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DISPERSAL IN RELATION TO POPULATION DENSITY IN WILD BOAR *(Sus scrofa)*

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ABSTRACT

Dispersal rate, the proportion of individuals in a population that emigrates, can be affected by population density and act as factor regulating a population. The purpose of this study was to determine whether dispersal distance and dispersal rate in wild boar are affected by variation in population density. Relative population density was estimated from root counts, and dispersal rates were estimated through capture/mark/recapture. In this study, population density and dispersal behaviour were not strongly correlated. In both sexes, dispersal distance was not correlated with population density, but the proportion of individuals dispersing tended to be negatively correlated with density. The correlations are, however, sensitive to changes in the home range diameter used in the analysis and the results should be interpreted with this in mind.

Keywords: dispersal, dispersal distance, dispersal rate, population density, *Sus scrofa*, wild boar

INTRODUCTION

Important issues discussed in recent wild boar symposia (Uppsala 2000, Lousã 2002) include local increases in population density, geographic expansion, damage caused to agriculture, the species' impact on nature reserves, the spread of disease, and the influence on other aspects of human interest.

The determinants of population density: mortality, reproduction, and dispersal, are regulated by extrinsic and intrinsic mechanisms. Extrinsic mechanisms comprise density-independent processes in the environment, while intrinsic mechanisms are density-dependent and driven by interactions among individuals in the population (Erb et al. 2001).

Theory shows that changes in population density affect the *per capita* availability of resources and make it profitable for individuals to disperse, if they have competitive advantages in doing so (Sutherland et al. 2002). Empirical studies support the theory that dispersal is positively correlated with density (Nilsson 1989, Rosenberg et al. 1997), although negative correlations (Janeau and Spitz 1990, Allen and Sargeant

1993), or no correlations (Byrom 2002) are known in some populations. In species where dispersal is sex-biased, male and female dispersal rates can respond differently to changes in population density (Sandell et al. 1990, Clutton-Brock et al. 1997).

In Sweden, local increases and the geographic expansion of wild boar populations has created concern about the management of the species because of the potential for wild boar to caused damage to agriculture, nature reserves, and facilitate the spread of disease.

If dispersal acts to regulate populations, both the movement of individuals between populations and the rate of geographic expansion will be affected by density.

From a management perspective, it is the proximate causes of dispersal, rather than the ultimate causes that are of interest because they can be manipulated in order to reach the objectives set for the population by the parties concerned.

In this study, our objective was to determine whether population density acts as a proximate cause of dispersal in wild boar. If dispersal is responsive to changes in density, the regulation of density might be a possible management method of reducing dispersal.

MATERIALS AND METHODS

This study was performed in the province of Södermanland in east-central Sweden (58º47'N-58º55'N and 16º20'E-16º52'E) during the period 1989-2000. The area is varied and mainly consists of forests, agricultural land, lakes, and wetlands. Forests are dominated by pine *Pinus sylvestris* and spruce *Picea abies*. In the border zones between forests and agricultural land, coniferous forests are mixed with birch *Betula* spp., aspen *Populus tremula* and oak *Querqus* spp. Cultivated areas are dominated by arable land, interspersed with pastures and meadows. Cereals are the main crop and constitute a substantial food-source for wild boars in the area. Since oak is sparse the availability of mast is limited. In the study area, artificial feeding is commonly used to attract wild boars during hunting events, to reduce the damage caused to crops, and supply wildlife with additional food during the winter. Between 1989 and 2000, at several locations in the area, wild boars were caught and ear-tagged (Truvé and Lemel 2003).

To estimate the geographic density distribution of wild boars in the area, we performed a root count. Roots are excavations in the soil created by wild boars when they search for food below ground. Roots indicate the presence of wild boars and, by estimating the density of roots, we assumed that their density can be used as an index of wild boar density, given that interannual food availability is stable. We used strip-transect sampling (Thomas et al. 2002), whereby observers counted all roots within five meters of the transect. We estimated the size of each root. The distance between transects was 1 km.

The survey was performed once between 27 September and 27 November, 1999. Hunting bag data were collected from seven properties covering a total area of 300 km^2. Between 1998 and 2000, the number of wild boars culled varied little and, on average, 0.6 animals/ km^2 were shot annually in the study area. Therefore, we assumed that population density was constant during those years, and that the results from the root-count in 1999 can be used as a density estimate for 1998 and 2000.

Dispersal distances were mainly based on ear-tags returned by hunters. Some animals were killed in traffic accidents or by other causes. We calculated dispersal distance as the straight-line distance between capture site and recapture site. An individual was considered to have dispersed if the distance between capture and recapture sites exceeded one home range diameter (4 km), which is based on the assumption that the home range is circular and has an area of 12 km^2, the mean 95% adaptive Kernel density-estimate for groups with sows and piglets in Sweden (Lemel 1999).

In wild boar, dispersal distance is age- and sex-dependent (Truvé and Lemel 2003); therefore, the data from males and females were analysed separately, and females younger than 7 months and males younger than 10 months were omitted from the analysis because those individuals had not reached the age at which dispersal begins (Truvé and Lemel 2003). Including younger animals in the analysis would have biased the results because none of them had dispersed, although they could have dispersed if they had reached an older age.

The root count in 1999 was the only estimate of population density that covered the entire study area; consequently, our analysis only included animals that were caught between 1998 and 2000 because we assumed that population density was constant during that period.

We estimated a population density-index associated with each captured animal by calculating the total rooted area within a 2-km radius of the capture site. That area is assumed to represent the home range of the animal, based on an average home range diameter of 4 km. When the proportion of individuals dispersing in relation to density index was analysed, the area was rounded to the nearest thousand.

To estimate the correlations between dispersal distance and density index, and between the proportion of individuals dispersing and density index, we used linear regression (SAS Version 8.02, SAS Institute Inc.)

Results

The density of roots was not uniformly distributed throughout the area. There were three areas with high densities interspersed with areas having lower densities (Figure 1). Density index and dispersal distance were not correlated in females

(R^2=0.007, P=0.247) or in males (R^2=0.024, P=0.087) (Figures 2 and 3). The proportions of females and males dispersing tended to be negatively correlated with density (R^2=0.53, P=0.062 for females, R^2=0.43, P=0.066 for males) (Figures 4 and 5). The correlations are not significant based on a p-level of 0.05 level, but the calculations can be sensitive to changes in the home range diameter, which changes the proportion of individuals dispersing and the density index.

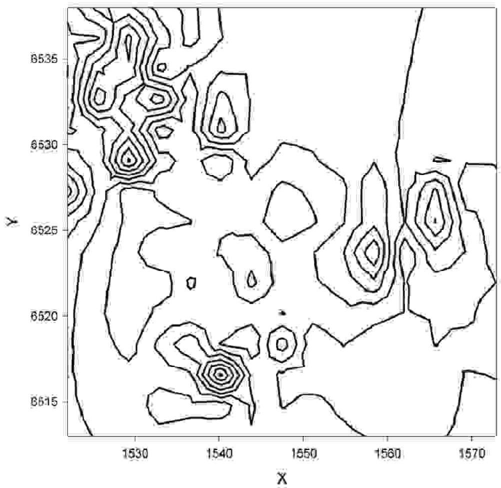

Figure 1. Contour plot illustrating the distribution of root density in the study area X and Y coordinates are in kilometre units (1 unit = 1 km)

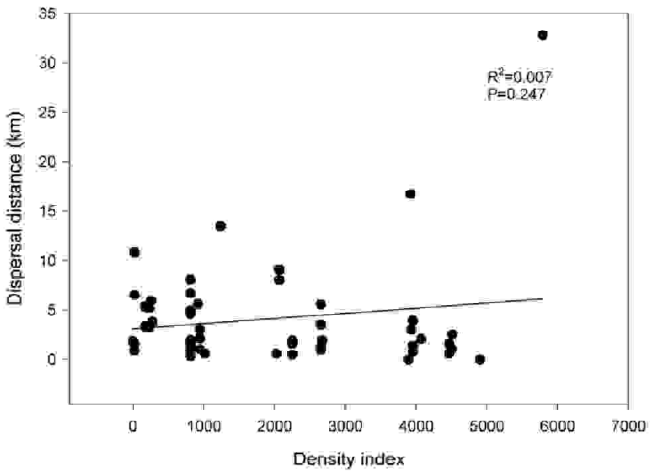

Figure 2. Female dispersal distance in relation to density index.

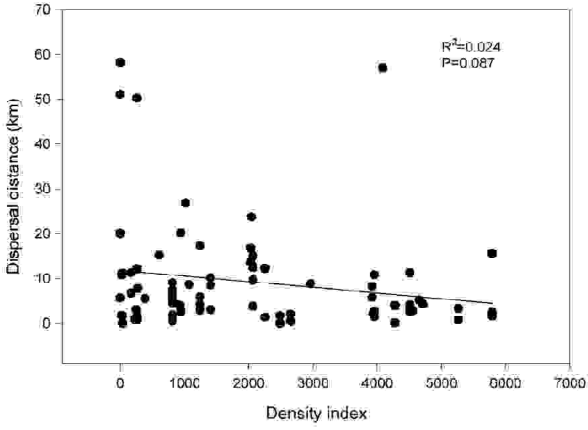

Figure 3. Male dispersal distance in relation to density index.

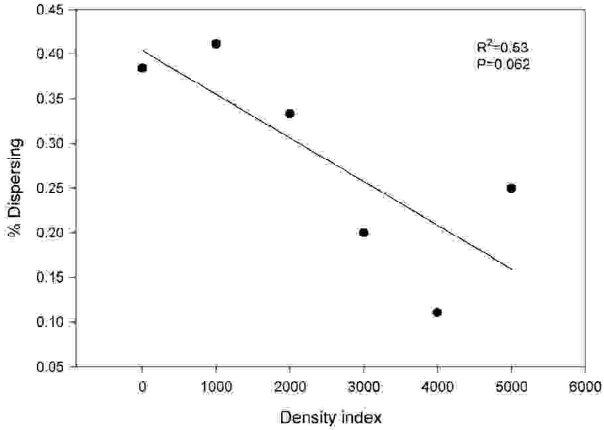

Figure 4. Proportion of females dispersing in relation to density index.

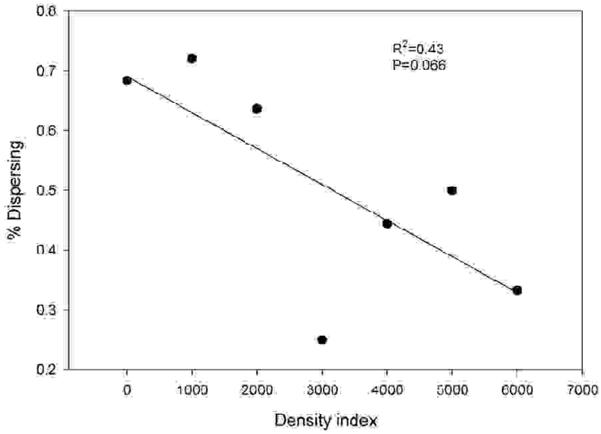

Figure 5. Proportion of males dispersing in relation to density index.

DISCUSSION

Our results do not suggest a strong correlation between population density and dispersal in the wild boar population we studied in east-central Sweden. Dispersal distances of males and females were not correlated with density, but the proportion of individuals dispersing tended to be negatively correlated with density. The correlations are, however, sensitive to changes in the home range diameter used in the analysis and the results should be interpreted with care.

Estimates of home range diameter affect both the limit that determines whether an individual has dispersed and the area associated with an individual, which contributes to the density index. Home ranges can be estimated in several ways that produce different estimates of area (Powell 2000). Therefore, the analyses of the data should be extended to include an estimate of the sensitivity of the correlation to different home range estimates.

Few studies have examined density-dependent dispersal in large mammals and, to our knowledge, only one examines the question in wild boar. Janeau and Spitz (1990) showed that dispersal rate, the proportion of individuals relocated more than 10 km from the marking site, was negatively correlated with density in wild boars in France. Their results are in accordance with the conclusions that we draw from our study and, therefore, the prevailing view should be that dispersal in wild boar is negatively correlated with density. Dispersal patterns might differ between populations that are widely distributed and those that are at the edge of an expanding population (Swenson et al. 1998). The populations we studied are recently established and expanding. We suggest that theories concerning density-dependent dispersal need to be extended to include the spatial distribution and succession state of populations. Furthermore, in addition to emigration, animals spend time searching for a new area before they settle as immigrants (Andreassen et al. 2002). If a population is regulated by dispersal, the colonisation rate of other areas will be affected if there is variation in the number of individuals dispersing. Consequently, population density might be an important determinant of the geographic expansion rate of populations.

The density of roots can vary considerably between years in some vegetation types, which might reflect variation in preferred foods, rather than variation in the density of wild boars (Welander 2000). Therefore, it might be difficult to use the density index as a precise estimate of population density. We assume, however, that root counts provide a relative estimate of population density, and we do not discount the possibility that, if developed, root counts can be used to estimate density precise enough to fulfil the requirements of several issues where it is used as an index.

If dispersal rate is negatively correlated with population density, the relationship has implications for the management of wild boar populations. To minimise the dispersal rate as a means of, for example, reducing the geographic expansion of the species, or to avoid spreading disease, the population should be kept at a high density; however, the number of individuals dispersing from a high-density population might be higher than the numbers dispersing at low density. To quantify the number of individuals dispersing, it is necessary to quantify the density and estimate its relationship with the dispersal rate. If the relationship between density and dispersal rate is non-linear, there might be threshold densities at which the number of dispersing individuals is minimised or maximised.

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