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ORIGINAL PAPER

First evidence of long-distance dispersal of adult female wild boar (*Sus scrofa*) with piglets

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Abstract Using GPS telemetry and ear tagging, we monitored wild boar sounder (a 2-year sow, a female yearling and eight piglets) captured in northern Slovenia. Five months after the capture, the sounder left its home range and first travelled 100 km west, to the three-border area between Slovenia, Austria and Italy, and from there toward southeast. The sow and three piglets were shot 2 months after start of dispersal 60 km from the capture site and in-between travelled at least 500 km. At least one piglet continued dispersal after the death of the sow, and the yearling split from the sounder during dispersal. This is the first documented case of long-distance dispersal of adult female wild boar with piglets. Several arguments suggest that long-distance dispersal of female wild boar is more common than previously reported in the literature. For wild boar and other species with predominant male dispersal, data on occasional far-dispersing females like presented here are important for understanding biology of species (e.g. metapopulations, rate of population expansion, local sex and age structure of population) and for management including control of diseases.

Keywords Breeding dispersal of females · Invasion · Long-distance dispersal · Management · Population expansion · Spread of diseases · *Sus scrofa* · Wild boar

Animal dispersal occurs when an individual moves from its natal range to a new area or succession of areas where it reproduces (Greenwood 1980). During dispersal, individuals make the longest move of their lifetime, which may thus affect several individual and population traits, such as local sex and age structure of the population, the speed of population expansion, genetic structure, competition for partners and food and the spread of diseases (Lidicker 1975; Greenwood 1980; Mundt et al. 2009). Knowledge of dispersal is therefore important for management of species and understanding of their biology.

In most (but not all) species of mammals, dispersal is male-biased, rarely equal or female-biased (Greenwood 1980). Mating systems are widely accepted as key determinants of the direction and magnitude in sex-biased dispersal. In polygynous mammals, males mostly compete for access to females (Clutton-Brock 1989). Spatial distribution of females should thus determine male dispersion and promote their dispersal.

Depending on time of dispersal, it can be divided to natal dispersal, when juveniles move from birth site to breeding site, and breeding dispersal, when adults move between breeding sites. In the majority of studied species, juveniles disperse more often and further than adults. Breeding dispersal may be related to the search for better breeding partners or breeding environment, or it could be a form of parental investment (Cockburn 1988). With few exceptions, such as chimpanzee (*Pan troglodytes*), field vole (*Microtus agrestis*) and red squirrel (*Tamiasciurus hudsonicus*), breeding dispersal of females has not been documented for most mammal species (Greenwood 1980; Berteaux and Boutin 2000).

Wild boar is a polygynous mammal with a social organization characterised by matrilineal territorial groups consisting of females and their offspring and solitary adult males (Keuling et al. 2010). Natal, male-biased dispersal would therefore be expected while adult females would not be expected to disperse, which has also been suggested in most previous studies (rev. in Keuling et al. 2010, but see also Cesas-Diaz et al. 2013). Present article documents the first

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recorded case of breeding dispersal of a sow with piglets and discusses the frequency and relevance of long-distance dispersal of wild boar females.

Materials and methods

We were capturing wild boars with cages at five feeding sites during May–July in subalpine Slovenia (N 46.3°, E 15.0°). All captured wild boars were ear-tagged, and adult females and males were also equipped with GPS collars (Vectronic, Berlin), which recorded locations every hour. The area is 65 % forested; the rest is comprised of arable land and meadows. Forests are dominated by common beech (*Fagus sylvatica*) and oaks (*Quercus* spp.). Supplementary feeding (mostly maize) is intensive over the entire year (1 feeding site/300 ha). Wild boar culling in the capture area was 1.1 animals/100 ha, slightly above the average in Slovenia (0.9 animals). Wild boar population size and distribution range have increased drastically in the past decades in Slovenia. For example, culling increased 12 % annually, but it has not kept up with population increase (Jerina 2006). Favourable natural conditions and indices of fitness (high fertility, body mass, rapid population growth) suggest that wild boar density is not yet close to the carrying capacity in the capture area or elsewhere in Slovenia.

Results

In total, 47 wild boars were captured, including a sounder with a 2-year sow (named Erika), eight piglets and a female yearling captured on 19 May. For 5 months after the capture, Erika remained in the forest area around the capture site (95 % min. convex polygon=212 ha). She moved a bit further in early September and regularly visited maize fields. At the beginning of October, Erika left her home range. We monitored her movements for another 2 months, until 4 December, when the GPS battery failed. In these 2 months, Erika travelled at least 500 km (sum of distances between hourly locations). She was culled on 18 December, close to the last recorded GPS locations. The aerial distance between the capture site and the cull site was 60 km, and the distance to the most remote location in the border area between Slovenia, Austria and Italy was 100 km (Figs. 1, 2). During dispersal, Erika was on average 58 km from the capture site, corresponding to 15 diameters of wild boar home range in Slovenia.

Erika dispersed with the entire sounder. The female yearling separated during dispersal, settled down and was culled on 13 December 42 km from the capture site. Two of the piglets (2♂) were culled soon after ear-tagging near the capture site, three piglets in the same hunt as Erika (2♂, 1♀) and one (♀) a year later 74 km from capture site and 24 km from the Erika's cull site (Fig. 2). For two piglets, we did not receive return data.

We captured additional 37 wild boars in the study area, of which four (1♂, 3♀, age 1–4 years) were GPS collared and 33 (27 piglets, 6 yearlings) ear tagged. The movements of these animals were substantially less extreme than those of Erika's group. The ear-tagged males were culled up to 30.6 km (average 4.9 km) and females up to 21.4 km (average 6.4 km) from tagging site. Home ranges (95 % min. convex polygon) of the four GPS-collared animals were 6.2–19.0 km^2 (average 14.8 km^2) and maximum distance from capture site 2.4–8.9 km (average 5.1 km).

Discussion

To our knowledge, Erika's case is one of the longest reported dispersals of female wild boar and the first documented dispersal of an entire wild boar matriarchal group. In other study areas, females dispersed on average 1.8–6.9 km and maximally 1.8–89.9 km (rev. in Keuling et al. 2010; Cesas-Diaz et al. 2013). These studies typically monitored juveniles/subadults, which generally disperse more (e.g. Prevot and Licoppe 2013; Truvé and Lemel 2003). In contrast, Erika dispersed as an adult. We found only one published unequivocal case of dispersal of an adult (3 years) female, but even that dispersed only short distance to a neighbouring sounder (Gabor et al. 1999).

In most mammal species, dispersal distances of both sexes inversely depend on population density (Greenwood 1980). In species with pre-saturation dispersal (incl. wild boar), females living in saturated populations are more philopatric compared to males; in contrast, in increasing and spatially expanding populations, the maximal dispersal distances of both sexes can be comparable (Swenson et al. 1998), as for example showed for brown bear in several parts of Europe (Jerina and Adamič 2008). In Slovenia, both the dynamics of population density (rapid increase of density) and saturation of populations of wild boar are at a level that might promote female dispersal. It is noteworthy that several years ago, a similar dispersal distance (75 km) was recorded for a female in the south of Slovenia (rev. in Keuling et al. 2010). Comparably long maximum dispersal distances for female wild boar were also recorded in a study in Spain (max. 89.9 km; Cesas-Diaz et al. 2013), in an area where wild boar population densities are increasing rapidly, as in Slovenia. However, the population densities there are considerably higher than in our study area (2.5–5.8 vs. 1.5 animals/100 ha). This indicates that absolute population density per se is not a key factor affecting long-distance dispersal of female wild boar and that such dispersal can occur in various environmental conditions and populations.

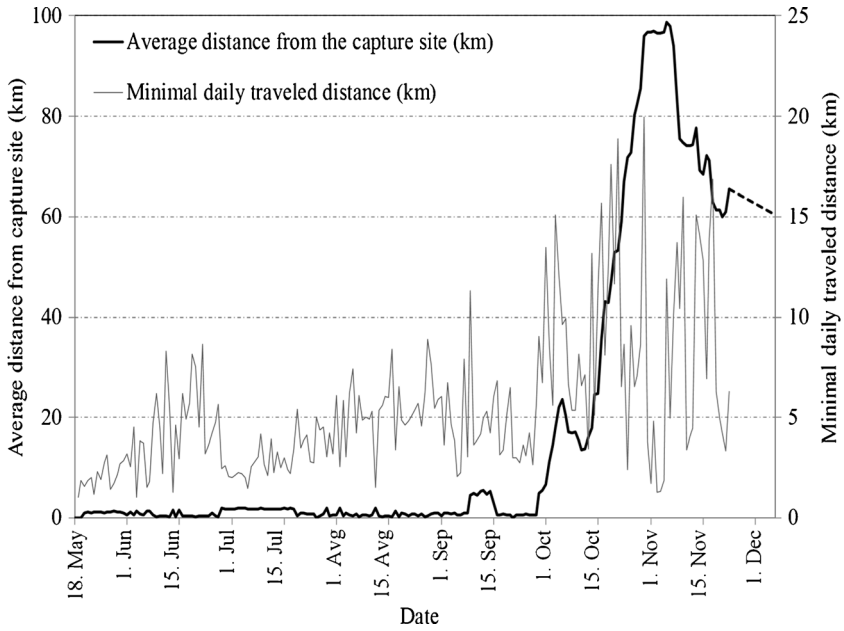

Fig. 1 Minimum daily distance (sum of distances between locations) travelled and distance from the capture site of dispersing sow in Slovenia. The sow started dispersing 5 months after capture, and its movement was monitored with GPS telemetry until 4 December, 2 weeks before it was culled (*dashed line*)

Majority of wild boar dispersal studies were based on mark–recapture data (e.g. ear-tagging; mostly piglets), with single recapture location. In contrast to GPS telemetry used in our study, such approach does not enable to assess whether the individuals settled down prior to recapture or if there was movement between consecutive breeding sites. Mark-recapturing also underestimates dispersal distances and inadequately detects the longest dispersal events (Barrowclough 1978; Baker et al. 1995). Animals that disperse the farthest are more likely to leave the study area, management unit or even the study country; therefore, the feedback of data for such animals is less likely. This may be even more expressed in reproductive females. Such females are less exposed to hunting mortality due to shorter hunting period and self-initiative protection by hunters, partially driven by ethics. Besides, hunters may tend to conceal killing of breeding female (e.g. report wrong sex or age) and thus less likely report their "recapture." According to these potential biases as well as our case of monitoring dispersal using GPS telemetry, we believe that long-distance dispersal of wild boar females

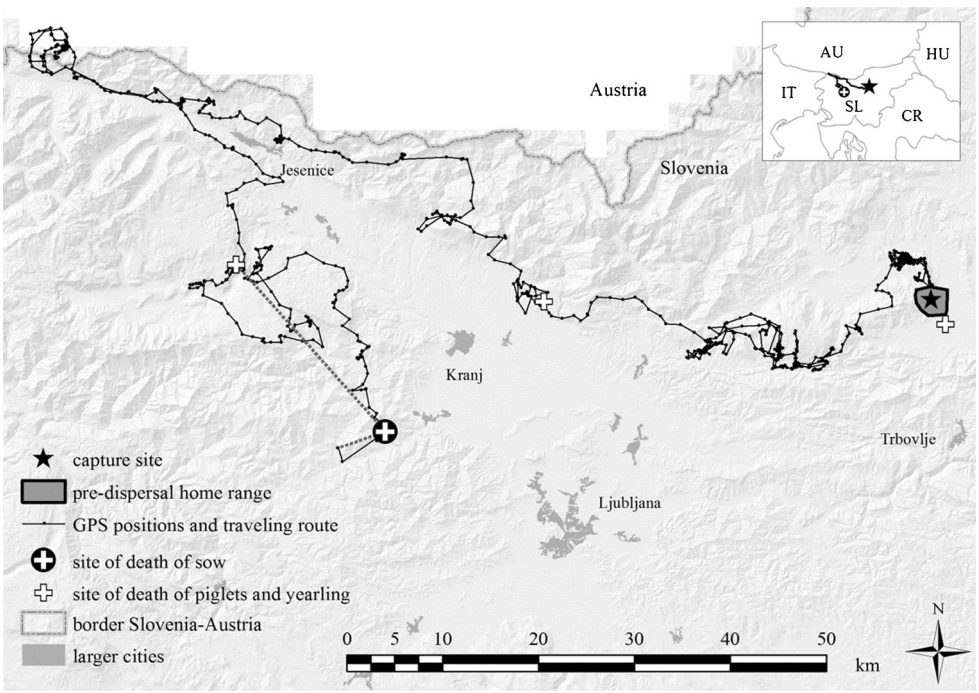

Fig. 2 Travelling route of the wild boar sow, its eight piglets and a yearling after they left their home range. The sow's 2-month dispersal ended with a culling 60 km from capture site. In between, it maximally moved 100 km away from its pre-dispersal home range

(juvenile and adult) is likely underestimated and underreported and occurs more frequently than suggested by existing literature.

Previous studies implicitly presumed that breeding dispersal does not occur in wild boar. Although our results base on a single case, they provide clear evidence that adult female wild boar can disperse far, even with entire sounder. In a male-biased dispersal species such as wild boar, this could be an important consideration in the biology, ecology, behaviour, epidemiology and management of the species. Even a few far-dispersing females can strongly increase the rate of population spatial spread (Goldwasser et al. 1994). In several parts of Europe, the expansion of the wild boar has been indeed so rapid (Apollonio et al. 2010) that it might be difficult to explain it without female long-distance dispersal. Female dispersal also makes species more successful in coping with fragmented habitats. This could explain why wild boar is one of the most successful game species in colonizing fragmented landscapes. Wild boar is also one of the most "problematic" species, mostly due to damages in agriculture (Apollonio et al. 2010) and spread of diseases to domestic animals and human (Ruiz-Fons et al. 2008; Meng et al. 2009). The main method to decrease conflicts is often culling (Keuling et al. 2013), used to reduce density or even establish wild boar-free zones. But effects are typically short lived, as the species can quickly occupy empty habitat. This may be enhanced by female long-distance dispersal, in particular when the females are accompanied by piglets, as reported in our study. Wild boars are known key reservoir hosts for a number of diseases affecting domestic animals and for several zoonoses (e.g. Ruiz-Fons et al. 2008; Meng et al. 2009). Long-distance dispersal of family groups can strongly enhance the spatial spread of diseases (Mundt et al. 2009), which should be taken into account in health surveillance and disease control programmes (Gortazar et al. 2007).

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