Abundance dynamics and reproduction success in the common dormouse, *Muscardinus avellanarius*, populations in Lithuania

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A b s t r a c t . This study in Lithuania showed that the abundance dynamics of the common dormouse (*Muscardinus avellanarius*) populations were comparatively "smooth", without outbreaks and crashes. Decreases and increases of abundance continued for some years, and abundance differed no more than three-fold in two successive years. A close negative correlation was revealed between spring population density and percentage of juveniles in the autumnal population. The last parameter is a consequence of reproduction success, which determined the scale of population increase in autumn and was due to several factors. Among them, proportion of breeding adult females had the greatest significance and was inversely proportional to population density in spring. Some young-of-the-year females usually joined the breeding process, when population density was low. The proportion of late breeding cases, when juveniles were born in September, was also negatively correlated with spring population density. The number of litters produced by one female during the season, and the average litter size also influenced reproduction success. The negative correlation between population density and reproduction success shows the presence of a reproduction success based pattern of density dependent self-regulation in *M. avellanarius* in the populations investigated.

Introduction

Mammalian population ecology is built around the study of fluctuations in population numbers together with investigations into population structure and demography, feeding, breeding, movement and social organisation. Habitat preference and interactions with other species also come under scrutiny. All these aspects of mammalian ecology may affect the fluctuations in numbers (F l o w e r d e w 1987). Of the small mammals, the voles and lemmings exhibit the most marked fluctuations in their populations and have been the subject of many generally excellent studies (see e.g., C h r i s t i a n 1971, S t e n s e t h 1999 for overviews). The majority of small mammals have short generation times and high reproductive rates. The common dormouse (*Muscardinus avellanarius* L.) is unusual among small mammals because of its long life, low recruitment rate and low population density (B r i g h t & M o r r i s 1996).

Data on long-term population dynamics of this species are scant. Numbers of nestboxes occupied by *M. avellanarius* during 17 years in Germany are presented in the dissertation of B a n g u r a (1988). Yearly variations in the spring occupation of nestboxes by *M. avellanarius* were observed in Italy during seven years (S o r a c e et al. 1998). The National Dormouse Monitoring Programme based on nestbox checks has been carried out in Great Britain (B r i g h t et al. 1996), but the results are not published yet. Only the total number of nestbox records each year of *M. avellanarius* at Siccaridge Wood between

1993–1998 are presented in a paper by M a r s h & M o r r i s (2000). However, in all these cases only the dynamics of relative abundance are presented, but there are no data on dynamics of other *M. avellanarius* population parameters.

L i k h a c h e v (1966a,b, 1967) collected valuable data on demographic structure, reproduction, winter mortality and many other aspects of *M. avellanarius* populations south of the Moscow region in 1956–1962. However, nestboxes at his study site were put up in lines and small groups (L i k h a c h e v 1967), and L i k h a c h e v could not estimate population density. Despite of this, in many cases only data by L i k h a c h e v from the Moscow region are suitable for comparison with the results obtained at two dormice study sites in Lithuania (J u š k a i t i s 1994, 1997a,b, 1999a,b).

Although, as mentioned above, many intrinsic and extrinsic factors influence abundance dynamics of mammalian populations, the aim of the present paper is to discuss the significance of only one of them – reproduction success – for abundance dynamics of *M. avellanarius* populations in the northern part of its distribution range.

Study Areas, Material and Methods

Investigations of the structure and dynamics of two isolated *M. avellanarius* populations were carried out in Lithuania in two locations: at study site A (south-western Lithuania, Šakiai district; 55°03'N, 23°04'E) in 1984–1990 and in 1997–2002 and also at study site B (eastern Lithuania, Moletai district; 55°09'N, 25°21'E) in 1984–1993. However data from 1990, 1997 (site A) and 1993 (site B) are not analysed in the present paper, because there were fewer investigations during these years.

Site A, with an area of 60 ha and 262 nestboxes (274 nestboxes, 1999–2002), covered about 22% of the whole habitat occupied by the *M. avellanarius* population in that locality. Forest here was middle-aged (30–80 year-old), with a great diversity of mixed tree stands. Within the study site, mixed birch (*Betula pendula*) stands with Norway spruce (*Picea abies*) and black alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*) stands with aspen (*Populus tremula*), and pure Norway spruce stands were prevalent. There was a mixed Norway spruce stand with oak (*Quercus robur*) at the southern edge of the site. The understorey contained many hazels (*Corylus avellana*) and in some places – buckthorn (*Frangula alnus*).

Site B, with an area of 85 ha and 341 nestboxes, covered approximately 17% of the whole habitat occupied by the *M. avellanarius* population in that locality. Mature (100–130 year-old) oak stands with Norway spruce, in some places with maple (*Acer platanoides*) and aspen, were prevalent in most of this site. In the eastern part of the site, 40–60 year-old aspen stands with Norway spruce grew. There were also small plots of Norway spruce, aspen and grey alder (*Alnus incana*) stands in this area. Hazel prevailed in the understorey.

The methods used to study *M. avellanarius* populations were based on the following three main principles:

1) even spacing of nestboxes in a grid system in large forest areas;
2) regular checking of the boxes;
3) marking of all dormice caught.

At both study sites, standard wooden nestboxes for small hole nesting birds were placed every 50 meters (see schemes in J u š k a i t i s 1997b, 2002). The density was four boxes in 1 ha. The boxes were checked once a month from April until October, and twice a month in

May and September (in some years also in October). All dormice caught were marked with aluminium rings (the straightened plate was 2.5 x 8.0 mm). The rings were placed on the right hind leg over the ankle. Suckling young weighing less than 10 g were marked by amputation of one toe phalanx, and ringed when caught repeatedly. All the animals were weighed and their sex and age determined. Dormice were considered adults if they had survived at least one hibernation. Body weight, fur coloration, which changes with age, and width of tail were used to identify independent juveniles and adults. The percentage of juveniles in the autumnal population was chosen as an index of reproduction success. Breeding females were considered to be not only females found in nestboxes with litters, but also those that were caught pregnant or with distinct nipples, having given birth to their litters in natural nests.

The spring population density was determined by dividing the total number of overwintered individuals, caught during the whole active season, by the trapping area of the study site (F l o w e r d e w 1976). The trapping area was considered 64 ha at site A and 90 ha at site B. This was calculated by adding a 50 m wide boundary strip to the sides of the study sites which were not delimited by forest edge (or forest road at site A).

The autumn number of dormice in the area of the site (N) was determined by the Petersen-Lincoln index (F l o w e r d e w 1976, C a u g h l e y 1977):

$$M/N = m/n,$$

where M is the number of dormice marked in autumn (August–October), m – the number of marked dormice caught next year, n – the total number of overwintered dormice caught next year. From this, density (ind./ha) was calculated. Pearson's correlation coefficient r was used to express relationships between population parameters.

During the whole period of investigation (1984–2002), 2379 individuals of *M. avellanarius* have been marked: 627 – at site A in 1984–1990, 598 – at renewed site A in 1997–2002 and 1154 – at site B. The total number of dormice captures reached 5843 at both study sites.

Results

The abundance of *M. avellanarius* was rather stable at site A during the years of investigation. The autumnal population density ranged within narrow limits: from 2.4 ind./ha to 3.4 ind./ha (Fig. 1a). Spring population density decreased slightly from 1.4 ind./ha in 1985 to 0.7 ind./ha in 1989, but again reached 1.1 ind./ha in 2001. At site B, the population density fluctuated more widely in comparison with site A during the years of investigation: the highest autumnal density was 3.6 ind./ha and the lowest – 0.9 ind./ha (Fig. 1b). In 1987, there was a clear decrease in abundance, but population density was restored later. The average population density of *M. avellanarius* was a little lower at site B than at site A in both spring (0.6±0.2 ind./ha and 0.9±0.2 ind./ha respectively) and autumn (2.3±0.8 ind./ha and 2.8±0.4 ind./ha respectively).

A very close negative correlation (r = –0.84, p = 0.002, n = 10) was revealed between spring population density and percentage of juveniles in the autumnal population at site A (Fig. 2). The proportion of juveniles in the autumnal population is a consequence of reproduction success, which determined the scale of population increase in autumn and was due to several factors. A significant inverse relationship between some of these factors and spring population density was established in *M. avellanarius* populations.
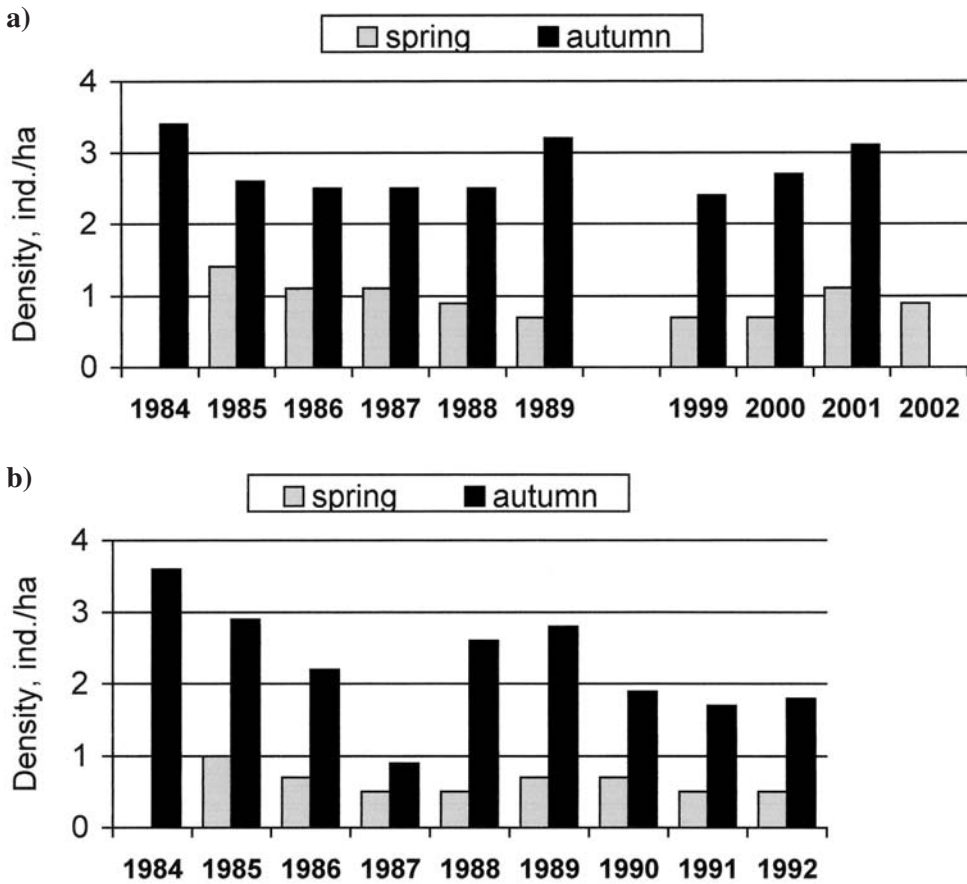
a)

b)

Fig. 1. Dynamics of *M. avellanarius* population density at two study sites in Lithuania: a) site A, b) site B.

Among the indices of reproduction success, proportion of breeding adult females had the most important significance. A direct relationship (r = 0.78, p = 0.004, n = 11) between the percentage of breeding females found in nestboxes and proportion of juveniles in the autumnal population was established at site A. Proportion of breeding adult females was inversely proportional to population density in spring, particularly at site A (r = –0.80, p = 0.005, n = 10). Some of the most evident examples of this relationship are presented below.

At site A, the highest spring population density (1.4 ind./ha) was registered in 1985 (Fig. 1a). However, only 24% of all adult females found in the nestboxes bred, and juveniles comprised only 57% in the autumnal population in this year. Data from 2000 illustrate the reverse case, when spring population density was 0.7 ind./ha at site A. Almost all adult females (94%) took part in reproduction, with the exception of one female, which was caught only in May, but never again. Young females, born in the same year joined the breeding process: two such females were found with their litters in nestboxes in September. As a consequence of intensive breeding, juveniles made up 78% of the autumnal *M. avellanarius* population in this year. However, there was also exceptionally low reproduction success in the case of low spring abundance at site B, as discussed below.
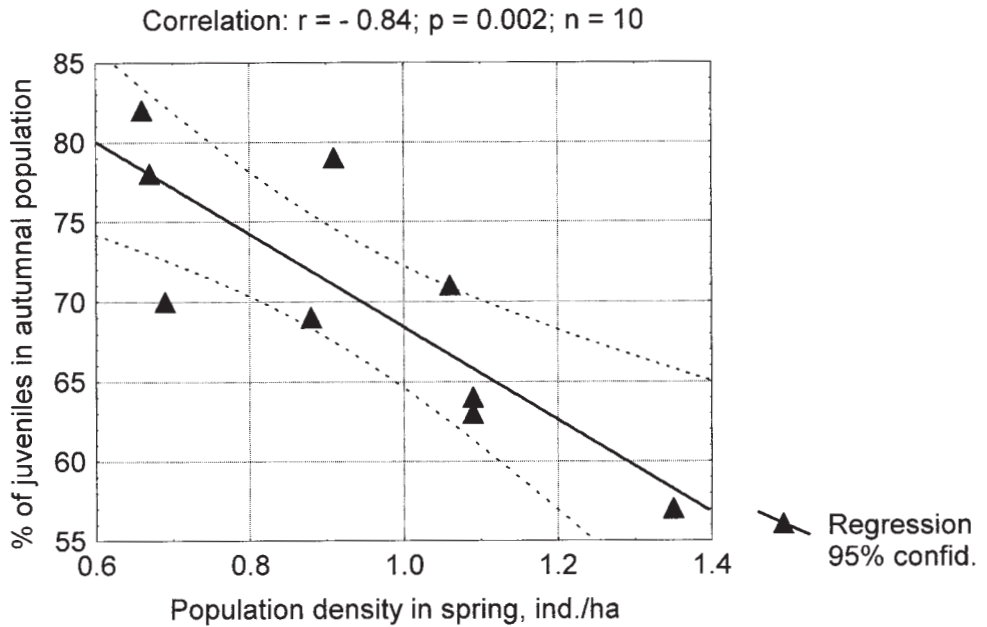
Fig. 2. Correlation between *M. avellanarius* population density in spring and percentage of juveniles in the population in autumn at site A in Lithuania (1985–1989, 1998–2002).

A significant negative correlation between *M. avellanarius* population density in spring and the percentage of breeding cases involving young-of-the-year females was established at site A (r = –0.71, p = 0.034, n = 9). Young-of-the-year females usually joined the breeding process when spring population density was low. The proportion of late breeding cases, when juveniles were born in September, was also negatively correlated with spring population density (r = –0.73, p = 0.027, n = 9). Thus, late breeding in *M. avellanarius* populations, as well as breeding by young-of-the-year females, may help to restore population abundance. However, favourable environmental conditions are necessary for successful realisation of late breeding.

Breeding by young-of-the-year females and late breeding were more frequent at site B, where average population density was lower than at site A. However, the inverse relationship between spring population density and reproduction success was less evident in this population. A distinct decrease in abundance was observed at site B in 1987 (Fig. 1b). However, despite a very low spring population density in 1987 (0.5 ind./ha), very low reproduction success was observed. Only 30% of all adult females caught in nestboxes were breeding this year, and mean litter size (3.4 juveniles per female) was the lowest during the whole study period. In the outcome, juveniles comprised only 48% in autumn, and autumnal population density was particularly low – only 0.9 ind./ha. Radioactive pollution after the accident at the Chernobyl nuclear power station and an abnormally prolonged breeding season in 1986 could have influenced reproduction success in 1987, but concrete evidence is lacking.

This exceptional case biased correlation between spring population density and reproduction success in pooled data from both sites A and B (r = -0.38, p = 0.119, n = 18).

When data from site B in 1987 were omitted, a statistically significant negative correlation was obtained between spring population density and percentage of juveniles in autumnal population (r = –0.74, p = 0.001, n = 17).

Discussion

Population density and its dynamics in *M. avellanarius*

The population density of *M. avellanarius* was rather low in both Lithuanian populations investigated. Considerably higher population densities were estimated in some other studies, e.g., from 2.6 to 15.6 adults/ha at separate sites in Southwest England (B r i g h t & M o r r i s 1990), 13.6 ind./ha in Croatia (T v r t k o v i ć et al. 1996), 3.4 adults/ha in Denmark (V i l h e l m s e n 1996), 3.0–6.7 adults/ha in Sweden (B e r g & B e r g 1999), up to 6 ind./ha in Italy (S o r a c e et al. 1999), up to 8.2 adults/ha in Sicily (S a r a et al. 2001).

It is noteworthy that in all these cases population density was estimated in comparatively small areas (e.g., 1.2 ha in England, 1.1 ha in Croatia, 1.9 ha in Denmark, 0.16–3.2 ha in Sweden, 2 ha in Italy, 1 ha in Sicily). For this reason, densities could be overestimated, in some cases because the results obtained at small study sites do not reflect average characteristics of the populations, and the edge effect also has a big influence (R. J u š k a i t i s, in prep.). By contrast, densities from Lithuania are average population densities in large forest areas (60 ha and 85 ha respectively). Also higher *M. avellanarius* population densities were observed in Lithuania (e.g., up to 2.4 adults/ha in 2002), but only in separate comparatively small plots of study site A with more favourable conditions for dormice (e.g., where the understorey was better developed).

L i k h a c h e v (1954) estimated densities of *M. avellanarius* similar to Lithuanian populations. In the Tula region, *M. avellanarius* spring population density was 0.8 ind./ha and autumnal density – 3.2 ind./ha in 1950, and 1.2 ind./ha and 3.9 ind./ha respectively in 1951 (area of the study site – 20 ha). In the Moscow region, spring density was 1.5 ind./ha, autumnal density – 3.5 ind./ha in 1953 (area of the study site – 4 ha). The very low density of 0.12 ind./ha obtained in northern Moravia is doubtful, and the authors themselves acknowledged this (G a i s l e r et al. 1977).

Long-term investigations of *M. avellanarius* population were carried out by L i k h a c h e v (1966a, b) in the south of the Moscow region in 1956–1962. L i k h a c h e v could not estimate the density for the reasons mentioned above. We can assess the abundance dynamics of this population by the number of adult individuals of *M. avellanarius* caught and marked in separate years (L i k h a c h e v (1966b). These data can be compared with dynamics of spring population density estimated in Lithuania.

The results obtained in Lithuania (our data) and in the Moscow region (L i k h a c h e v 1966b) showed that abundance dynamics of *M. avellanarius* populations investigated were comparatively "smooth": there were no sudden changes of abundance. Decreases and increases of abundance usually continued for some years, and abundance differed no more than three-fold in two successive years. Also L o z a n (1970), who investigated dormice in Moldavia, numbered *M. avellanarius* among the species whose population abundance does not fluctuate markedly.

Other small mammals living in similar forests (e.g., yellow-necked mouse (*Apodemus flavicollis*) and bank vole (*Clethrionomys glareolus*) distinguish themselves by considerably

higher fluctuations of abundance with outbreaks and crashes in successive years (e.g., P u c e k et al. 1993, J u š k a i t i s 2000).

R e l a t i o n s h i p   b e t w e e n   p o p u l a t i o n   d e n s i t y   a n d
r e p r o d u c t i o n   s u c c e s s   i n   *M. a v e l l a n a r i u s*

Results obtained in Lithuania and in the Moscow region showed that abundance dynamics in *M. avellanarius* populations were connected very closely with the process of reproduction, which included several factors:
    1) proportion of breeding adult females;
    2) number of litters, bred by one female during the season;
    3) average litter size;
    4) breeding by young-of-the-year females.
    The index – proportion of breeding adult females – used both by L i k h a c h e v (1966a) and J u š k a i t i s (1994, 1997a) could be somewhat underestimated for two reasons:
    1) some females produced their litters in natural nests, and they were not caught in nestboxes while still showing signs of breeding;
    2) some females were caught only in spring, but never later, and they could have died before joining the breeding process.
    Despite these circumstances, the percentage of breeding females recorded in nestboxes shows the general tendency of breeding success. A direct relationship between the percentage of breeding females found in nestboxes and proportion of juveniles in the autumnal population was established both in Lithuania and in the Moscow region (r = 0.90, p = 0.006, n = 7).
    The percentage of breeding adult females found in nestboxes in different years fluctuated from 24% to 94% in Lithuania and from 18% to 68% in the Moscow region (L i k h a c h e v 1966a), and was inversely related to spring population density. In the Moscow region, the highest abundance of *M. avellanarius* was observed in 1958, but only 26% of all adult females bred, and the proportion of juveniles was only 14% in autumn (L i k h a c h e v 1966a). A very high proportion of non-reproducing adult females (61%) was estimated in Sweden, where a relatively high population density (3.0–6.7 adults/ha) was found (B e r g & B e r g 1999). The high proportion of adult females not showing signs of reproduction may be an indication that reproductive suppression occurred in this dormouse population (B e r g 1997).
    Is it possible that some adult females were non-reproducing? Maybe all adult females were breeding: some of them in nestboxes, the others in natural nests? The fact that some adult females were really non-breeding was confirmed by L i k h a c h e v (1966a). This researcher controlled his nestboxes very frequently (28–53 times in separate years from 15 April until November) (L i k h a c h e v 1966b), and some females used to be caught regularly during the whole summer without showing signs of breeding. For example, 13 non-breeding females were registered in 1958: most of them were caught from five to eight times during the summer, and one female – 11 times, another – 18 times.
    As mentioned above, the proportion of breeding adult females was the most important, but not the only factor, which can determine reproduction success. During the summer, *M. avellanarius* may produce two litters, at least in some parts of its distribution area (see J u š k a i t i s 1997a for review). In exceptional cases even three litters during a season are possible (R. J u š k a i t i s, unpublished). The importance of the second litters was shown

by L i k h a c h e v (1966a). On average, one reproducing female bred 3.4 juveniles in 1956, when there were no second litters, and 6.1 juveniles in the next year, which included second litters. The proportion of two-year-old and older females in the population is very important in this respect, because these females can produce two litters, meanwhile one-year-old females, born in late summer of the previous year, can manage only one litter (L i k h a c h e v 1966a, J u š k a i t i s 1997a).

In Lithuania, the average litter size of *M. avellanarius* varied insignificantly from year to year and was close to 4 (from 3.4 to 4.4 in separate years) (J u š k a i t i s 1997a). In the Moscow region, average litter size ranged more widely (from 3.4 to 5.4 in separate years). Fluctuations of the average litter size in *M. avellanarius* depends mainly on environmental factors, e.g., weather and feeding conditions (L i k h a c h e v 1966a, B r i g h t & M o r r i s 1996). The latter factors can also influence the presence of second litters in *M. avellanarius* populations.

Young females born in the same year can join the breeding process at the age of 2–3 months (L i k h a c h e v 1966a, J u š k a i t i s 1997a, B ü c h n e r 1998). L i k h a c h e v (1966a) suggested that such a phenomenon could be observed only in years with very good feeding conditions. Results obtained in Lithuania show that it is associated with decreased population density, when young females can find their own space to rear offspring (W o l f f 1997).

Late breeding also can influence reproduction success in *M. avellanarius* populations. In certain years, some *M. avellanarius* litters are born in September, i.e. at the time, when dormice normally accumulate fat reserves and prepare for hibernation (R. J u š k a i t i s, in prep.). Late breeding is not included among the reproduction success factors named above, because late born litters can be the second litters of adult females as well as the first litters of young-of-the-year females.

Negative correlation between population density and reproduction success suggests that reproduction success followed a pattern of density dependent self-regulation in the *M. avellanarius* populations investigated. It is noteworthy that this pattern of self-regulation was found in *M. avellanarius* populations with comparatively low spring population density (about 1 ind./ha), and predetermined comparatively low autumnal population density (about 3 ind./ha).

Many populations of mammals appear to occur at population densities, which are adapted to the environment in which they live (F l o w e r d e w 1987). Self-regulatory internal mechanisms reduce population growth before resource limitation. If self-regulation is going to occur, it will be mediated through territoriality and reproductive suppression, which limit the number of breeding females in the population (W o l f f 1997). In *M. avellanarius* populations, both males and females are territorial (L i k h a c h e v 1967, B r i g h t & M o r r i s 1991, J u š k a i t i s 1997b) and reproductive suppression was found (L i k h a c h e v 1966a, B e r g 1997, our data). According to W o l f f (1997), this means that *M. avellanarius* should be considered as an intrinsically regulated species.

Presented here are examples of abundance dynamics and reproduction success that were established in the northern parts of *M. avellanarius* distribution area, where population density was comparatively low. In other southern parts of its range, where living conditions are more favourable and population density is higher, different patterns of abundance dynamics and reproduction success are possible. Comparative long-term investigations are necessary in other parts of the distributional range of *M. avellanarius*, and it is necessary to estimate population density together with other population parameters.

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