Inter-Research Science Publisher

Endangered Species Research
Volume 57:119–141

Published June 5, 2025
https://doi.org/10.3354/esr01409

OPEN ACCESS

Extinction lurks for a flagship species in agricultural habitat: three years of supplementation of the common hamster in Belgium

Sarah Descamps[1,2,*], Alain De Vocht[1,2]

[1]PXL BIO-Research, 3590 Diepenbeek, Belgium
[2]Hasselt University, Centre for Environmental Sciences, 3590 Diepenbeek, Belgium

ABSTRACT: The first common hamster *Cricetus cricetus* species protection program in Belgium was conducted between 2015 and 2021. Within this Flemish government program, annual introductions of captive-bred hamsters into the population in Widooie (Tongeren) occurred from 2019 to the present. Monitoring of motion, survival, habitat selection, and reproductive parameters of introduced individuals was carried out to evaluate the success of the conservation actions. Remote sensing techniques; specifically, VHF transmitters, camera traps, and desktop spatial analyses, were used during 3 consecutive years to acquire and analyze data from 52 introduced hamsters (12 males, 40 females). The overall survival rate of introduced males in the first months after introduction (75.00% after the first month, which dropped to 8.33% by the end of the third month) was significantly lower than findings from other studies. We identified a lack of local optimal habitat with connecting elements as a possible driver for this reduced survival. The reproductive data showed that the introduced females in Widooie produced a limited number of litters in a season. Also, the median number [IQR] of pups per litter 1 [1–2] is too low to keep the population size of this prey species at a stable population level. We hypothesize that the females cannot consume enough animal and/or plant proteins before and during the reproductive period, which could endanger pregnancy, lactation, and thus litter size. Failing to address the declining reproductive rate in the wild poses a substantial threat to the conservation of endangered hamster populations.

KEY WORDS: *Cricetidae* · Agricultural biodiversity · Telemetry · Reproduction · Locomotor behavior · Survival · Prey species

1. INTRODUCTION

The biodiversity crisis has been acknowledged for at least 30 yr (Bellard et al. 2022, Prakash & Verma 2022, Hochkirch et al. 2023). Current extinction rates of mammals and other taxa are higher than would be expected from the fossil record, highlighting the need for effective conservation measures (Barnosky et al. 2011). This sixth mass extinction of the earth's biodiversity distinguishes itself from previous comparable events due to the origin of the decline, initiated by human activities (Cowie et al. 2022). Some major drivers are global warming along with habitat fragmentation and loss caused by the spatial expansion of human activities such as agricultural intensification, with human population growth and increasing per capita consumption acting as the overarching drivers (Green et al. 2005, Malcolm et al. 2006, Pimm 2008, Kehoe et al. 2017a, Bellard et al. 2022). Moreover, the extinction rate of critically endangered mammals has more than doubled since 1900 (Pimm et al. 2014).

One mammalian species on the brink of extinction is the common hamster *Cricetus cricetus*. Originating from the Asian steppes in the Pleistocene, during the

*Corresponding author: sarah.descamps@pxl.be

Publisher: Inter-Research · www.int-res.com

Holocene, the hamster populations extended to western, central, southeast, and eastern Europe due to a changing climate and landscape dynamics. In particular, the cultivation of agricultural crops, resulting in the creation of a secondary (cultural) steppe, has facilitated the spread of several rodent species in the last centuries (Kozyra et al. 2021). In the past, the common hamster was considered to be an agricultural pest species, with densities up to 2000 ind. ha^{-1} (Nechay 2005). However, since the 1980s, its populations have been declining at a dramatic rate, beginning in the western part of Europe and later extending throughout the rest of the continent. Some major drivers include global warming, habitat fragmentation, and the spatial extension of human activities including agriculture and its intensification (Kehoe et al. 2017b, Spooner et al. 2018). Currently, the species' range is highly fragmented across different European countries (Surov et al. 2016).

1.1. Conservation status in Europe

The adverse and diminishing conservation status of the common hamster is systematically documented in the latest Article 17 of the EU Habitats Directive Species Assessment, in which it is categorized as a U2 species for the European Atlantic region (European Commission 2019). In 2008, a Standing Committee of the Bern Convention underscored the imperative to prevent the extinction of *C. cricetus*, listed in Annex II of the Bern Convention, specifically in Germany, France, Belgium, and the Netherlands (Convention on the Conservation of European Wildlife and Natural Habitats 2008). The enhancement of this conservation status is additionally mandated through the Habitats Directive (92/43/EEC) for EU Member States in which the common hamster is designated as an Annex IV species. This obligation led to a formal notice by the European Commission in 2004 to the Flemish and Walloon governments, elucidating their non-compliance with Article 10 of the Habitats Directive (European Commission 2004). The Commission concluded that Belgium had inadequately exerted efforts to achieve a favorable conservation status and displayed insufficient emphasis on a comprehensive inventory of the species. The Western European countries aim to achieve these conservation goals through national and regional species protection programmes (SPPs) for the common hamster, primarily encompassing breeding, introduction/restocking of the species, and habitat enhancement through Agri-Environmental Climate Measures (AECM). Presently, most of the SPPs fall short of their objectives due to a lack of knowledge, innovation, and allocation of financial resources.

In response to the drastic decline in Western Europe, a breeding program was initiated in the Netherlands in 1999, aiming to preserve the genetic lineage of the common hamster in the westernmost distribution of the species (La Haye et al. 2012b). Initially, individuals from the population in Heer (the Netherlands) were bred, and in subsequent years, 2 Belgian males from Bertem (Belgium) and 1 male from Neuss (Germany) were introduced to the Dutch breeding program. Multiple breeding lines were maintained (La Haye et al. 2012a), forming the genetic lineage of the BNN region (Belgium, the Netherlands, and the German state of North Rhine-Westphalia) (Fig. 1). Surplus individuals from the breeding program were used to supplement wild populations in the Netherlands and Belgium (Agentschap voor Natuur en Bos 2015). In 2017, the Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen (LANUV) established a breeding station for the species with the BNN genetic lineage in Metelen (Thimm & Geiger-Roswora 2021).

At the end of the 20th century and the onset of the 21st century, 4 extant wild hamster populations existed in Belgium, situated in loam soil in the south and southeast of the province of Limburg and Flemish-Brabant, and the north of the province of Liège. Despite a formal warning to the Flemish and Walloon governments in 2004 (European Commission 2004), negative advice by the Standing Committee of the Bern Convention in 2008 (Convention on the Conservation of European Wildlife and Natural Habitats 2008), and supplementation of wild populations in 2007 and 2008 (La Haye et al. 2012a), 3 of the 4 remaining populations in Belgium became extirpated after 2012, with only 1 population remaining in Widooie (Fig. 1). Consequently, in 2015, the Flemish Minister of Environment endorsed the 'Hamster Protection Plan' with the aim of achieving the European nature target for hamsters in Flanders (Agentschap voor Natuur en Bos 2015). In the context of the 6-yearly reporting obligations to Europe, the Flemish LSVI-tables (Lokale Staat van Instandhouding) indicate that a favorable state of the species is achieved when a local population size exceeds 500 burrows and the metapopulation consists of at least 19 490 individuals connected through functional corridors (Lommaert et al. 2020).

The restricted size of the relic population in Widooie (Tongeren), wherein the observed count of summer burrows is notably low (Fig. 2), led to the decision in

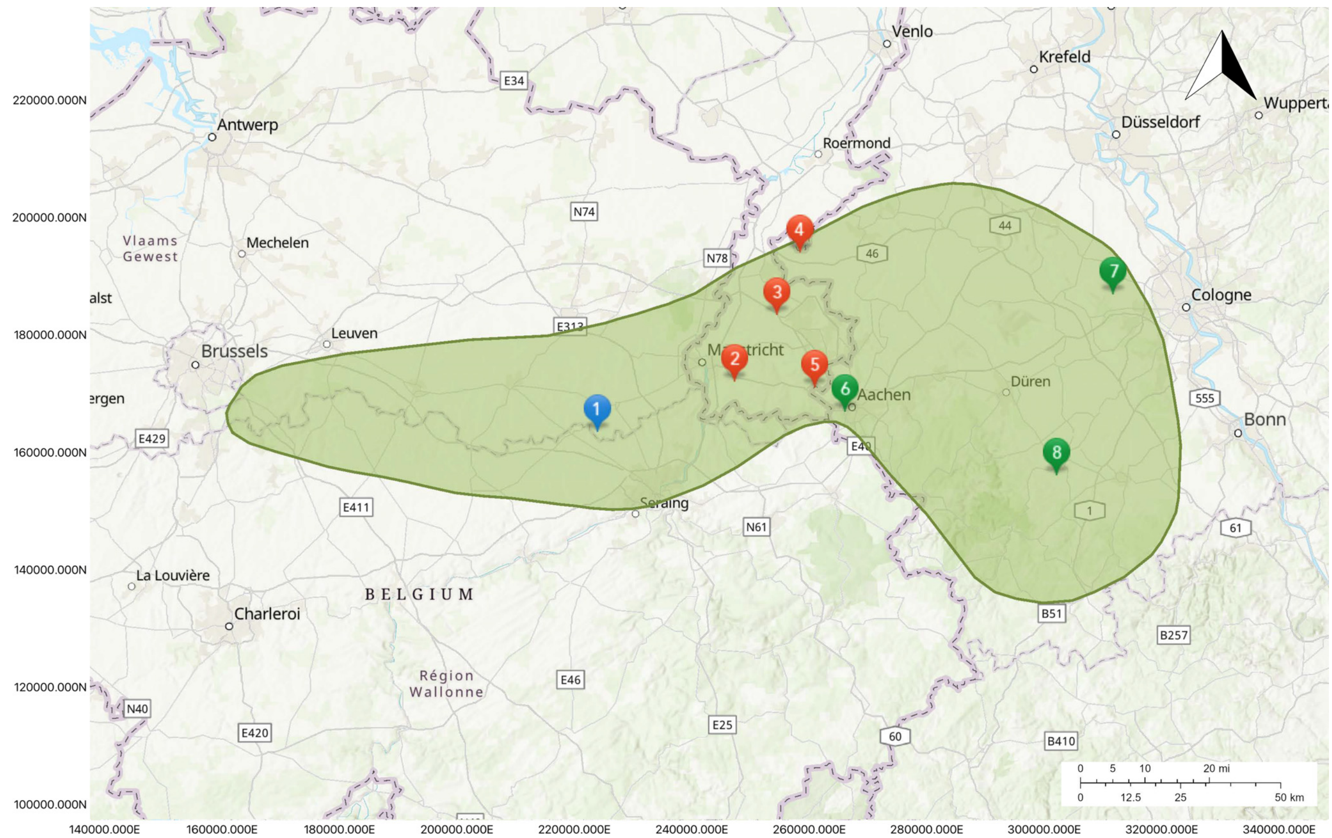

Fig. 1. Remaining populations of the common hamster within the BNN region (Belgium [blue], the Netherlands [red], and North Rhine Westphalia-Germany [green]). Green area: historical distribution of the species until the middle of the previous century. 1: Widooie; 2: Amby-Heer-Sibbe; 3: Sittard-Puth-Jabeek-Bingelrade; 4: Koningsbosch; 5: Heerlen-Wittem; 6: Aachen; 7: Rommerskirchen/Pulheim; 8: Kreis Euskirchen. Coordinates are given in the EPSG:31370 Belgian Lambert 72 projection

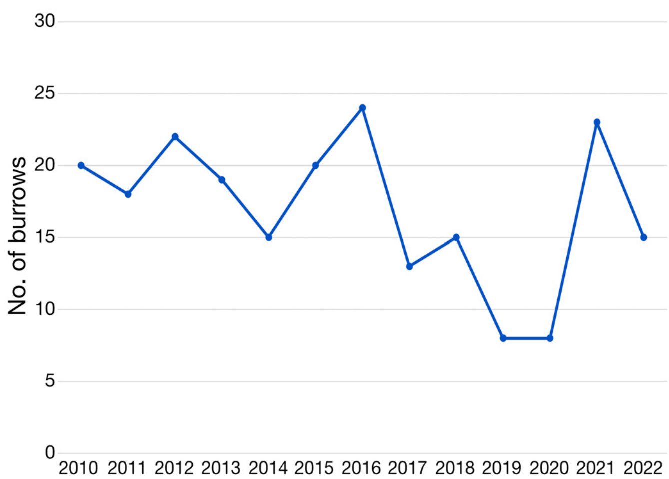

Fig. 2. Absolute number of detected common hamster burrows during the summer monitoring in Widooie from 2010–2022 (Ruyts et al. 2023)

the regional SPP to introduce hamsters through a breeding program, along with habitat improvement. The first introduction of captive-bred hamsters from the BNN line in Widooie took place in the spring of 2019, followed by second and third introductions in 2020 and 2021. To assess the performance of these introduced animals within the relic population in Widooie, an ecological study was initiated. Monitoring encompassed the tracking of movement patterns, survival rates, habitat selection, and reproductive success. This investigation aimed to assess the efficacy of the introductions in Widooie, serving as a crucial method to assess processes and improve the actions taken in introduction programmes.

1.2. Activity period and reproduction

The common hamster, a species characterized by solitary behavior and burrow excavation, exhibits an activity period extending from the beginning of April to the onset of November, with a subsequent entry into hibernation (Monecke & Wollnik 2004, Franceschini-Zink & Millesi 2008a). Its average lifespan is estimated to be around 2–3 yr (Weinhold & Kayser

2006). However, only a minority of individuals in the field live longer than 1 yr, with females exhibiting a higher annual survival rate than males (Kuiters et al. 2010, La Haye et al. 2020).

Functioning as an *r*-strategist, the common hamster exhibits a polygamous reproduction system, whereby the production of numerous litters, each comprising a substantial number of pups, upholds its population dynamics. In Western Europe, the reproductive season spans from early May to mid-September, theoretically allowing the production of 3–4 litters with 4–12 pups (Weinhold & Kayser 2006, Franceschini-Zink & Millesi 2008a, Harpenslager et al. 2011, Surov et al. 2016, Wilson et al. 2017). The gestation period ranges from 17–20 d for the initial litter to 37 d for subsequent litters (Vohralík 1974, Wilson et al. 2017). Females can undergo postpartum estrous, leading to subsequent fertilization (Franceschini-Zink & Millesi 2008a, Harpenslager et al. 2011). In adequate habitats that offer substantial cover against predators and an ample food supply, hamster populations can persist under high predation pressure. This pressure becomes problematic when agricultural measures cut back the hamster's reproductive season or when the number of offspring is insufficient to offset predation-induced mortality. Analysis of historical and contemporary data on reproduction in the entire dispersion region of the common hamster revealed that a negative trend in litter size has persisted since 1954 (Surov et al. 2016). The mean number of pups per litter dropped to 3.43 in the period 1996–2015, with a sharp decline of the mean annual litter number post-1986 to 1.63 per female. Possible factors contributing to this decline include climate change, landscape fragmentation, light pollution, pesticides, altered reproductive cycles, fur harvesting, population density, and decreased lifespan (Surov et al. 2016).

A study in the Netherlands observed a stable population when each female raised 2 nests per season, consisting of 5–6 pups each, highlighting crop management during the breeding season as the key limiting factor, heightening predation risk and limiting the mobility of pregnant and lactating individuals (La Haye et al. 2010, 2014). Two intrinsic factors were found to influence yearly offspring production: the age of females and their spring body condition (Siutz & Millesi 2021). Early spring emergence of reproductive females is correlated with an increased number of litters and offspring production compared to those with later vernal emergence (Franceschini-Zink & Millesi 2008a). Modern agricultural constraints typically permit only one nest due to limited time until harvest (Harpenslager et al. 2011). Adequate cover in the form of unharvested crops with minimal visibility is crucial for females to survive and produce multiple litters during the reproductive season. Following birth, a minimum of 3 wk of sufficient coverage is imperative to prevent predation of the female or to avoid abandonment of the burrow and offspring. Subsequently, the offspring can venture out to find a suitable field and construct a burrow of their own (Müskens et al. 2019).

Reproductive data from studies conducted between 2010 and 2023 across various West European farmland regions with hamster populations indicate a decrease in the number of litters per female and reduced pup counts per litter (Table 1).

1.3. Survival and movements

The survival rate of adult animals bred in captivity and then introduced into the field is 63% in the first month; this rate increases to 89% in the third month after introduction and at that point is roughly equal to the survival rate of wild individuals (Harpenslager et

Table 1. Reproductive success of the common hamster *Cricetus cricetus* in West European countries during the period 2010–2023. NA: not available

Pups litter^{-1}	Litters female^{-1}	% Females with a second litter	% Females with no litter	Year	Country	Reference
NA	Wild: 2.47 ± 0.96 (SD) Introduced: 1.57 ± 1.07 (SD)	50	35.00	2011	Netherlands	Harpenslager et al. (2011)
First litter: 3, 4 Second litter: 3	1.5	36.84	26.32	2013	Germany	Albert (2013)
3.3 ± 0.8 (SE)	NA	NA	NA	2015	France	Tissier et al. (2018)
2.67 ± 1.47 (SE)	0.90 ± 0.95 (SE)	8.82	45.16	2014–2017	France	Kourgy et al. (2019)
1.03	NA	27	NA	2022	Germany	Kondla (2023)

al. 2011). It must be noted that this estimate includes both sexes; however, males are known to have a high death rate in the first month due to their risk-taking behavior in traveling long distances in the search for females and territory, which makes them more vulnerable to predation. The average survival of a captive-bred hamster in the wild is <3% for 1 yr compared to 20% for wild hamsters, with wild female hamsters having the highest average survival rate (La Haye 2008). It is assumed that the high mortality rate of introduced animals is caused by unfamiliarity with the habitat and the associated predators. The fact that females exhibit less risk-taking behavior than males is shown by the smaller home range of females (0.2–0.44 ha) compared to males (1.66–2.48 ha) (Weinhold 1998, Kayser 2002, Ulbrich & Kayser 2004). The longest average distance covered by hamsters in Germany was 220 m for male individuals versus 191 m for female hamsters (Ulbrich & Kayser 2004), although individuals have been recorded traveling >1 km (Kupfernagel 2008). Juvenile dispersal in France reached a maximum of 1.9 km (Kourgy et al. 2019). Predation is the leading cause of death during the activity season in the Netherlands and Germany, with foxes, mustelids, and birds of prey serving as main predators (Kayser et al. 2003, La Haye et al. 2010, Van Wijk et al. 2011).

2. MATERIALS AND METHODS

2.1. VHF transmitter implant procedure

Prior to introduction, a radio-transmitter (Advanced Telemetry System [ATS], R1170, 4 g; Fig. 3) was inserted intraperitoneally under brief isoflurane anesthesia in 46 introduced captive-bred hamsters (12 males, 34 females). Six hamsters (all females) trapped in the wild were also equipped with this transmitter (Fig. 4). Captive-bred individuals had a recovery time of at least 4 d. Wild-caught animals were released the same day of the procedure. All applicable national and institutional ethical guidelines for the care and use of animals were followed.

The objective of observing the 6 wild-caught females was to explore potential differences in reproductive success between introduced and wild females. From 21 April to 14 May 2021, a total of 15 live traps were deployed daily around the locations of the winter burrows for a period of 17 d to capture and tag female animals. During this interval, 11 males and 6 different females were caught. The males were immediately released and the females received an implant transmitter on the day of capture. Following a recovery period and a health check on the same day, which included an assessment of the animal's alertness, eating, and excrement behavior, the female was released back into her original burrow.

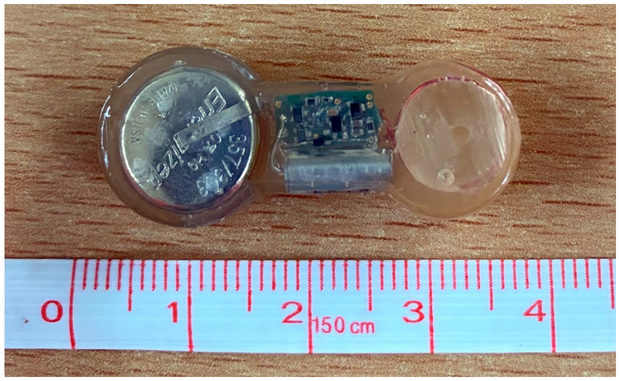

Fig. 3. Example of an ATS R1170 radio transmitter used to monitor the movements of captive-bred and wild common hamsters

2.2. Introductions

In the years 2019–2021, a total of 165 captive-bred hamsters from the BNN breeding line, bred at GAIA-zoo (NL), were released by the Agency of Nature and Forest (ANB) at various introduction sites with AECM measures within a small area of arable land with high agricultural activity in Widooie (Tongeren; 50° 45′ 54″ N, 5° 24′ 24″ E) (Fig. 4). These individuals were placed into artificially constructed burrows. Briefly, holes measuring approximately 8 cm in diameter and 120 cm in length were drilled at a 45° angle using a hand drill. The burrows were provisioned with a mixture of grains and sunflower seeds, along with a piece of apple. Following the placement of the animal in the burrow, the entrance was sealed with a plug made of grasses or alfalfa (Müskens et al. 2020). This measure was implemented to prevent immediate roaming-induced stress after introduction, thereby reducing the susceptibility of the introduced individuals to predation.

2.3. Mobility, survival, and reproductive parameters

Animals fitted with VHF transmitters were located through triangulation 3 times per week during the first month after being introduced to the field, using a

Date of introduction	No. introduced		No. with VHF transmitter		Crop type	Electric fence
	M	F	M	F		
11/06/2019	16	10	2	3	AECM alfalfa/grasstrip mix (3)	X
10/07/2019	8	8	2	3	AECM alfalfa/grasstrip mix (1)	
08/05/2020	15	12	4	7	AECM alfalfa/grasstrip mix (5)	X
	14	13	4	7	AECM alfalfa/grasstrip mix (1)	X
20/05/2021	7	8	0	5	AECM alfalfa/grasstrip mix (5)	X
	7	8	0	5	AECM alfalfa/grasstrip mix (1)	X
30/07/2021	13	7	0	4	AECM fauna crop mix (2)	
	13	6	0	0	AECM fauna crop mix (4)	
	93	**72**	**12**	**34**		
Wild			0	3	AECM alfalfa/grasstrip mix (5)	X
23/04-15/05/2021			0	2	AECM alfalfa/grasstrip mix (1)	X
			0	1	AECM mixed crop (6)	
	Total introduced	**165**	**Total tagged**	**52**		

Fig. 4. Overview of the introduced and radio-tagged common hamsters (M: male; F: female) from 2019 to 2021 with the respective crop type and whether or not the introduction site was surrounded by an electric fence to protect the hamsters from ground-dwelling predators. All captive-bred hamsters were introduced in an artificial burrow within a field under Agri-Environmental and Climate Measures (AECM) which provided sufficient cover and food at that time

VHF receiver (ATS R410, 150 MHz) and a low-frequency loop antenna. The precise geographical coordinates of the tagged animals were systematically recorded in a geo-referenced database (Field Maps, ArcGIS). After this initial month, the tracking frequency of the hamsters was adjusted to 2 times per week, which persisted until the end of September. Thereafter, the tracking regimen transitioned to a weekly frequency until the termination of the monitoring period: the end of September in 2019 and the end of October in 2020 and 2021. Individuals who were not found in the vicinity of their previous location were subsequently sought within a 500 m action radius (representative of the average hamster activity radius) of their prior location. The minimal convex polygon (MCP), which is a measure of home range, the maximum distance from the introduction point, and the maximal distance between 2 consecutive location points (approximately 2–3 d displacements) were determined for each individual.

Hamsters that could not be located within a 1000 m range were assumed to have been depredated and subsequently removed from the surveyed area, as the batteries of the ATS VHF transmitters demonstrated reliability in a prior long-term telemetric study (Descamps & De Vocht 2016). Causes of death were determined from tagged hamsters whose remains were found. Individuals displaying a slow VHF signal in their burrows were considered deceased. Monthly survival was determined for each sex, and to obtain a more precise understanding of the survival of all animals equipped with VHF transmitters, the Kaplan-Meier estimate (which accounts for variability in group sizes and non-constant survival over the years) was used (Kaplan & Meier 1958). To gain a more nuanced understanding of whether the introduction of individuals within an electrically wired enclosure (hereafter, fence) in Widooie might influence their survival, female hamsters were stratified based on this variable. Males were excluded from this analysis due to the observation that most of them commenced movement beyond the fence on the initial day of release. The mesh size of the fence enabled hamsters to move freely in and out, while ground predators such as large mustelids and foxes could be kept out. Reproductive activities were monitored using cameras strategically positioned at the entrance of the burrows for each female. The cameras were set up 10 d prior to the earliest anticipated emergence of pups from the burrow (30 d after introduction or previous birth date). The reproductive period of the individuals was mapped based on the different timing of introductions.

2.4. Habitat mapping

To understand the habitat selection patterns of the hamsters, a weekly habitat survey was conducted throughout the activity periods in both 2020 and 2021. The survey comprised all agricultural plots within a 500 m radius (141 plots, 295 ha; hereafter designated as the 'hamster area') surrounding the most central release site. Crop type, crop height (m), crop density (% coverage m^{-2}), and executed measures were recorded in a geo-referenced database (ArcGIS Field Maps).

2.5. Data analysis

Given that most of the collected data were skewed (Shapiro-Wilk's test, $p < 0.05$), statistics were performed using non-parametric tests, such as the Kruskal-Wallis test for multiple samples and the Mann-Whitney *U*-test for 2-sample comparisons. The data were analyzed using IBM SPPS Statistics (v.25). Spatial analyses were executed with QGIS (v.3.30) (QGIS.org 2023). To analyze the impact of the habitat and movements on the survival of the hamsters, boosted regression trees (BRTs) were used. This technique aims to improve the performance of a single model by fitting multiple models and combining (boosting) them for prediction (Elith et al. 2008). BRT models are known to have several advantages, including the capacity to combine predictor variables of different data types and accommodate missing data values. We developed BRTs using the 'gbm' package in R (Ridgeway et al. 2024). The optimal values of the learning rate and tree complexity were derived by performing a grid search using the 'train' function of the 'caret' package in R (Kuhn 2008). The habitat and movement variables used to model the survival of *Cricetus cricetus* are provided in Table 2.

3. RESULTS

3.1. Movements

Based on the localizations of the animals, the median [IQR] of the maximum distance from the release location and maximum distance covered between 2 consecutive location points (approximately 3 d of movements) was calculated for the different sexes for the years 2019–2021 (Table 3). The data revealed an overall median [IQR] maximal distance from the introduction site of 96.73 [49.98–244.07] m for males and 133.19 [55.95–410.46] m for females. The overall

Table 2. Boosted regression tree model habitat and movement variables for introduced captive-bred common hamsters

Sex	0 Male 1 Female
Year	0 2019 1 2020 2 2021
Introduction crop	0 AECM Alfalfa 1 AECM Fauna crop mix 2 AECM Crop Rotation
Introduction period	1 May 2 June 3 July
Period out of alfalfa	1 Not leaving 2 May 3 June 4 July 5 August 6 September
To which crop	Crop where the individual is found after the largest distance between 2 subsequent locations 0 AECM Alfalfa 1 AECM Fauna crop mix 2 AECM Crop rotation 3 Wheat 4 Sugar beet 5 Mustard 6 AECM Gras strip mix 7 Barley 8 Potatoes 9 Spelt
Residence same plot	Does the hamster stay in the introduction plot throughout its entire survival period? 0 No 1 Yes
Survival days	Number of survival days during the monitoring period

median [IQR] distance between 2 consecutive localizations was 78.23 [40.80–167.26] m for males and 111.67 [35.83–322.47] m for females. Moreover, the median [IQR] of the MCPs for the different monitoring years were determined (Table 3, Fig. S1–S3 in the Supplement at www.int-res.com/articles/suppl/n057p119_supp.pdf). The overall median [IQR] MCP area covered a surface area of 1707.53 [812.37–12 884.32] m^2 for the males and 2456.18 [495.97–17 978.13] m^2 for the females.

Statistical analyses (Kruskal-Wallis) on all introduced females (n = 34) revealed a significant difference in the maximal distance covered between 2 locations (H_2 = 8.377, p = 0.015) during the different monitoring years. Moreover, a significant difference was found between the maximal distance from the introduction point (H_2 = 8.672, p = 0.013). Post hoc tests (Mann-Whitney U) (Table S1) demonstrated a statistically significant difference in the distance from the introduction point (U = 86.00, p = 0.027) and the maximal distance between 2 localizations (U = 83.00, p = 0.021) between the years 2020 and 2021, respectively. A significant difference in MCP area for the females was detected between the consecutive monitoring years (H_2 = 6.671, p = 0.036), specifically between 2020 and 2021 (U = 88.00, p = 0.032).

A Pearson correlation analysis revealed a statistically significant correlation between survival days and the maximal distance from the burrow where introduced (r = 0.333, p = 0.016), the maximal distance between 2 points (r = 0.355, p = 0.010), and the MCP area (r = 0.389, p = 0.004) covered by all tagged individuals (n = 52) in this study.

3.2. Habitat selection

Weekly habitat mapping conducted within a 500 m action radius of the main hamster residences, covering an area of 295 ha, offered a more detailed overview of the changes in the agricultural landscape over the course of several months during the hamster's active season (Fig. 5). A comparison of the percentage of favorable cover within the designated 'hamster area' for the years 2020 and 2021, based on spatial analyses, indicates that the area suitable for the hamster during its activity season was smaller in 2020 than in 2021 (Fig. 6). At the time that the captive-bred hamsters were introduced in 2020, only 7.52% of the total area displayed a suitable coverage percentage of 80% or more. The suitable plots were primarily confined to those featuring AECM alfalfa and were fragmented within the area. In contrast, during the corresponding period in 2021, a total of 45.73% of the area provided a suitable habitat, predominantly comprising plots with AECM alfalfa, AECM fauna crop mix, AECM crop rotation, wheat, and barley. These suitable habitats were more strategically arranged in a connected patchwork configuration. A comparison of crop differentiation in the selected area between June 2020 and June 2021 (Fig. S4) indicated no remarkable differences in crop distribution, with the only notable

Table 3. Overview of the movement analyses from male (M) and female (F) tagged common hamsters from 2019–2021. Wild-caught females in 2021 are shown separately (2021 wild) MCP: minimum convex polygon; IQR: interquartile range; (–) no data

Year	N		Median [IQR] max. distance from introduction location (m)		Median [IQR] distance between 2 consecutive localizations (m)		Median [IQR] MCP area (m^2)		Max. distance between 2 consecutive localizations—single individual (m)	
	M	F	M	F	M	F	M	F	M	F
2019	4	6	315.08 [287.43–507.37]	170.75 [77.37–380.54]	305.05 [214.20–372.46]	157.88 [51.34–260.75]	26724.07 [16689.25–42108.94]	4702.59 [598.71–18398.85]	389	395
2020	8	14	96.73 [49.98–109.01]	452.36 [117.07–703.26]	59.41 [40.80–98.18]	344.87 [112.42–630.19]	1439.24 [812.37–4340.06]	15807.41 [559.20–36438.72]	214	852
2021	0	14	–	62.97 [31.84–105.85]	–	36.82 [27.12–85.81]	–	913.02 [192.73–3786.56]	–	397
2021 wild	0	6	–	146.70 [69.36–238.70]	–	141.04 [61.21–210.83]	–	3408.58 [369.82–24711.73]	–	348
Overall	12	40	96.73 [49.98–244.07]	133.19 [55.95–410.46]	78.23 [40.80–167.26]	111.67 [35.83–322.47]	1707.53 [812.37–12884.32]	2456.18 [495.97–17978.13]		

change being a reduction in wheat cultivation and an increase in sugar beets in 2021.

Most female hamsters were introduced into an alfalfa plot (n = 36), which offered the best coverage and food availability at the time of introduction, and the majority of the individuals remained there for a while after being introduced (Fig. 4). In total, 17 of the 40 female hamsters stayed within their respective introduction plots during the complete monitoring period. When comparing short- and long-living female individuals (<90 versus ⩾90 survival days), more short-living individuals moved to different plots (n = 14) than long-living individuals (n = 9), but this difference was not significant (Fisher's exact test, p = 0.52). The proportion of the residence time in alfalfa versus other crops was not significantly different between the short- and long-living females (χ^2_1 = 0.035, n = 40, p = 0.85) (Table S2).

In this study, female hamsters that exceeded 120 d of lifespan (n = 7) consistently exhibited a tendency to relocate to alternative crops after their stay in the AECM alfalfa. Sugar beets, in particular, emerged as a favored choice towards the end of the season, preceding hibernation. During this period, sugar beets not only offered shelter but also served as a source of nutrition next to the AECM fauna crop mix and crop rotation (Fig. 7).

The 4 female hamsters that survived throughout the extended monitoring period until November 2021 established their winter burrows in specific plots featuring AECM. Two of them selected a winter residence within crop rotation, one within the fauna crop mix, and another within the gras strip mix.

3.3. Survival

The relative survival rates of male (n = 12) and female hamsters (n = 34) from the first to third month post-introduction were determined for 2019–2021 (Fig. 8, Table 4). In 2021, these same variables were determined for the 6 wild-caught females. Overall, the male and female hamsters had a first-month survival of 75 and 92.50%, respectively. This dropped to a third-month survival of 8.33% for the males and 47.50% for the females. The total median [IQR] number of survival days was 36.50 [22.25–48.25] d for males and 86.00 [56.50–113.75] d for females. At the end of the 3 mo monitoring period in 2019, 1 male and 4 females were still alive. At the end of the 5.5 mo monitoring period in October 2020, none of the 22 hamsters tagged that year had survived. At the end of the 6 mo monitoring period at the end of October

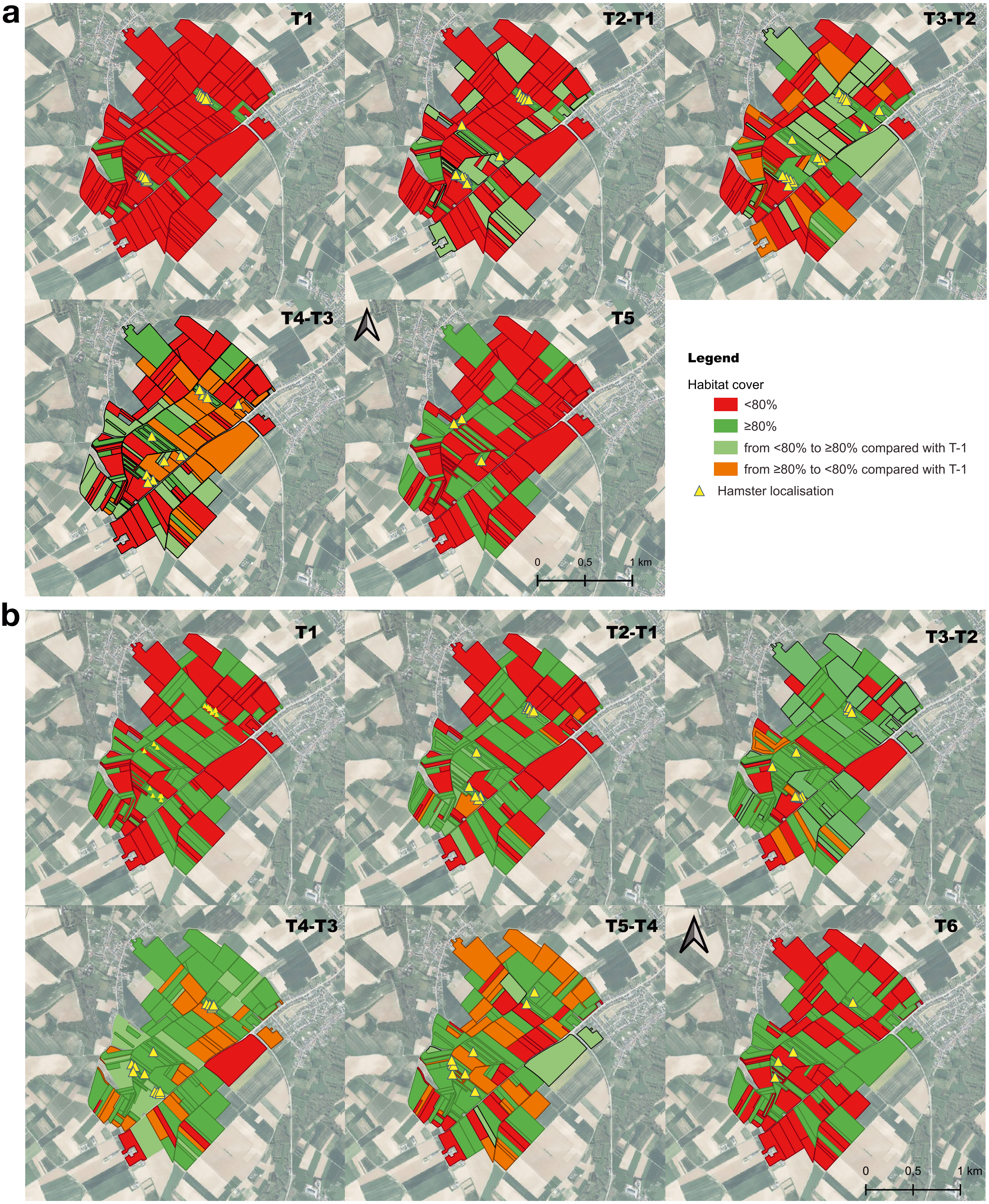

Fig. 5. Temporal composite of the change in habitat coverage and common hamster localization within the designated hamster area in (a) May to September 2020 and (b) May to October 2021. Colors represent habitat favorability: light green indicates plots that became more favorable for the hamster compared to the previous time point (T − 1); orange represents the plots that became more unfavorable compared to T − 1 (T1: May; T2: June; T3: July; T4: August; T5: September; T6: October)

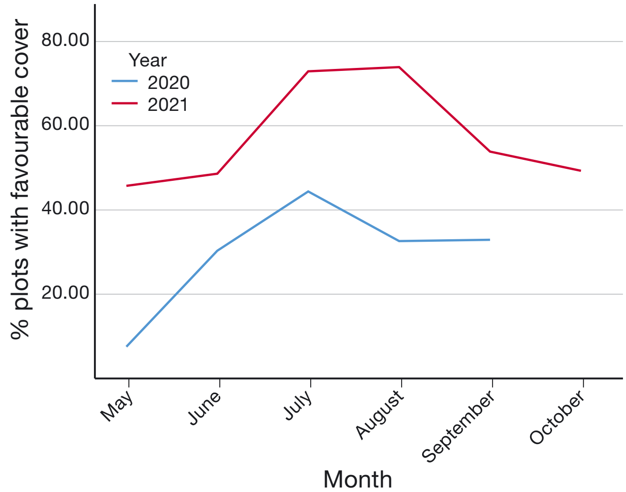

Fig. 6. Plots with favorable cover (>80%) during the activity season of the common hamster within the designated hamster area in 2020 and 2021

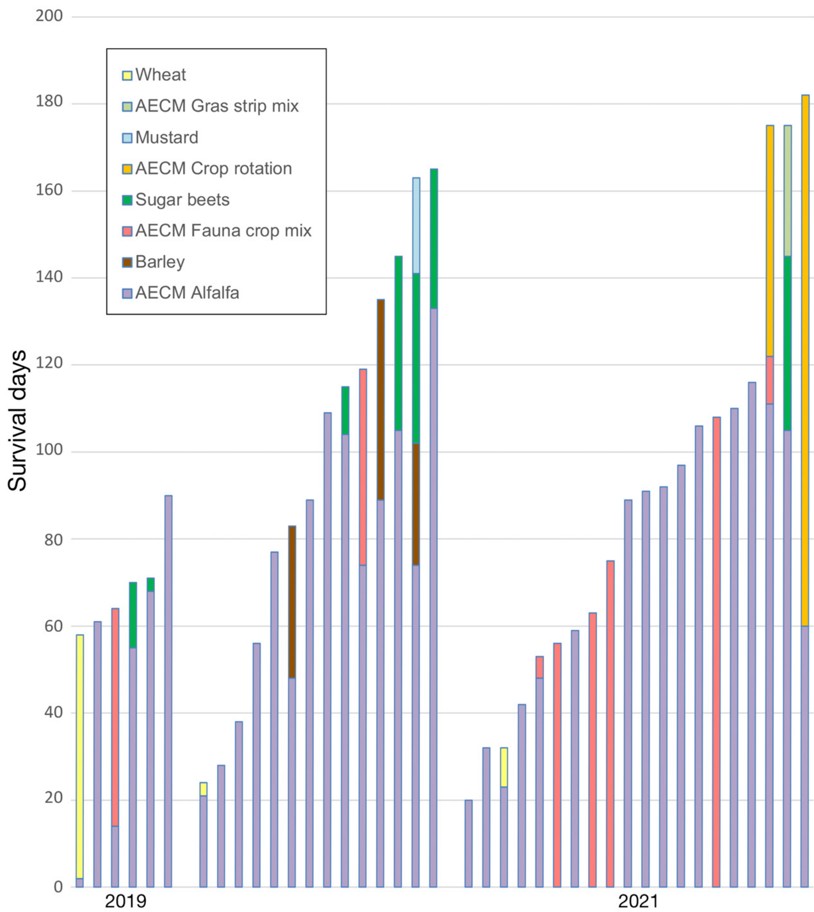

Fig. 7. Proportion of survival days for female common hamsters in different crop types during the monitoring period 2019–2021 (n = 40). Crop types with Agri-Environmental and Climate Measures (AECM) are adopted by farmers to provide sufficient cover and food for agricultural species such as the common hamster

2021, 4 tagged females were still alive: 2 that had been introduced and 2 that had been wild-caught in early spring. The wild-caught females (n = 6) in 2021 had slightly higher first- to third-month survival rates than their introduced female counterparts (n = 14): 100, 83.33, and 50% compared to 92.86, 64.29, and 35.71%, respectively.

A survival analysis (Mann-Whitney U) of all the tagged male and female individuals (n = 52) revealed a significantly higher number of survival days for females (n = 40) than for males (n = 12) (U = 66.00, $p \leqslant 0.001$) (Table 4). A Kruskal-Wallis test showed no statistically significant difference in the number of survival days for females across different monitoring years (H_2 = 1.482, p = 0.476).

An examination of the survival rate between wild-caught females (n = 6) and females introduced in spring (May–June, n = 27) or summer (July, n = 7) revealed a median [IQR] of 75.00 [32.00–186.00] survival days for the wild group and 90.00 [56.00–116.00] survival days for the captive-bred individuals introduced in spring. The individuals that were introduced in summer had a median [IQR] of 61.00 [61.00–75.00] survival days. A Kruskal-Wallis test showed no statistically significant difference between the number of survival days of wild-caught and captive-bred individuals introduced in spring or summer (H_2 = 1.094, p = 0.579).

Females introduced within a plot equipped without an electric fence (n = 10) exhibited a median [IQR] of 61.00 [50.00–83.25] survival days, whereas those within a fenced enclosure (n = 30) demonstrated 90.50 [57.50–120.75] survival days (Fig. S5). A Mann-Whitney U-test reported no significantly greater number of survival days between females introduced within or outside an electric-fenced enclosure (U = 107.50, p = 0.187).

The raw data from the monitoring periods reveal that 5 of the deceased female hamsters died within their burrow following the weaning of the first or second litter (Fig. 9). A total of 22 fell prey to predators while engaging in activities outside their permanent burrows or during dispersal in search of more favorable habitat. The remaining individuals perished directly (har-

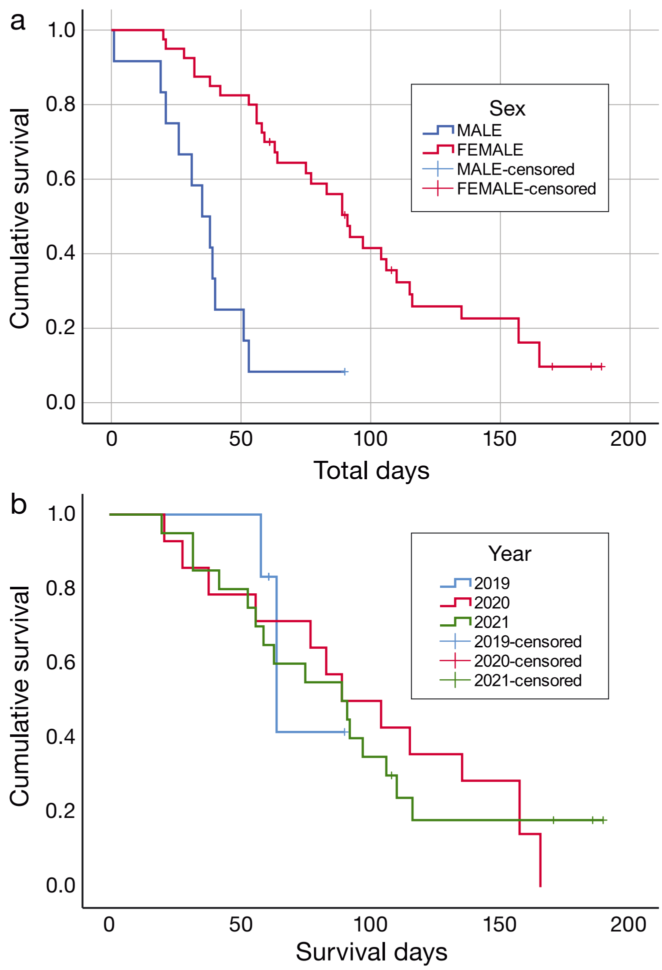

Fig. 8. Kaplan-Meier survival analysis showing cumulative survival versus number of survival days for (a) male (n = 12) and female (n = 40) common hamsters during 2019–2021 and (b) females (n = 40) from 2019–2021. Censored individuals were still alive at the end of the monitoring period

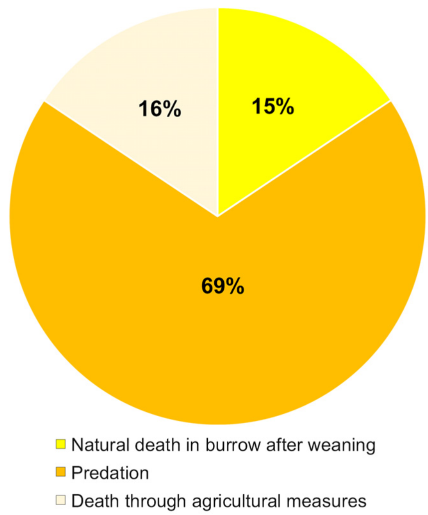

Fig. 9. Cause of death of tagged female common hamsters (n = 32) during the monitoring period (2019–2021)

vesting machines) or indirectly because of agricultural measures, such as the mowing of wheat and alfalfa, which resulted in an immediate loss of coverage and subsequent predation (n = 2). A total of 75% of those inhabiting sugar beet plots (n = 4) died during harvest at the end of the activity season.

3.4. Boosted regression trees

The optimal meta-parameter values for the BRT model included an interaction depth of 2, a learning rate of 0.001, a bag fraction of 0.7, and a minimum of 2 observations (Fig. S6). These settings resulted in an optimal final model with 3000 trees. The model led to a

Table 4. Overview of the relative survival over the first 3 mo post introduction of the tagged male and female common hamsters in Widooie from 2019 to 2021. Wild-caught females in 2021 are shown separately (2021 wild). (—) no data

Year	No. tagged		Relative first-month survival (%)		Relative second-month survival (%)		Relative third-month survival (%)		Median [IQR] cumulative no. of survival days	
	M	F	M	F	M	F	M	F	M	F
2019	4	6	75.00	100	25	83.33	25.00	66.67	42 [27.25–80.75]	61 [60.25–70.5]
2020	8	14	75.00	85.71	0.00	71.43	0.00	50.00	36.50 [19.50–39.75]	96.50 [51.50–157.00]
2021	0	14	—	92.86	—	64.29	—	35.71	—	90.50 [31.00–108.50]
2021 wild	0	6	—	100	—	83.33	—	50.00	—	75.00 [32.00–186.00]
Overall	12	40	75	92.50	8.33	72.50	8.33	47.50	36.50 [22.25–48.25]	86.00 [56.50–113.75]

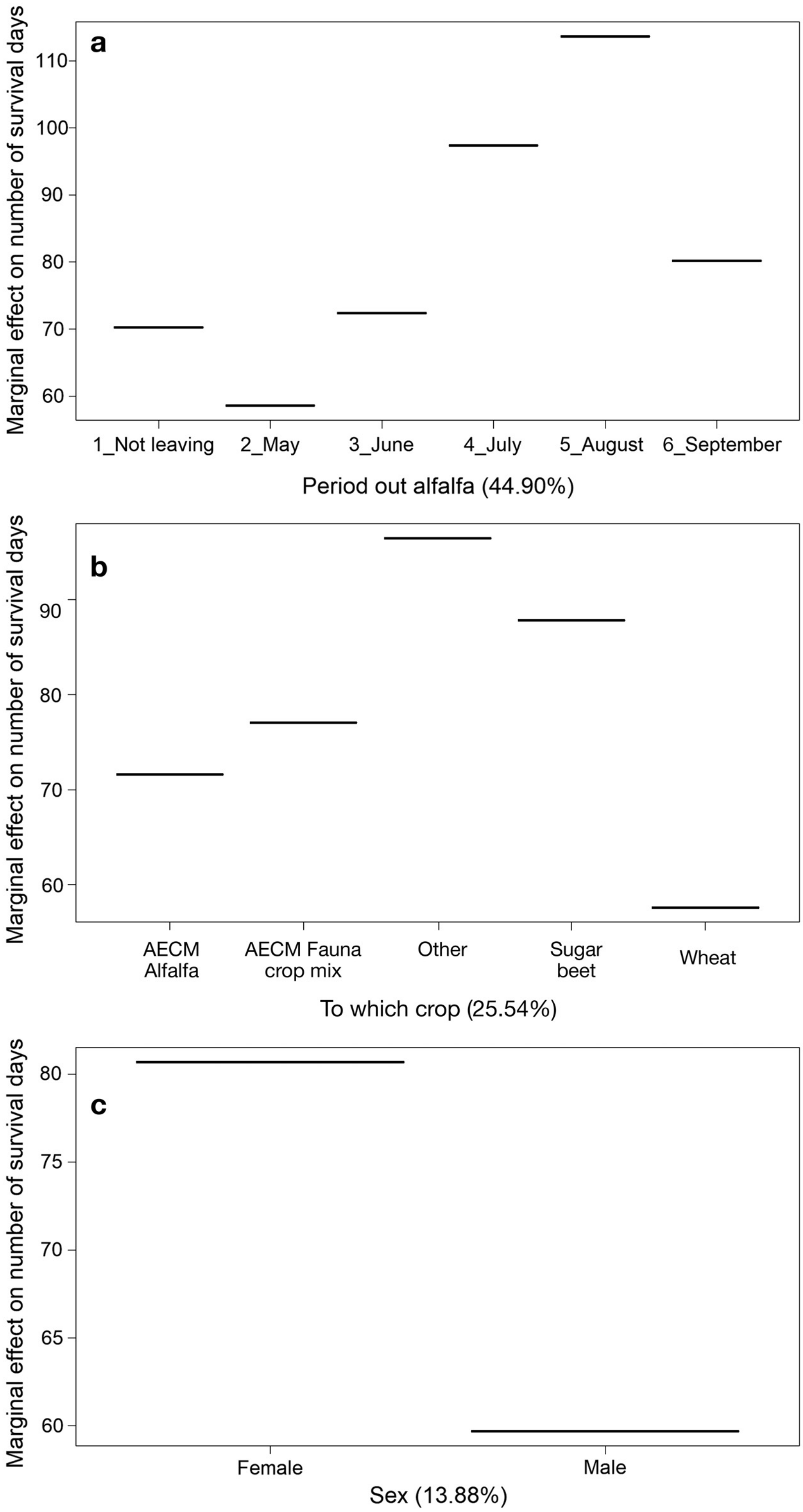

Fig. 10. Partial dependence plots of the response to the predictors in the boosted regression trees. The plots indicate the effect of each predictor on survival days of the studied common hamsters, given the average effects of all other predictors in the model. The relative importance (%) of each predictor is given in parentheses. (a) Effect of the month in which the hamster leaves the alfalfa plot, (b) effect of the crop type to which the hamster moves after leaving the alfalfa plot, (c) effect of sex

good fit of the training data ($R^2_{adj.train}$ = 0.490). After a 10-fold cross-validation, the model showed a $R^2_{adj.CV}$ = 0.416.

In the model, all 7 variables (Fig. S7) demonstrated a non-zero impact on survival days: 'year', 'sex', 'introduction crop', 'introduction period', 'period out of alfalfa', 'to which crop', and 'residence in same plot'. Furthermore, the relative importance of each variable was estimated, considering the number of times a variable was selected for splitting and the improvement to the model as a result of each split. The relative importance of each variable was scaled so that the sum added to 100%. The coefficients of the model confirmed the strong positive influence of 3 variables on the number of survival days: 'period out of alfalfa' (44.90%), 'to which crop' (25.54%), and 'sex' (13.38%) (Fig. 10). 'Year' (8.0%), 'introduction period' (6.61%), 'residence in same plot' (1.03%) and 'introduction crop' (0.04%) showed a lower relative influence on survival days (Fig. S8).

3.5. Reproduction

The reproductive success of females was calculated for the consecutive years in which they were tagged and released (Table 5). Over the course of 3 reproductive seasons, 26 tagged females produced a total of 44 pups, with 37 originating from first litters and 7 from second litters, produced by 5 of the 26 reproductively successful females (Fig. 11). Notably, 15% of a total of 40 females carrying a transmitter experienced no litters or had litters that failed, evident by their departure from the permanent reproductive burrow around the anticipated birth period, without any additional agricultural stimuli prompting their exit. Additionally, 20% of the females met an early demise due to predation or agricultural measures before having the chance to give birth or wean the pups (Fig. S9).

Table 5. Overview of the yearly and overall reproductive success of all tagged female common hamsters from 2019–2021. Wild-caught females in 2021 are shown separately (2021 wild)

Year	No. tagged	First litter (%)	Median [IQR] no. of pups in first litter	Second litter (%)	Median [IQR] no. of pups in second litter	Litter size	Total no. of pups	Median [IQR] total no. of pups per female
2019	6	50.00	1.00 [1.00– .]	0.00	0 [0.00–0.00]	1–3	5	0.50 [0.00–1.50]
2020	14	64.28	2.00 [1.00–2.00]	14.28	0 [0.00–0.50]	1–3	17	1.00 [0.00–2.00]
2021	14	78.57	1.00 [1.00–1.00]	14.28	0 [0.00–0.00]	1–2	15	1.00 [0.00–1.25]
2021 wild	6	50.00	1.00 [1.00– .]	16.67	0 [0.00– .]	1–3	6	0.50 [0.00–2.25]
Overall	40	65	1.00 [1.00–2.00]	12.50	0 [0.00–0.00]	1–3	43	1.00 [0.00–2.00]

The reproductively successful females had a median [IQR] of 1.00 [1.00–2.00] pup in their first litter and 0 [0.00–0.00] pups in their second litter. Reproductive success of all tagged females during the 3 reproductive seasons (2019–2021) amounted to a median [IQR] of 1.00 [0.00–2.00] pup per female. Fig. 11 illustrates that females who gave birth to a second litter already possessed a pup count surpassing the median of the number of pups of the first litter of all females. No statistically significant difference in reproductive success was found between the wild and introduced females.

Fig. 11. Number of pups per litter of all tagged reproductively successful female common hamsters from 2019–2021

The temporal scheduling of introductions for captive-bred individuals in consecutive years exhibited variation due to the dependence on breeding success within the colony. Consequently, the emergence date of the first litter of pups was contingent upon the introduction date of their respective mothers (Fig. 12). In general, for a first litter, the pups emerged from the burrow 44–70 d after the introduction of the female, whereas for a second litter, the emergence occurred between 27 and 64 d after the previous litter. Introductions in May allowed the animals the possibility of producing 2 litters. Introductions of females into the wild in June onward resulted in the production of only 1 litter, with the exception of 4 females that produced their first litter at the breeding center in 2021.

4. DISCUSSION

As an integral component of the Flemish hamster species protection plan, 52 common hamsters *Cricetus cricetus* (also known as European hamsters) were equipped with VHF transmitters under the auspices of the ANB throughout their active seasons from 2019 to 2021. The monitoring encompassed tracking demographic parameters, including movement patterns, survival rates, and reproductive success combined with habitat mapping in 2020 and 2021. This investigation aimed to assess the efficacy of the introductions within Widooie and facilitate the refinement of optimal habitat conditions to enhance introduction success accordingly.

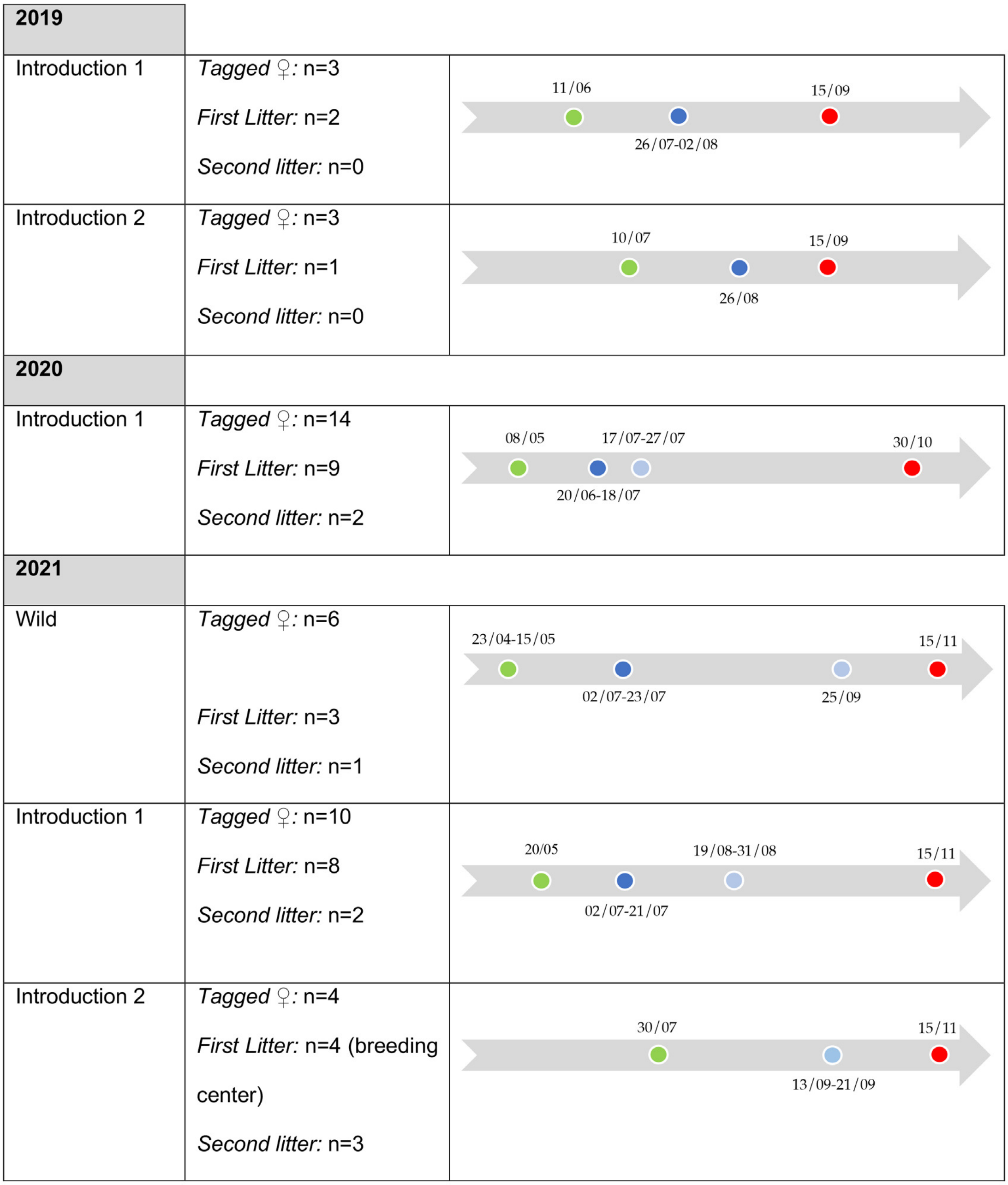

Fig. 12. Overview of the introduction date (green dot), date of the first reported emerging young of the first or second litter (blue and light blue dot, respectively), and end of the monitoring period (red dot) for the tagged female common hamsters from 2019 to 2021 in Widooie

4.1. Movements and habitat selection

The monitoring of male and female common hamsters in Widooie revealed median maximum distances from the release site of 96.73 m for males and 133.19 m for females. The findings for males are notably lower than the greater distances reported in previous studies on reintroduced or translocated individuals (Kupfernagel 2008, Van Wijk et al. 2011). This discrepancy is likely a result of the early predation of male individuals during the monitoring period, which limited their representation in the data set. Existing literature suggests that male hamsters typically traverse larger distances, primarily for reproductive purposes, a behavioral trait widely documented in rodents (Loew 1999, Song et al. 2005, Ishibashi & Saitoh 2008, Gauffre et al. 2009).

The median home range (i.e. MCP) for females varied across the monitoring years, with values of 0.47 ha in 2019, 1.58 ha in 2020, and 0.091 ha in 2021. The ranges observed in 2019 and 2021 align with values reported in the literature (Weinhold 1998, Kayser 2002, Ulbrich & Kayser 2004). The statistically significant differences in distances and area covered by females between 2020 and 2021 (Table S1) in Widooie may be attributable to variations in suitable habitat for the species between the consecutive years. The spatial analyses indicated that the percentage of habitat offering food and shelter, with a favorable cover of ⩾80%, was considerably lower and more scattered in the landscape in 2020 than in 2021 (see Figs. 5 & 6).

In this study, 27.5% of the females exhibited a maximal distance from the introduction site exceeding 350 m. Notably, one individual traveled 852 m between 2 consecutive locations in 2020. Instances of outliers surpassing 1 km were documented in the Netherlands, where long-living males were also included in the study (Van Wijk et al. 2011). Our study did not include long-living males, and given the significant correlation between survival days and movement, our results are understandable. It was observed that females exhibit their longest displacements after weaning their pups, as they seek potential new locations for burrow construction, and following the reproductive period, when they search for suitable areas to store winter food and potentially hibernate. During mid- to late-August, when suitable parcels in Widooie with appropriate crops and adequate cover are becoming scarce due to harvesting and other agricultural measures, these animals traverse considerable distances in their quest (see Figs. 5 & 6). This supports the observations in Germany, where predation pressure is linked to vegetation cover and is highest in mid-July to August after the harvest of barley and wheat (Kayser et al. 2003).

Previous studies have shown that the common hamster has a preference for alfalfa and grains due to its high cover and foraging opportunities (Ulbrich & Kayser 2004, La Haye et al. 2020). Our hamster movement data and the presence of successful reproduction confirm this preference; however, given that the early introduced hamsters were released into alfalfa fields, the results may be biased. Barley and wheat were occasionally chosen by females for cover and food availability from May to July. Nonetheless, the selected plots were subjected to regular management practices, forcing hamsters to cover extensive distances due to inadequate cover in neighboring plots, which often resulted in predation. As the season progressed, hamsters living over 120 d tended to leave the alfalfa in search of more suitable habitats for winter stockage, as the alfalfa in AECM plots became more woody and less nutritious. Towards the end of August and the beginning of September, sugar beets and the fauna crop mix were most often selected, which offered sufficient cover and abundant food resources during this period. However, the harvesting of beets resulted in direct mortality for 75% of the hamsters residing in beet fields at that time (n = 7).

It is recommended to introduce hamsters into a cluster of plots managed under AECM measures, ensuring a minimum cover percentage of 80% and food availability throughout the reproductive season. Alfalfa plots under hamster-friendly management are typically mowed late in the fall, coinciding with the time when clover has hardened, reducing its capacity to provide cover. Implementing partial cyclic management of alfalfa plots would promote the growth of sprouting plants and reduce crop desiccation. Furthermore, incorporating partially unharvested corridors would mitigate predation risks for males in search of females, and for females in search of suitable habitat for their reproductive burrows with appropriate cover and food. Indeed, the AECM grass strip mix, containing 85% grasses and 15% herbs (Vlaamse Landmaatschappij 2017), such as the very nutritious wild chicory, emerged as a suitable habitat or corridor. It is recommended that a fixed percentage of this mix is composed of herbs that are nutritionally important for the hamster. Currently, farmers may choose seeds freely, which does not always provide the best connectivity and resources for the species. Additionally, it is crucial to have adjacent plots or corridors that offer sufficient cover during and after hibernation to mitigate predation risk in spring. The absence of cover after hibernation increases susceptibility to predation. Many hamsters delay their above-ground activities after hibernation until the vegetation around their burrows provides adequate cover, with an optimal scenario comprising 80% cover by 15 April (Müskens et al. 2019).

4.2. Survival

The monthly survival rates observed in this study were higher in the initial month after introduction than those documented in existing literature (Harpenslager et al. 2011). High mortality of introduced animals is primarily caused by their unfamiliarity with the new habitat and predators (Norrdahl & Korpimäki 1998). With a first-month survival of 75% for the males and 92.50% for the females, the introductions of captive-bred individuals in Widooie within AECM alfalfa and fauna crop mix gave them suitable coverage and the accompanying protection against predators.

The majority of introduced animals were placed within fenced alfalfa, with females exhibiting a tendency to remain within the confines of the release plots, thereby benefiting from additional protection against terrestrial predators. The most pronounced mortality during the initial month of this investigation was observed among males that had ventured beyond the confines of the enclosed release plots. It should be noted that only ferrets, weasels, and stoats are able to traverse the gaps in the fencing. Additionally, male or female hamsters may have been taken from the release plot by birds of prey and subsequently consumed at a different location. The literature reports a survival rate of 60.7% in the first month after introduction within a fenced enclosure (Villemey et al. 2013) and concludes that survival and reproduction are significantly higher inside than outside the enclosure. The data from this study cannot confirm this conclusion, as we found a trend but no significant difference in the average number of survival days between the females inside or outside the electric fences. The small sample size for females inhabiting unfenced plots (n = 10) compared to fenced plots (n = 30) may have reduced statistical power. A more extensive study involving a larger group of females in areas without an electric fence is necessary to draw a more substantiated conclusion.

It is noteworthy that after the initial month, the observed survival rates were lower than anticipated based on existing literature on introduced hamsters. Specifically, in the third month after introduction, the female survival rate in Widooie of 47.50% was below the anticipated normal range of 89% (Harpenslager et al. 2011). In the present study, the mortality observed during the second month was attributed to females departing from the enclosed alfalfa plots. It is assumed that a permanent departure of a female from a nest within 40 d suggests that she experienced a failed litter (Harpenslager et al. 2011). Concurrently, male individuals exhibit extensive movements outside the enclosures during this period, rendering them highly susceptible to predation due to a lack of connective elements in the surrounding landscape. The mortality of males was extremely high, with none surviving more than 90 d after introduction. Subsequently, in the fourth month, female movements coincide with post-harvest activities within the plots and the search for an appropriate location to store food reserves for the upcoming winter season.

In this study, the BRT model indicates that the survival days of captive-bred, introduced hamsters are most influenced by their sex, the timing of their departure from the alfalfa plots, and the type of crop they move to. Hamsters introduced into AECM-managed alfalfa plots tend to survive longer if they leave these plots only in July or August (Fig. 10). All introduced hamsters either abandoned the alfalfa plots or died within them during the monitoring period. Since moving out of well-covered plots into landscapes with limited suitable connectivity increases predation risk, hamsters that remained in the alfalfa plots until July or August showed the longest survival in this study. During these months, the percentage of suitable cover within their movement range is highest, reducing the risks associated with movement compared to other months (Fig. 6).

Interestingly, those hamsters that survived longer tended to transition primarily to sugar beet fields, which offer nutritious resources at this time of year. This explains why the presence of sugar beets correlates with increased survival days. The crop category that surpasses all others in terms of supporting the longest-living individuals, however, is mustard. One hamster that did not succumb to harvest in the sugar beet fields moved to a mustard field, where it remained until the end of the monitoring period.

This study was unable to fully map the natural habitat preferences of hamsters over time due to their introduction into artificial burrows within alfalfa plots. However, female hamsters found this habitat suitable for reproduction, as evidenced by their successful reproduction within those plots. Conversely, male hamsters exhibited extensive dispersal typical of rodent reproductive behavior, leading to increased predation risk, as observed by high male mortality in the initial months. Given the observed predation of male hamsters during their movements, it is advisable to incorporate connectivity elements between different plots when designing hamster habitats. In this study, the spatial analyses of the habitat in conjunction with the survival data indicate insufficient cover across the landscape, hindering safe movement between different, mostly distant, suitable plots. This pattern can be attributed partially to the differing growth and harvest phases of crops. Therefore, integrating management agreements that include planting edges or strips of suitable crops and herbs within regular plots could create a mosaic of suitable habitats tailored to the hamsters' needs and still provide an income for the farmers.

4.3. Reproduction

Rodents play a crucial role in ecosystem maintenance owing to their rapid reproduction and their status as a key component in the diet of various predatory species. Access to food resources is a primary determinant of reproductive capacity (Dantas et al. 2021). Additionally, abiotic factors such as photoperiod, rainfall, and temperature can exert a considerable influence on reproductive outcomes (Hufnagl et al. 2011). Historically, it is assumed that various factors, such as fur hunting and the use of rodenticides, have indirectly led to an evolutionary selection for animals that emerge from hibernation late (Surov et al. 2016). Hamsters that emerge from hibernation earlier (March–April) have on average more litters compared to animals that emerge in May (Hufnagl et al. 2011, Surov et al. 2016). This can be an explanation for the drastic decline in the number of litters per year and the number of young per litter over the past 70 yr. Historically, the average was 2.46 litters per female per year, and more recently it was recorded as 1.64 across Europe (Surov et al. 2016). Additionally, postnatal mortality can occur due to infanticide or inadequate maternal care stemming from stress, insufficient food, or high hamster density (Franceschini-Zink & Millesi 2008a).

For a prey species such as the common hamster, with an average life expectancy of only 1–3 yr (Kayser & Stubbe 2002, Franceschini-Zink & Millesi 2008b), a sufficient number of litters and pups per litter are essential to maintain the population, especially in the face of predation pressure. This study reveals a markedly low number of pups (median: 1) emerging from the reproductive burrows of maternal hamsters. This value is notably lower than the reported litter sizes documented in recent literature pertaining to Western Europe (Table 1). Moreover, the occurrence of a second litter was only observed in 12.5% of the introduced females. These findings far undershoot the minimum requirement of 2 litters, each comprising 5–6 pups, necessary for population sustainability (La Haye et al. 2014). In contrast, hamsters from the BNN lineage, which were not released but instead bred within the controlled environments of the breeding stations of GAIA-zoo and Metelen, exhibited a mean (±SD) number of pups per litter of 5.66 ± 0.23 and 7.10 ± 1.01 during the period 2019–2021 (M. Geense et al. unpubl.). Moreover, a study by La Haye (2012a) showed that litter size does not correspond to inbreeding. These facts allow us to exclude the inbreeding of introduced individuals in the BNN region as a potential factor in low reproductive success.

A hypothesis regarding the hamsters in Widooie posits that owing to a nutritionally suboptimal habitat, maternal infanticide may lead to a reduction in litter size. Infanticide is observed in solitary breeders, such as the common hamster, and is more likely to occur in areas with heightened resource competition. Species with intense resource competition invest substantially more energy into offspring production, often reaching up to 1.0 times their own body mass (Ebensperger 1998, Lukas & Huchard 2019, Bose 2022). Infanticide by females, including self-inflicted harm, has been documented in *Cricetus* spp. (Labov et al. 1985). In the golden hamster, pup cannibalism occurs during the first few days postpartum, allowing females to adjust litter size based on their ability to rear young in prevailing environmental conditions at the time of their parturition (Day & Galef 1977). Reproductive failure, attributed to enhanced infanticide, resulted from a vitamin B_3 deficit induced by a maize diet in captive common hamsters (Tissier et al. 2017). In a mesocosm experiment, Tissier et al. (2018, 2021) observed that organic monocultures reduced the species richness of weeds and invertebrates by 82% compared to organic mixed crops. Additionally, wheat–soybean crop associations showed the highest reproductive success compared to maize–sunflower and maize–radish associations. Laboratory mice that were provided with supplemental food containing proteins, unsaturated fatty acids, vitamins, and minerals exhibited reduced cannibalistic behavior towards pups (Lecker & Froberg-Fejko 2016).

An additional factor contributing to a low pup count may involve partial resorption of the litter during later stages of gestation, particularly when the growth rate and, consequently, the energy and nutrient requirements of the embryos increase significantly. Nutritional deficits have been shown to trigger this phenomenon in Rodentia (Robbins 1983, Loeb & Schwab 1987, Tissier et al. 2017, Giacchino et al. 2020). The breeding program in Germany demonstrated that providing a continuous supply of high-protein food significantly increased the average litter size from 5 to 8 offspring (Monecke et al. 2021). Extrapolating this to the field, it could be hypothesized that female hamsters may experience a deficiency in animal or plant proteins during pregnancy and/or lactation. It is conceivable that the female hamsters in Widooie lacked the necessary energy reserves to invest in rearing their offspring, leading to instances of resorption of the embryos or infanticide and leaving the reproductive burrow early. Notably, 15% of the female hamsters in Widooie left their burrow early, while an additional 15% died in their burrows post-weaning.

The shortest interval recorded between 2 litters during 2019–2021 was 28 d, suggesting postpartum estrus followed by fertilization, consistent with findings in hamsters reported by Franceschini-Zink & Millesi (2008b). Since monitoring relies solely on wildlife cameras, determining the initial litter size was not feasible. To address this limitation, temperature loggers could be used to continuously record the females' body temperatures. These data would allow the number of pups to be inferred from distinct body temperature peaks associated with birthing events (S. Monecke et al. unpubl.). This method would also provide a clearer assessment of offspring survival, offering deeper insights into the reproductive population dynamics of these animals.

Crop management practices during the breeding season often emerge as the limiting factor influencing the attainment of multiple litters. This temporal limitation amplifies the risk of predation and imposes challenges for the mobility of pregnant and lactating individuals (La Haye et al. 2010). Following parturition, a minimum of 3 wk with substantial cover is imperative to mitigate predation risks and prevent the female from prematurely abandoning the burrow and offspring. After this period, the offspring attain self-sufficiency, enabling them to seek suitable fields and independently construct burrows (Müskens et al. 2019). The fact that females need a minimum of 3 wk with substantial cover after parturition is corroborated by observations in this study in Widooie regarding the impediment to multiple litters. A subset of introduced female hamsters left the release plots post-weaning and sought refuge in barley and wheat fields, eventually departing after the harvest, thus precluding the opportunity to establish a reproductive burrow. The supply of differentiated food, as offered in breeding programs, disappears once the animals are introduced. The common hamster has an opportunistic and highly flexible diet, consisting of 10–13% animal foods (primarily young hamsters, Coleoptera, Hymenoptera, Lepidoptera larvae, and small rodents). As a result, food availability significantly influences its nutrient intake (Gorecki & Grygielska 1975, Tissier et al. 2019). Intensive agriculture leads to reduced soil biodiversity, resulting in less diverse food webs and smaller organisms (Tsiafouli et al. 2015), which ultimately limits the availability of invertebrate food sources. This can lead to reduced fitness of individuals and, consequently, less energy to invest in reproduction. The reproductive success of hibernating animals is influenced not only by food quality but also by body condition upon awakening from hibernation. A lipid-rich diet before hibernation leads to increased torpor, resulting in poorer body condition upon waking, reduced reproductive success, and slower offspring growth compared to a high-protein diet (Weitten et al. 2018). In that matter, the availability of high-protein sources is essential not only in spring and summer to support reproductive success but also in autumn, provided through healthy soil biodiversity and leguminous crops in the field.

Of the 40 introduced female hamsters, only 5 produced a second litter, with 60% of these offspring being born in the same reproductive burrow as the first litter. Notably, females introduced in June or July did not produce a second litter. Although the breeding season theoretically extends until mid-September for animals released in early May, allowing the potential for 2–3 litters, landscape management practices must be adapted to meet the needs of the species (La Haye et al. 2014, Müskens et al. 2019). All hamsters in this study that were released in May were just over 1 yr old. Given that young hamsters can reach sexual maturity within 2.5 mo, those born early in the season are crucial for population growth (Franceschini-Zink & Millesi 2008a, Monecke et al. 2014).

Another noteworthy finding in this study was that successful reproductive females who had a second litter exhibited a higher pup count compared to the median number observed in their first litters (Fig. 11). Since those introduced females had the same breeding background and age, this finding may indicate that certain microhabitats offer a more nutrient-rich environment for foraging or that some females have superior reproductive traits.

Since all females built their reproductive burrows within fields with AECM measures, the agricultural management did not have an influence on the first litter. However, for the second litter, it may have had an influence, as many females had moved from the alfalfa fields to regularly managed fields after their first litter. Due to the agricultural activities in these fields, the second litter was affected by the management in some cases.

5. CONCLUSIONS

This study highlights the challenges and insights gained from monitoring common hamsters reintroduced to Widooie as part of the flemish hamster species protection plan. The last existing population of the common hamster in Belgium is on the verge of extinction due to some critical points that prevent the recovery of the local hamster population. Key findings underscore the importance of habitat quality, connectivity, and crop management for the survival and reproductive success of this endangered species.

Female hamsters were observed to travel considerable distances, especially post-weaning, in search of suitable habitat and resources for winter storage. However, due to limited well-connected habitats, both males and females faced increased predation risks when moving between fragmented plots. Initial survival rates were high, particularly among females within their introduction plot. However, male survival declined rapidly due to extensive movements outside protected plots. Survival beyond the first month dropped significantly, primarily due to habitat-related risks and predation, indicating that additional landscape connectivity and predator-safe corridors are essential.

This study showed a very low reproductive outcome for both captive-bred and wild females. Both the number of offspring per litter and the average number of litters must be drastically increased for the species to survive in the wild. The cause of the low number of offspring must be investigated and mitigated, otherwise future introductions will be pointless. Factors like crop harvesting schedules and lack of nutrient-rich food sources likely constrained reproduction. Furthermore, the lack of diverse plant and animal protein sources in the environment may have impacted maternal care, resulting in infanticide, embryo resorption, and ultimately smaller litter sizes.

To enhance survival and reproduction, conservation efforts should focus on the following priorities:

• Improving habitat connectivity: establish strips or edges of arable land to facilitate movement and reduce predation risks.

• Ensuring year-round cover: maintain adequate cover, particularly during critical periods such as post-hibernation and the reproductive seasons.

• Adopting strategic agricultural practices: manage alfalfa and other suitable crops in phases to retain their nutritional value and cover. Practices such as late-season mowing and creating unharvested corridors can extend habitat cover and reduce predation.

• Boosting nutritional value: increase the availability of proteins by improving soil biodiversity and cultivating protein-rich crops or herbs.

• Timing of introductions: release hamsters early in the reproductive season (late April to early May) in suitable areas, allowing females to produce 2 litters. This timing also enables female offspring from the first litter to reproduce within the same year.

• Building partnerships with farmers: foster collaboration with farmers to innovate crop management practices and create a biodiverse landscape that supports both conservation goals and a sustainable income. This is especially vital given the current uncertainties surrounding EU regulations and the increasing pressures on farmers.

This study demonstrates the complexities of reintroducing common hamsters in agricultural landscapes and highlights the need for tailored habitat management to ensure long-term viability of the reintroduced populations. Addressing nutritional and habitat challenges could increase reproduction and survival, ultimately enhancing the population's sustainability in Widooie and similar areas.

Acknowledgements. This study was partly funded by the Agency of Nature and Forest of the Flemish Government and LIFE BNIP (LIFE14 IPE BE002BNIP). The authors owe gratitude for the successful completion of the fieldwork to the PXL BIO-Research team. Special acknowledgment is extended to Sam Ottoy, Erik Nuyts, Ben Ramaekers, Timon Smeets, Robbe Ghysens, Aleksandra Pudjak, and Leona Milic. Additionally, appreciation is extended to the editors and reviewers for their meticulous review and valuable suggestions, contributing significantly to the enhancement of the manuscript. The study was conducted in accordance with the national and institutional ethical guidelines. The implant protocol was approved by the Ethics Committee of Hasselt University.

LITERATURE CITED

Agentschap voor Natuur en Bos (2015) Soortbeschermingsprogramma voor de Europese hamster in Vlaanderen (2015–2020) Agentschap voor Natuur en Bos, Brussel

Albert M (2013) Erfassung des Reproduktionserfolges des Feldhamsters (*Cricetus cricetus*) in Hessen [Logging the reproductive success of female European hamsters (*Cricetus cricetus*) in Hesse]. MSc thesis, Forschungsinstitut Senckenberg / Justus-Liebig University, Giessen

Barnosky AD, Matzke N, Tomiya S, Wogan GOU and others (2011) Has the Earth's sixth mass extinction already arrived? Nature 471:51–57

Bellard C, Marino C, Courchamp F (2022) Ranking threats to biodiversity and why it doesn't matter. Nat Commun 13: 2616

Bose APH (2022) Parent–offspring cannibalism throughout the animal kingdom: a review of adaptive hypotheses. Biol Rev Camb Philos Soc 97:1868–1885

Convention on the Conservation of European Wildlife and Natural Habitats (2008) Draft European Action Plan For the conservation of the common hamster (*Cricetus cricetus*, L. 1758). Council of Europe, Strasbourg

Cowie RH, Bouchet P, Fontaine B (2022) The sixth mass extinction: fact, fiction or speculation? Biol Rev Camb Philos Soc 97:640–663

Dantas MRT, Souza-Junior JBF, Castelo TS, Lago AEA, Silva AR (2021) Understanding how environmental factors influence reproductive aspects of wild myomorphic and hystricomorphic rodents. Anim Reprod 18:e20200213

Day CS, Galef BG (1977) Pup cannibalism: one aspect of maternal behavior in golden hamsters. J Comp Physiol Psychol 91:1179–1189

Descamps SMR, De Vocht AJP (2016) Movements and habitat use of the invasive species *Lithobates catesbeianus* in the valley of the Grote Nete (Belgium). Belg J Zool 146: 88–98 doi:10.26496/bjz.2016.44

Ebensperger LA (1998) Strategies and counterstrategies to infanticide in mammals. Biol Rev Camb Philos Soc 73: 321–346

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J Anim Ecol 77:802–813

European Commission (2004) Letter of formal notice to Belgium concerning the common hamster. European Commission, Brussels

European Commission (2019) Biogeographical assessments of conservation status of species and habitats under Article 17 of the Habitats Directive. https://nature-art17.eionet.europa.eu/article17/ (accessed 12 Feb 2024)

Franceschini-Zink C, Millesi E (2008a) Reproductive performance in female common hamsters. Zoology (Jena) 111: 76–83

Franceschini-Zink C, Millesi E (2008b) Population development and life expectancy in common hamsters. In: Millesi E, Winkler H, Hengsberger R (eds) The common hamster (*Cricetus cricetus*): perspectives on an endangered species. Austrian Academy of Sciences Press, Vienna, p 45–59

Gauffre B, Petit E, Brodier S, Bretagnolle V, Cosson JF (2009) Sex-biased dispersal patterns depend on the spatial scale in a social rodent. Proc R Soc B 276:3487–3494

Giacchino M, Claver JA, Inserra PIF, Lange FD, Gariboldi MC, Ferraris SR, Vitullo AD (2020) Nutritional deficiency and placenta calcification underlie constitutive, selective embryo loss in pregnant South American plains vizcacha, *Lagostomus maximus* (Rodentia, Caviomorpha). Theriogenology 155:77–87

Gorecki A, Grygielska M (1975) Consumption and utilization of natural foods by the common hamster. Acta Theriol (Warsz) 20:237–246

Green RE, Cornell SJ, Scharlemann JPW, Balmford A (2005) Farming and the fate of wild nature. Science 307:550–555

Harpenslager SF, La Haye MJJ, van Kats RJM, Müskens GJDM (2011) Reproduction of the female common hamster (*Cricetus cricetus*) in Limburg, the Netherlands. Säugetierkund Inf 8:131–138

Hochkirch A, Bilz M, Ferreira CC, Danielczak A and others (2023) A multi-taxon analysis of European Red Lists reveals major threats to biodiversity. PLOS ONE 18: e0293083

Hufnagl S, Franceschini-Zink C, Millesi E (2011) Seasonal constraints and reproductive performance in female common hamsters (*Cricetus cricetus*). Mamm Biol 76:124–128

Ishibashi Y, Saitoh T (2008) Role of male-biased dispersal in inbreeding avoidance in the grey-sided vole (*Myodes rufocanus*). Mol Ecol 17:4887–4896

Kaplan EL, Meier P (1958) Nonparametric estimation from incomplete observations. J Am Stat Assoc 53:457–481

Kayser A (2002) Populationsökologische studien zum Feldhamster *Cricetus cricetus* (L., 1758) in Sachsen-Anhalt. PhD dissertation, Martin-Luther-Universität Halle-Wittenberg, Halle

Kayser A, Stubbe M (2002) Untersuchungen zum Einfluss unterschiedlicher Bewirtschaftung auf den Feldhamster *Cricetus cricetus* (L.), einer Leit- und Charakterart der Magdeburger Börde. Tiere im Konflikt 7:3–148

Kayser A, Weinhold U, Stubbe M (2003) Mortality factors of the common hamster *Cricetus cricetus* at two sites in Germany. Acta Theriol (Warsz) 48:47–57

Kehoe L, Romero-Muñoz A, Polaina E, Estes L, Kreft H, Kuemmerle T (2017a) Biodiversity at risk under future cropland expansion and intensification. Nat Ecol Evol 1: 1129–1135

Kehoe L, Romero-Muñoz A, Polaina E, Estes L, Kreft H, Kuemmerle T (2017b) Biodiversity at risk under future cropland expansion and intensification. Nat Ecol Evol 1:1129–1135

Kondla MR (2023) Monitoring der Auswilderung des Feldhamsters (*Cricetus cricetus*) im Sommer 2022 in Rommerskirchen (Rhein-Kreis Neuss, Nordrhein-Westfalen). Bachelor dissertation, Universität Duisburg-Essen

Kourgy MS, Souchay G, Eidenschenck J (2019) Evaluation of innovative agricultural practices for common hamsters: results of 5 years of survey in the fields: the final results of the LIFE Alister program. In: Conference presentation abstract, 26th meeting of the International Hamster Workgroup, Kerkrade

Kozyra K, Zając TM, Ansorge H, Wierzbicki H, Moska M, Stanko M, Stopka P (2021) Late Pleistocene expansion of small murid rodents across the Palearctic in relation to the past environmental changes. Genes (Basel) 12:642

Kuhn M (2008) Building predictive models in R using the caret package. J Stat Softw 28:1–26

Kuiters AT, La Haye MJJ, Müskens GJDM, van Kats RJM (2010) Perspectieven voor een duurzame bescherming van de hamster in Nederland. Alterra-rapport 2022. Alterra Wageningen UR, Wageningen

Kupfernagel C (2008) Movements in translocated common hamsters. In: Millesi E, Winkler H, Hengsberger R (eds) The common hamster (*Cricetus cricetus*): perspectives of an endangered species. Austrian Academy of Sciences Press, Vienna, p 27–37

La Haye MJJ (2008) Is there a future for the common hamster (*Cricetus cricetus*) in Western Europe? In: Peschke E, Gattermann R, Moritz G (eds) Cricetinae Internationales Ehrensymposium im Gedenken an Rolf Gattermann. Centre for Ecosystem Studies, Stuttgart, p 54–59

La Haye MJJ, Müskens GDJM, van Kats RJM, Kuiters AT, Siepel H (2010) Agri-environmental schemes for the common hamster (*Cricetus cricetus*). Why is the Dutch project successful? Asp Appl Biol 100:1–8

La Haye MJJ, Koelewijn HP, Siepel H, Verwimp N, Windig JJ (2012a) Genetic rescue and the increase of litter size in the recovery breeding program of the common hamster (*Cricetus cricetus*) in the Netherlands. Relatedness, inbreeding and heritability of litter size in a breeding program of an endangered rodent. Hereditas 149: 207–216

La Haye MJJ, Neumann K, Koelewijn HP (2012b) Strong decline of gene diversity in local populations of the highly endangered common hamster (*Cricetus cricetus*) in the western part of its European range. Conserv Genet 13:311–322

La Haye MJJ, Swinnen KRR, Kuiters AT, Leirs H, Siepel H (2014) Modelling population dynamics of the common hamster (*Cricetus cricetus*): timing of harvest as a critical aspect in the conservation of a highly endangered rodent. Biol Conserv 180:53–61

La Haye MJJ, van Kats RJM, Müskens GJDM, Hallmann CA, Jongejans E (2020) Predation and survival in reintroduced populations of the common hamster *Cricetus cricetus* in the Netherlands. Mamm Biol 100:569–579

Labov JB, Huck UW, Elwood RW, Brooks RJ (1985) Current problems in the study of infanticidal behavior of rodents. Q Rev Biol 60:1–20

Lecker J, Froberg-Fejko K (2016) Using environmental enrichment and nutritional supplementation to improve breeding success in rodents. Lab Animal 45:406–407

Loeb SC, Schwab RG (1987) Estimation of litter size in small mammals: bias due to chronology of embryo resorption. J Mammal 68:671–675

Loew SS (1999) Sex-biased dispersal in eastern chipmunks, *Tamias striatus*. Evol Ecol 13:557–577

Lommaert LDA, Adriaens D, Pollet M (2020) Criteria voor de beoordeling van de lokale staat van instandhouding van de Habitatrichtlijnsoorten in Vlaanderen. Versie 2.0. Instituut voor Natuur- en Bosonderzoek, Brussel

Lukas D, Huchard E (2019) The evolution of infanticide by females in mammals. Philos Trans R Soc B 374:20180075

Malcolm JR, Liu CR, Neilson RP, Hansen L, Hannah L (2006) Global warming and extinctions of endemic species from biodiversity hotspots. Conserv Biol 20:538–548

Monecke S, Wollnik F (2004) European hamsters (*Cricetus cricetus*) show a transient phase of insensitivity to long photoperiods after gonadal regression. Biol Reprod 70: 1438–1443

Monecke S, Amann B, Lemuth K, Wollnik F (2014) Dual control of seasonal time keeping in male and female juvenile European hamsters. Physiol Behav 130:66–74

Monecke S, Kritschker J, Müller N, Löhrmann B, Müskens G, Thimm S (2021) A new concept for conservational breeding of the European hamster. In: 28th meeting of the International Hamster Workgroup (IHWG), 15–16 October 2021, Hessen (online conference)

Müskens GJDM, La Haye M, van Kats RJM (2019) Re-establishment of a viable network-population of the common hamster in South-Limburg, the Netherlands: impact of crop management and survival strips on burrow distribution in the release sites. Alterra Centre for Ecosystem Studies, Wageningen, p 59–62

Müskens G, La Haye M, van Kats R, Moonen S, van der Grift E (2020) Ontwikkeling van de hamsterpopulatie in Limburg: Stand van zaken 2019–2020. Wageningen University & Research, Wageningen

Nechay G (2005) Peak numbers of *Cricetus cricetus* (L.): Do they appear simultaneously? In: 13th meeting of the International Hamster Workgroup. Austrian Academy of Sciences Press, Vienna, p 69–77

Norrdahl K, Korpimäki E (1998) Does mobility or sex of voles affect risk of predation by mammalian predators? Ecology 79:226–232

Pimm SL (2008) Biodiversity: climate change or habitat loss — Which will kill more species? Curr Biol 18:R117–R119

Pimm SL, Jenkins CN, Abell R, Brooks TM and others (2014) The biodiversity of species and their rates of extinction, distribution, and protection. Science 344:1246752

Prakash S, Verma A (2022) Anthropogenic activities and biodiversity threats. Biol Invasions 4:94–103

QGIS.org (2023) QGIS geographic information system. Open Source Geospatial Foundation Project. http://qgis.org

Ridgeway G, Edwards D, Kriegler B, Schroedl S and others (2024) Generalized boosted regression models: package 'gbm'. https://cran.r-project.org/web/packages/gbm/gbm.pdf

Robbins CT (1983) Wildlife feeding and nutrition. Academic Press, New York, NY

Ruyts S, Delief A, Descamps S, Westra T, Van den Berghe K (2023) Is de soort nog te redden? Hamsters in Vlaanderen. Zoogdier 34:16–19

Siutz C, Millesi E (2021) Reproductive success in female common hamsters — results from a long-term study. In: 28th meeting of the International Hamster Workgroup (IHWG), 15–16 October 2021, Hessen (online conference)

Song M, Zhang Z, Neumann K, Gattermann R (2005) Sex-biased dispersal of greater long-tailed hamster (*Tscherkia triton*) revealed by microsatellites. Can J Zool 83: 773–779

Spooner FEB, Pearson RG, Freeman R (2018) Rapid warming is associated with population decline among terrestrial birds and mammals globally. Glob Change Biol 24: 4521–4531

Surov A, Banaszek A, Bogomolov P, Feoktistova N, Monecke S (2016) Dramatic global decrease in the range and reproduction rate of the European hamster *Cricetus cricetus.* Endang Species Res 31:119–145

Thimm S, Geiger-Roswora D (2021) Artenschutzprogramm Feldhamster Nordrhein-Westfalen Natur in NRW. Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen, Recklinghausen, p 11–18

Tissier ML, Handrich Y, Dallongeville O, Robin JP, Habold C (2017) Diets derived from maize monoculture cause maternal infanticides in the endangered European hamster due to a vitamin B3 deficiency. Proc R Soc B 284:20162168

Tissier ML, Kletty F, Handrich Y, Habold C (2018) Monocultural sowing in mesocosms decreases the species richness of weeds and invertebrates and critically reduces the fitness of the endangered European hamster. Oecologia 186:589–599

Tissier ML, Marchandeau S, Habold C, Handrich Y, Eidenschenck J, Kourkgy C (2019) Weeds as a predominant food source: a review of the diet of common hamsters *Cricetus cricetus* in farmlands and urban habitats. Mammal Rev 49:152–170

Tissier ML, Kletty F, Robin J, Habold C (2021) Sustainable agriculture: nutritional benefits of wheat–soybean and maize–sunflower associations for hibernation and reproduction of endangered common hamsters. Sustainability 13:13521

Tsiafouli M, Thebault E, Sgardelis SP, De Ruiter PC and others (2015) Intensive agriculture reduces soil biodiversity across Europe. Glob Chang Biol 21:973–985

Ulbrich K, Kayser A (2004) A risk analysis for the common hamster (*Cricetus cricetus*). Biol Conserv 117:263–270

Van Wijk R, La Haye M, Van Kats R, Müskens G (2011) Movement characteristics of the common hamster (*Cricetus cricetus*) in Limburg, the Netherlands. Säugetierkund Inf 8:79–91

Villemey A, Besnard A, Grandadam J, Eidenschenck J (2013) Testing restocking methods for an endangered species: effects of predator exclusion and vegetation cover on common hamster (*Cricetus cricetus*) survival and reproduction. Biol Conserv 158:147–154

Vlaamse Landmaatschappij (2017) Tips voor het succesvol inzaaien van graskruidenstroken, bloemenstroken en voedselgewassen. https://www.vlm.be/nl/SiteCollectionDocuments/Beheerovereenkomsten/Fiches%20BO%20PDPOIII/2017%2006%2023_FICHE_succesvol%20inzaaien%20graskruidenstroken%20voedselgewassen.pdf

Vohralík V (1974) Biology and reproduction of the common hamster, *Cricetus cricetus* (L.). Věstn Československ Spol Zool 38:228–240

Weinhold U (1998) Zur Verbreitung und Ökologie des Feldhamsters (*Cricetus cricetus* L. 1758) in Baden-Württemberg, unter besonderer Berücksichtigung der räumlichen Organisation auf intensiv genutzten landwirtschaftlichen Flächen im Raum Mannheim-Heidelberg. PhD thesis, Ruprecht-Karls-Universität, Heidelberg

Weinhold U, Kayser A (2006) Der Feldhamster, Vol 625. Westarp-Wissenschaften-Verlagsgesellschaft, Hohenwarsleben

Weitten M, Tissier ML, Robin JP, Habold C (2018) Dietary proteins improve hibernation and subsequent reproduction in the European hamster, *Cricetus cricetus.* Am J Regul Integr Comp Physiol 315:R848−R855

Wilson DE, Mittermeier RA, Lacher TE (2017) Handbook of the mammals of the world, Vol 7: Rodents II. Lynx Edicions, Barcelona

Editorial responsibility: Alexandros A. Karamanlidis, Thessaloniki, Greece
Reviewed by: M. La Haye, and previous version reviewed in ESR by S. Monecke and 1 anonymous referee
Submitted: December 19, 2024; Accepted: April 1, 2025
Proofs received from author(s): May 31, 2025