Timing and distance of natal dispersal for wild boar *Sus scrofa* in Sweden

Johan Truvé & Jonas Lemel

In order to estimate age at natal dispersal and dispersal distance, wild boars *Sus scrofa* were studied in Sweden by use of mark-recapture and telemetry. To describe the average natal dispersal in the population, we applied a sigmoid regression model to analyse the age specific distance to the natal site. We used the first and second order derivatives of the model to determine at which average age dispersal begins, reaches its maximum rate and ceases. The average dispersal distance was estimated by the maximum value of the model. Using this method, we reached the conclusion that male wild boars begin to disperse at the age of 10 months, reach their maximum dispersal rate at the age of 13 months, and that dispersal ceases at the age of 16 months. At that age, they have dispersed 16.6 km from their natal sites. For females, the corresponding ages were 7, 9 and 11 months, with a dispersal distance of 4.5 km. The results follow the prevalent opinion on natal dispersal in polygynous mammals. Dispersal distances are generally short with a negative exponential probability distribution. Dispersal reaches its maximum rate during the age at which sexual maturity is occurring, and males disperse longer distances than females.

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Animal dispersal occurs when individuals leave their social group or home range, causing population redistribution that leads to spatial spread (Turchin 1998). Depending on when in life dispersal occurs, it can be divided into natal dispersal if juveniles move from birth sites to breeding sites, and breeding dispersal if adults move between breeding sites (Greenwood 1980). Juveniles generally disperse in higher proportions and roam longer distances than adults, and are assumed to gain advantages by dispersing as they would otherwise be competing with their parents for food, dens and reproductive opportunities (Waser & Jones 1983).

Many species show sex differences in their dispersal patterns (Greenwood 1980, Dobson 1982). Pusey (1987) theorises that the reason for this difference in dispersal patterns may be caused by inbreeding avoidance and sex differences in competition. In polygynous mammals, males disperse in higher proportions and roam longer distances than females. Females are supposed to benefit from the familiarity of an area because of higher parental investment. Males, who are competing for access to mates, should benefit from dispersal (Pusey 1987). In mammals, where individuals of one sex live in social groups, it is common that all members of the opposite sex disperse (Packer 1979, Pusey 1987).

The distance and rate of animal dispersal are of

importance in many fields of population biology. Meta-populations, source sink dynamics, invasion, colonisation, gene flow and genetic structure are issues strongly associated with dispersal (Paradis, Baillie, Sutherland & Gregory 1998). The probability distribution of dispersal distances is usually assumed to be negative exponential ($f(x) = ae^{-bx}$; McCallum 2000). It has been suggested that the distributions are shaped this way, because dispersal distance is a function of home range turnover probability, and because individuals settle in the first uncontested home range area they encounter (Murray 1967, Waser 1985). However, many of the described distributions of animal dispersal distances are assumed to be incorrect because of measurement errors (Koenig, Van Vuren & Hooge 1996). If the study area is limited, long distance dispersers may not be detected, and the results may thus become biased towards shorter distances.

The wild boar *Sus scrofa* is a polygynous mammal with a social organisation characterised by matrilineal groups consisting of females and their offspring and solitary adult males (Martys 1991). Among the characteristics of the species are high rates of reproduction (Mauget 1991) and adaptation to a wide variety of habitats (d'Huart 1991). Wild boars and feral pigs have increased in density and geographic distribution in many countries, primarily due to introductions by humans (Waithman, Sweitzer, Van Vuren, Drew, Brinkhaus & Gardner 1999).

The wild boar was present in Sweden until the sixteenth century, when it became extinct. During the last decades, wild boars have been kept in confined populations maintained for sport hunting or breeding. Escaped or deliberately released individuals from confined populations have established free-living populations, and today, the wild boar is locally and regionally abundant in Sweden. The species is currently expanding geographically, but the expansion rates of the populations are still unknown. Prediction of the rate of spread of a population usually requires data on the dispersal of individuals (McCallum 2000).

The purpose with our study was, on the basis of collected data on the dispersal traits of wild boars in Sweden to consider the described general traits associated with mammalian dispersal to see if they are applicable to wild boars as well. Consequently, we performed a study to describe the dispersal distribution for wild boars. We also intended to estimate the age at dispersal and to test for sex difference in dispersal distance.
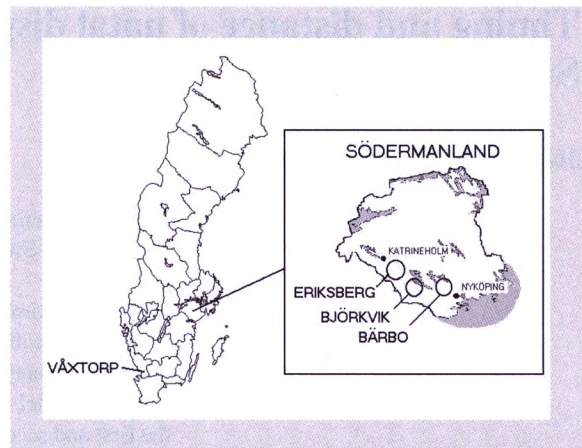

Figure 1. Location in Sweden of the four areas in which the study was performed during 1989-2000.

Methods

The major part of our study was performed in the province of Södermanland in east-central Sweden during 1989-2000 (Fig.1). In 1989-1994, wild boars were caught within a single location in the Björkvik area (58°47'N, 16°30'E). The trapping effort was increased in 1995 when animals were caught on adjacent locations nearby, ranging over an area of about 10,000 ha. In 1997, we began to trap animals in the Eriksberg area (58°55'N, 16°20'E), 20 km northwest of Björkvik, and in 1998 we included a third area Bärbo (58°47'N, 16°52'E), located 20 km east of Björkvik. The Eriksberg and Bärbo areas are of similar size as the Björkvik area. In 1995 and 1996, animals were also caught on a single location near Våxtorp (56°15'N, 12°70'E) in the province of Halland in southwestern Sweden. All study sites are situated in lowland areas consisting mainly of arable land, coniferous and mixed forests.

To capture and mark animals, we used traps of different sizes but based on the same principle, i.e. a wooden box with a one-way swing-door entrance, which permits several juveniles to be caught at the same occasion. The entrance and the exit were sized to permit juveniles only (width 20 cm, height 30 cm). Traps were baited with corn and set by blocking the exit when the animals got used to entering them. Caught animals were marked with plastic eartags (Allflex Inc.), one in each ear, and some individuals were also provided with a radio transmitter. In 1995-1997, we used both collar (Telonics Inc.) and ear-transmitters (Televilt International AB), and in 1998-2000 implant-transmitters (Telonics Inc.).

We placed the traps on feeding sites used to supply wildlife with supplemental food during winter and to attract animals during hunting events. Wild boar fre-

quently visit such sites and this makes trapping possible. In each study area in Södermanland, we used about 10 different feeding sites. The locations of the feeding sites were determined by the landowners before we began our study, and they usually intended to distribute them evenly on their premises. Trapping was carried on from early April to early July, usually with 1-3 trapping events per week and 3-5 traps set at each occasion.

Data on dispersal distances were mainly obtained through eartags returned by hunters. Hunting is permitted all year round, the exception being females accompanied by juveniles. Some animals were either killed in traffic accidents or found dead by other causes. We also recaptured juveniles in traps and occasionally re-sighted animals and identified their eartags. However, data on recaptures in traps and resightings may cause bias in the results because they depend on the location of traps and observers. Therefore, we did not include these data in the analysis.

We calculated the dispersal distance as the straight-line distance between the sites of capture and recapture. Dispersal rate is often defined as the proportion of individuals in a population that disperse. Some authors set a minimum distance requirement for dispersal. Such *a priori* limits are arbitrary (Johnson & Gaines 1990), since it is usually difficult to decide whether an individual has dispersed or not. In our below model we consider dispersal as a continuous age-dependent process. The dispersal rate, as we define it, is the age-dependent rate of increasing distance between capture sites. We do not categorise individuals as dispersers or non-dispersers as we are aware of the difficulty in differentiating them. However, we are also aware of the importance of estimating the proportion of individuals that disperse, so we will consider the issue in the discussion of our results.

We assume that dispersal consists of three phases: predispersal, explorative phase and settlement. Consequently, to describe the average natal dispersal in the population, and to analyse the age specific distance to the natal site, we applied a sigmoid regression model to the data: $f(x) = ax^b/(c^b+x^b)$. We chose this model for phenomenological reasons, assuming that it would represent the observed distribution. The parameters, therefore, have no mechanistic relation, but the model helps us to estimate the timing and distance of dispersal. We used the maximum value of the model to estimate the average dispersal distance. The maximum value of the first derivative of the model estimates the age when dispersal reaches its highest rate. The maximum and minimum values of the second derivative of the model estimate the beginning and the end of dispersal, respectively.

Age of captured juveniles was based on the following relationship between age and body mass (J. Lemel, unpubl.data):

Birth date = Trap date - ((Body mass - a)/b)+c)

where a = 6.21, b = 0.16 and c = 30, and age dependent growth is equal for males and females up to the age of 10 months (Lemel 1999).

To determine whether recoveries of marked animals were representative, and not biased due to the finite study area, we compared the movements of ear-tagged and radio-tagged animals. The distribution of maximum distances that radio-tagged individuals had moved from marking sites should preferably be within the same distance limits as the distribution of dispersal distances of ear-tagged individuals.

We used non-linear regression to fit the negative exponential model ($f(x) = ae^{-bx}$) to the distribution of dispersal distances. The difference in dispersal distance between sexes was tested using logistic regression. Non-linear regressions were made with Sigmaplot (version 5.00, SPSS Inc.) and derivations were made with Mathcad (version 2000 professional, Mathsoft Inc.). For logistic regression we used SAS (version 6.12, SAS Institute Inc.).

Results

Capture-recapture

Between 1989 and 2000, we caught and marked 873 wild boars; 432 females and 441 males. In the Södermanland area we provided 33 males and 67 females with radio
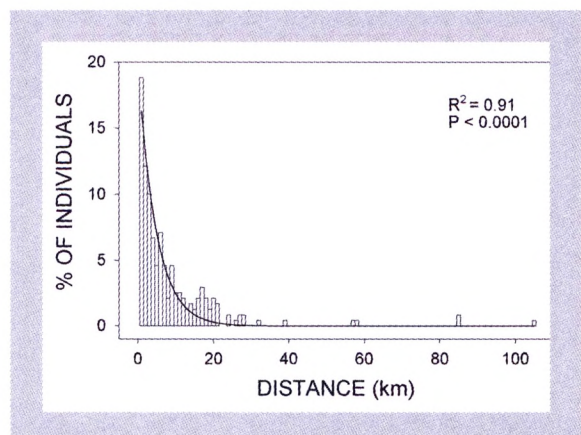

Figure 2. Frequency distribution of dispersal distances in wild boar males (N = 239) with regression model $f(x) = a*e^{-bx}$. Distances are rounded off to the nearest higher integer.
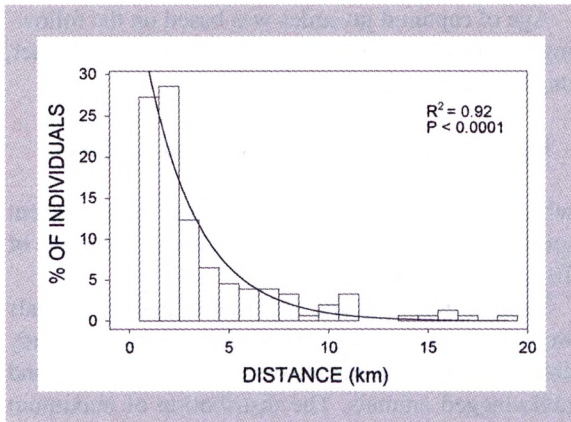
Figure 3. Frequency distribution of dispersal distances in wild boar females (N = 154) with regression model f(x) = a*e^(-bx). Distances are rounded off to the nearest higher integer.
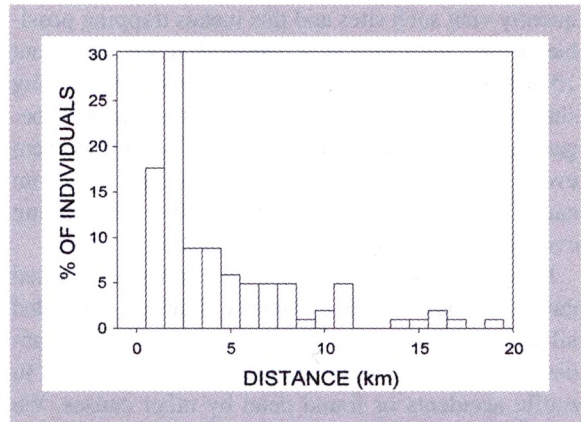

Figure 5. Frequency distribution of dispersal distances for wild boar males recaptured when they were older than 11 months (N = 102). Distances are rounded off the the nearest higher integer.

transmitters. Of the total number of marked animals, 56 were caught in Halland. A total number of 393 individuals were relocated; 154 females (eight in Halland) and 239 males (15 in Halland).

Dispersal distance

The distribution of dispersal distances shows that males are distributed over a wider range than females, with some individuals being relocated more than 50 kilometres from their natal sites (Fig. 2). Females differ from males in this respect and the majority is relocated within a few kilometres distance from their natal sites (Fig. 3).The distribution of both sexes was well described by the negative exponential model $f(x) = ae^{-bx}$ ($R^2 = 0.91$, P < 0.0001 for males, $R^2 = 0.92$, P < 0.0001 for females; see Figs. 2 & 3). There was a significant difference

between sex and dispersal distance ($\chi^2 = 27.11$, P < 0.0001). The distribution of the dispersal distances for individuals, which are older than the age when natal dispersal ends, are presented in Figures 4 & 5. These distributions are skewed more to the right and the negative exponential model could not be fitted to the data. The maximum distances moved by radio-tagged individuals are within the same distance limit as for the ear-tagged individuals (Figs. 6 & 7).

Timing of dispersal

Males become sexually mature at the age of 10 months (Mauget 1991), and they tend to increase their average dispersal distance from the capture site at that age (Fig. 8). From the maximum of the first order derivative of our model we reached the conclusion that male wild
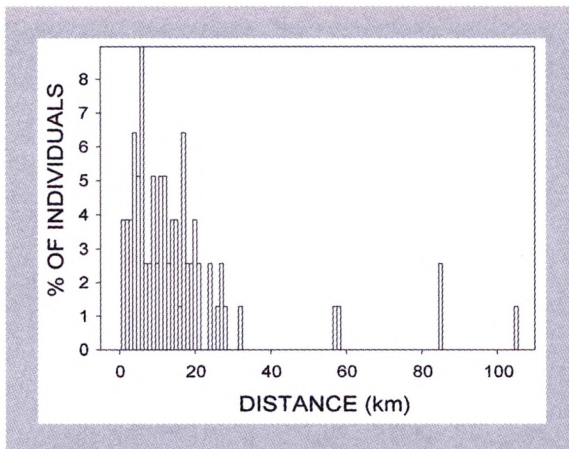

Figure 4. Frequency distribution of dispersal distances for wild boar males recaptured when they were older than 16 months (N = 78). Distances are rounded off the the nearest higher integer.
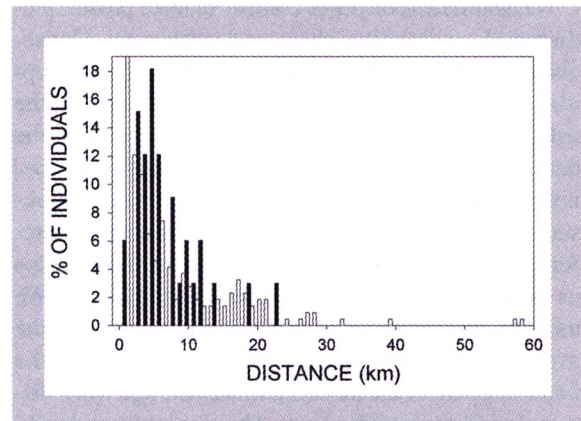

Figure 6. Dispersal distance in ear-tagged wild boar males (▨; N = 215;), and maximum distances that radio-tagged males (■; N = 33) moved. Among the ear-tagged males, two individuals at distances of 85 and 105 km are excluded from the figure.
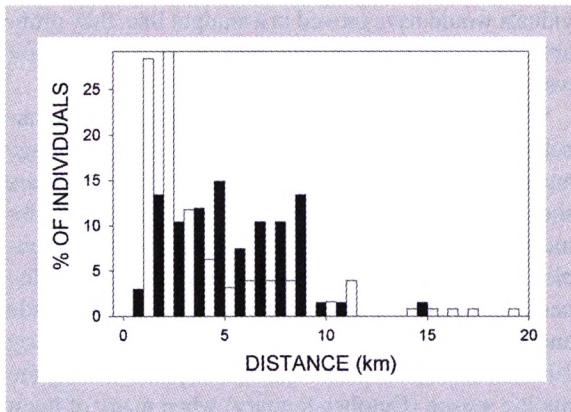
Figure 7. Dispersal distance in ear-tagged wild boar females (▥; N = 127), and maximum distances that radio-tagged females (■; N = 67) moved.

Figure 9. Dispersal distance in relation to age in wild boar females (N = 154), and results of the regression model (—), first derivative of the regression model (—) and the second derivative of the regression model (- - -).

boars reach their highest dispersal rate at the age of 13 months. From the maximum and minimum of the second order derivative, it appears that the dispersal begins at the age of 10 months, and ceases at the age of 16 months. At that age, the male wild boars have dispersed 16.6 km.

Females show a more uniform distribution of dispersal distances in relation to age (Fig. 9) than do males. Using the same procedure as for males, we reached the conclusion that female wild boars begin to disperse at the age of seven months, reach their maximum dispersal intensity at the age of nine months, and cease dispersing at the age of 11 months. At that age the female wild boars have dispersed 4.5 km from their natal sites. Sexual maturity for females occurs between the age of 7 and 22 months (Mauget 1991).
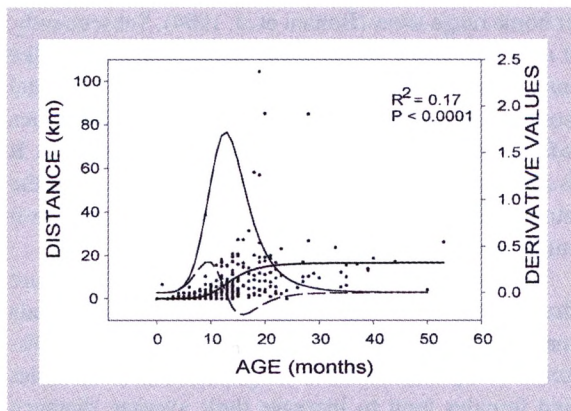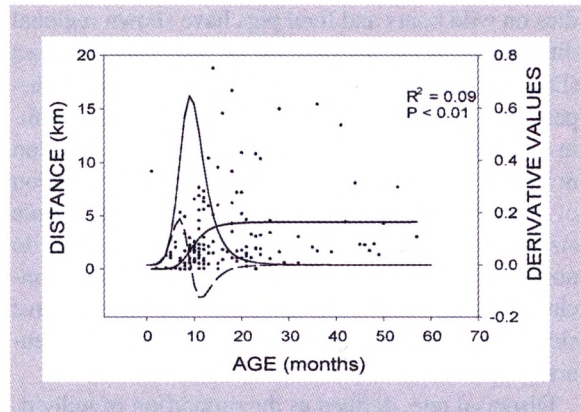

Figure 8. Dispersal distance in relation to age in wild boar males (N = 239), and results of the regression model (—), the first derivative of the regression model (—) and the second derivative of the regression model (- - -).

Discussion

The distributions of dispersal distances in our study are skewed towards short distances. Bias in dispersal distance due to finite study areas occurs if individuals disperse outside the study area from which they can not be relocated (Koenig et al. 1996, Paradis et al. 1998). In our study, we received information about animals killed outside our study area. Maximum distances of radio-tracked individuals were located within the same distance limits as ear-tagged individuals, but the distributions were not similar in shape. That was expected because one distribution represents average values of movement and the other maximum values of movement. Our purpose with the comparison of the distributions was merely to show that ear-tagged individuals were relocated even though some of them moved outside our study area, here represented by the extreme boundary of the home range of individuals with radio transmitters. Thus we conclude, that our estimates of dispersal distributions are unaffected by the limits of our study area.

Studying game species for which mortality is dominated by hunting, the bias caused by finite study areas can be overlooked. In our study area, hunting causes more than 90% of the mortality of marked wild boars (Lemel 1999). All marked animals killed by hunters were probably not reported, and animals might also have dispersed to areas with low hunting pressure, or other variables of mortality. Still, few areas are exempted from hunting in Sweden, and the hunting pressure is most likely about the same on all established wild boar populations in the country.

In our study, we focused on local dispersal in established wild boar populations in Sweden. Previous stu-

dies on wild boars and feral pigs have shown regional differences in the distribution of dispersal distances (Dardaillon & Beugnon 1987). Still, few individuals disperse long distances, and the majority is relocated within a few kilometres from the marking site (Dardaillon & Beugnon 1987). The data sets with a high proportion of long distance dispersers are few, have small sample sizes and it could be argued that these populations do not differ markedly from the first mentioned. Our conclusion is, that wild boar populations in Sweden behave similar to other populations, and that wild boars generally settle in or near their natal areas.

Dispersal rate, defined as the proportion of individuals in a population that disperse, is difficult to estimate. The maximum distance moved by radio-tracked animals in our study rarely exceeded 10 km, suggesting that ear-tagged individuals that were relocated further away represent a minimum of individuals that actually dispersed. If we sum the proportion of individuals (in Figs. 4 & 5) that were relocated at distances exceeding 10 km, it will include 11% of the females and 55% of the males. These numbers could then be interpreted as the proportion of individuals in the population that has dispersed after they reached the age when natal dispersal ends. However, this estimate is probably underestimated if dispersing animals mainly settle in areas close to their natal home range and do not exceed the 10 km limit we used to identify dispersing individuals.

Dispersal is a life history trait (Johnson & Gaines 1990), and it is probable that phenotypic plasticity could cause different dispersal patterns depending on environmental conditions. A comparison between different studies of wild boar suggests a remarkable plasticity of the spatial and activity patterns of the species (Boitani, Mattei, Nonis & Corsi 1994). The populations we studied are still expanding. Based on our results we find it plausible that the expansion is continuos and not stratified. We have not estimated the expansion rate, but the data from our study give us reason to believe that it amounts to an average of a few km²/year for females. We believe that the great difference in dispersal distance between sexes is due to the fact that females are philopatric and stay in their natal sites, forming social units with their mother and female siblings. Males, on the other hand, leave their social group and disperse, in search of territories that are vacant or possible to 'conquer'. In a spatially heterogeneous population like the one we studied, this search may last for a long time and result in long distance dispersers. In our study, the male wild boars that dispersed longer than 30 kilometres, all ended up in areas with either low densities or without previous observations of wild boars. If these indi-

viduals would have moved in a straight line, they probably would not have encountered any females on their way either.

What causes the big difference in dispersal behaviour between males and females? Dominance is related to age and size (Packer 1979), and subadult male wild boars should be outcompeted by adults in gaining access to females. According to Wolff (1993), there are few examples where juveniles are forced by resident adults to disperse, but there are cases in which adult males intrude and force both adults and subadults to leave (Pusey 1987). Male wild boars start to disperse during the mating season (October-January) when many of them also become sexually mature. Home ranges of adult males overlap except during this period when they compete for access to females (Boitani et al. 1994). If subadults leave their natal areas during the mating season, either voluntarily or forced by intruders, they probably encounter aggressive adults in neighbouring areas. Consequently, the movement activity of subadults ought to be intensive during the mating season when they are forced to move on by aggressive adults. The following period should give them opportunities to settle, as aggressive territorial males become more tolerant to male conspecifics. Our data support these conclusions as they match the timing of the different events. There may be another period of dispersal in the following mating season, during which adult males redistribute, but it would require further investigation to have this verified.

Wild boars are often supplied with food to prevent damage on farmland, to help them survive during the winter and to attract animals during hunting events. In our study area, supplementary feeding is a widespread phenomenon, and many landowners supply wild boars with food all year round. Supplemental feeding affects the spatial behaviour of wild boars and results in smaller home range areas (Boitani et al. 1994). Subsequently, it may also affect the dispersal distance in a study like ours. If an individual is randomly recaptured in its natal home range, the average distance between capture sites will be correlated to the size of the home range area. It is also possible that supplemental food could affect the number of individuals that leave for another area as it might decrease competition for food.

The majority of wild boars become sexually mature during their first year of life with some individuals maturing about their seventh month (Mauget 1991). Distance of dispersal in relation to age shows that both males and females tend to increase their average distance from the capture site when they reach maturity. Wild boars in Sweden mainly farrow during February-May (Lemel 1999), and consequently juvenile females start

to disperse during the period September-December. This is also the time of the year during which the hunting season is open. Wild boar movements increase when hunting dogs disturb the animals, and occasionally some boars move to refuge areas. The probability of getting killed is also higher during this period, and if an increased number of individuals are killed during a period with increasing movements due to disturbance, this will affect the results. We assume that disturbance does not affect the results in our study. It is only the onset of the dispersal activity for females that is correlated in time with disturbance. The season for hunting with dogs closes by the end of February, and following our model, maximum dispersal activity occurs later than this for the greater part of the individuals. Interestingly and worth mentioning in this case is, that disturbance could be a proximate cause of dispersal if individuals choose to settle in the refuge area instead of returning to their natal sites.

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