Movement characteristics of the Common hamster (*Cricetus cricetus*) in Limburg, the Netherlands

Überblick über den Ortswechsel des Feldhamsters (*Cricetus cricetus*) in Limburg, Niederlande

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Zusammenfassung: Diese Studie gibt einen Überblick über Ortswechsel des Feldhamsters in seinem Lebensraum in den Niederlanden. Die benutzten Daten wurden von September 2002 – November 2008 während des Wiedereinbürgerungsprojektes des Feldhamsters in der Provinz Limburg gesammelt. Erwachsene Männchen verlagerten sich im Vergleich mit erwachsenen Weibchen und Jungtieren am meisten und über die größten Distanzen. Parzellenränder und kleine Sandwege bildeten keine Barrieren während eines Ortwechsels. Diese und andere Landschaftsmerkmale können Ortswechselverhalten steuern.
Eine durchschnittliche jährliche Expansionsrate wurde berechnet, um die Populationsausbreitung zu simulieren. Exponentieller Populationszuwachs und Ortswechsel ohne Barrieren waren die Annahmen. Das Ergebnis zeigte, dass in Limburg zwei größere Populationen existieren könnten. Das ist aber nicht der Fall. Empfohlen wird, mögliche Ursachen zu untersuchen.
Schlagworte: Feldhamster, Verbreitung, Nagetiere, Wiedereinbürgerung, Simulation von Populationsausdehnung

Abstract: This study presents a first overview of the movement characteristics of the Common hamster (*Cricetus cricetus*) in the Netherlands. Data were gathered from September 2002-November 2008, during the reintroduction project of the Common hamster in Limburg. Adult males moved most often and over the longest distances, when compared to adult females and juveniles. Parcel boundaries and small (sand) roads formed no barriers in their movements. These and other landscape features might steer their movement path. An average annual expansion rate was calculated to simulate population expansion. Exponential population growth and movement without barriers were assumed. The results of this simulation show that two large populations should exist in Limburg by now. However, this is not the case. It is recommended to investigate possible causes.
Key words: Common hamster, dispersal, rodents, reintroduction, population expansion simulation.

Introduction

Movements and especially dispersal was of no interest for ecologists for a long time. Dispersal movements, one way movements to establish a new home range, create chances to explore new environments and colonize new habitat patches, forming new populations (ENDLER 1977; GAINES & MCCLENAGHAN 1980; STENSETH & LIDICKER 1992; SINCLAIR et al. 2006). But it is difficult to distinguish between occasional movements of an individual for foraging, mating or exploring and 'classical' dispersal. Given this complication to distinguish between data for dispersal and for occasional movements, they are both comprised in the term 'movements' in this study.

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Dispersal was supposed to be 'a desperate way to get out of an inhospitable environment with minimal chances of survival' (ELTON 1927; ELTON 1930). Only during the 1960's ecologists started to acknowledge the importance of movements in general. First by means of the 'island biogeography theory' (MACARTHUR & WILSON 1967). Secondly, LEVINS (1969) published his theory on metapopulations: several spatially separated populations of the same species which have an interaction at some level. A so-called 'population of populations'. The theories of MACARTHUR & WILSON & LEVINS were the start of conservation biology and form a basis to understand the importance of movements. Both theories show that in order for small populations to sustain, interaction between populations via movements of individuals is essential. This situation occurs often in the case of reintroductions. When reintroducing a species into its former habitat, it is of vital importance that the populations can interact and expand by means of (dispersal) movements.

Due to fast declines of Common hamster populations in large parts of Europe in the last decades, several reintroduction projects of Common hamsters were started in Europe (NECHAY 2003; NEUMANN et al. 2004). Although it is acknowledged that knowing their movement characteristics is essential to sustain the small populations, still a lot is unknown. Based on studies on other rodent *spp* some predictions can be made. Most often dispersal distances range from 20-500 meters. Females were found to disperse for the shortest distances and less often compared to males (FRENCH et al. 1968; HOLEKAMP 1986; BOYCE & BOYCE 1988; VANVUREN & ARMITAGE 1994; GUNDERSEN & ANDREASSEN 1998; OLSON & VAN HORNE 1998; BYROM & KREBS 1999; BERTEAUX & BOUTIN 2000; NEUHAUS 2006).

Studies concerning Common Hamsters found that males move for the longest distances compared to females. The average distances were 220 and 191 meters respectively (KUPFERNAGEL 2008). But these hamsters were deliberately translocated to another area to see if they would return. Another study found a mean annual recapture distance for males of 346 meters and 387 meters for females (WEINHOLD 2008). Both studies involved low numbers (N=34 and N=22 respectively) and stressful measuring methods. This study uses data of about 300 hamsters, all tracked using radio transmitters.

The aim of this study was to describe the movement characteristics of the Common hamster. Secondly, to calculate an average annual expansion rate to simulate population expansion in an optimal environment, that is without barriers and with an exponentially growing population. For the first aim the following was investigated: (1) the percentage of individuals moving per month; (2) the chance of a movement in a given month; (3) the mean distance of a movement; and (4) whether they are able to overcome barriers when moving.

Based on literature it is expected that for adult males: (1) the percentage of moving males will be lower than (2) the chance of a movement, because it is expected that only some of the adult males will move. For females and juveniles no differences are expected (FELDHAMER et al. 2003). In general it is expected that adult males move more often compared to females and juveniles (VANVUREN & ARMITAGE 1994; GUNDERSEN & ANDREASSEN 1998; BYROM & KREBS 1999; BERTEAUX & BOUTIN 2000). It is expected that (3) the distance covered by the adult males is the longest and distances are expected to be between 20 and 500 meters (FRENCH et al. 1968; HOLEKAMP 1986; BOYCE & BOYCE 1988; VANVUREN & ARMITAGE 1994; BERTEAUX & BOUTIN 2000; KUPFERNAGEL 2008). It is expected, based on findings in the field, that (4) they can cross parcel boundaries.

Materials and methods

General approach

Common hamsters were implanted with radio transmitters in the abdominal cavity. These transmitters usually last for about half a year to one year. Hamsters were tracked weekly until they went missing or until they died. On average 8% of the males survived until the next spring and 30% of the females. Most of the time hamsters did not reach an age older than 2 years in the wild (KUITERS et al. 2007).

Study area

The reintroduction of the Common hamster took place in Limburg in reserves, mainly in cultivated fields with cereals and alfalfa (LA HAYE 2008). They were released, in chronological order, in Sibbe, Amby, Heer, Sittard, Puth, Koningsbosch and Wittem (figure 1). Currently hamsters are also released in between the populations, connecting them (LA HAYE 2008). Table 1 shows the number of tracked hamsters per reserve over the years.

Tab. 1 Number of tracked hamsters per reserve per year.

	2002	2003	2004	2005	2006	2007	2008	Total
Sibbe	0	6	10	20	16	12	6	**70**
Amby		6	8	15	17	12	0	**58**
Heer			2	9	18	8	10	**47**
Sittard				11	17	16	19	**63**
Puth					10	11	3	**24**
Koningsbosch						9	11	**20**
Wittem						8	2	**10**
Total	**0**	**12**	**20**	**55**	**78**	**76**	**51**	**292**

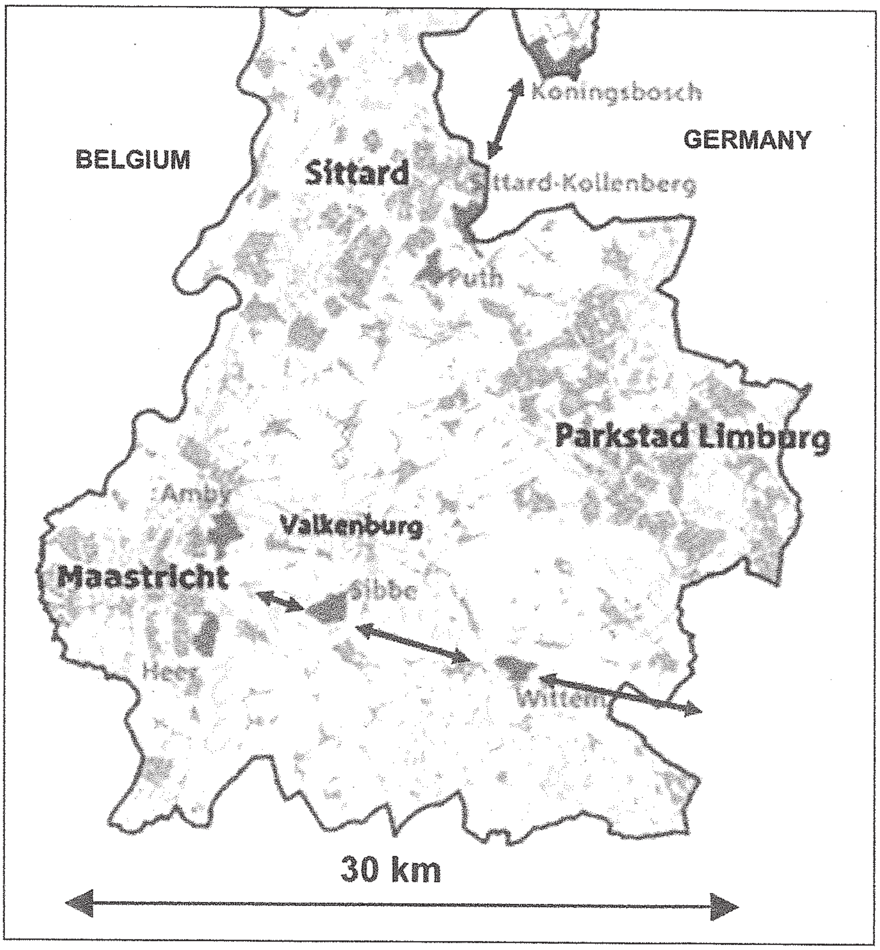

Fig. 1 Hamster reserves in Limburg. Hamsters were released in the dark grey areas and some of the corridors (represented as arrows).

Data

The data used in this study were gathered from September 2002 till November 2008. A total of 171 males and 121 females were equipped with implanted radiotransmitters and tracked weekly, all year round in this period. Of these animals, 54 males and 43 females moved. Data collected consisted of the GPS location of the hamster's burrow, the date on which an individual was checked, the type of vegetation and the cover of the vegetation around the burrow. Several criteria were applied to these data: minimum occupation time of a burrow had to be 7 days, the hamster should not have been translocated by humans and sex and age should be known. Other data from the reintroduction study were used to add more information about: (1) the age of the hamsters (adult or juvenile) and (2) the parcel boundaries in the different reserves.

Data analysis

To get a first impression of what a population of hamsters did during a year, an overview was made using the number of movements and the number of tracked hamsters per month. For adult males the 'population' was founded with all individuals tracked from the 15th of April onwards. For adult females this was the 1st of May. An overview was made with the number of individuals moving and not moving per month. Also the number of living hamsters was counted at the end of each month.

For the research questions, the number of moving hamsters was calculated per month as a percentage of the total number of tracked hamsters in a given month.

The chance a hamster moves was calculated using the theory underlying the Mayfield method (BEINTEMA 1992). Instead of calculating nesting success, 'movement success', the chance a movement will take for a hamster of given sex and age, was calculated per month. Therefore (1) the number of movements, $N_{movements}$ (2) the total number of days hamsters were followed during that month, N_{days} and (3) the number of days per month, N_{month} were determined:

$$\text{Movement}_{chance} = \left(\frac{N_{movements}}{N_{days}/N_{month}} \right) * 100$$

Distance of the movements was calculated using the X and Y coordinates before and after the movement. Because of the accuracy of the GPS device (5 metres), 10 meters was the shortest distance counted as a movement. To calculate the effective movement distance, the Pythagoras theorem was used. x represents the distance of the movement in the 'horizontal' direction, y in the 'vertical' direction.

$$\text{Distance}_{movement} = \sqrt{(x_{new} - x_{old})^2 + (y_{new} - y_{old})^2}$$

Possible barriers of all the movements were investigated using satellite images. The images were verified with field data. This was possible for the reserves Amby, Heer, Puth and Sittard.

Statistics

The percentage of hamsters moving per month and the chance a movement takes place in a month did not require any statistics. Also the overview of barriers they cross did not involve statistics. These findings are presented graphically.

The statistical tests were conducted with SPSS 16.0 (SPSS Inc.). For distance first a Kruskal-Wallis test was used to test for possible differences between the hamster reserves. The same test was then conducted to find possible group differences between the sex and age classes. Differences between 2 groups were examined with the Mann-Whitney U test.

Simulation of population expansion

For this simulation only data of the adult females were used, because they are assumed to move for the shortest distances and are of the greatest importance for a population to sustain. The movement distance and the fraction per number of movements (table 2) were used to calculate an annual movement distance. Mean movement distance was used for a minimum estimation, mean distance of outliers for a maximum estimation. The populations were assumed to grow exponentially, so the number of animals would not be a restriction in this simulation. Also it was assumed that there were no barriers while moving. Finally, it was assumed that all surrounding habitats were equally suitable for their survival.

Results

Figure 2 shows what happens with a population of adult hamsters, considering their survival and movements. Survival rates are low, especially for males. Thus the number of tracked hamsters is different per month.

Percentage of hamsters moving versus movement success

An overview of moving and not moving adult hamsters as a percentage of all tracked hamsters for the entire research period, is given in table 2. Juveniles were not taken into account, because the number of movements were too low. If a hamster was tracked for a second year, the two years were handled as two different events. For moving hamsters an overview of the number of

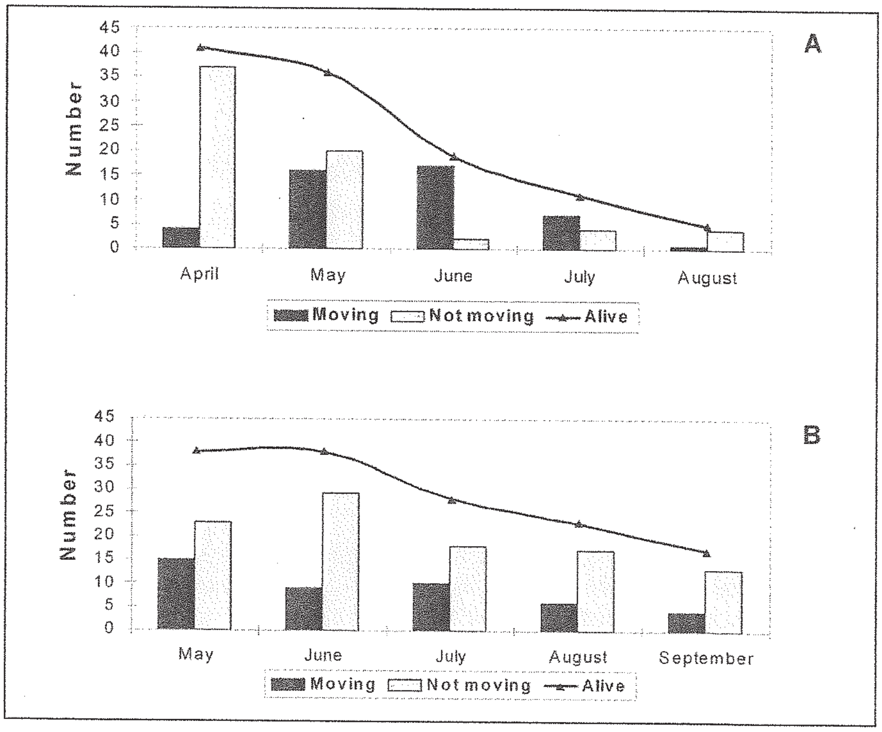

Fig. 2 Summary of what happens to a hamster-population starting for A) males with all radio tracked individuals on the 15th of April (N= 41) and for B) females on the 1st of May (N= 38). Data of all the study years were used.

Tab. 2 Overview of the percentage of adult hamsters not moving and the percentage of adult hamsters per number of movements (adult males N=82 and adult females N=100).

MALES (%)						FEMALES (%)			
0x	1x	2x	3x	4x	=5x	0x	1x	2x	3x
72	9,8	5,9	5	1,4	5,9	67	20,1	7,3	5,6

movements per year is added. Percentage was used, because the number of tracked hamsters was not the same for each month. It can be seen that adult males move more often compared to adult females.

Figure 3 shows the combination of the percentage of hamsters moving and the chance of a movement in a particular month for both sex and age classes. A movement chance larger than 100% indicates that there should be more than one movement per individual in that month. It can be seen that the chance of a movement for adult males is larger during the breeding season (May-August), than the actual percentage of moving hamsters. This difference is not that profound

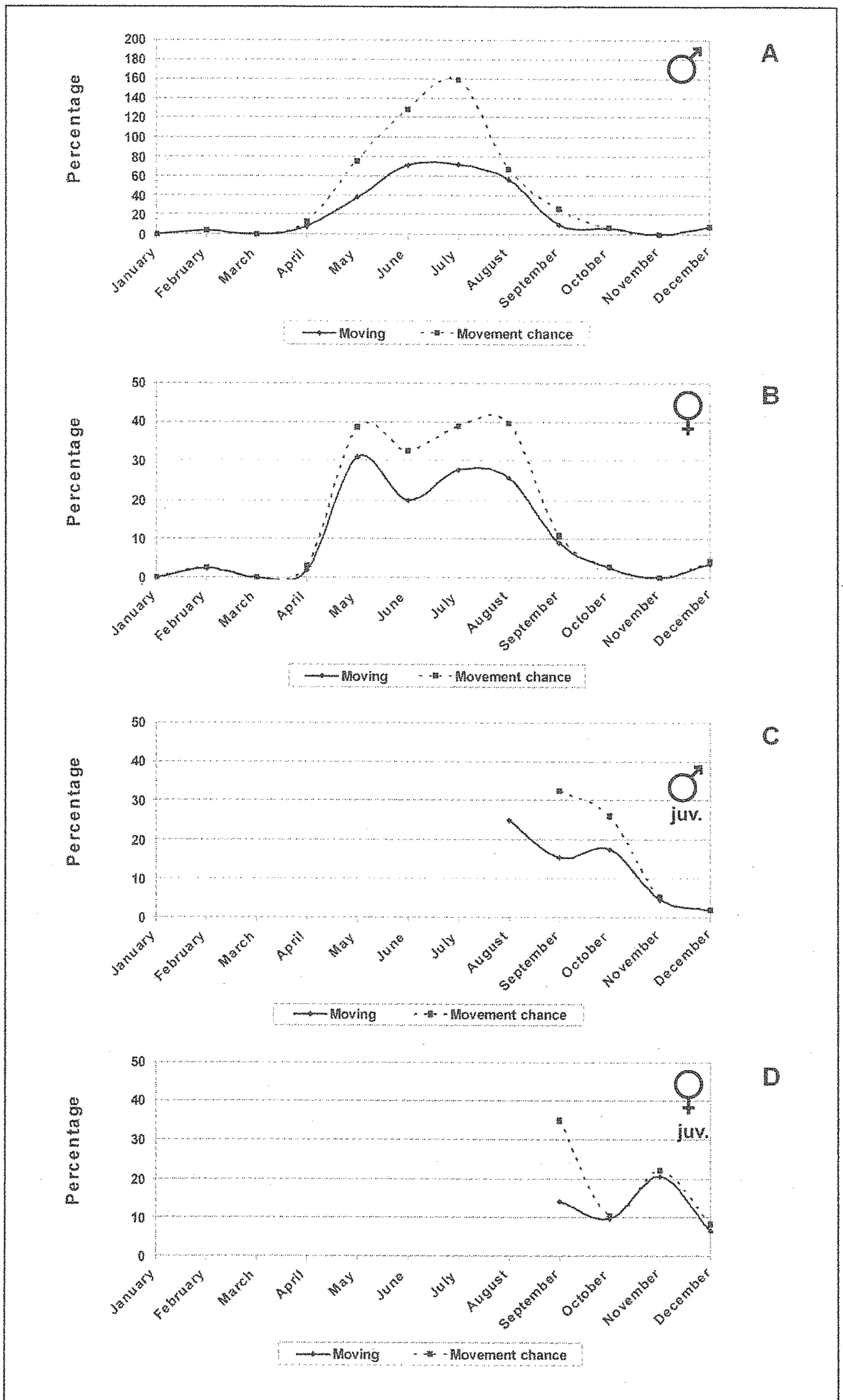

Fig. 3 The percentage of moving hamsters versus the chance of a movement per month for A) adult males, B) adult females, C) juvenile males and D) juvenile females. The scale of adult males was set to 0-200% (instead of 50%) in order to fit the graph.

for females and juveniles. Further more adult females show a distinct peak in July/August (after successfully raising a litter ?), following the first 'movement peak' after the hibernation period. Juveniles start moving around in August for males and September for females, but numbers were very low !

Distance of the movements

Figure 4 shows the distance frequency distribution for movements of both sex and age classes. All data of moving hamsters were used. Table 3 summarizes the characteristics of the move-

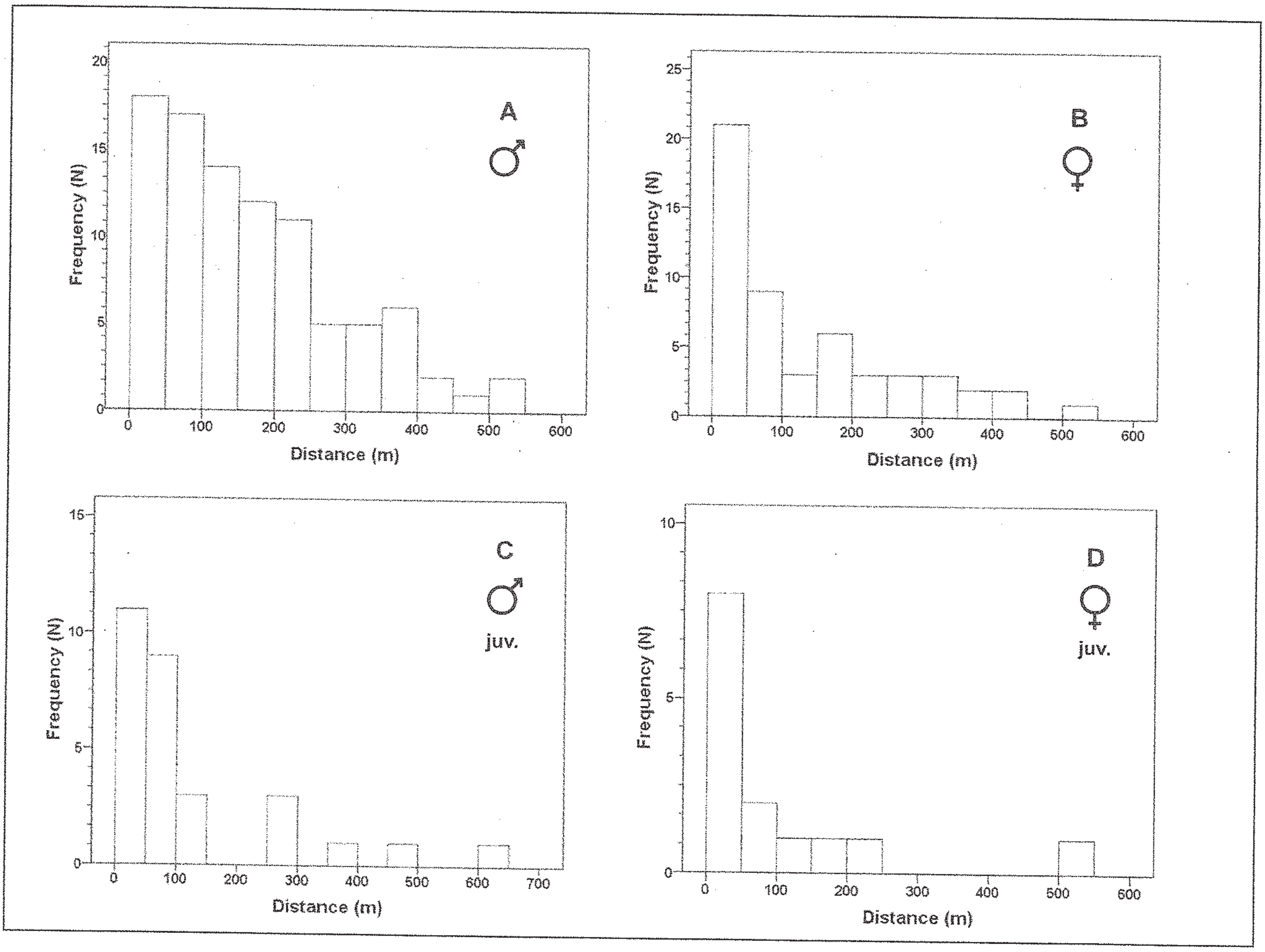

Fig. 4 Distance frequency distribution of A) adult males, B) adult females, C) juvenile males and D) juvenile females (number of movements is noted in the figures). Note the different scales in distance and frequency.

Tab. 3 Mean and median distances in meters with 95% range of all data for all sex and age classes.

	Mean	Median	95% range
Adult males (N=101)	172,4	135,8	22-506
Adult females (N=60)	131,6	69	20-400
Juvenile males (N=30)	120,6	68	18-459
Juvenile females (N=17)	90,9	40,3	12-228

ments. Adult males were found to move for significantly longer distances (P_{af}=0.010, P_{jm}=0.004 and P_{jf}=0.001). Overall group difference were found significant ($P_{overall}$=0.001), but when adult males were removed from the group, overall differences were not significant (P=0.374). Overall, distances varied between 12-506 meters (95% range of all data).

Barriers in their movements

Figure 5 shows the type of barriers hamsters crossed. For a complete overview also the number of movements without crossing barriers are shown. The amount of data for juveniles was insufficient for a separate overview of males and females. It can be seen that besides parcel boundaries, adult hamsters occasionally cross small (sand) roads during the breeding season. Juveniles also cross parcel boundaries as well as small (sand) roads.

Population expansion simulation

The average annual expansion rate of adult females was found to be approximately 200 meters. These data were used to simulate the population expansion by the year 2009, taken into account how many years/generations ago they were released. Figure 6 shows the spatial distribution

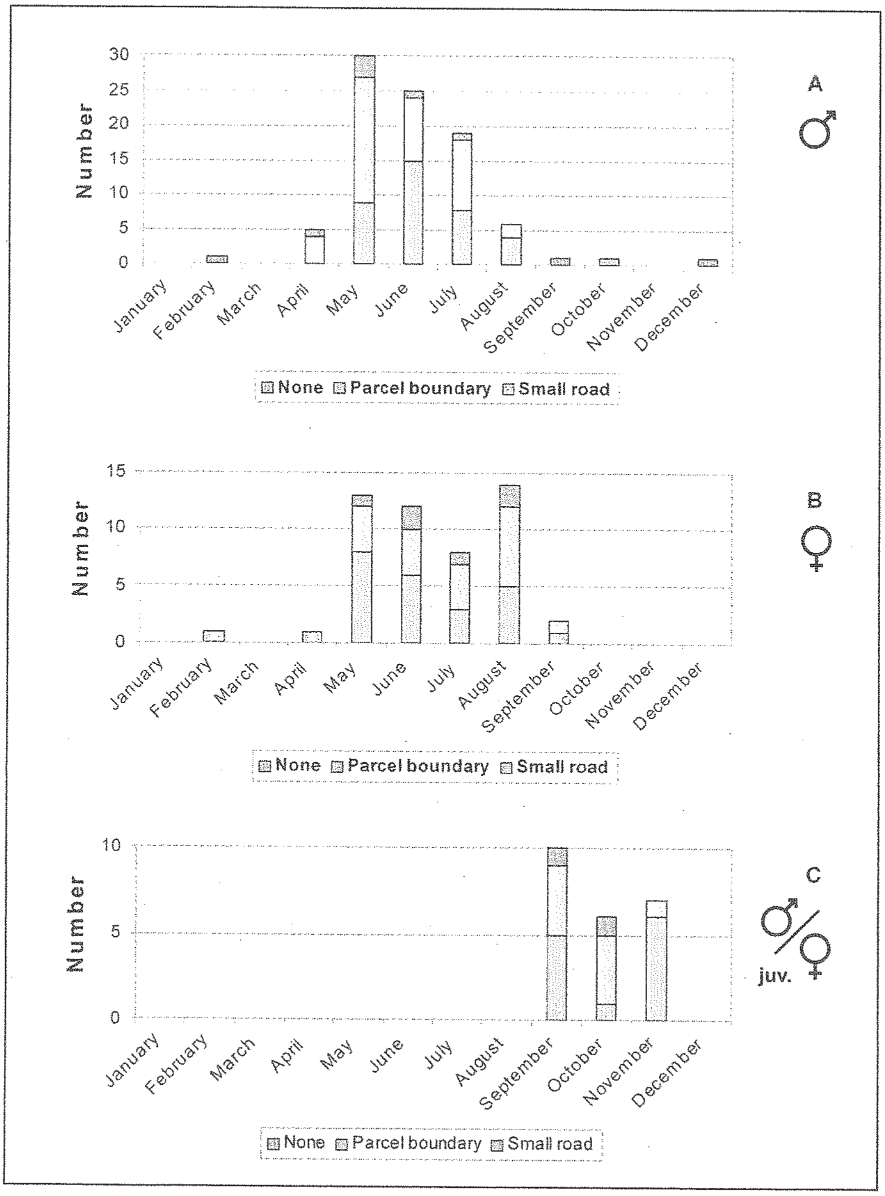

Fig. 5 Number of movements per month that crossed: no barriers, small (sand) roads and parcel boundaries for A) adult males, B) adult females and C) juveniles (adult males N=89, adult females N=51 and juveniles N=23). Note that the scales are different for number.

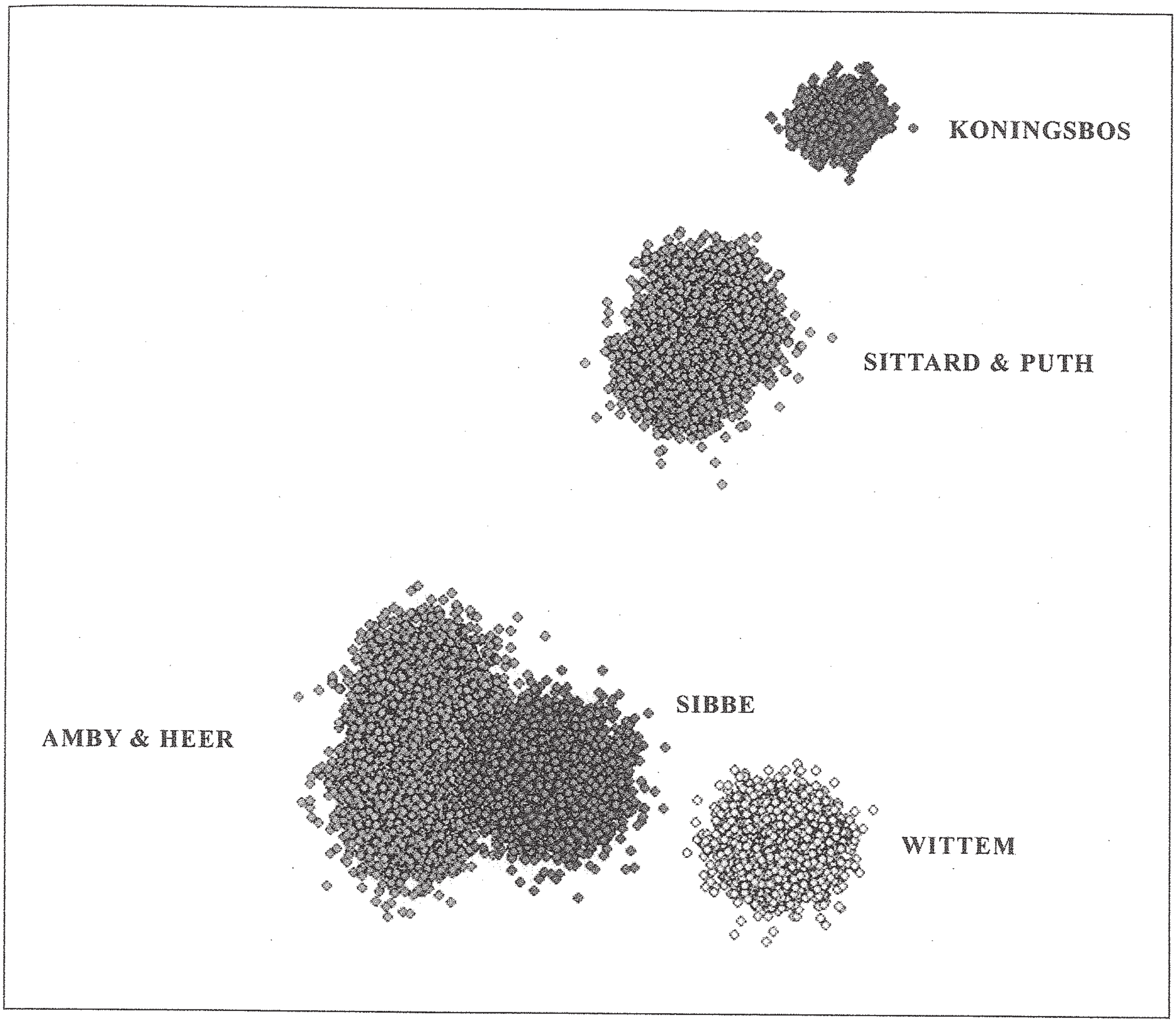

Fig. 6 Expected population expansion in 2009 based on adult females for the different reserves with an average expansion rate of 200 meters.

of the different populations, using the coordinates of the different reserves as starting points (compare with figure 1). In this simulation Amby, Heer and Sibbe form a connected population, as well as Sittard and Puth. Except for the adding of Sibbe to the Amby-Heer population, this simulation reflects more or less the current situation in the field.

Discussion

Although it is acknowledged that knowledge on the movement characteristics of Common hamsters is essential to sustain and improve reintroduction projects throughout Europe, still a lot was unknown.

The summary of what happens to a hamster-population (figure 2), first of all clearly shows that survival rates of hamsters are low, especially for adult males (KUITERS et al. 2007). Therefore in order to sustain a population, hamsters need to be highly reproductive. Probably only some of the males are responsible for reproduction, as the difference between the percentage of moving adult male hamsters and the chance of a movement indicate (figure 3A). That only some males reproduce, is not uncommon in rodents (FELDHAMER et al. 2003). This might be further investigated, *e.g.* using genetic tools.

Adult females show a distinct second peak in the percentage of moving hamsters in July/August. This might indicate that they deliberately move to leave their first litter with a territory. Maybe they get a second litter in a different location. This type of movement is called female breeding dispersal. Other rodents *spp* also show this type of dispersal, often as a parental care strategy (BERTEAUX & BOUTIN 2000; RAJSKA-JURGIEL 2000; NEUHAUS 2006). From the movements investigated in this study, three more types of dispersal can be distinguished: the first movement of adults after hibernating, say 'spring dispersal', dispersal as a consequence of agricultural disturbance like ploughing, 'human induced dispersal', and dispersal of juveniles, 'natal dispersal'.

'Spring dispersal' might be triggered by waking up in an unsuitable habitat with low ground cover and therefore low protection of predators. During the year a habitat altered as a consequence of agricultural work might also cause hamsters to disperse to a more suitable habitat. Thus absence of ground cover seems to be an important trigger for movement.

Juveniles might disperse after being weaned, 'natal dispersal'. This is seen in other rodents *spp* as well (HOLEKAMP 1986; GUNDERSEN & ANDREASSEN 1998; BYROM & KREBS 1999). Whether juveniles do disperse might depend on their body fat, as found in ground squirrels (NUNES et al. 1998). Movements of adult males during the breeding season differ from females and juveniles: they seem to be relatively short walks in one or maybe two parcels, probably for reproduction. Figure 7 summarizes this movement pattern of adult males during the year, often they die before the end of the year (figure 2).

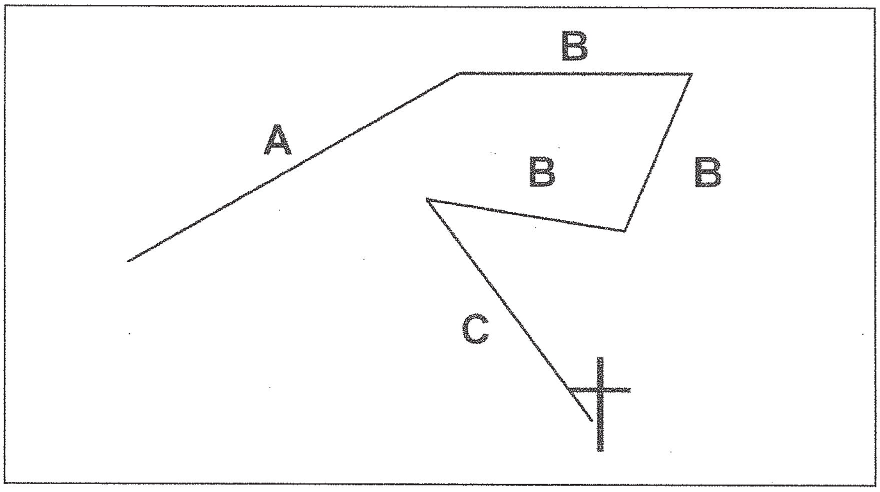

Fig. 7 Schematic outline of the movements of adult males during the year. A) spring dispersal, B) movements during the breeding season and C) final movement before hibernating.

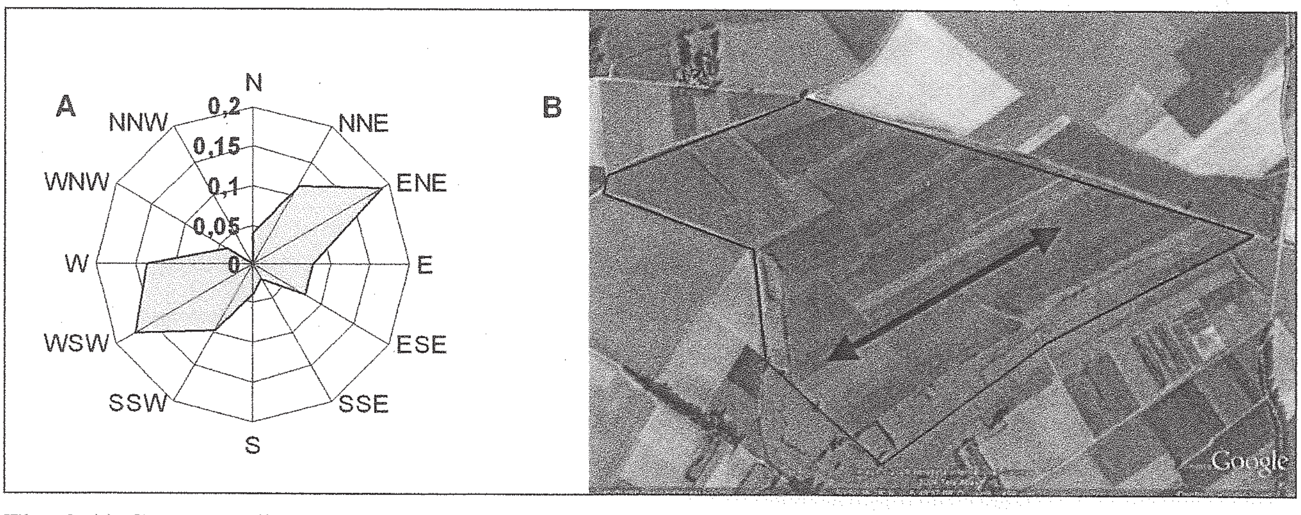

Fig. 8 A) Compass direction as a fraction of the total number of movements in Sibbe compared to B) an overview of the reserve (GoogleEarth), with the most common parcel outline (arrow).

Two outliers were not used for the calculations: an adult female moving over 1439 meters in two months and an adult male moving over 1789 meters in one month. The female came from Heer, crossed a main road and had a litter on the other end in the Amby reserve. Such an outlier can be of major importance when connecting populations.

Distances covered by hamsters varied between approximately 20-500 meters for males and 15-400 meters for females (table 3). Adult males move more often compared to females and juveniles. These findings correspond with studies on other rodents *spp* (FRENCH et al. 1968; HOLEKAMP 1986; BOYCE & BOYCE 1988; VANVUREN & ARMITAGE 1994; GUNDERSEN & ANDREASSEN 1998; OLSON & VAN HORNE 1998; BYROM & KREBS 1999; BERTEAUX & BOUTIN 2000; NEUHAUS 2006).

The movements in the Sibbe reserve (figure 8A) suggest that hamsters follow landscape features, in this case, the parcel outlines (figure 8B). Although it was not found in the other areas, landscape features acting as 'guidelines' for movement are not uncommon (DIFFENDORFER et al. 1995; OLSON & VAN HORNE 1998; MACDONALD & RUSHTON 2003; MCDONALD & ST CLAIR 2004; EPPS et al. 2007). But hamsters were also found to regularly cross these parcel boundaries, as well as small (sand roads), figure 5. To determine whether landscape features really act as 'guidelines' for Common hamster's movement patterns more study is required.

The population expansion simulation shows that two large populations could have formed by now: one with Sittard and Puth, the other with Sibbe, Amby and Heer. Sittard and Puth are still separated by a main road, but actually they already interact, forming one population. Amby and Heer show similar interaction over a main road, but Sibbe is not included in this metapopulation yet. Possible causes for the differences between the simulation and the current situation may be a lower population growth rate and the occurrence of barriers. But also the low survival rates outside the reserves (figure 2) might cause the populations to first expand, but then to go extinct again. Another explanation for the difference might be that they do encounter barriers in their movement, like roads and buildings. A problem with the data in general is first of all that the number of movements are sometimes low, especially when dividing the data into groups (take for instance figure 4). Increasing the number of tracked hamsters, chiefly females and juveniles, is highly recommended. Besides that, it is assumed that the movement from the old to the new location took place in a straightforward manner. It could also be that the movement took place in more than one step. Or that its path was curved and because of that longer and with a different angle (figure 9). Distance would be longer and maybe other barriers were crossed. But what is actually calculated, is the mean dispersal distance or, in this case, the mean movement distance. This has been a useful tool for simulating population expansion (BYERS 2001), one of the two aims of this study. This mean movement distance is therefore used for the population expansion simulation in this study.

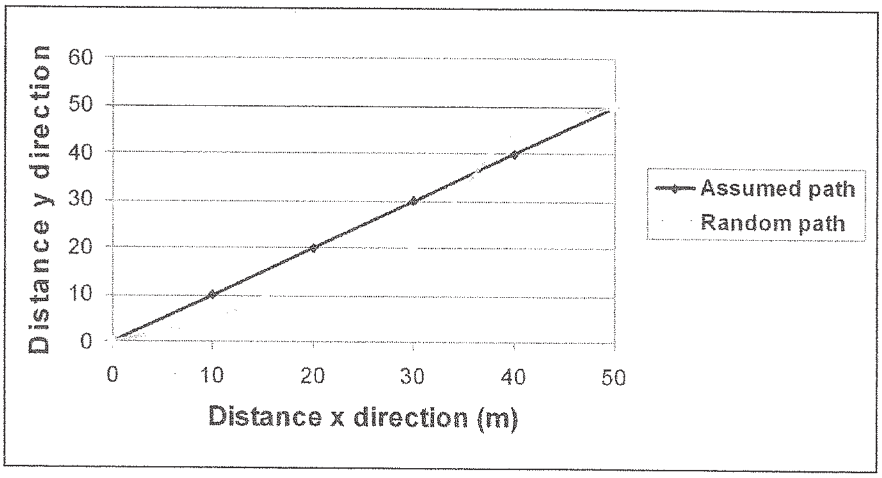

Fig. 9 The path calculated with the Pythagoras theorem versus a random path assuming more than one step and curved pathways.

Another point on the expansion simulation, is that in another study an annual expansion rate for females of 387 meters was found (WEINHOLD 2008), so in theory they might have even expanded further.

Recommendations

In order to further investigate questions that arose from this study, it is recommended to closely monitor one or two populations. Best would be to start with an equal number of males and females and track them as often as possible, preferably once every day. It would be very useful for conservation/reintroduction to know what actually causes the low survival rates (especially for adult males) and what determining factors for movement (direction) are. Is, for instance, ground cover indeed of high importance? Insight in the number of males reproducing using genetic tools is useful, but might be difficult because of low genetic variance in the hamster populations (NEUMANN et al. 2004) More insight in what happens when adult females have produced a litter is important, because what happens to the young and where do the females go?

Conclusion

It was found that the chance of a movement for adult males is much larger than the actual percentage of moving individuals. This supports the suggestion that only some of the adult males account for the reproduction.

For adult females the second peak in moving hamsters in July suggests the occurrence of breeding dispersal of some kind (BERTEAUX & BOUTIN 2000; RAJSKA-JURGIEL 2000). More research is needed to investigate the causes of this second peak. Movement of juveniles might indicate natal dispersal, but more study is needed.

It was found that adult males move over the longest distances and most often. Distances of males ranged from 18-506 meters, for females 12-400 meters.

The finding that landscape features might guide the hamster's movements encourages further research. Subsequently it was found that parcel boundaries appear to form no barrier for their movements, but a more extensive study is recommended.

The population expansion simulation shows the situation with an average annual expansion rate, exponential growth and no barriers versus the real life situation at present. To improve conservation of the Common hamster it is recommended to investigate possible causes.

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