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Population parameters of fallow deer at Doñana National Park (SW Spain)

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In order to know the reproductive and social status of fallow deer *Dama dama* (Linnaeus, 1758) populations at Doñana National Park and analyze the influence of climatic factors and population density on the reproductive performance of females and males, periodic counts were conducted from September 1982 to September 1988. The size of the study population increased in the period 1982–1983 and remained relatively stable from 1983 to 1988 (mean $= 267.79 \pm 11.26$). The mean group size of the female groups was the largest (8.67 ± 1.44); mixed groups showed a mean size of 8.09 (± 1.05), the mean group size of the male ones being the smallest (5.21 ± 0.9). The results indicate that density as well as temperature during the last month of gestation have repercussions on the reproductive performance of the females. No sexual differences have been detected in juvenile mortality during the first year of life.

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Key words: population parameters, *Dama dama*, Doñana National Park

Introduction

In scientific literature only scparce information exists about natural population dynamics of fallow deer *Dama dama* (Linnaeus,1758). Thus, the four monographs which have been published about this species up to the moment (Ueckermann and Hansen 1968, Heidemann 1973, Chapman and Chapman 1975, 1980) furnish only few data on this matter. Nevertheless, in recent years the study of population dynamics of herbivores has become very important, especially because of its direct relation to environment and primary producers. Specifically, detailed information about some aspects of population dynamics is found with respect to a species in close phylogenetic relation to fallow deer, which is *Cervus elaphus* (Lowe 1969, Mitchell and Crisp 1981, Clutton-Brock *et al.* 1982, Nelson and Peek 1982, Ratcliffe 1984, Bobek and Kosobucka 1985, Hornbeck 1985). However, as indicated by Clutton-Brock *et al.* (1982) studies about population dynamics of large mammals have scarcely paid attention to the comparative aspects of dependent and independed variables of male and female density.

As regards the National Park of Doñana, the density of wild ungulates has been increasing due the absence of large predators. High utilization by these wild ungulates and the domestic herbivores has restricted the regeneration of riparian woodlands within the ecotone between the scrubland and the marshland, and a serious conservation problem now exists. Riparian woodlands of Doñana provide an important nesting habitat for a variety of resident and migratory birds. Furthermore, past management practices have reduced the extent of these riparian woodlands to only a few isolated deteriorating stands.

Previous studies on fallow deer *Dama dama* in Doñana National Park (Braza 1975, Ojeda *et al.* 1983, Braza *et al.* 1984) indicate that approximately 80 percent of the population lives in the meadows of the ecotone zone, rarely in vading the surrounding habitats. It is believed that this species has a profound effect on vegetation that occurs in the ecotone. The aim of this study was to know the reproductive and social status of fallow deer population at Doñana, to analyze the influence of climatic factors and population density on the reproductive performance of females and males, and finally, to obtain information about these population parameters that permits to elaborate a management plan for these ungulate populations.

Study area

The National Park of Doñana is located on the southwest coast of Spain at the mouth of the Guadalquivir river (37°N, 6°30′W). Three main biotopes are recognized: sand dunes, Mediterranean scrubland, and marshes (Allier *et al.* 1974) (Fig. 1).

The ecotone a marshland border is an area of acid water outcrop from the brushwood over the same limits of the marshland. In this area we find dry meadows with *Tuberaria guttata*, *Trifolium campestre*, *Plantago coronopus*, *Cynodon dactylon* etc. and also extensions of mosaic complexes of *Trifolium fragiferum*, *Cynodon dactylon*, *Paspalum vaginatum* and *Glaudina fragilis*, as well as a forest of *Quercus ruber* with some specimens of *Populus alba*.

We concentrated on fallow deer living in a narrow ecotonal zone of approximately 6 km by 1.5 km in the inner Biological Reserve. About 25 percent of the total fallow deer population occurs there (San José 1988). The chosen study area can be considered absolutely representative for the rest of the ecotone in the National Park as for the utilization standard for ungulates (Braza *et al.* 1984). Annual rainfall in Doñana averages about 500 mm, 87 percent of which falls between October and April. The average annual temperature is 17°C, with August the hottest (mean = 24°C) and January the coldest (mean = 11°C) months. This study began just after a period of drought (1980 – 1981) with annual mean value of falls below 400 mm.

Overhunting resulted in the extirpation of fallow deer in Doñana in the middle of the 18th century. The species was reintroduced into the Park at the end of the last century, and the population has continued to increase. Braza (1975) estimated that there were about 1200 fallow deer living within the National Park in 1973. By 1979 this number had more than doubled to 2500 individuals (Ojeda *et al.* 1983). The drought of 1980/1981, resulted in a population decline, caused during that summer when almost all the fawns and a high proportion of breeding females died. After that, the first complete census in the National Park was taken in 1984 with a result of 1900 fallow deer (F. Braza *et al.*, unpubl.).

Methods

Periodic counts were conducted by vehicle at least once a month from September 1982 to September 1988 to ascertain an index of population size and determine grouping patterns of fallow deer. Counts followed a fixed path during early morning hours. Two observers (apart from the driver) recorded the

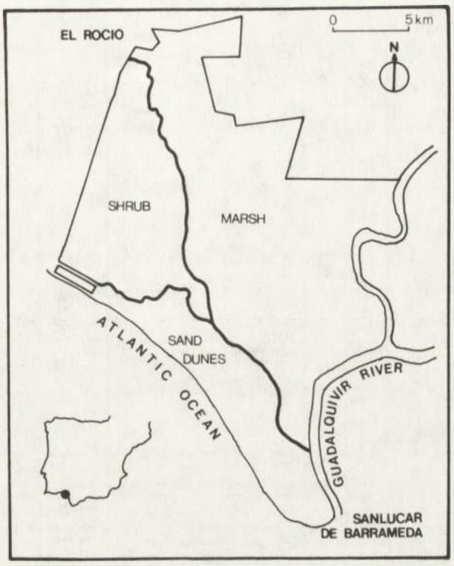

Fig. 1. Study area: Doñana National Park.

number, group size and composition of all fallow deer observed. Individuals were considered to belong to the same group if they were no farther than 50 m apart. The following sex and age classes were recognized: adult males older than 2 years; juvenile males, 1 year old; females older than 1 year; fawns of both sexes younger than 1 year.

For data analysis, census which correspond to summer months were chosen because then the different age classes considered are easier to distinguish. The young born in June have then already joined the groups of females and the males' antlers are completely developed. Furthermore, during this season the groups are relatively stable as to their composition, almost without any emigration or immigration (San José 1988). In order to evaluate mixed groups census of autumn were used. During the second half of June it is furthermore possible to distinguish between the juvenile females one year old and the adults does due to the marked curvature of the latter's belly during pregnancy. Thus, we were able to approximate to the sexual differences in survival during the first year of life calculating the relation between the juvenile–male/doe ratio and the juvenile–female/doe ratio to a half fawn/doe ratio of the previous year (considering a birth sex ratio of 1:1; Braza *et al.* 1988).

For statistical analysis, ANOVA was used to test for differences among years and between sexes, using a VAX-11 computer and BMDP Statistic Software (Dixon 1981). When appropiate, the data were arc-sine transformed prior to statistical testing. Pearson correlation coefficients were also used.

Results

Population size and structure

As Table 1 shows, the size of the study population significantly increased in the period 1982/1983. From 1983 to 1988 the population size remained relatively stable ($F=1.297$, $p=0.2889$, ANOVA). While the number of females did not significantly fluctuate during this period ($F=2.202$, $p=0.007$, ANOVA), the number of males

Table 1. Population size and structure (N = number of census).

Year	N	Total		Adult males		Juvenile males		Females		Fawns		Op. sex ratio	
		$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
1982	4	173.50	18.77	20.00	6.37	1.00	–	100.50	12.97	40.25	3.09	5.50	2.10
1983	12	254.91	19.17	27.16	6.57	24.58	6.72	125.25	7.66	79.91	9.18	4.92	1.50
1984	10	264.20	32.71	46.90	4.77	31.49	5.75	114.70	16.49	71.20	11.88	2.45	0.41
1985	7	264.42	33.96	41.42	11.60	23.71	3.94	126.00	18.85	73.28	9.37	3.12	1.11
1986	5	274.25	14.68	49.50	7.04	18.50	1.91	129.75	9.53	76.25	5.50	2.65	0.41
1987	3	287.00	15.71	62.00	2.00	34.00	3.00	137.33	15.56	53.66	3.21	2.22	0.32
1988	2	262.00	1.41	50.50	19.09	18.50	0.70	136.50	13.43	57.00	4.24	2.96	1.38
$\bar{x}$		254.32		42.49		21.67		124.29		64.50		3.40	
SD		37.07		14.46		10.85		12.97		14.48		1.28	

increased gradually till 1987 ($F=17.004$, $p=0.001$, ANOVA).

Operative sex ratio

The gradual increment in the number of males determined a statistically important decrease of the sex ratio ($F=8.397$, $p=0.0001$, ANOVA), which was specially marked in the beginning of the study period. From 1984 onwards the sex ratio stabilized ($F=1.65$, $p=0.1974$, ANOVA), at a mean value of about 2.68 females per male (SD=0.36; Table 1).

Grouping parameters

Fallow deer live in unisexual groups during most of the year, with an average size of 8.67 ± 1.44 individuals as for female groups and 5.21 ± 0.91 individuals as for male groups during the period of 1982 to 1987 (Table 2). In general, an increase in the number of individuals also means an increase in the number of groups ($n=6$, $r=0.923$, $p<0.01$ and $r=0.885$, $p<0.05$, for males and females respectively). No significant correlation was found between population density and group size.

Table 2. Group size (N = number of census; N* = census of mixed groups corresponding to autumn while the rest were made in summer).

			Years					
			1982	1983	1984	1985	1986	1987
Total	N		3	8	6	5	4	2
	No Groups	x̄	17.33	33.62	29.16	30.20	36.33	46.00
		SD	1.52	4.30	2.56	2.77	2.08	0.00
	Group size	x̄	8.93	7.41	8.43	8.01	7.43	5.80
		SD	0.59	1.22	1.47	0.45	0.90	0.67
Females	N		3	8	6	5	4	2
	No Groups	x̄	13.66	28.75	18.83	21.25	27.00	31.00
		SD	1.55	3.32	2.22	2.50	3.00	5.60
	Group size	x̄	9.80	7.53	10.29	9.56	8.24	6.60
		SD	0.93	1.25	1.84	0.29	1.54	0.08
Males	N		3	8	6	5	4	2
	No Groups	x̄	3.66	4.87	10.33	8.40	9.33	15.00
		SD	0.57	1.12	1.21	2.70	1.15	5.65
	Group size	x̄	5.60	6.74	5.17	4.18	5.16	4.43
		SD	1.15	1.83	0.83	0.57	0.96	1.43
Mixed	N*		3	4	8	3	2	6
	No Groups	x̄	4.66	14.50	13.37	18.66	22.50	20.40
		SD	2.50	2.88	4.30	2.08	2.12	6.22
	Group size	x̄	7.82	6.74	7.66	8.94	7.73	9.69
		SD	1.46	0.93	1.10	1.46	0.02	1.81

Table 3. Calf ratio.

Year	N	$\bar{x}$	SD
1982	4	40.44	5.16
1983	12	62.24	6.79
1984	10	62.04	5.31
1985	7	58.38	2.58
1986	5	58.83	4.38
1987	3	39.26	2.71
1988	2	41.80	1.00

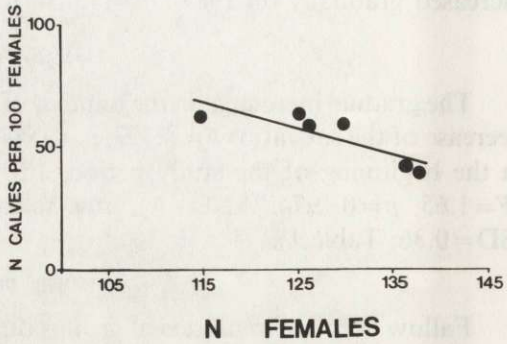

Fig. 2. Calf/hind ratios plotted against the number of females in the study area.

Table 4. Calf birth weight (in grams).

Year	Total			Females			Males		
	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD
1982	12	4491.66	418.66	5	4380.00	438.17	7	4571.42	419.18
1983	18	4847.22	574.59	8	4581.25	683.44	10	5060.00	383.55
1984	14	5757.14	815.61	9	5588.80	886.27	5	6060.00	642.65
1985	13	4984.61	698.62	6	4616.66	545.58	7	5442.85	621.44
1986	27	4929.62	560.26	13	4950.00	471.69	14	4910.71	649.31
1987	32	4834.37	566.03	14	4457.14	443.28	18	5127.70	475.03
1988	49	4891.83	752.38	27	4725.92	734.50	22	5095.45	739.67

As regards mixed groups, which form during the rutting season (Table 2), we detected a positive correlation between the number of females and the number of males present in the study area and the number of harems (n = 6, $r = 0.933$, $p < 0.01$ and $r = 0.861$, $p = 0.05$ respectively), but without finding any correlation between the mentioned parameters and the average size of the harems (n = 6, $r = 0.438$, ns).

Fawn/doe ratio

The fawn/doe ratio (number of fawns/100 females) increased from 40.44 fawns/100 females in1982 to 62.24 fawns/100 females in 1983. From 1983 to 1986 this ratio remained stable ($F = 1.159$, $p = 0.3416$, ANOVA) decreasing to an average value of 40.54 in 1987 and 1988 (Table 3). Excluding the value which corresponds to 1982, we detected a negative correlation between the calf ratio and the number of females present in the study area during the study period (1983 – 1988) (n = 6, $r = -0.848$, $p < 0.05$; Fig. 2).

Calf birth weight

Excluding the data which correspond to 1982, just like in the case of the fawn/ /doe ratio, there was a clearly negative correlation between the number of females

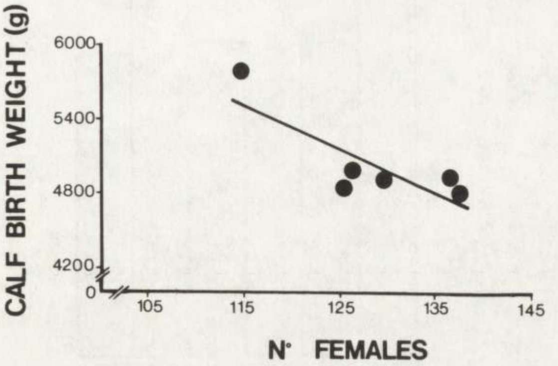

Fig. 3. Calf birth weight plotted against the number of females in the study area.

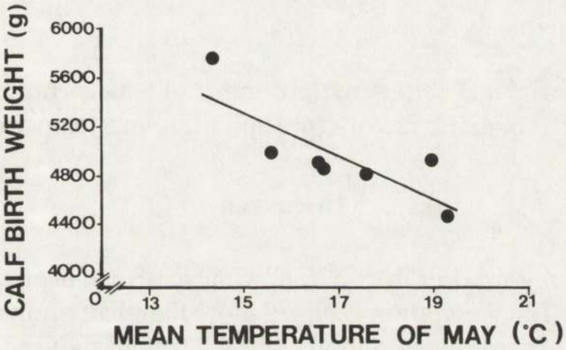

Fig. 4. Calf birth weight plotted against the mean temperature of May.

present in the study area and the average weight of the new-borns (n=6, $r=-0.882$, $p<0.05$; Table 4, Fig. 3). Taking into account the fawns sex, the afore-mentioned correlation remains in force for males (n=6, $r=-0.846$, $p<0.05$) whereas it is not statistically important in case of the females (n=6, $r=-0.692$, ns).

Likewise, a negative correlation was detected between calf birth weight and the average temperature recorded during the month of May (last month of gestation) (n=7, $r=-0.817$, $p<0.05$). This correlation remained statistically significant in the case of males (n=7, $r=-0.931$, $p<0.01$) but not for females fawns (n=7, r=−0.611, ns; Fig. 4)

Fawn mortality

With respect to fawn survival during their first year of life, no significant sexual differences were detected ($F=0.327$, $p=0.5745$, ANOVA). A 90.16% of the fawns (SD=11.51) got past their first year of life (Fig. 5). Despite variations in the course of the study period ($F=6.495$, $p=0.0013$, Two Way ANOVA) this low toll did not seem

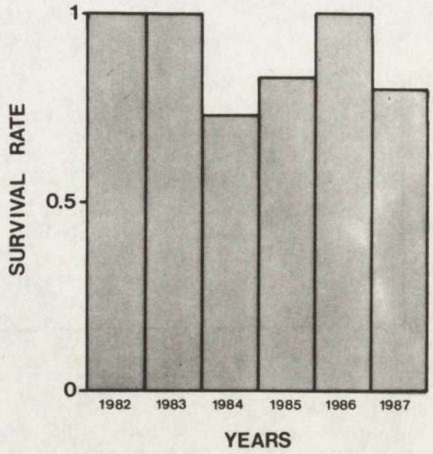

Fig. 5. Fawn survival rate during the first year of life.

to be significantly correlated neither to the number of females present in the study area nor to the considered climatic factors (precipitation and temperature).

Discussion

This study of fallow deer began following a severe drought that resulted in a population crash. The population declined more than half and was characterized by high levels of mortality for fawns and juveniles. Drought induced population decline has been documented for many large mammals (Caughley 1970), and disproportionate mortality among younger age classes is common in these situations (Clutton-Brock *et al.* 1985). The recovery of this population after drought was rapid and by 1983 the population size reached a value of 255 individuals that remained rather stable during the last six years of the study period (mean = 267.79 ± 11.26). We talk of a general quick recovery in the entire National Park, so that, as indicated in the introduction, in 1984 the fallow deer population reached values close to those furnished by Ojeda *et al.* (1983) for years before the drought. Likewise, the number of females in the study area experienced similar fluctuations, *i.e.* quick recovery in 1982/1983 to stabilize at an average value of 128.25 ± 8.37 individuals during most of the study period.

Due to the fact that the adult male class included only those more than two years old whereas the female class also includes one year old juveniles, the sex ratio did not stabilize until 1984 as there were no juvenile males in 1982. While the female population did not significantly change during the last six years of the study period, there was a progressive increase in the number of males until 1987 which declined again in 1988.

The birth sex ratio in the study population does not differ from parity (Braza *et al.* 1988) and according to our results there are no significant sexual differences in fawn survival during the first year of life. Therefore sexual differences must, without doubt, exist with respect to survival rates of animals more than one year old, which would justify the different observed recovery patterns as to the size of male and female populations. As it is known for many *Cervidae*, males are more susceptible to environmental variations than females due to higher food requirements (Julander *et al.* 1961, McEwan 1968, Wegge 1975). Nevertheless, we would like to point out herewith that males have been hunted in Doñana until 1982. In our opinion, this together with the effects of the drought might have conditioned the fact that at the beginning of the study period the number of males was so much below the potential size with respect to the available resources in their habitual home range.

Furthermore, it is interesting to bear in mind the known sexual differences in habitat preferences of fallow deer (Heidemann 1973, San José and Braza, in print) and also for red deer *Cervus elaphus* it is known that females use other habitats and have different food preferences (Staines and Crisp 1978, Clutton-Brock *et al.* 1982, Staines *et al.* 1982). In other circumstances the gradual increase in the number of males would have been perhaps relatively more limited because of the impact of density via increased mortality of males, as happens in other populations (Clutton-Brock *et al.* 1982, 1984, 1985). According to our data, the increase in number of males does not seem to have been limited until 1988. In short, the results seem to suggest that the population recovery after the severe drought followed different patterns with respect to males and females in accordance with distinct growth potentials and survival rates.

Fallow deer remain sexually segregated for a large part of the year. Male groups normally consist of adult males, sometimes accompanied by subadult or juvenile males. Female groups are primarily the mothers with their fawns. Mixed groups, usually an adult male and females with individuals of other sex-age classes, appear mainly during the rutting season. Groups of this type were uncommon in other seasons, with the exception of the unusually long rutting season 1982 during which mixed groups were recorded until spring 1983 (Braza *et al.* 1986). These authors demonstrated that the rutting season of 1982 was atypical, influenced by the poor physical condition of deer following the drought. The mean size of the female group type was the largest with a mean value of 8.67 ± 1.44. Mixed groups showed a mean size of 8.09 ± 1.05 and the mean group size of the males had the smallest value (5.21 ± 0.91). The mean size of harems in Doñana coincides with the one indicated by Schaal (1982) for a European population in Alsace in forest habitats. Nevertheless, the size of female as well as male groups is slightly superior to the number found by this author in the said populations. Whereas the size of mixed groups must be conditioned by aspects of reproductive behavior, variations in parameters of unisexual groups are certainly influenced by structural differences of habitats (Hirth 1977, Schaal 1982).

Although unisexual groups are more sensitive to structural characteristics of their habitat, the group size of fallow deer populations in Doñana, which are used to living in the marshland borders, is affected by variations in the population density. Nevertheless, the number of groups increases as soon as the number of males and females increases in the study area. Important factors like, for example, escaping from predators or competing for trophic resources probably contribute to the stability of the size of these groups. Mixed groups, whose number but not their size is influenced by variations in female density in the study area, rather depend on the competition between males and their capacity to defend a harem, thus conditioning the stability of the harem size.

As to reproductive performance, it has to be taken into account that the increase observed in fawn/doe ratio in 1982/1983 is strongly biased by the catastrophic effects of the drought in 1980/1981. Starting from 1983, the value of the fawn/doe ratio (0.54 ± 0.1) was within the range reported for other European deer populations (Ueckermann and Hansen 1968, Lowe 1969, Clutton-Brock *et al.* 1982). Nevertheless, our results indicate that density as well as temperature during the last month of gestation have repercussions on the reproductive performance of the females. Thus, an increase in said variables cause the number of fawns/100 females as well as the calves' birth weight to decrease. A similar relationship between calf/hind ratio and population density was found across Scottish deer populations (Clutton-Brock *et al.* 1982). The said authors observed a negative (but statistically not significant) relation between calf birth weight and the number of females present in the study area, the calf birth weight being lower in population with high female density.

Nevertheless, during the last month of gestation climatic factors play a more important role because of their effect on food availability (Clutton-Brock *et al.* 1982). This was, without doubt, what happened to the study population in 1982, *i.e.* the effects of the severe and lengthily drought were superior to the detected influences of density on female reproductive performance during the rest of the study period. Analysing the influence of these factors bearing in mind the fawns' sex it is interesting to point out that only the males' birth weight was negatively correlated with an increase in the number of females in the study area and the environmental temperature during gestation.

In accordance with the theories of Parental Investment (Trivers 1972, Trivers and Willard 1973, Clutton-Brock and Albon 1982) and as demonstrated in the study population (Braza *et al.* 1988, San José 1988), fallow deer does invest more in their males fawns especially with respect to body size and birth date. The results of the present study seem to indicate that this major investment in male fawns is also conditioned by environment and population factors, which directly affect the physical condition of the females during gestation.

Finally, no sexual differences have been detected in juvenile mortality during the first year of life; neither have they been found for red deer (Guinness *et al.* 1978). Furthermore, it seems that the survival rate of fallow deer in Doñana is, in fact, high (90.15 ± 11.51), and much higher that that reported in other European deer populations (37 % and 28 %, Lowe 1969 and Guinness *et al.* 1978, respectively). The mildness of the Doñana winters and the absence of large predators may account for this low mortality rate. Considering the absence of predators and the low incidence of juvenile mortality of fallow deer in Doñana processes of migration and juvenile dispersal as well as sexual differential mortality rates and reproductive performance are probably relevant on the dynamics of these populations.

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