Vol. 31: 119–145, 2016
doi: 10.3354/esr00749

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published October 6

FEATURE ARTICLE
REVIEW

Dramatic global decrease in the range and reproduction rate of the European hamster *Cricetus cricetus*

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ABSTRACT: Although the European hamster is probably the fastest-declining Eurasian mammal, its IUCN Red List status is still Least Concern. In addition to the huge distribution area, this categorization is based on the assumptions (1) that the decline affects only Western Europe, where (2) modern agriculture has led to (3) an increase in the mortality of the species. Since mortality-reducing protection measures in Western Europe have been unable to stop the decline, we reviewed the literature from 1765 to the present and reappraised the situation. We found support for none of these assumptions. The species has also vanished from more than 75% of its range in Central and Eastern Europe. In 48 of 85 Russian, Belarussian, Ukrainian and Moldovan provinces, its relative occurrence has decreased. It is now rare in 42 provinces and extinct in 8. Mortality has not increased, but the reproduction rate has shrunk since 1954 throughout the distribution area. Today the reproduction rate is only 23% of that between 1914 and 1935. Taking into account the mortality of this prey species, 1 female today raises only 0.5 females for next year's reproduction. The extrapolation of the literature data points to an extinction of the species between 2020 and 2038. We strongly recommend (1) changing the status of the European hamster on the IUCN Red List from Least Concern at least to Vulnerable or even Endangered and (2) supporting scientific research on the reproduction of European hamsters as a protection measure. Global threats such as climate change, light pollution or (in the past) fur trapping are more likely to be the ultimate reason for the decline of this species than modern agriculture.

KEY WORDS: *Cricetus cricetus* · Distribution · Reproduction · Climate change · Light pollution · Global threats

Adult female European hamster *Cricetus cricetus*.
Photo: Holger Fuchs

INTRODUCTION

Until the 1970s, European hamsters were a much feared agricultural pest throughout their distribution area. In 'normal' years, densities of 10 to 80 individuals per hectare were common (Ružić 1977, Nechay 2000). During pest outbreak years, which were frequent until the 1980s, population densities could increase to more than 2000 individuals per hectare as counted in Slovakia in 1971 (Grulich 1980, Nechay 2008). Thereafter, populations experienced a remarkable decline, which was first reported in Western Eu-

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

rope. In areas where the European hamster still exists, densities are often lower than 1 to 2 individuals per hectare (Kayser et al. 2003a, Kuiters et al. 2011). The species was included in Appendix II (strictly protected species) of the 1979 Bern Convention on the Conservation of European Wildlife and Natural Habitats, and since 1992, it has been listed in Appendix IV of the Habitats Directive, which provides strict legal protection in all European Union countries (Ziomek & Banaszek 2007). In France, Belgium, the Netherlands and Germany, protection measures have been implemented for at least 15 yr. Since European hamsters prefer agricultural areas as habitat, farmers are compensated by 450 to 2250€ per year and hectare (Laussmann & Fabry 2008, Amand et al. 2012, MKULNV 2013) for so-called hamster-friendly field management. This type of management aims to reduce mortality (Villemey et al. 2013) presumably caused by industrialized agriculture and includes small-scale cultures, restricted ploughing and late or no harvest to provide year-long food and cover for hamsters (Kayser & Stubbe 2002, Köhler et al. 2014, La Haye et al. 2014). The French national action plan for the European hamster for 2012 to 2016 provided 4 400 000€ just for this purpose (Amand et al. 2012).

The latest census data have revealed that this hamster-friendly management has thus far not had the desired effect. In spite of protection measures, the European hamster has vanished from 75% of the Alsatian sites (France) that were still inhabited in 1997 (Amand et al. 2012, Reiners et al. 2014). In Germany, the species has been lost from one-third of the inhabited grid-squares since 1998 (compare Weidling & Stubbe 1998 and the national Fauna-Flora-Habitat Report of Germany 2013, Bundesamt für Naturschutz 2013); however, in some regions, the animal vanished from 90% of the areas (compared to 1990; Meyer 2009). Moreover, hamster densities have declined dramatically within the still-inhabited areas, for example by 90% from 250–280 animals in 2006 to ca. 25 in 2015 (D. Geiger-Roswora pers. comm.) or by 97% from 9292 active burrows in 2002 to 283 in 2011 (Mammen 2011a). Moreover, we could not find any report which indicates that hamster-friendly field management increases the numbers of European hamsters. If at all, it stabilizes the populations, but most often hamster numbers continue to decrease (Martens 2005, Mammen 2011b, Walz 2011, Weinhold 2011). Since 2001, European hamsters have been bred in captivity for reintroduction programmes to hamster-friendly areas in 3 regions (Alsace/France, Limburg/the Netherlands, Mannheim/Germany). This measure was more successful than the approach with only hamster-friendly management. In the Netherlands, population size increased (Kuiters et al. 2011), and in Germany (U. Weinhold pers. comm.) and France (Amand et al. 2012), populations could be stabilized to very low levels. However, if the number of reintroduced animals is lowered, the populations break down immediately (Kuiters et al. 2011).

The protection of the European hamster is as yet not sufficient, suggesting that the reasons for its decline are not fully understood. Moreover, the IUCN still classifies the European hamster as Least Concern (Kryštufek et al. 2008). This classification and current measures are based on 3 assumptions: (1) the decline is restricted to Western Europe, where (2) modern industrial agriculture has led to an increase in the mortality of European hamsters. Focussing on this argumentation, we reviewed literature from across the distribution area. Moreover, by reviewing historical literature from 1765 to the present, we explored other reasons for the decline, such as fecundity. We added our own data on present distribution and reproduction. Based on these results, we define properties of the potential factors impairing the survival of the species and finally discuss additional factors that merit consideration. The aim of this study is to contribute to a better understanding of the decline of the European hamster.

DECLINE OF EUROPEAN HAMSTERS IS NOT RESTRICTED TO WESTERN EUROPE

The original distribution area of European hamsters (between 42 and 55° N and between 5 and 95° E; Nechay 2000) covered nearly the whole temperate zone of Eurasia and extended roughly from the Rhine River in the West to the Yenissei River in the East (Nechay et al. 1977).

In Western Europe, i.e. the Netherlands, Belgium, France, Germany and Switzerland, the decline of European hamster populations was noticed first (for a review, see Nechay 2000) (Fig. 1a,b and see Table S1 in the Supplement at www.int-res.com/articles/suppl/n031p119_supp.pdf), and thus it was assumed that this problem concerned only the western limit of the species' distribution. However, it soon became clear that the range reduction also dramatically affected many Central European countries (Fig. 1c, Table S1). In almost all countries in which monitoring was performed recently, the species has lost large parts of its original territory so that today its range is usually fragmented (Ambros et al. 2003, Bihari 2003, Ziomek & Banaszek 2007, Tkadlec et al. 2012). Even in East-

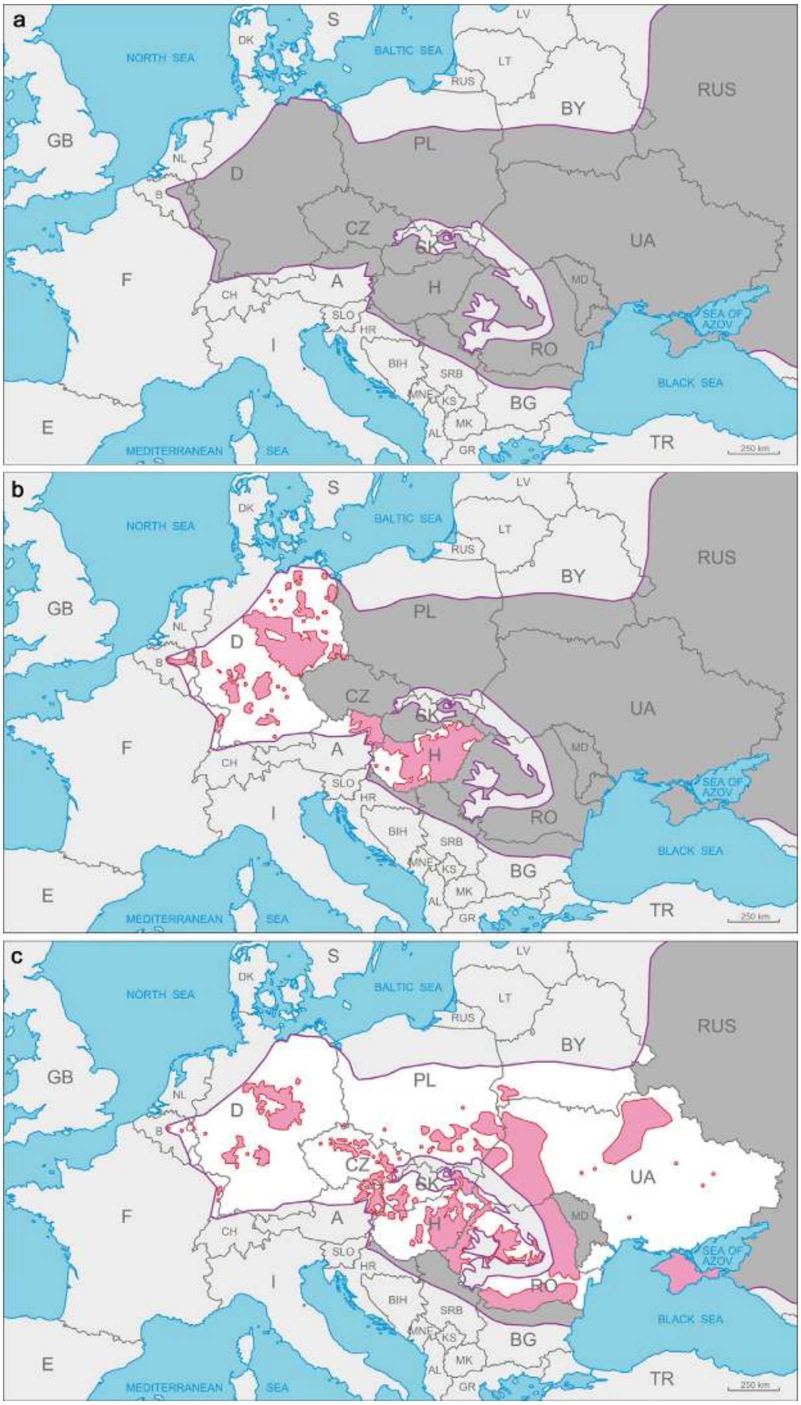

Fig. 1. Distribution of European hamsters *Cricetus cricetus* in Europe, excluding Russia. (a) Range before 1982 according to Niethammer (1982) (dark grey, violet borders; also applies to panels b and c). (b) Updates (Weidling & Stubbe 1998, Nechay 2000, Weinhold 2008) as of 1998 (red) show a strong decline in hamster populations in Western Europe. (c) Current (status as of 2015) distribution in Europe according to literature given in Table S1 in the Supplement at www.int-res.com/articles/suppl/n031p119_supp.pdf, with further declines in Western Europe and remarkable declines in Central and Eastern Europe. Where no recent data are available, the distribution is left unchanged (dark grey). Further literature used to create this figure is listed in the Appendix. A: Austria, B: Belgium, BG: Bulgaria, BY: Belarus, CH: Switzerland, CZ: Czech Republic, D: Germany, F: France, HR: Croatia, H: Hungary, MD: Moldova, NL: the Netherlands, PL: Poland, RO: Romania, RUS: Russia, SK: Slovakia, SRB: Serbia, SLO: Slovenia, UA: Ukraine

ern Europe, for example in Ukraine, where it was common belief that the hamster was abundant all over the country, recent studies confirmed only 3 areas of occurrence: Western Ukraine, Northeastern Ukraine and the Crimea (Korbut et al. 2013, Rusin et al. 2013). The species became extinct in most parts of the steppe zone and declined within the forest–steppe zone (Rusin et al. 2013). In summary, the European hamster has lost more than 75% of its range in most European countries. Exceptions are Hungary, where two-thirds of the range remain but populations are decreasing (Bihari 2003), and Romania, in which the range seems to be largely unchanged (Hegyeli et al. 2015).

In the Western European part of the range, where conservationists and governments have been aware of the decline of European hamsters for at least 20 yr, populations are observed carefully. Such intense monitoring is not possible across the entire Eurasian range, especially since in many countries, the species, although legally protected, does not receive any active protection on the governmental level. The studies in Central and Eastern Europe, on which Fig. 1 is based, used several sources of information (Table S2 in the Supplement) which were verified by careful fieldwork.

There are only a few European countries for which no recent data exist (Fig. 1c). However, in the light of the present data, it is unreasonable to expect that the distribution and numbers of European hamsters are unchanged in unsearched parts of the range. Likewise, since searching for hamsters in thousands of hectares of agriculture fields is akin to looking for a needle in the proverbial haystack, it is possible that in some areas considered not inhabited any more, the hamsters may still be present in extremely low numbers. In Poland, an active locality was found in Lower Silesia (Auguścik & Ziomek 2013), which was thought to be abandoned by the species (Ziomek & Banaszek 2007). However, such findings do not change the general picture of the dramatic distribution decline, as small isolated populations are subjected to random demographic and genetic processes and may disappear at any moment (Banaszek et al. 2011).

Mapping an exact distribution is even more difficult when it comes to the hamster's huge eastern and Asiatic distribution area. For Russian, Belarussian, Ukrainian and Moldavian provinces, we thus compiled data on the relative occurrence of European hamsters before and after 1970. To make them comparable, we used 4 categories: extinct, rare, common and abundant. The information is based on the literature, museum data and a historic map of intense fur harvesting of European hamsters (Neronov 1965) (see Table S3 in the Supplement). 'Extinct' was assigned to a province when it was explored in numerous locations and the species was absent everywhere. This term was used with great care and was not assigned to a region when the slightest doubt existed. 'Rare' was assigned to a province if we had reports about the species' presence in 1, 2 or 3 locations or if the studies did not satisfy the strict criteria for extinct. 'Common' was used when species was reported from numerous localities in a province, but the numbers of individuals in these localities were low. The same accounts for 'abundant', but here the species' presence in the reported localities was notable. In this case, locals often reported hamsters in agricultural areas, in natural conditions and even in human settlements.

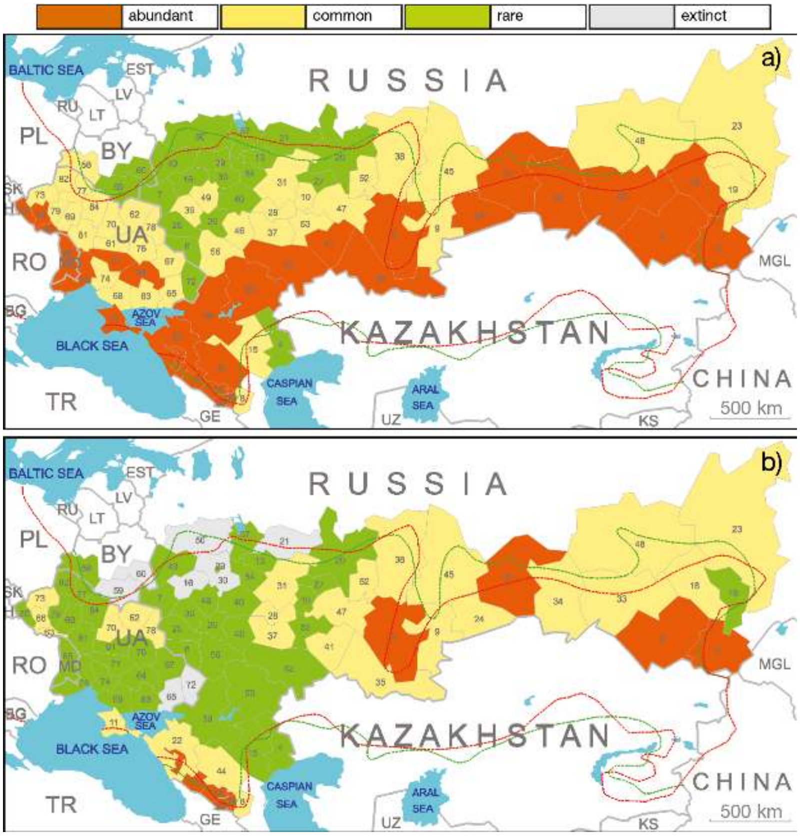

Fig. 2. Relative abundance (orange: abundant, yellow: common, green: rare, grey: extinct) of European hamsters *Cricetus cricetus* in their eastern range (a) before and (b) after 1970. Numbers replace the names of provinces, which are listed in Table S3 in the Supplement. The red line indicates the historical species range in the 1940s and 1950s according to Kucheruk (1959) and the green line in the 1960s according to Neronov (1965). Sources are given in Table S3 and in the Appendix. BG: Bulgaria, BY: Belarus, EST: Estonia, GE: Georgia, H: Hungary, KS: Kyrgyzstan, LV: Latvia, LT: Lithuania, MD: Moldova, MGL: Mongolia, PL: Poland, RO: Romania, RU: Russia, SK: Slovakia, TR: Turkey, UA: Ukraine, UZ: Uzbekistan

The density of European hamsters declined in most of the 85 provinces in this part of the distribution area (Fig. 2). Before 1970, the European hamster was abundant in 28 provinces, common in 37 and rare in 20. Today, the species is abundant only in 8 and common in 27 provinces, but it is rare in 42 and extinct in 8 provinces.

The rate of decline of the European hamster in Ukraine, Belarus, Moldova and Russia differs between regions (Fig. 3). In some regions we see dramatic changes and even full extinction (Eastern Europe), but in others (Caucasus and Siberia) the species is still abundant. We did not observe an increase in the relative occurrence in any province. In 37 regions, the category did not change (0). Deterioration by 1 category (−1) was found in a total of 39 provinces. A severe deterioration by 2 categories (−2) occurred in 9 provinces. The decline predominantly affected provinces in the west and in the south, with provinces in the southwest being most affected. This development suggests a fragmentation of populations in this part of the distribution area. When considering only areas in which the European hamster has the best chances for survival, i.e. where it is (i) common or abundant and (ii) has not declined, the maps suggest that populations will separate into 7 fragments (Fig. 4). Two are in Ukraine in the western

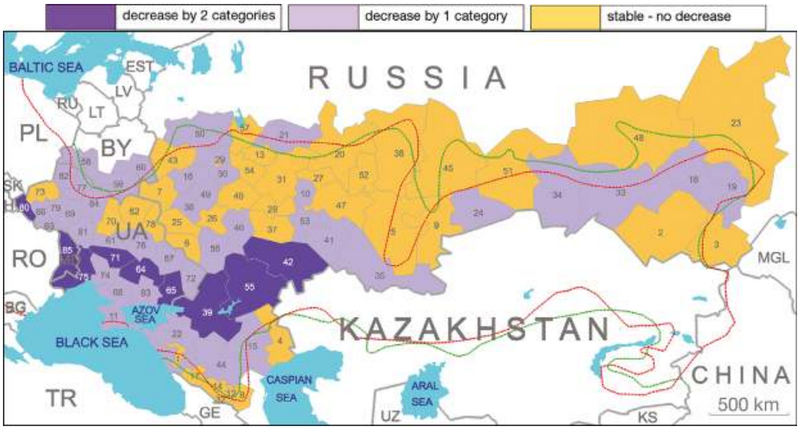

Fig. 3. Rate of decline in the relative occurrence of European hamsters *Cricetus cricetus* in their eastern range based on the comparison of historic (before 1970) and recent (since 1970) sources (see Table S3 in the Supplement). Literature used to create this figure is listed in the Appendix. We distinguish between densities (0), moderate declines by 1 category (–1) or dramatic declines by 2 categories (–2). For further details see Fig. 2

Fig. 4. Likely future occurrence of European hamsters *Cricetus cricetus* in Eastern Europe and Russia based on past changes in the relative abundance (see Table S3 in the Supplement). In provinces marked in yellow, hamsters are presently (i) common or (ii) abundant and not declining and should thus have better chances of survival than in other provinces. For further details see Fig. 2. For literature used to create this figure see the Appendix and Table S3

(province 73) and northern parts (provinces 70, 62, 78), which fits well with the distribution data (see Fig. 1). Of the 5 remaining fragments, 1 is mainly in the North Caucasus (provinces 17, 11, 12, 32, 8), 1 is in the western Volga region (provinces 31, 28, 37), a large fragment is in the eastern Volga and Ural region (provinces/republics 5, 47, 52, 38, 45, 9), and 2 are in Siberia (provinces 48, 23 and province/republic 2, 3) (Fig. 4).

From Kazakhstan we only have density data for the past (Neronov 1965) but not for the present. According to Lindeman et al. (2005), hamsters were abundant in Western Kazakhstan up to the mid-1970s. The number declined dramatically thereafter, except for a short increase between 1988 and 1990, after which the species became extremely rare. Moreover, the number of suitable habitats declined. Nevertheless, the European hamster is not in the Red Book of Kazakhstan and is not considered threatened (A. Shmalenko pers. comm.) In Kostanai oblast of Kazakhstan, the European hamster is quite common in wet biotopes within natural and grazed steppe areas (A. Shmalenko pers. comm., Oct 2015). More data on the recent distribution of European hamsters in Kazakhstan are needed.

According to Kucheruk (1959), the European hamster was present in northeastern China in the region of Xinjiang. Today the species is categorized as near threatened on the Chinese Red List, although it nearly meets the criteria for vulnerable (Smith & Xie 2008).

Despite the declines of European hamsters in rural areas, stable populations were found in cities across the distribution area, including Brno, Košice, Lublin, Moscow, Nalchik, Omsk, Simferopol and Vienna (Feoktistova et al. 2013, Feoktistova et al. 2016) where synurbanization is observed. This shows that the factors affecting population dynamics are still unclear and must be studied in more depth.

In summary, except for very few countries such as Romania and very few regions in Ukraine and Russia, a dramatic decline in range and/or relative occurrence of the European hamster has occurred throughout its distribution area. Consequently, there is a high probability of interrupted gene flow, which has already been confirmed in many European areas (Neumann et al. 2005, Banaszek et al. 2011, La Haye et al. 2012b) where population fragments are separated by hundreds of kilometers. Highly fragmented urban areas can impair gene flow over distances as short as 2 km (Feoktistova et al. 2016), and this can lead to a reduction in variability; for example, colour variants of the European hamster such as flavistic, piebald, albinistic and melanistic variants have decreased since the 1950s and are now seldom reported (Kayser & Stubbe 2000).

'Modern agriculture' seems unlikely to be the main reason for the decline

Originally, 'modern agriculture' seemed to be the most obvious reason for the decline of European hamsters (for a review, see Weinhold 2008). However, the fact that the species declined all over the distribution area, with different landscapes, field sizes, main crops, agricultural philosophies, and under both conventional and organic or under traditional and modern farming, makes it unlikely that 'modern agriculture' is the main reason. Moreover, we could not find literature which defines the term 'modern agriculture' or which relates different agricultural practices to population densities. Experiences from hamster-friendly field management, which includes profound changes in the agricultural practices, are thus the only source of information. However, after the implementation of hamster-friendly practices, no increase in hamster numbers could be ascertained (Martens 2005, Mammen 2011b, Walz 2011, Weinhold 2011, Amand et al. 2012). Finally, the onset of the decline of the European hamster also makes it appear highly unlikely that modern agriculture is one of the main causes, since modern farming methods started much later than the decline of European hamsters. In Germany, hamsters declined as early as the 1920s (Eisentraut 1928, Petzsch 1933, Stubbe & Stubbe 1998, Monecke 2013); in Hungary between 1960 and 1980 (Bihari 2003); and in the Omskaya oblast in Siberia in the late 1950s (Sidorov et al. 2011).

No literature evidence for increased extrinsic mortality

We could not find any literature showing that in European hamsters, the extrinsic mortality by predation or anthropogenic factors has increased. The monthly mortality rate of adults is currently rather low and is similar in both hamster-friendly (3–17%, La Haye et al. 2014; 5–19%, Kuiters et al. 2011, both for the Netherlands) and intensely farmed large fields (depending on culture, mortality ranges from 2–7 to 3–18% in eastern Germany, Kayser et al. 2003a). Only in 1 area in western Germany did it increase temporarily to 43% directly after harvest (Kayser et al. 2003a). These numbers are surprisingly low for a prey species.

Furthermore, the percentage of European hamsters in the diet of birds of prey such as the red kite *Milvus milvus* decreased from 49.5% between 1962 and 1967 (Traue 1970) to 0 to 15% between 1992 and 2010 (Allert & Löw 2011) in East Germany. In a Hungarian study of the eastern imperial eagle *Aquila heliaca* it declined from ca. 20% between 2005 and 2008 to 4% in the years 2011 and 2013 (Szabó 2013); moreover, many predators are also in decline.

In contrast, historically the extrinsic mortality of European hamsters due to fur trapping and pest control was exorbitant. Early reports of fur trapping in Germany date from the 16th to the 19th century (Hofmeister 1965, Stubbe & Stubbe 1998). Between the early 20th century and the 1970s, the number of hamsters trapped annually reached hundreds of thousands or even millions in many regions across Eurasia (see Table S4 in the Supplement). Fur hunting alone killed more hamsters in a region than are presently estimated to inhabit the whole of Europe. In addition, intensely targeted pest control actions against European hamsters, such as poisoning, gassing or drowning, were implemented throughout the range (Hofmeister 1965, Hubert 1968, Nechay et al. 1977, Adler & Zimmermann 2013), which killed additional high but undefined numbers of hamsters. To our knowledge, fur hunting ceased in most countries at the latest in the 1990s, since low hamster numbers rendered trapping uneconomical. In Hungary it lasted longer, although today it is very rare (G. Nechay pers. comm.). In Russia, harvesting sharply decreased after 1970–1972. It continues to the present only in 8 regions on a very small scale. Targeted pest control actions against European hamsters have largely ceased because there is no further need. Even though European hamsters may still succumb to general rodenticides, it seems safe to assume that the 2 most severe causes of mortality in European hamsters are no longer present.

Due to increasing vehicle traffic, road mortality might have gained in importance as a reason for the decline in numbers of European hamsters. High traffic mortality was already reported in the 1960s when streets were covered with hamster cadavers in mass-outbreak years (for a review, see Grulich 1980). In such a mass-outbreak year, Kemper (1967) counted 2400 dead hamsters per week on a 12 km long road stretch in Austria. In contrast, between 2001 and 2007, a total of only 197 hamster carcasses were found on ca. 50 km of country lanes in Thuringia, the region with the highest population density of European hamsters in Germany (Zimmermann 2008). As Grulich (1980) suggested, the number of road-killed hamsters seems to reflect the population densities, and thus traffic is considered to be of minor importance as a mortality factor today.

The only indication of increased mortality is linked to the eastward shift of the oceanic–continental climate gradient leading to increasing oceanic climate in Western Europe. Historically in Germany, snow covered the ground in winter, but due to higher winter temperatures, soils are now saturated from huge quantities of rain, which affects hibernacula and food stores. In Germany, European hamsters are thus increasingly reported by locals as being active above ground in winter with their fur soaked (U. Weinhold, M. Görner pers. comm. 2015). Thus, rising winter temperatures in precipitation-rich areas such as Western Europe might increase mortality.

In summary, the literature suggests that the extrinsic mortality of European hamsters is much lower at present than historically. To what extent a climatic shift has affected mortality in recent years remains to be studied. It appears unlikely that modern farming practices are killing European hamsters on a larger scale than fur trapping and pest control did in the past.

Reproduction rate has dramatically decreased

A population is stable when the reproduction rate compensates the mortality rate. Since the extrinsic mortality of European hamsters does not seem to have increased, we reviewed literature on their reproduction rate published since 1765 from across the distribution area, i.e. embryo numbers, litter size (pups per litter) and the number of litters a female has in a year. Data until 1986, i.e. before the decline was noticed in Western Europe, are summarized as historic data, while later data are called recent data.

Most historical data came from field guides, encyclopaedias or from 'natural histories', i.e. detailed monographs on European hamsters. The recent data for number of litters and litter size come from scientific articles in which the reproduction rate of focal females was observed. Historic and recent litter numbers and litter sizes might have been measured by different techniques. Today, exact litter numbers are determined by the observation of focal females, while in historic works, farmers, who knew the local fauna, were probably the source of information. In historic times, litter size was often determined by digging out or floating a burrow. More recently, pups are counted only when they leave the maternal burrow, i.e. at an older age, reducing the chances that the litter is still complete. However, in historic studies, pups might have been overlooked in the burrow or drowned before they appeared at the surface (Górecki 1977b). The consistency between historic and recent data of litter size (see Fig. 7) shows that the potential losses are similar with all techniques.

Data on maculae cyanae, uterine scars that indicate a previous implantation of an embryo, were not included, since it is unknown how long they stay. Their number typically ranges between 1 and 45 and might reach up to 140 (Weber & Stubbe 1984, Grulich 1986).

Mean embryo number, assessed from dead-trapped females (historic data, Table S5 in the Supplement) or by palpation of living females (recent data, Table S6 in the Supplement), was stable until 1986: between 1925 and 1950 it was 12.00 ± 1.08 (± SEM, n = 8 studies), between 1951 and 1975, it was 12.02 ± 1.12 (n = 6), and between 1976 and 1986, it was 12.61 ± 1.12 (n = 7). After 2000, it decreased slightly to 9.95 ± 0.83 (n = 4; Fig. 5). This decrease might be attributed to the different methods used. Moreover, the data show high variance, which might result from counting embryo numbers at various unknown ages of females and embryos. Embryo resorption reduces their number with increasing prenatal age (Weber & Stubbe 1984). Moreover, embryo numbers are higher in older females (Gyurkó 1975). Females which gestate in their birth year have, on average, 5 embryos while older females have 10 (Nechay et al. 1977).

Data on number of litters and litter size are clearer. Literature sources and details are given in Tables S7–S10 in the Supplement. Some articles give several data, e.g. Grulich (1980) indicated a litter number of 3 for young females and 4 to 5 for old females. In such cases, both values, 3 and 4.5, were included in the graph.

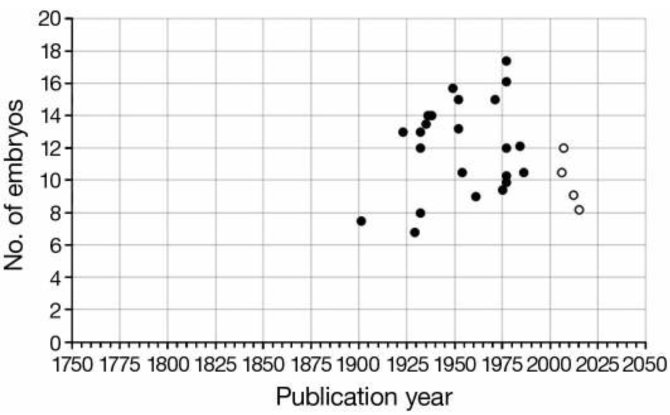

Fig. 5. Mean number of embryos in European hamsters *Cricetus cricetus* in various regions of their distribution area plotted against the publication year of the original studies (see Tables S5 & S6 in the Supplement). (●) Historic data (n = 23); (○) recent data (n = 4). Literature used to create this figure is listed in the Appendix

Before 1986, a female produced mostly 2 to 2.5 litters per year (Fig. 6), but there was a large range from 1.5 to 4.5 between 1925 and 1985. From a modern point of view, a mean litter number of 4.5 (Nechay et al. 1977, Grulich 1980, Sládek & Mošanský 1985) might appear too high, although 5 gestations per year have been reported for females in captivity (Samosh 1975) and are thus within the possible range. The overall mean yearly litter number from historic data was 2.46 ± 0.1 (n = 59; mean ± SEM). In contrast, recent litter numbers are considerably lower, at 1.64 ± 0.1 (n = 6) and their range is reduced (between 1.4 and 1.9, Fig. 6). There was no east–west gradient in the yearly litter number as previously assumed (Leirs 2002). Mean litter numbers from historical data are: France 2.5 ± 0.3, Germany 2.3 ± 0.1, Czech/Slovakia/Czechoslovakia 2.8 ± 0.3, USSR 2.2 ± 0.1.

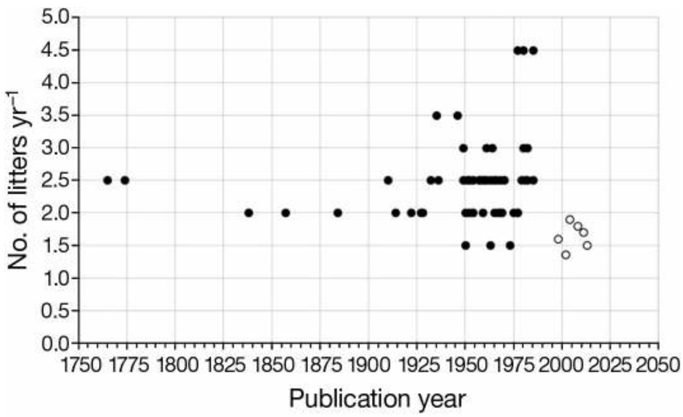

Fig. 6. Mean number of litters produced per year by European hamsters *Cricetus cricetus* across their distribution area plotted against the publication year of the literature source (Tables S7 & S8 in the Supplement). (●) Historic data from 1765 until 1985 (n = 59); (○) recent data after 1996 (n = 6). Literature used to create this figure is listed in the Appendix

The litter size before 1910 was ca. 8 (5.5–11) pups per litter (Fig. 7a). Between 1914 and 1955, a litter usually had 10 to 11 pups, but after this period, litter size decreased dramatically (Fig. 7a, Tables S9–S11 in the Supplement). To estimate the start of the decline, we performed a segmented regression analysis in Sigma Plot (SPSS) from the past 100 yr. This procedure is based on a change-point model, in which the linear relationship may change at a point that is not fixed in advance (Vieth 1989):

$$fx = Ax \leq \mathrm{t}$$
$$fx = A + b\,(x - t)\; x > \mathrm{t} \qquad (1)$$

where fx is the predicted value of the n^{th} data point, x is the n^{th} time point, and A is the amplitude of the plateau. Constant b describes the slopes of the decrease, and t is the abscissa of the change point. For further details see Monecke et al. (2006). The regression revealed that the decline started in 1954 ± 4.03 yr (± SE, Fig. 7b). The data strongly suggest that this decline is ongoing. The extrapolation of the regression line points towards a litter size of 0, i.e. an extinction of the species, in 2038; however, when the range of the data is considered, extinction could occur as early as 2020 (Fig. 7b). Theoretically, the extinction could also occur as late as 2050 (Fig. 7b), although we consider this possibility unlikely, since the reproduction rate is so low that in any year with a

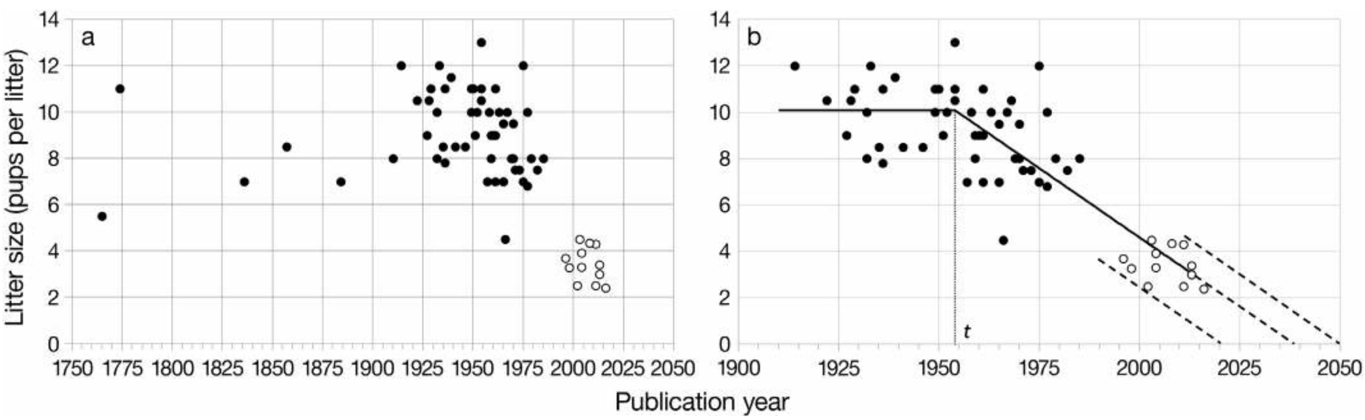

Fig. 7. Mean litter sizes in European hamsters *Cricetus cricetus* plotted against the publication year of the respective literature sources (Tables S9 & S10 in the Supplement). (●) Historic data from 1765 until 1985; (○) recent data after 1995. Data are from across the distribution area. Literature used to create this figure is listed in the Appendix. (a) All data, (b) results of the segmented regression analysis. Data points from 1914 and thereafter were fitted with a regression consisting of 2 straight lines (solid) with a correlation coefficient of r = 0.84. Their crossing point (t) gives the beginning of the decline in litter size, which is in 1954 ± 4.03 yr (± SE). The x-axis crossing of the extrapolation of the regression line and its parallel translations through the upper and lower limit of the data (dashed lines) show the time frame during which the extinction of the species can be expected

reproduction rate below average, regional populations might be so weakened that random unfavourable circumstances could lead to spontaneous extinction at any moment.

When data are split into different geographical regions, it becomes evident that this dramatic decrease in litter size affects most, if not all, regions of the distribution area (Fig. 8). Except for the former USSR, the decline rate was similar in all regions, as were the litter sizes at any given time.

That this effect is less clear in the former USSR might be due to the short time span covered by the available data. However, it might also reflect a difference in the reproduction rate between stable, declining and rapidly shrinking populations in Russian, Ukrainian, Belarussian and Moldavian provinces (Fig. 4), since the data cover an enormous geographical range. Indeed, a recent review (Sidorov et al. 2011) (which was not included in the graphs on reproduction because it does not constitute original work on focal females and it is not clear whether the data originated from recent studies) gives a yearly litter number of 2 (Russia, midlands) or even 3 (southern Russia) and a mean litter size of 10.5 pups (Siberia). The extent of the data exceeds by far all recent data from studies on focal females, but the data originate from regions in which the occurrence of the European hamster is mainly stable and high (Figs. 2 & 3). A confirmation of these data and a comparison of the reproduction rate between declining and stable

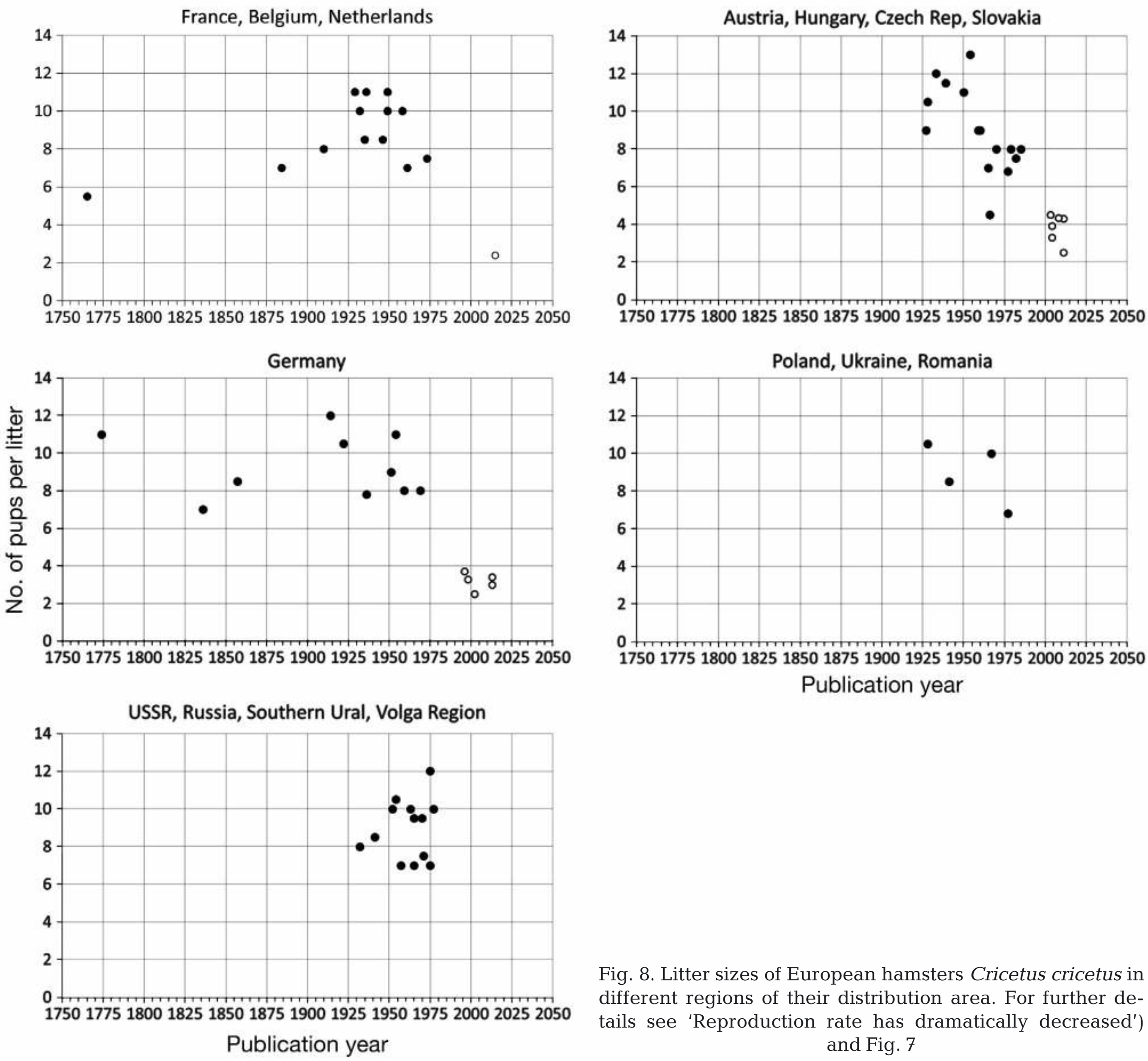

Fig. 8. Litter sizes of European hamsters *Cricetus cricetus* in different regions of their distribution area. For further details see 'Reproduction rate has dramatically decreased') and Fig. 7

populations as well as between phylogeographical lineages (Neumann et al. 2005, Banaszek et al. 2010, Banaszek et al. 2012) would be highly desirable.

The yearly reproduction rate of a female is given in Table 1. Between 1914 and 1935, a female raised ~25 pups per year. Between 1965 and 1985, it was only 21, due to a clear reduction in litter size, which was partly compensated by a slightly increased litter number. Between 1996 and 2015, both litter size and litter number were so reduced that a female now raises only slightly more than half of the offspring in 1 year (5.6) than it did in a single litter during the 1914–1935 period (10.2). The calculated yearly offspring number of 5.6 is supported by several field studies following focal females: Franceschini-Zink & Millesi (2008b) found 6.3 pups, Hufnagl et al. (2011) reported 6.9 and 3.7 pups, and Albert (2013) found 5.4 pups per year and female. Recapture studies showed that no more than 20% of the pups survive until the following spring (Karaseva 1962, Górecki 1977a, Kayser & Stubbe 2002, Franceschini-Zink & Millesi 2008a). Given that the sex ratio is balanced (Vohralík 1974, Grulich 1986, Monecke & Wollnik 2008), half of the pups are females, of which roughly 15% fail to reproduce (Weber & Stubbe 1984, Franceschini & Millesi 2004, Franceschini-Zink & Millesi 2008b, Albert 2013). Consequently, a female effectively raises only 0.5 females for next year's reproduction (Table 1).

European hamsters can only survive as a species if each female effectively produces at least 1 female for next year's reproduction. This is no longer the case. Moreover, since in recent years the life span of European hamsters has barely exceeded the yearling state (Kayser & Stubbe 2002, Franceschini-Zink & Millesi 2008a), most animals have only 1 reproductive phase in their lifetime. The strong negative trend in litter size since 1954 (Fig. 7) accompanied by a sharply reduced litter number after 1986 (Fig. 6) closely mimics the decrease in hamster occurrence and range recorded over the past decades (see Figs. 1 & 2) and can thus be considered as the proximate reason for the decline of this species. The ultimate reasons causing this decrease in reproduction must now be identified.

The data on the reproduction rate show that the European hamster is very close to extinction. If the reproduction rate, especially the litter size, for only a single year is lower than average, the species will become extinct. This is certainly true on a regional level, but it might also affect the whole distribution area. Studies on hamster pests revealed (1) that in outbreak years the reproduction rate and/or the duration of the reproductive phase was increased (Sládek & Mošanský 1985, Grulich 1986) and that (2) such years occurred simultaneously over huge parts (300–4000 km) of the distribution area (Nechay 2008). Thus, the opposite scenario, viz. a high synchrony of bad years with low reproduction, might be possible, and as a result, could cause a widespread breakdown of hamster populations.

Table 1. Mean annual reproduction rates of female European hamsters *Cricetus cricetus* and the resulting number of reproducing females in the next year

	1914–1935	1965–1985	1996–2015
Mean no. of litters per year and female	2.43	2.56	1.63
Mean no. of pups per litter	10.17	8.24	3.43
Mean no. of offspring per female and year	24.69	21.11	5.58
No. of pups that survive until the next spring (20%[a])	4.94	4.22	1.12
No. of survivors that are female (50%[a])	2.47	2.11	0.56
No. of surviving females that reproduce (85%[a])	2.10	1.79	0.47

[a]Percentages according to literature given under 'Reproduction rate has dramatically decreased'

IUCN STATUS OF THE EUROPEAN HAMSTER NEEDS TO BE CHANGED

Surprisingly, the IUCN Red List status of the European hamster is Least Concern (LC) (Kryštufek et al. 2008). This categorization is mainly based on the very wide European-Asiatic range and on the assumption that the species is abundant in the eastern part of the range, especially in Russia and Ukraine (Kryštufek et al. 2008). However, this assumption was in no way based on any literature or research, but on personal communications and simple assumptions. For example, one of the authors (I. Zagorodnyuk pers. comm. in Kryštufek et al. 2008) stated personally that the species is abundant in Ukraine. However, this is quite surprising, as Gorban et al. (1998) published several years earlier that the hamster had become rare or disappeared from some parts of the country. These data were later confirmed by Rusin et al. (2013). Similarly, opinions on the species' status in Russia are simply assumptions, demonstrated in statements like:

> Less is known about the status of the species in eastern Europe and Russia, but it is certainly more abundant there than in the west (Kryštufek et al. 2008, p. 4)

even though data showing a decrease in hamster populations in several Russian provinces were already available (see Table S3). Our review shows with well established and new data that the assumptions for the present Red List categorization of the European hamster are not valid. The range and/or relative abundance of the species is rapidly shrinking all over the huge Eurasian range. The inhabited area is, or is quickly becoming, fragmented, and the number of populations is decreasing. Moreover, we have also shown a dramatic decrease in reproduction, which may cause the complete collapse of the species within a few years.

Although further research is needed, the findings on the decrease in range and relative abundance suggest that the global status of European hamsters should at least be Vulnerable (VU) according to criterion A2 of the IUCN Red List (minimum 30% of decline within 10 yr; IUCN 2012), especially since the IUCN criterion is matched that

> the reduction or its causes may not have ceased or may not be understood or may not be reversible (IUCN 2012, p. 21).

The reduction in population size is based on A1 a and c criteria (direct observation and decline in area of occupancy, extent of occurrence and/or quality of habitat). If the low reproduction rate, which suggests a shrinking of the population by 50% each year in large parts of the distribution area, is also incorporated, then the status of Endangered (EN) criterion A4 might be considered:

> A projected or suspected population size reduction of ≥50% over any 10 year period, [...] where the time period must include both the past and the future, AND where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible (IUCN 2012, p. 19)

In Europe, the species is present in 18 countries, 9 of which currently consider the European hamster to be Vulnerable (VU), Endangered (EN), Critically Endangered (CR) or Extinct (EX) at the national level (Table S1). Moreover, despite reports on a severe decrease in Poland and Ukraine (Ziomek & Banaszek 2007, Rusin et al. 2013), which also suggest the status of Endangered, the species there is still considered Data Deficient (DD) and Not Evaluated (NE), respectively. Furthermore, 14 Russian and Belorussian provinces or regions consider the European hamster as Near Threatened (NT), Vulnerable, Endangered or Critically Endangered (Table S3). None of these data support the global IUCN status of Least Concern (LC). In many of the other countries or regions the status is Data Deficient or Not Evaluated or unknown. For the sake of the species' protection it is imperative that these countries, as well as Kazakhstan and China, evaluate the range and densities of the European hamster in their area.

POSSIBLE REASONS FOR THE DECLINE IN REPRODUCTION

This review shows that the original assumptions for the decline in European hamster populations are not supported by the literature. Instead, it revealed that since about 1954, a dramatically declining reproduction rate has increasingly impaired survival of the species throughout its distribution area. The reproduction rate is already so low that it alone is sufficient to cause extinction, even if anthropogenic mortality is reduced to 0. Research is urgently needed to identify the causes.

In general, our data suggest that the reasons for the decline in the hamsters' reproduction apply (1) all over Eurasia (2) since ca. 1954 (3) with increasing importance and (4) that they are most likely not directly related to modern agriculture. The significance of these factors might differ between regions. Some possible hypotheses which fit these characteristics are discussed in the following.

Reproductive cycle of European hamsters

To identify what might impair reproduction in wild European hamsters, a summary of the neuroendocrine processes controlling reproduction is helpful. In this species, the seasonal reproductive cycle is driven by an endogenous timing mechanism, the circannual clock, which times the onset and end of hibernation and reproduction and initiates the necessary physiological changes, even if the animals have no information about the season (for a review, see Monecke et al. 2014b). This circannual clock ticks only approximately but not exactly in a 365 d stroke and thus needs to be reset once per year to maintain synchrony with the environmental cycle (Gwinner 1986). This is achieved by an interaction of the circannual clock and the circadian clock, which drives daily rhythms, for example the activity rhythm. The circadian clock is located in the hypothalamic suprachiasmatic nuclei (SCN) (Dunlap et al. 2004), and one of its tasks is to measure the length of day or photoperiod for the circannual clock, since this is the most reliable environmental signal for seasons (Gorman et al. 2001). In mammals, the SCN receives the information about light or darkness from special photoreceptors in the retina, the ganglion cells, which perceive light of wavelengths around 500 nm (Dunlap et al. 2004).

The synchronization process in European hamsters is based on a so-called sensitive phase to short photoperiods, from mid-May to mid-July, when the shortening of photoperiod after the summer solstice is perceived (Saboureau et al. 1999). Normally, the European hamster has an arrhythmic activity pattern that is highly unpredictable for predators, but during the sensitive phase it is very precise (and risky; Monecke & Wollnik 2005). During this period, activity starts in the late afternoon several hours before sunset, at exactly the same time each day. This precise activity onset is a stable reference to measure the tiny advances of sunset (Monecke et al. 2006) after the summer solstice. When in mid-July the shortening of the photoperiod is detected, the animals initiate gonadal regression (visible only 4 wk later; Saboureau et al. 1999), the activity pattern switches back to the default arrhythmic pattern (Monecke & Wollnik 2005), and the circannual clock, which times the onset of the next year's reproductive phase by a complex neuroendocrine pathway (Sáenz de Miera et al. 2014), is reset (Monecke et al. 2009).

To survive in a seasonally varying environment, very precise timing is essential. The circannual clock allows the animals to anticipate the upcoming seasonal changes in the environment, so that all necessary physiological changes (at least 73 are known; Monecke et al. 2014b) from the hibernation state (Waßmer & Wollnik 1997) to the reproductive state are completed in early spring, allowing the animals to raise their offspring during the most favourable seasons. It also allows them to anticipate the harsh winter conditions by preparing a winter stock in late summer when food abundance is high.

The above timing process might be disturbed at different points, potentially resulting in the impairment of the reproduction rate in European hamsters as observed since 1954. Indeed, several studies have reported a delay in the onset of reproduction. In a population in Austria, conception of the first litter occurred only in early to late May (Hufnagl et al. 2011), in the Netherlands from early May to early June (La Haye et al. 2014) and in Germany from early May to mid-June (Kayser & Stubbe 2002, Weinhold & Kayser 2006). This is a delay of 0.5 to 2 mo compared to older literature, which in general indicates mid-April as the onset of the reproductive phase (Table S12). Such a delay severely reduces the possible number of yearly litters. Moreover, late-reproducing females have smaller litters (Hufnagl et al. 2011) so that the total number of offspring they produce in a year is lower than in early females, even if both spend the same amount of time (from the first conception to the last weaning) on reproduction (Franceschini-Zink & Millesi 2008b).

Fur harvesting

One possible reason for a delay in reproduction might be fur trapping, although this practice ended several decades ago. More critical than the number of hamsters which were trapped was probably the timing of trapping, which occurred early in the year, since fur quality is best directly after hibernation. Thus, each year, the part of the population which terminated hibernation and started reproduction early was trapped, and this occurred over centuries.

These early-emerging animals represent the most valuable part of the population, since they have the chance to raise 3 litters in a year instead of 2. Moreover, they are the only animals which would reproduce early enough in the year for their offspring to become reproductive in their year of birth at an age of a few weeks, while later-born animals reach puberty only after months, i.e. after hibernation (Kirn 2004, Monecke et al. 2014a). The probability that these early-born animals survive until they are able to reproduce is thus much higher than that of late-born animals, of which only 20 % reach the age of sexual maturity (Table 1). Animals which reproduce in their birth year have seldom been observed in recent years.

Early fur trapping may also have had an evolutionary effect. It is very likely that analogous to circadian rhythms (Ralph & Menaker 1988, Monecke et al. 2011b), the timing of circannual rhythms has a heritable component with early- and late-reproducing genotypes (Monecke 2013). In this case, fur trapping would have caused a strong selection pressure against early-reproducing animals, which may have led to a progressive decline of animals carrying the early-reproducing genotype. Since late-reproducing females raise fewer offspring (Franceschini-Zink & Millesi 2008b), a continuous decline in the mean litter size since 1954 and finally a reduction in the mean number of litters might be the consequence of having removed early-reproducing individuals over decades in the past. Thus, a reason for the decline in the reproduction rate may well derive from the past. If this hypothesis is true, individual monitoring of the timing of reproduction in the wild and in breeding programmes and protection of the early-reproducing phenotype/genotype might be an effective protection measure, particularly since these animals may become crucial in the adaptation of the species to climate change.

Climate change

Following this argument, climate change induces high selection pressure against late-reproducing European hamsters. Since harvest timing has advanced due to increasing temperatures, the second litter is born around harvest (Albert 2013), so that the pups are challenged with a food shortage early in life when energy requirements are high. Survival chances of these late-born animals are considered low (Deutsche Wildtierstiftung 2014).

In general, offspring should be born when food abundance is highest. However, the increasing temperatures due to climate change induce an advance in the peak seasons of food resources, i.e. plants and insects, resulting in a temporal mismatch with the breeding phenology in vertebrates such as mammals and birds (Both et al. 2006). This occurs because the former use temperature and the latter use the unaltered seasonal changes in photoperiod as seasonal timetellers (Dunlap et al. 2004). Bird species which fail to advance their breeding phenology in adaptation to the advanced food abundance peak are in decline (Both et al. 2006, Møller et al. 2008, Husby et al. 2010, Saino et al. 2011). Some mammals have succeeded in advancing their phenology (Réale et al. 2003, Moyes et al. 2011). For example, an advanced spring emergence in recent years due to climate change has led to a strong increase in the number of the hibernating yellow-bellied marmots *Marmota flaviventris* (Ozgul et al. 2010). In contrast, 2 other hibernators, Columbian ground squirrels *Urocitellus columbianus* (Lane et al. 2012) and European hamsters (Kayser & Stubbe 2002), have delayed their reproduction phenology and are experiencing rapid population declines.

Although climate change induces selection pressure against late-reproducing animals, it might ironically cause the disadvantageous delay in reproduction of European hamsters. Climate change has advanced cereal harvests; for example, in many French, Belgian and German regions, the harvest has advanced to June or early July. At least in these regions, it coincides, and might interfere, with the hamsters' phase of sensitivity to the short photoperiod and thus the resetting of their circannual clock which determines the onset of reproduction in the following spring. A case study showed that European hamsters become completely nocturnal after harvest due to a lack of cover (Wendt 1989). If they leave the burrow only at night in the summer, they would not see the advances in sunset, which are the resetting signal for the circannual clock (Monecke et al. 2006). Instead, they experience constant darkness — in the burrow during the day, and outside at night — which could be interpreted as an (extremely) short photoperiod during the sensitive phase. Such a false short day signal would be perceived too early compared to the endogenous season of the animal, resulting in a slightly premature gonadal regression (Saboureau et al. 1999), which is supported by field data (Kayser & Stubbe 2002, Weinhold & Kayser 2006). Such a false short day signal perceived too early in the season also causes a profound delay of the circannual clock and thus of the onset of the next reproductive phase (Monecke et al. 2009), which is also confirmed by field data (Kayser & Stubbe 2002, Hufnagl et al. 2011, La Haye et al. 2014). Climate change could therefore account for the delay in reproduction and thus the reduction in litter numbers after 1986, since temperature has increased since the 1980s (Hartmann et al. 2013).

Light pollution

Artificial light is a global factor which is increasingly becoming a threat for animals. The decline in range (Fig. 1) and relative abundance (Fig. 3) of the European hamster shows a remarkable coincidence with highly light-polluted areas (Fig. 9). Both decline in range and relative abundance are predominantly observed in Europe and western Russia, and farther east in a stretch at the southern border of Russia. European hamsters are not only subjected to light pollution from nearby villages and street lights but also to the bright headlights of cars, which shine at eye level of these animals. Moreover, there is not only a spatial but also a temporal coincidence of increased light pollution and declining hamster populations, since the use of artificial light and its intensity increased rapidly after the Second World War. Finally, light pollution matches the criteria for identifying potential causes for the decrease in the reproduction rate: It has affected huge parts of Eurasia since the 1950s with increasing importance, and it is not related to agriculture.

Fig. 9. Light-pollution across Eurasia. (Earthlights dmsp 1994–1995; data courtesy of Marc Imhoff [NASA GSFC] and Christopher Elvidge [NOAA NGDC]. Image by Craig Mayhew and Robert Simmon [NASA GSFC]: http://eoimages.gsfc.nasa.gov/ve//1438/land_lights_16384.tif. Licensed under Public Domain via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Earthlights_dmsp.jpg#/media/File:Earthlights_dmsp.jpg; image has been modified to show only Eurasia)

Today, the brightness of the night sky around most urban settlements is greater than in a full moon night or than at nautical twilight (Cinzano et al. 2001). Thus, such areas never experience true nightfall. Light pollution is known to severely affect physiology and behaviour through endocrine and neurobiological processes (Navara & Nelson 2007). Across taxa, light pollution can induce cancer or impair immunity, it can alter circadian rhythms, behaviour, energy metabolism, reproductive state and foraging/eating behaviour, and it can influence predation and migration (for a review, see Navara & Nelson 2007, Gaston et al. 2013). Moreover, the spectral composition of street light types has changed from predominantly orange sodium-based lighting in the 1960s over metal halide lamps to high-brightness, light-emitting diodes (LEDs) with a broader spectrum of wavelengths (Gaston et al. 2013). In contrast to the sodium-based lighting, the light emitted by metal halide lamps and LEDs includes wavelengths around 500 nm, which are perceived by the retinal ganglion cells, which in turn project to the circadian clock in the suprachiasmatic nuclei (Dunlap et al. 2004). These wavelengths are thus also relevant for the correct resetting of the circannual clock. In European hamsters, they might increasingly impair the perception of the natural shortening of the photoperiod after the summer solstice and consequently the timing of the reproductive cycle. Moreover, this environmental signal might be further blurred by the continuously increasing nightly light intensities.

In other species, light pollution initially seems advantageous, but after longer exposure it leads to profound impairment of seasonal physiology. Birds interpret light pollution as an increase in day length (Dominoni & Partecke 2015); consequently, it advances the reproductive phase including the lay date (Kempenaers et al. 2010, Dominoni et al. 2013a, Dominoni & Partecke 2015) and increases the extra-pair siring success (Kempenaers et al. 2010). However, after long-term exposure over 2 yr, the reproductive system of the birds fails to develop (Dominoni et al. 2013b). Likewise, Siberian hamsters *Phodopus sungorus* initially adapted their physiology faster to a shortening of the photoperiod under dim-light nights versus dark nights (Gorman & Elliott 2004); however, they failed to switch completely to the winter phenotype (Ikeno et al. 2014). In Siberian hamster pups, a brief nightly illumination of only 15 min on postnatal Day 18 induced gonadal growth (Spears et al. 1990) even though the animals were maintained under a short photoperiod and should have been in a winter state.

In European hamsters, artificial light during 2 nights in winter shifted the circannual reproductive cycle by 3 to 4 wk (Monecke et al. 2010). Outdoors, they showed a slightly modified activity pattern in an urban versus a rural area in July and August (Kaim et al. 2013). Since the activity pattern changes profoundly at this time of the year, it might indicate a difference in the seasonal timing of reproduction and thus its success. Light pollution may therefore present a hitherto underestimated threat for European hamsters and other species.

Fragmentation of the landscape

Highly light-polluted areas are usually highly fragmented by streets, highways and railway tracks. The coincidence between the maps showing the decline of European hamsters (Figs. 1 & 3) and the light-pollution map (Fig. 9) might thus be a result of the coincidence of population decline and habitat fragmentation, which has been discussed to be a reason for the decline of many species (Hanski 1998), including European hamsters (Weinhold 2008). Besides a risk for increased mortality due to traffic and a long-term reduction in genetic diversity due to isolation (Neumann et al. 2004, Feoktistova et al. 2016) habitat fragmentation might pose an additional possible threat to reproduction. In captive European hamster colonies, higher litter sizes were observed after a male from another colony was introduced (La Haye et al. 2012a, L. Heimann pers. comm., S. Monecke unpubl. obs.), possibly due to an increase in genetic variability. In general, the genetic diversity of European hamster populations is low (La Haye et al. 2012b). Since even comparably small natural barriers, such as a 20 km belt of sandy soils, are able to separate 2 huge phylogeographical lineages of the European hamster (Banaszek et al. 2012), it is likely that the increasing number of artificial barriers is insurmountable. In highly structured urban areas, distances as short as 2 km isolate different demes of hamsters (Feoktistova et al. 2016). Fragmentation might thus be another reason for the ongoing decrease in the reproduction rate.

Population density

A similar case in history when a dramatic decline in reproduction led to the extinction of a severe pest and game species is illustrated by the passenger pigeon *Ectopistes migratorius*. Once probably the world's most abundant bird species, passenger pigeons declined within a century from several billions of birds per flock to extinction in 1914 (Frenz 2012). A recent model calculation found that habitat loss did not play a role in the decline of passenger pigeons; neither did hunting, except when it impacted reproduction. Instead, a failure to reproduce was identified as the primary reason for the decline (Stanton 2014). One hypothesis is that steadily declining population densities increasingly failed to stimulate reproduction. There is a striking similarity between the fate of passenger pigeons and the decline of European hamsters (Hutterer & Geiger-Roswora 1997, Monecke 2013). The decline of hamsters might have started with overhunting leading to decreasing population densities, which negatively affected the reproduction rate. This hypothesis is supported by extremely high population densities, an extended reproductive phase and high numbers of juveniles in pest years (Grulich 1986).

However, observations by Sludsky (1977) suggest that an increased mortality rate supports a high reproduction rate. At present, we observe low rates of both mortality and reproduction. The effect of density and mortality on the reproduction rate remains to be studied. An effective protection measure might be to cause an artificial hamster pest situation by releasing high numbers of captive-bred hamsters in small areas and follow the reproductive success of the population.

Pesticides

The use of pesticides increased rapidly after the Second World War. Simultaneously, reproduction of the European hamster decreased, suggesting a causal relationship. In the American mink *Mustela vison*, reproduction rates and embryo numbers decreased due to exposure to polychlorinated biphenyls (Aulerich & Ringer 1977). Various persistent organochlorines used in pesticides, among them DDT and Dieldrin, have been detected in the tissue of European hamsters, although the concentrations barely exceeded the detection limit (Kayser et al. 2001). Likewise, only traces of lead, cadmium, mercury and copper could be detected (Kayser et al. 2003b). These results were thus considered not dangerous for the hamster or its reproduction. Moreover, if these agrochemicals were responsible for reduced embryo numbers, one would expect an increase in the reproduction rate after the ban of such pesticides in many countries (e.g. in Germany, DDT and Dieldrin were banned in the 1970s), which did not happen. Furthermore, the number of embryos produced by European hamsters has decreased only slightly and only very recently (Fig. 5). Thus, agrochemicals do not appear very likely to be the main cause for a reduction in the reproduction rate of European hamsters.

Decrease in lifespan

Older European hamster females produce a larger number of embryos (Gyurkó 1975), larger litter sizes (Monecke et al. 2011a) and more litters (Grulich 1980) as yearlings. They also emerge earlier from hibernation (Ružić 1976) and can reproduce earlier. However, in recent years, it has been reported from many regions that wild European hamsters barely exceed the yearling stage (Kayser & Stubbe 2002, Franceschini-Zink & Millesi 2008a, participants of the International Hamster Workgroup pers. comm.). This potential decrease in lifespan is not caused by a higher extrinsic mortality, such as predation or anthropogenic reasons, but rather by unknown intrinsic reasons such as cancer (Ghadially & Illman 1965, Brandes et al. 2004) or other predispositions, since even in captivity, the mean lifespan is currently only 1 to 1.5 yr for males and 1.5 to 2 yr for females (S. Monecke unpubl. obs.), and this is only rarely exceeded (Monecke et al. 2011a, Wenisch & Godman 2011). According to its physiology as a circannual hibernator, this species should have a lifespan of several years, and this is indeed stated in older literature (Mohr 1954, Karaseva 1962, Reznik et al. 1976, Nechay et al. 1977, Ernst et al. 1989). A possible decrease in lifespan might thus be a major reason for the species' decline and might explain the lower reproduction rate. In accordance with this suggestion, a recent study found remarkable parallels with our study for body weight, which has also declined since the 1950s (Tissier et al. 2016). This might reflect a younger mean age or a poorer fitness of the animals. Both would lower the reproduction rate of the animals.

CONCLUSIONS

This literature review does not exclude the possibility that particular agricultural practices increase the mortality of European hamsters; however, it shows that reduced fecundity is a far better explanation for the decline of this species than an increased mortality due to changes in agricultural practices. The continuous decrease in the reproduction rate is so severe that it alone is sufficient to cause extinction within an extremely short period of time, but the factors which negatively affect the reproduction rate still need to be identified. Without considering mortality, our data suggest an extinction of the species between the years 2020 and 2038. Thus, fundamental research is presently the most important protection measure to develop effective protection strategies in the short remaining time and should thus have highest priority. Conservation breeding programmes for the weakest populations might buy some additional time and postpone local extinctions of hamsters by a few more years. The decline in European hamster populations may have started with overhunting and continued as the result of an ongoing decline in the reproduction rate. Modern farming practices seem less likely to be responsible for losses than threats acting on the genetics (reduced genetic variability or potential extinction of an early-breeding genotype) or physiology (climate change, light pollution, altered age structure) of the animals. We strongly recommend immediately changing the IUCN Red List status of European hamsters from Least Concern to Vulnerable or even Endangered.

Acknowledgements. Our study was done under the framework of the IUBS/ISZS International Research Program: Biological Consequences of Global Change (BCGS). We thank Marcel Visser (NIOO, the Netherlands) for sparking the idea for this literature research. We are very grateful for the committed literature search by the interlibrary loan service of the library of the Karlsruhe Institute of Technology (KIT, Germany), especially by Nadia Zappe, the University of Heidelberg (Germany) and Petra Widmer from Motz & Kadner Literature Service (Germany). Further, we thank the German National Library in Leipzig, the State Library of Baden, Karlsruhe (Germany), the State Museum of Natural History Karlsruhe (Germany), Carina Siutz (University of Vienna, Austria), Clara Stefen (Senckenberg Natural Historic Collections, Dresden, Germany), Gabor Nechay (Gödöllő, Hungary), Maurice La Haye (Radboud University of Nijmegen, the Netherlands), Mikhail Rusin (National Academy of Science, Kiev, Ukraine), Stefani Martens (Großrettbach, Germany) and Ulrich Weinhold (Institute for Faunistic, Heiligenkreuzsteinach, Germany). We also thank Ilse E. Hoffmann (University of Vienna, Austria), Jennifer Hatlauf (University of Natural Resources and Life Sciences Vienna, Austria), Elke Schmelzer (Nature Conservation Alliance Burgenland, Austria), Ayona Shmalenko and Sergey Sklyarenko (Association for the Conservation of Biodiversity of Kazakhstan) for their help in obtaining distribution data and also Dr. Valery Neronov (Severtsov Institute of Ecology and Evolution, Moscow) who provided us with unique data on fur harvesting of European hamsters in the former USSR and with a number of respondents from the regions, reserves and universities for recent information. We are also grateful for excellent transcription and translation services by Stepan Khalimonov and Dina Ershova (University of Hohenheim, Stuttgart, Germany) as well as for the revision of the English by Katrin Monecke (Wellesley College, USA).

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Appendix. Literature used to create the figures

Source	Figures	Source	Figures
Albert (2013)	6, 7 & 8	Hamar et al. (1959)	6
Amand et al. (2012)	1	Hanzák (1970)	6, 7 & 8
Ambros et al. (2003)	1	Hediger (1944)	1
Anděra & Horáček (1982)	6, 7 & 8	Hegyeli et al. (2015)	1
Andreychev & Kuznetsov (2012)	2, 3 & 4	Hufnagl et al. (2011)	6, 7 & 8
Aubry (1961–1962)	7 & 8	Husson (1949)	6, 7 & 8
Babina (2009–2010)	2, 3 & 4	Ilin et al. (2006)	2, 3 & 4
Baldaev (2002)	2, 3 & 4	Isaev & Dmitriev (2010)	2, 3 & 4
Bašenina et al. (1957)	6, 7 & 8	Ivanchev & Kazakova (2011)	2, 3 & 4
Bašenina et al. (1961)	5	Jennison (1929)	7 & 8
Bayanov & Kucherov (1995)	2, 3 & 4	Kapitonov (2009)	2, 3 & 4
Berdyugin & Bolshakov (1998)	2, 3 & 4	Karaseva (1962)	2, 3 & 4
Bihari (2003)	1	Karaseva et al. (1999)	2, 3 & 4
Blasius (1857)	6, 7 & 8	Karpenko (2013)	2, 3 & 4
Bobrinskiy et al. (1965)	6, 7 & 8	Kayser & Stubbe (2002)	6, 7 & 8
Bolšhakov (1977)	6, 7 & 8	Kiku et al. (2011)	1, 2, 3 & 4
(Botnariuc & Tatole 2005)	1	Kirikov (1952)	2, 3, 4 & 5
Brehm (1914)	6, 7 & 8	Konstantinov (2006)	2, 3 & 4
Buffon (1765)	6, 7 & 8	Korbut et al. (2013)	1, 2, 3 & 4
Bundesamt für Naturschutz (2013)	1	Kowalski (1964)	6
Čanády (2013)	1	Kratochvíl (1966)	6, 7 & 8
Chebakova (ed) (1996)	2, 3 & 4	Kryshtal (1929)	5
Demyanchik (2004)	1, 6, 7 & 8	Kuilik (1962)	2, 3 & 4
Didier & Mathias (1936)	7 & 8	Kuiters et al. (2011)	1
Didier & Rode (1935)	6, 7 & 8	Kuzmin (2006)	2, 3 & 4
Dukelskaja & Stepanova (1932)	5, 7 & 8	Kuznecov (1952)	5 & 6
Dupond (1932)	6, 7 & 8	Kuznetsov (1975)	6, 7 & 8
Enzinger et al. (2010)	1	La Haye & Müskens (2014)	1
Eóry (1959)	7 & 8	Laptev (1958)	2, 3 & 4
Fedorowicz (1928)	6, 7 & 8	Larina et al. (1968)	2, 3 & 4
Feoktistova et al. (2016)	2, 3 & 4	Le Louarn & Saint Girons (1977)	6
Feriancová-Masárová & Hanák (1965)	6, 7 & 8	Lindeman et al. (2005)	2, 3 & 4
Flint et al. (1965)	6, 7 & 8	Lovassy (1927)	6, 7 & 8
Flint et al. (1970)	6	Lozan (1971)	5, 7 & 8
Franceschini-Zink & Millesi (2008b)	6, 7 & 8	Lyapunov (2008)	2, 3 & 4
Franceschini & Millesi (2004)	6, 7 & 8	Manninger (1960)	6, 7 & 8
Frechkopf (1958)	6, 7 & 8	Markov (1998)	1
Gaffrey (1961)	6, 7 & 8	Martin (1910)	6, 7 & 8
Gelashvili et al. (1999)	2, 3 & 4	Marvin (1968)	6, 7 & 8
Geptner et al. (1950)	6	Marvin (1966)	2, 3 & 4
Gerber (1951)	6, 7 & 8	Melnikov & Buslaev (2012)	2, 3 & 4
Gershenson (1941)	7 & 8	Minoransky & Dobrovolsky (2013)	2, 3 & 4
Gershenson (1945a)	2, 3 & 4	Mironov et al. (1965)	2, 3 & 4
Gershenson (1945b)	2, 3 & 4	Mishta & Sitnikova (2005)	2, 3 & 4
Gershenson (1945c)	2, 3 & 4	Mohr (1954)	1, 6, 7 & 8
Gershenson (1945d)	2, 3 & 4	Morozova-Turova (1938)	2, 3 & 4
Glas (1961)	6, 7 & 8	Moskvitina & Sushkova (1988)	2, 3 & 4
Glotov (1969)	2, 3 & 4	Munteanu (1998)	1
Gorbachev (1915)	2, 3 & 4	Müskens et al. (2003)	1
Górecki (1977b)	5, 6, 7 & 8	Muzaev (2013)	2, 3 & 4
Grizmek (1969)	6, 7 & 8	Myasnikov (1977)	2, 3 & 4
Gromov et al. (1963)	6, 7 & 8	Nechay (2000)	1
Grulich (1975)	1	Nechay et al. (1977)	1, 5 & 6
Grulich (1980)	6	Negrobov (2011)	2, 3 & 4
Grulich (1986)	5	Nehring (1901)	5
Guryleva (1968)	2, 3 & 4	Neronov (1965)	1, 2, 3 & 4
Gyurkó (1975)	5	Neronov & Prokofieva (1969)	2, 3 & 4
Hainard (1949)	6, 7 & 8	Niethammer (1982)	1 & 6
Hamar (1967)	6, 7 & 8	Novikova & Novikov (2007)	5

Appendix (continued)

Source	Figures	Source	Figures
Ognev (1916)	2, 3 & 4	Spitzenberger (1998)	1
Oken (1838)	6, 7 & 8	Spitzenberger (2001)	1
Pelikán et al. (1979)	6, 7 & 8	Starikov et al. (1989)	2, 3 & 4
Petzsch (1936)	6, 7 & 8	Štěpánek & Baum (1939)	7 & 8
Petzsch (1952)	6	Stroganova (1954)	5, 6, 7 & 8
Pfeffer (1954)	6, 7 & 8	Sulzer (1774)	6, 7 & 8
Polushina et al. (1988)	2, 3 & 4	Surdacki (1971)	1
Polyakov (1968)	6	Surov et al. (2016)	2, 3 & 4
Popov (1960)	2, 3 & 4	Sysoev (1970)	2, 3 & 4
Prisny (2004)	2, 3 & 4	Tauscher et al. (2003)	7 & 8
Prokopov (2008)	2, 3 & 4	Tkadlec et al. (2012)	1
Pucek (1981)	6	Tovpinetz et al. (2006)	2, 3, 4 & 5
Rebel (1933)	7 & 8	Trouessart (1884)	6, 7 & 8
Reiners et al. (2014)	1	Turček (1950)	6, 7 & 8
Rode & Didier (1946)	6, 7 & 8	Varlygina et al. (2008)	2, 3 & 4
Rusin et al. (2013)	1, 2, 3 & 4	Vinogradov & Gromov (1952)	6, 7 & 8
Ružić (1978)	1	Voronin (2004)	2, 3 & 4
Saint Girons (1973)	6, 7 & 8	Voronov (1982)	2, 3 & 4
Savchenko (2014)	2, 3 & 4	Voronov (1993)	2, 3 & 4
Sazonova & Gashev (1999)	2, 3 & 4	Vorontsov (1982)	2, 3 & 4
Schmelzer & Herzig-Straschil (2013)	1	Vyshegorodskih (2015)	2, 3 & 4
Seluga et al. (1996)	6	Weber & Stubbe (1984)	5
Shlyakhtin et al. (2009)	2, 3 & 4	Weidling & Stubbe (1998)	1
Sidorov et al. (2011)	2, 3 & 4	Weinhold (1998)	6, 7 & 8
Simak (1990)	2, 3 & 4	Weinhold (2008)	1
Sládek & Mošanský (1985)	6, 7 & 8	Yudin et al. (1979)	2, 3 & 4
Sludsky (1977)	5	Zimmermann (1959)	6, 7 & 8
Soffel (1922)	6, 7 & 8	Ziomek & Banaszek (2007)	1
Sokur (1963)	6	Zlobin & Plesski (1978)	2, 3 & 4
Sorokin (2002)	2, 3 & 4		

Editorial responsibility: Nils Bunnefeld, Stirling, UK

Submitted: January 29, 2016; Accepted: July 19, 2016
Proofs received from author(s): September 22, 2016