothesis that survival and reproduction would be higher inside electric fences and within unharvested wheat plots, i.e. in condition where individuals are protected against predators.

In the best release conditions, i.e. in unharvested wheat plots surrounded by fences, we were able to achieve successfully the first step of a reintroduction process: establishment and reproduction of reintroduced animals (Armstrong and Seddon, 2008). In these release conditions, monthly survival rate was about 0.607 [0.362, 0.851] (meaning 0.368 [0.072, 0.665] after 2 months and 0.050 [0.000, 0.017] after 6 months) and we detected 0.86 (±0.25) litter per female.

This result is much better than the results obtained by the previous French experiment (without fences) for which the survival rate after 11 days was 0.50 and no reproduction occurred (Losinger and Petiteau, 2004). In the Netherlands, an experiment showed yearly survival rates of 0.05 [0.03, 0.08] for released females and 0.01 [0.00, 0.01] for released males (La Haye et al., 2010). Two experiments without electric fences led to survival rate of 0.37 seventy-two days after release in Belgium (Verbist, 2008), and 0.25 survival after 2 months in Germany (Sander and Weinhold, 2008). Our results are consistent with these reintroduction programs. In the best release conditions, the survival rate we observed was similar to that of the Belgium experiment, lower than the Dutch experiment but better than the German one. However, these differences may be due to the use of non-similar release techniques (anti-predator measures), monitoring and analyses. Moreover, diverse climatic conditions which have a strong impact on rodent populations prevented us from making direct comparisons.

4.1. Impact of release methods

Our experiment showed that exclusion of medium sized terrestrial predators had a positive impact on survival and, as a consequence, on the reproduction of released hamsters. Indeed, this result is in accordance with Weinhold (2008) who found that red fox is a major predator of common hamsters. Fences restricted medium-sized terrestrial predators from getting through but allowed hamsters going out. Nevertheless, less than 10% of released hamsters were located at least once outside fenced areas which may not significantly change our results. The positive impact of fences could have been more obvious because in 2010, we had to deal with power outage due to theft, vandalism and inappropriate maintenance of the vegetation under fences. Maintenance of fences during the whole aboveground active period helped released animals to reproduce during this first year; fences were removed at the end of the restocking year. In the following spring, when hamsters emerge from hibernation, almost all captive born hamsters will have died because of the species' natural lifetime (Weinhold, 2008), but we can wonder about the fate of wild born animals which will have to deal with terrestrial predation. Wild born hamsters would have a more appropriate anti-predator behaviour because, unlike their parents, they have not experienced captivity. After fences' removal, we expect a population with a higher recruitment rate than the death rate, but long term monitoring of hamsters born in situ is needed to assess the success of such a restocking program in the long run (Reiners et al., 2011).

Our results tended to prove that hamsters released in the alfalfa plots had lower survival rates and lower number of litters per female whereas this crop is assumed to be the most suitable cover for the species (Out et al., 2011). This result could be due to differences between alfalfa and wheat management: in regular agriculture, wheat is cut once whereas alfalfa is mown regularly. However, in our experiment, almost all hamsters died before the first cut of alfalfa. Another explanation can be that in 2011, we faced an exceptional dry spring which induced a low height of alfalfa at the release date, which in turn favoured raptors' hunting success. Indeed, hunting success increases when height and density of vegetation decrease (Toland, 1987). In very intensive arable landscapes, alfalfa plots are also the only semi-perennial habitat (alfalfa cultivation 3–5 years in a row on the same plot), providing a good source of shelter and food and supporting a high density of rodents like common voles, *Microtus arvalis* (Heroldová et al., 2007). Predators could thus be especially attracted to this crop (Koks et al., 2007), and then develop a specialization inducing the lower survival rates of animals released on alfalfa.

Batch effect found in the vegetative cover experiment for unharvested wheat and alfalfa plots (monthly survival rates 2 to 3-fold higher between batches, Table 3) raised some questions. Indeed, in the two plots of each crop, other factors could have influenced hamster survival. Batches could have been subject to different local conditions like cover density and/or predation pressure and more detailed studies controlling these parameters are required to conclude on crops' effect. In addition, further studies in various climatic conditions are also needed to conclude on the impact of alfalfa vegetation cover on released animals.

As expected, harvest increased mortality and timing of harvest also had a negative impact on the number of litters that could be born (Out et al., 2011). Negative impact of cover removal has already been reported for wild hamsters (Kayser et al., 2003) and other rodents (meadow vole *Microtus pennsylvanicus* and montane vole *Microtus montanus*, Jacob, 2008). Our experiment thus confirmed this general result. For prey species, shelter is crucial for hiding from predators (Jacob, 2008). Harvest, by reducing cover, makes rodents easier to detect for birds of prey, leading to an increased hunting success (La Haye et al., 2010; Toland, 1987). In addition, cover removal drastically reduces food availability, and can compromise food storage and thus winter survival (Kayser et al., 2003; La Haye et al., 2010). To alleviate the impacts of this agricultural practice and because unharvested wheat is not sustainable, it would be wise to test alternative agricultural management. In the future, it would be beneficial, for example, to assess the impact of postponing harvest date by cultivating late wheat varieties, leaving high stubble after harvest or sewing intermediate crops immediately after wheat harvest.

4.2. Time effect

We did not detect any critical period after the release date, contrary to what has been observed in another experiment on released hamsters (Müskens et al., 2008) or on other species (rabbit *Oryctolagus cuniculus*, Rouco et al., 2008). In both our experiments, released animals had constant survival rates over time except for the groups that had to face harvest.

Unlike other reintroduced endangered species (Jule et al., 2008), our results suggested that reproduction of common hamster after restocking is not a critical point of such conservation programs. Our experiments showed that reproduction was always effective if females survived long enough (>10 weeks) to adapt to their new environment, mate and wean their young. Moreover, second litters were almost always raised successfully if they survived at least seven additional weeks. Even if we did not have information about the behaviour of released hamsters, they seemed to mate successfully in the wild and females were able to wean their litters. It also seemed that survival time after release was the most critical point to ensure reproduction in situ. Hamster conservationists have to delay released animals' death as much as possible to ensure a reproductive success high enough to compensate for losses and drive a positive demography.

4.3. Effects of individual characteristics

In the fence experiment, we found a higher survival in females than in males. Lower survival in male hamsters was also reported in the Netherlands (4 months survival rates: 60% for females, 40% for males, Müskens et al., 2008). Females have smaller home ranges than males (van Wijk et al., 2011), they are thus more familiar with their surrounding than males are. In addition, during the mating season, males are actively roaming for females over longer distances (van Wijk et al., 2011) leading to higher chances of being detected by predators. This sex-specific difference in survival is widespread among mammals, the 'risky male behaviour hypothesis' is also known for Vancouver island marmot (*Marmota vancouverensis*, Aaltonen et al., 2009), grey mouse lemur (*Microcebus murinus*, Kraus et al., 2008), field and sibling voles (*Microtus agrestis and rossiaemeridionalis*, Norrdahl and Korpimäki, 1998).

Finally, we detected a simple linear negative impact of frequency of burrow change on individual survival. Our results tended to demonstrate that higher mobility increased the predation risk, which is in accordance with studies on field and sibling voles (Norrdahl and Korpimäki, 1998). Rather than mobility per se increasing encounter probability with predators, it is probably the unfamiliarity with the environment which is responsible for higher mortality (Norrdahl and Korpimäki, 1998). Indeed, when inhabiting an unfamiliar area, rodents show more active behaviour, prospecting their surrounding to discover resources, threats, congeners, and to create a complex system of chemical scent-marked trails (Andrzejewski, 2002). Animals reintroduced in an unknown environment may suffer from foraging deficiency and decreased ability to find shelter and avoid predators (Calvete and Estrada, 2004). Behavioural studies are needed to understand the mechanism underlying the positive relationship between frequency of burrow change and predation rate.

4.4. Management implications

Threatened species like the common hamster, which should be the primary target of reintroduction, translocation and restocking programs, are also the ones for which demographic parameters are the least available (Sarrazin and Barbault, 1996). As a consequence, conservation programs are launched even with deficient knowledge, because time needed to understand the system as a whole can compromise the survival of the species. This study highlights the benefit of modelling survival probabilities of reintroduced animals thanks to post-release monitoring to determine how survival and reproduction are influenced by components of restocking strategies. Despite the low sample size, it seems that restocking success is greater if hamsters are released inside electric fences and within unharvested wheat plots which provide sufficient protective cover for a long period of time. In addition, it would be better to release hamsters in early spring, thereby extending the breeding season, allowing released females to raise two litters (Harpenslager et al., 2011) and giving enough time for their offspring to store food for hibernation. The level of predation mainly depends on the seasonal availability of vegetation cover, but fluctuations in vegetation height are inherent to agro-ecosystems (Jacob, 2008). Hence in the Alsatian agricultural landscape, cultivated mostly with spring crops, which leads to an increased predation risk due to bare soil during the reproductive period in spring, small fields cultivated with a diversity of suitable crops for the species have to be promoted to allow displacement and survival after yearly environmental changes (Ulbrich and Kayser, 2004). In this kind of landscape, release areas have to be chosen by favouring high density of favourable crops but also by ensuring a permanent vegetation cover during several years on the release sites, in accordance with farmers, who are key actors for the preservation of this species which is dependent on the agricultural landscape.

For a prey species like the common hamster, predation vulnerability after release seems to be a critical factor (La Haye et al., 2010). Given the fact that captive bred hamsters are not exposed to predators during their early development stage, their behavioural response to predation risk can be altered (Jule et al., 2008). For this reason, any direct or indirect reduction of predation pressure can have a positive impact on the fate of reintroduced animals. Predation pressure can be reduced either thanks to extrinsic factors such as anti-predator device and improvement of shelter availability, tested in this study, but also by relying on the intrinsic characteristics of released animals (anti-predator behaviour, innate fearfulness; Griffin et al., 2000). It would be wise to focus on this last point in the following years. Direct comparisons between captive and wild animals (Aaltonen et al., 2009) could help to evaluate the suitability of captive born individuals for release, and if necessary, to develop new breeding methods (Griffin et al., 2000).

Acknowledgments

We thank J. Hoffmann and S. Rostaing for field assistance, P. Aubry and C. Calenge, for their participation in developing the sampling scheme and their contribution to preliminary data analyses. We are in debt to G. Daniel who planned the fence experiment and contributed to develop field methods and Dutch scientists: M.J.J. La Haye, G.J.D.M. Müskens, and R.J.M. Van Kats for invaluable advice. This project could not have been successful without support of local and agricultural authorities and, most of all, without involvement of all the farmers of Blaesheim district. We thank the association "Sauvegarde Faune Sauvage" which carefully breeds hamsters to be released and continuously improves the breeding units. We acknowledge F. Capber, the veterinarian who cares for the breeding units and performed all surgeries to implant transmitters. Thoughtful and patient suggestions from M.J.J. La Haye, G.J.D.M. Müskens, Y. Paillet, M. Pellerin, T. Reiners, M. Sage, proofreading by C. Carter, English translator, and relevant comments from three reviewers improved this manuscript. Financial support was provided by the French Ecology Ministry and Sanef Abertis group.

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