

Social organization of the wild boar (*Sus scrofa*) in Doñana National Park

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Social organization of the wild boar (Sus scrofa) in Doñana National Park.—The composition of social groups in the wild boar was observed in Doñana National Park over a one-year cycle. Mean group size was 3.21 ± 0.69 (mean \pm SE, N = 842) individuals per group, and significant changes were observed throughout the year reaching a maximum during the birth season in spring. Ten types of groups were defined, and among them, those that predominated throughout the year were the following seven: male groups; mixed groups with adult animals of both sexes; adults with subadults; adult females with subadults; adult females with piglets; females with subadults and piglets; mixed groups of adult animals with piglets. Most groups made similar use of the habitats in Doñana, the main exception being family groups without piglets that were found less frequently in the shrub/forest on mobile dunes and more in the ecotone habitats. Contrasting with other ungulates, group size did not appear to be related to the use of different kinds of habitat. The particular period of the biological cycle appears to be the main factor shaping the social organization of wild boar in Doñana.

Key words: Wild boar, *Sus scrofa*, Social organization, Social groups, Doñana.

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Introduction

The social organization of a species throughout the yearly cycle is a key to understanding the relationships between individuals and the ecological factors they face in a particular environment (JARMAN, 1974). It is also useful to determine the conditions that produce other

behavioural characteristics such as the mating system (EMLEN & ORING, 1977; DAVIES, 1991).

The wild boar is a very common and widely distributed large mammal, but the knowledge we have on many aspects of its ecology and behaviour is still limited. The social organization of the wild boar seems to be highly dynamic, with many

different kinds of groups which change throughout the year (MAUGET, 1972; MAUGET et al., 1984; KRATOCHVIL et al., 1986; DARDAILLON, 1985, 1988). However, the factors modelling such changes are still not clear. In the Iberian peninsula, little attention has been paid to this topic with the exception of Doñana National Park (VENERO, 1983; CUARTAS, 1988; BRAZA & ÁLVAREZ, 1989).

The size and composition of groups in all different habitats in Doñana National Park was studied over a one-year cycle. The main factors affecting the changes of the dynamic social organization were evaluated.

Material and methods

The study was carried out in the protected area of Doñana National Park and includes the following habitats, all of which are inhabited by the wild boar (VALVERDE, 1960):

- Marsh: the eastern half of Doñana, constituting almost 50% of the total extension of the park and mainly covered by *Scirpus maritimus*.

- Shrub/forest on fixed dunes: located mainly in the center and north. Covered by *Eucalyptus* sp. in some areas and by autoc-tonous scrub in others. This scrub includes two main communities: 'monte blanco' consisting mainly of *Pteridium aquilinum* and *Halimium halimifolium*, and 'monte negro' with *Erica scoparia* as the most common bush species.

- Shrub/forest on mobile dunes: in the south, with *Pinus pinea* as the main over-story species.

- Beach: in the west, between the scrub and the Atlantic Ocean.

- Ecotone: longitudinal area between the scrub and the marsh, north-south oriented along most of the Park, and covered by *Juncus* sp. patches and *Cynodon dactylon* meadows.

Field work was done over a one-year cycle, from November 1992 to November 1993. The commencement of the study coincided with the onset of the mating period which lasts until early January. Mid-January to mid-March was defined as the gestation period. Mid-March to early June was the birth season. From June to the end of October was defined as the growing pe-

riod, during which the piglets developed to the subadult age. Although our yearly cycle started with the mating period in November, some results are presented from January for clarity.

A group was defined as those individuals of the same species with a relationship of spatial proximity with respect to others, that moved together, and tended to synchronize their behaviour. Mean group size was calculated by dividing the total number of individuals in a sample by the number of groups. The analysis of variance (ANOVA) was used to test the variations in the size of groups throughout seasons and in each habitat.

Two criteria were used to define the group types, one based on those used in

Table 1. Mean group size throughout the year. MGS. Mean group size; N. Number of groups recorded; SE. Standard error; CI. Confidence intervals.

Tamaño medio del grupo a lo largo del año. MGS. Tamaño medio del grupo; N. Número de grupos; SE. Error estándar; CI. Intervalos de confianza.

Months	N	MGS	SE	95% CI
Nov	44	2.48	0.22	1.83-3.08
Dec	75	2.89	0.20	2.43-3.35
Jan	63	2.63	0.22	2.13-3.14
Feb	83	2.99	0.19	2.55-3.42
Mar	130	3.47	0.19	3.12-3.82
Apr	100	2.97	0.18	2.57-3.36
May	86	3.79	0.25	3.36-4.22
Jun	55	3.71	0.34	3.17-4.24
Jul	57	3.28	0.28	2.75-3.81
Ago	53	3.51	0.30	2.96-4.05
Sep	66	3.33	0.27	2.84-3.82
Oct	30	3.03	0.29	2.31-3.76
Total	842	3.21	0.07	3.07-3.35

the literature, and the other based on the groupings resulting from the cluster analysis of proximity of age-sex classes occurring in the groups. The cluster analysis has been used in previous studies to determine types of groups from a sample (STAUFFER & BEST, 1986). The kind of cluster analysis used herein assigns each observation to one of the group types previously defined according to the literature (DARDAILLON, 1985, 1988; BRAZA & ÀLVAREZ, 1989). A final value is calculated on how each age-sex class fits into every group type. The relationship between age-sex classes and group types allows us to test whether the groupings previously defined from the literature fit well with our observations (see BROWN et al., 1990). Analysis was done using the BMDP statistic package.

Changes in the frequency of observation of group types throughout the year were studied by means of the chi-square

and the correspondence analysis (BMDP statistic package). The chi-square was also used to analyze the relationship between group types and the habitats in Doñana.

Results

Group size

The size of wild boar groups ranged from one to 11 individuals per group, with a mean of 3.21 ± 0.69 SD (N = 842 groups). Group size changed significantly throughout the year (ANOVA: $F = 1.95$; $df = 11,830$; $p = 0.03$; table 1). Groups were smaller in November (2.48 ± 0.22 SD), increasing until peaking in May (3.79 ± 0.25 SD), from when they slowly started to decrease. Maximum group size coincided with the birth season and the initial growth of piglets (fig. 1).

There was no significant relationship be-

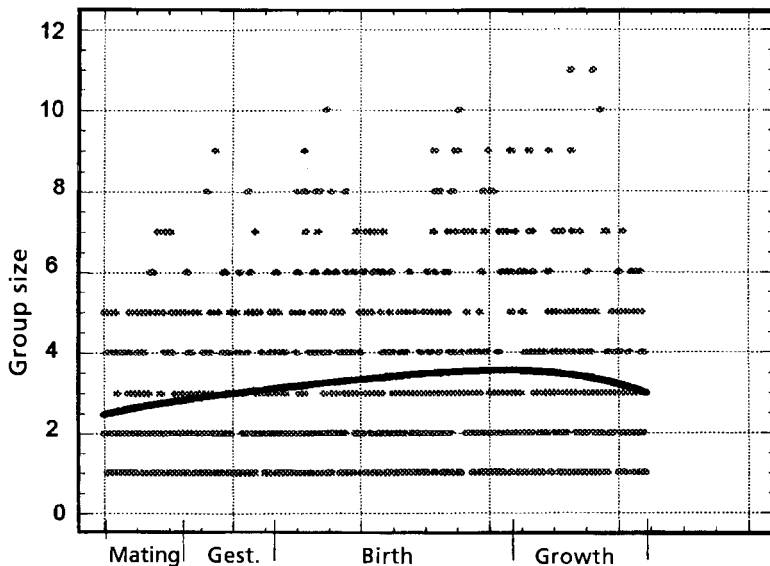


Fig. 1. Changes in group size throughout the annual cycle. Points are cases of individual groups recorded. The line results after adjusting the data to a fourth degree polynomial by using the minimum squares method.

Cambios a lo largo del año del tamaño de los grupos. Los puntos son casos de grupos registrados. La línea resulta tras el ajuste de los casos a un polinomio de cuarto grado, según el método de mínimos cuadrados.

tween group size and habitat (ANOVA: $F = 1.933$; $df = 3,838$; $p = 0.123$).

Group types

The cluster analysis indicated that our observations fitted well into the ten group types defined according to literature on the species (ANOVA: $F = 354.56$, $df = 27,2496$; $p < 0.0005$). Table 2 shows the values of presence of each age-sex class in each group type. Two values are presented per class and group type, a theoretical value used in the cluster analysis and the actual value obtained from our observations. Such actual values revealed cases where some non-typical individuals were found in a group type.

The resulting group types were as follows: type A. All-male groups, with one or several adult males; type B. Mixed adult group, with adult males and adult females; type C. Mixed group with adults and subadults; type D. Mixed group including piglets; type E. Mixed subadult group; type F. Female group, with one or several adult females; type G. Female group with subadults of either sex; type H. Female group with piglets; type I. Female group with subadults and piglets; type J. Mixed adult group with piglets.

Group types and the annual cycle

The occurrence of each group type varied significantly throughout the year (Chi-square = 63.19; $df = 27$; $p = 0.0001$). Figure 2 shows the relative frequency of each group type in the four main seasons of the yearly cycle. Groups of adult males (type A) occurred almost constantly in all seasons. Mixed groups with adult and subadult animals (types B and C) were most common during the mating and gestation periods, decreasing to the birth season, when some included piglets (type D), and when females tended to separate into unisexual groups (type F) and family groups with piglets (type H). Later, the growth of piglets produced an increase of type G (females and subadults) and type I (females, subadults and piglets) groups. Groups including only subadult animals (type E) were present throughout the year with a slight

peaking in the mating period. Most of these groups (77 out of 96: 80.21%) included only subadult males. Mixed groups including adult animals and piglets without subadults (type J) occurred occasionally in the second half of the year.

The correspondence analysis performed to study the relationship between group types and period of the biological cycle showed an association between mating and

Table 2. Average number of individuals in each type of group following cluster analysis. 1. Theoretical value; 2. Real value.

Número medio de individuos en cada tipo de grupo después del análisis de cluster. 1. Valor teórico; 2. Valor real.

Types		n			
		Adults		Subad Piglets	
		♂♂	♀♀		
A	1	1.00	0.00	0.00	0.00
	2	1.08	0.00	0.09	0.01
B	1	1.00	1.00	0.00	0.00
	2	1.06	1.09	0.36	0.04
C	1	1.00	1.00	2.00	0.00
	2	1.06	1.20	2.80	0.06
D	1	1.00	1.00	2.00	3.00
	2	1.04	1.50	2.64	3.00
E	1	0.00	0.00	2.00	0.00
	2	0.00	0.00	1.84	0.00
F	1	0.00	1.00	0.00	0.00
	2	0.02	1.64	0.13	0.36
G	1	0.00	1.00	2.00	0.00
	2	0.00	1.12	2.03	0.07
H	1	0.00	1.00	0.00	3.00
	2	0.00	1.16	0.13	3.64
I	1	0.00	1.00	2.00	3.00
	2	0.00	1.26	2.47	2.65
J	1	1.00	1.00	0.00	2.00
	2	1.07	1.14	0.50	2.64

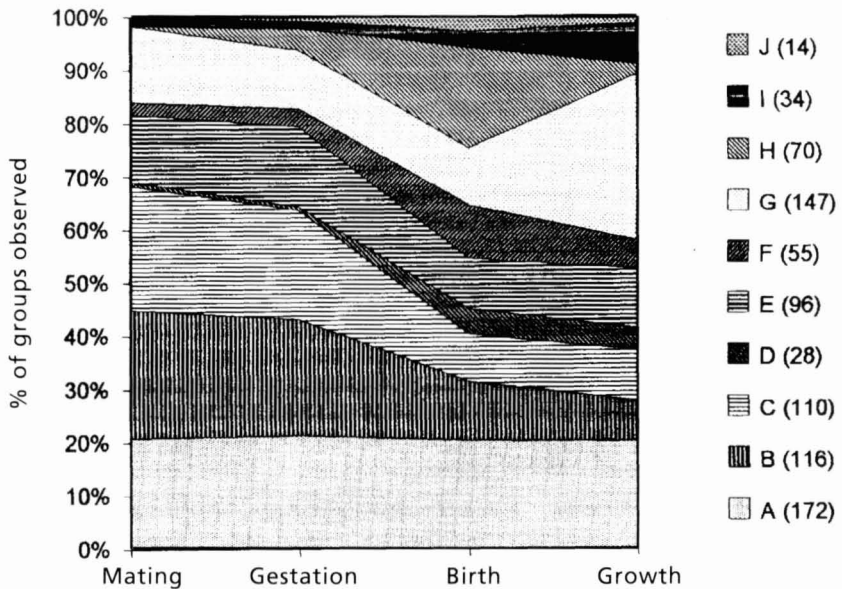


Fig. 2. Changes in the proportion of each type of group throughout a one year cycle (n in brackets): A. Males; B. Mixed adult group; C. Adults and subadults; D. Mixed group including piglets; E. Subadults; F. Females; G. Female group with subadults; H. Adult females with piglets; I. Females with subadults and piglets; J. Adults with piglets.

Cambios en la proporción de cada tipo de grupo a lo largo de un ciclo anual (n entre paréntesis): A. Machos; B. Mixto de adultos; C. Adultos y subadultos; D. Mixto con crías; E. Subadultos; F. Hembras; G. Hembras con subadultos; H. Hembras con crías; I. Hembras con subadultos y crías; J. Adultos con crías.

gestation periods, while birth and growing seasons appeared well-differentiated not only from each other but also in relation to mating and gestation seasons (fig. 3). Associations in the analysis showed that male groups (type A) and subadult groups (type E) occurred independently of the season, mixed groups with adults (type B) and subadults (type C) were associated to mating and gestation periods, females alone (type F) or with piglets (type H) occurred in the birth season, groups with females and subadults (type G) were typical of the growing period, and the remaining groups (types J, D and I) appeared between the birth and growing seasons (fig. 3).

Group types and habitat

All types of groups occurred in all four main habitats in Doñana. However, there were small but significant differences in the occurrence of the ten types of groups depending on the habitat (Chi-square = 41.13; df = 27; p = 0.04). Within family groups, there were differences in habitat use (Chi-square = 34.47; df = 18; p = 0.011), mainly because those groups without piglets (B, C, G) tended to use the shrub on mobile dunes less and the ecotone more than groups including piglets (D, H, I, J). The overall use of habitats by groups of any type was 11.99% marsh area, 38.36% ecotone, 33.49% shrub on mobile dunes and 16.16% shrub on fixed

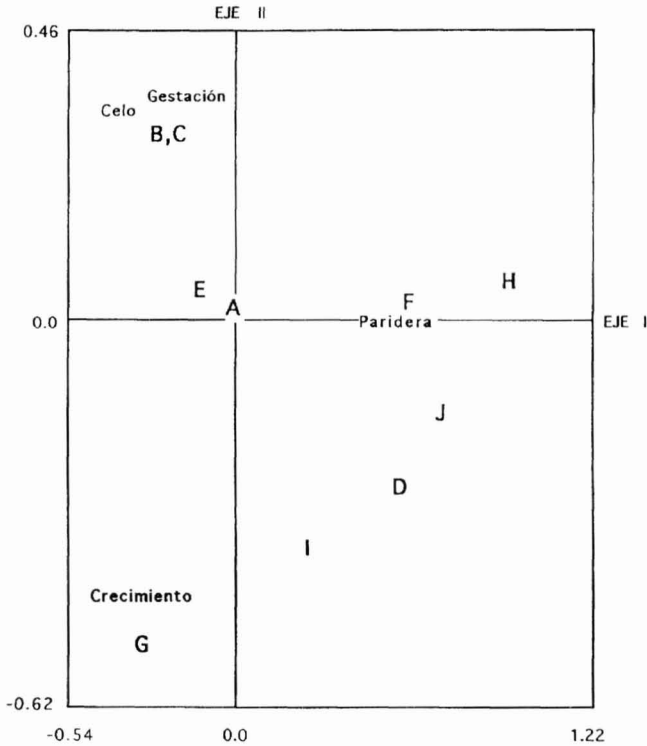


Fig. 3. Correspondence analysis relating the periods in the biological cycle with group types. Types of groups according to the cluster analysis. (For abbreviations see figure 2).

Análisis de correspondencias que relaciona los periodos del ciclo biológico con los tipos de grupo. (Para abreviaturas ver figura 2).

dunes. In order to see the relationships more clearly, the ten group types were summarized into the following six groups: family groups including piglets (types D, H, I, J), family groups without piglets (B, C, G), all-male groups (A), family groups including adult males (B, C, D, J), all-female groups (F) and subadult groups (E). On comparing each groups with the general pattern, the results show that only family groups without piglets differed from the general pattern (see fig. 4). This group type used the shrub on mobile dunes less and the ecotone more as compared with the general pattern. Some non-significant tendencies also appeared: (1) subadult males used the shrub

on fixed dunes more and (2) all female groups used the ecotone more.

Discussion

The mean group size for the wild boar in Doñana in 1993 is somewhat lower than the figures obtained in previous studies in this area (see table 3) and also below the average group size reported for La Camarge in France by DARDAILLON (1988). The tendency in Doñana seems to be a decrease over the last decade. Interpopulational differences in group size could be related to differences in habitat structure. On the basis of

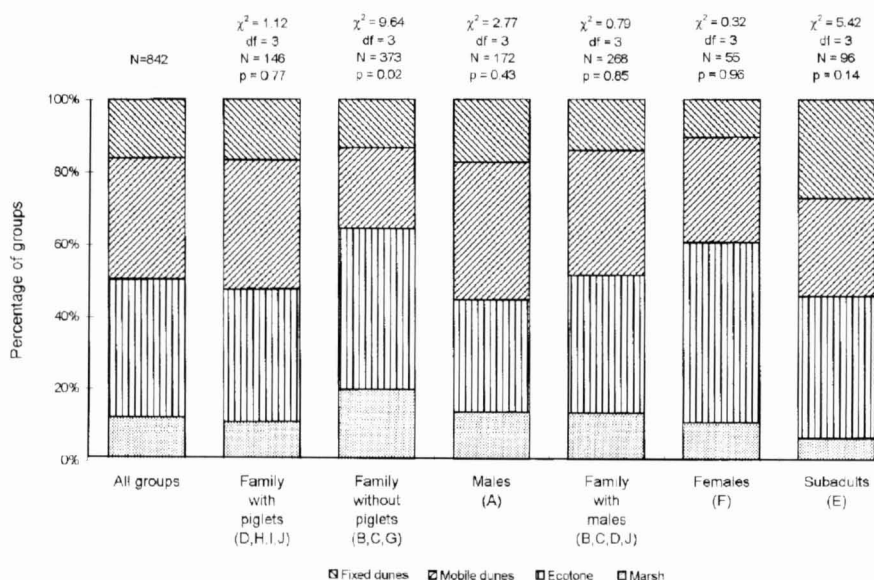


Fig. 4. Percentage of habitat used by each group type. The first bar is the total use by all groups, and chi-square tests are the comparisons between each type and the total.

Porcentajes de uso de los diferentes hábitats para cada tipo de grupo. La primera barra es el uso por parte de todos los grupos y los tests Chi-cuadrado muestran la comparación entre cada tipo y el total.

antipredatory strategies in many vertebrates (PULLIAN & CARACO, 1984) including ungulates (JARMAN, 1974) it is expected that social units aggregate when using open habitats, thus resulting in larger group sizes. However, our results show that group size in the wild boar does not appear to be affected by the use of different habitats. The wild boar is a prey species, commonly included in the diet of larger carnivores such as the wolf (*Canis lupus*; OKARMA, 1995). Wolves were present in Doñana until early this century and current potential predators of piglets are foxes (*Vulpes vulpes*) and lynx (*Lynx pardina*). One possible explanation for the lack of antipredatory aggregation in this species in Doñana could be the high level of feeding competition, particularly during the year of study which took place after a period of several years of drought and which could have prevented the clumping of animals when searching for food in open habitats.

Intrapopulational differences in group size may be explained by ecological fac-

Table 3. Mean group size of wild boar in Doñana.

Tamaño medio de los grupos de jabalí en Doñana.

Year	n	Period	Reference
1980	4.44	year	VENERO, 1983
1983	3.85	year	BRAZA & ÁLVAREZ, 1989
1985	3.34	summer	CUARTAS, 1988
1986	3.74	summer	CUARTAS, 1988
1993	3.21	year	present study

tors affecting the population over time. Again, the long period of drought could possibly account for the decrease in group size over recent years. Family groups contribute greatly to average group size, and accordingly the maximum size of groups occurs at the end of the birth season, when most females are with piglets. Poor climatic conditions during 1993 may be responsible for several associated effects observed in Doñana during the same period such as the low proportion of lactant females and low mean litter size (MASSEI et al., 1996), the high mortality of piglets (FERNÁNDEZ-LLARIO, 1996), and hence the low mean group size.

The social organization of the wild boar in Doñana, as in other populations, appears to be highly dynamic and closely related to the biological cycle of the species. Throughout most of the year sexes are separate, perhaps as a result of differences in nutritional requirements or in abilities for feeding competition as in other ungulate species (JARMAN, 1974; GEIST, 1982). The tendency of females to separate from other individuals when giving close to birth may also contribute (MARTÍNEZ-RICA, 1980; MARTYS, 1982). In the birth season most female groups appear with piglets, their proportion depending on the particular conditions of the year (GELDOF, 1983). Later, during the growing period (summer and autumn), the presence of subadult animals in female groups becomes more frequent due to the growth of piglets.

Groups of subadult animals, mainly including males, follow a different pattern, their relative frequency increasing during the mating period. This may occur because they are expelled by adult males (DARDAILLON, 1985, 1988; SPITZ, 1989) when the latter join female groups. Subadult males experience a faster rate of growth, their food demands increase (AKHERNE & KIRKWOOD, 1985; GAILLARD et al., 1992), and their mortality risk from natural predators is also high at this age (SCHAUSS et al., 1990). These animals make long foraging movements (DOUAUD, 1983; SPITZ, 1991), and their foraging strategy is highly opportunistic (VENERO, 1982; DARDAILLON, 1989). The scarce presence of subadult females is likely because, in contrast with males, they are not

forced to leave the family groups (DARDAILLON, 1988).

All types of groups appear to make similar use of the habitats in Doñana. The main difference in the overall statistical significance is family groups without piglets. This may be the result of the interaction between occurrence of group types and food availability throughout the seasons in each habitats of Doñana. Family groups without piglets are mainly found either before or after the birth period, when offspring of the year are included in the subadult category. During the birth period (late winter and spring) an important source of food is found in the shrubs on mobile dunes, when the pines (*Pinus pinea*) release mature seeds, and many wild boars collect there (FERNÁNDEZ-LLARIO, 1996). Most group types made use of this food resource. Because in this period most family groups include piglets, families without piglets appeared to use the habitat on mobile dunes less and the ecotone more used mainly during the rest of the year. The main result is therefore a seasonal by-product rather than a consequence of the peculiarities of the composition of this group type. In contrast, the non-significant tendencies found for subadult groups and for female groups can be explained by features of the kind of individuals included. Subadult groups (mostly subadult males, see above) used the habitats on fixed dunes more probably because such individuals are dispersing from the familiar home ranges, and dispersing young animals are more likely to be found in least preferred areas (GERARD et al., 1991). On the other hand, all female groups tended to use the ecotone more than other group, probably because they consisted mainly of females parturient, and best birthing places in Doñana are located in this area (FERNÁNDEZ-LLARIO, 1996).

Resumen

Organización social del jabalí (Sus scrofa) en el Parque Nacional Doñana

En este trabajo se analizan las variaciones en el tamaño y composición de los grupos

de jabalí en el Parque Nacional Doñana durante un ciclo anual completo, y en diferentes tipos de hábitats. El tamaño medio de los grupos fue de $3,21 \pm 0,69$ (media \pm ES, N = 842) individuos. Este tamaño cambió significativamente a lo largo de los meses del año (tabla 1). No se encontraron diferencias entre hábitats en el tamaño de los grupos.

En cuanto a la composición de los grupos en clases de edad/sexo, un análisis cluster indicó que se ajustan bien a diez grupos (tabla 2), de los cuales los más frecuentes a lo largo del año fueron: grupos de machos; adultos de ambos sexos; adultos con subadultos; hembras adultas con subadultos; hembras adultas con crías; hembras con subadultos y crías; mixtos de adultos con crías. La organización social de la población mostró diferencias a lo largo del ciclo anual (fig. 2), de modo que los grupos de machos y de subadultos ocurrían independientemente de la estación, mientras que los mixtos se asociaban a los periodos de apareamiento y gestación, y las hembras con o sin crías/subadultos aparecían más frecuentemente en las épocas de paridera/crecimiento (fig. 3). La mayoría de los tipos de grupo se encontraron por igual en todos los tipos de hábitat de Doñana, siendo la principal excepción los grupos de hembras sin crías que se encontraron en menor frecuencia en el matorral/bosque que ocupa las áreas de dunas móviles, y más frecuentemente en el ecotono (fig. 4).

Al contrario de lo que ocurre con otros ungulados, en los que grupos grandes se asocian a hábitats abiertos probablemente como estrategia antipredadora, estos resultados no indican que el tamaño de grupo en el jabalí se vea afectado por el tipo de hábitat. Para el jabalí en Doñana, los cambios en el modo en que los animales se agrupan parecen venir determinados principalmente por el momento en que se encuentren en el ciclo biológico anual de la especie.

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