Common Fallow Deer *Dama dama* (Linnaeus, 1758)

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Common Names

English	Common fallow deer
German	Damhirsch
French	Daim
Spanish	Gamo
Italian	Daino
Russian	лань

Taxonomy and Systematics

The International Commission on Zoological Nomenclature with the Opinion 581 (China and Melville 1960) validated *Dama* Frisch, 1775 as the generic name for fallow deer. However, several authors (e.g., Corbet 1978) have continued to consider it congeneric with *Cervus*. Molecular analyses support the monophyly of the genus *Dama* (e.g., Gilbert et al. 2006). Different divergent times were estimated for this genus in relation to the selected calibration point, for example 5.1 mya, just after the start of the Pliocene, or 3 ± 0.4 mya, during the Pliocene, according, respectively, to Pitra et al. (2004) and Gilbert et al. (2006).

The genus *Dama* includes the common fallow deer and the Mesopotamian fallow deer. These deer can be distinguished on the basis of body size (Mesopotamian is larger) and antler shape, and by some minor differences in coat and tail color, rhinarium, and skull morphology. The common and Mesopotamian fallow deer *Dama dama*

Fig. 1 Common fallow deer. A male (left) during the rutting season and a group of females with fawns (right) (photographs by A. M. De Marinis)

(Linnaeus, 1758) (Fig. 1) and *Dama mesopotamica* (Brooke, 1875) have been regarded as sister taxa on the basis of molecular and morphological analyses (e.g., Heckeberg 2020, Pitra et al. 2004). On the contrary, Masseti et al. (2008), estimating a divergence time of 423,021 years (95% CI = 430,000–116,000 years) between haplotypes of these two taxa, supported the subspecific classification of *D. d. dama* and *D. d. mesopotamica*. At present, the taxonomic debate is still open.

Paleontology

The ancestry of the modern fallow deer (Fig. 1) has been tentatively traced back to several Pliocene/Early Pleistocene forms whose relationships to *Dama* are still unclear (see Heckeberg 2020).

The common fallow deer belong to the group of Asian biota that immigrated to the European regions. At the beginning of the Late Pleistocene, fallow deer lived in continental Europe and commonly occur in faunal assemblages from the last interglacial (*c.* 130–115 kya) of mid-latitude Europe (Masseti and Vernesi 2014). During the last glacial period, common fallow deer retreated into the southern areas of its former distribution, and survived in southern Anatolia and perhaps in southern Italy, Sicily, and the southern Balkan Peninsula (Uerpmann 1987; Stuart 1991; Masseti 1996; Masseti and Vernesi 2014). There is no clear archaeological evidence of the early colonization of the Iberian Peninsula. Davis and MacKinnon (2009) suggest that the species was absent in this peninsula before Roman times and that the Romans were responsible for its introduction. Osteological remains from the island of Mallorca, Spain, recovered in Iron Age (Talayot culture) settlements, could instead suggest a pre-Roman introduction chronology for the species, but these remains "came from insecure contexts more likely associated with Roman activity" (Valenzuela et al. 2016). Paleontological evidence of deer presence in glacial refugia is very fragmentary. As far as is presently known, several artistic Epipaleolithic representations of the common fallow deer from southern Italy and Sicily constitute the latest chronological evidence for the persistence of this cervid in Italy during the Late Glacial Maximum (Masseti and Rustioni 1988; Masseti 1996). Subsequently, the fallow deer did not return as far north as its previous range, unlike many other temperate species (Masseti and Vernesi 2014). This lack of expansion from southern refugia is atypical, but not unique (see Bilton et al. 1998).

Post-glacial expansion of the genus *Dama* was limited almost exclusively to the northern Mediterranean and the Near East (Chapman and Chapman 1997; Masseti and Vernesi 2014), where, despite the contiguity of their native geographical distribution, the common and Mesopotamian fallow deer were not sympatric. Fallow deer of the

Taurus range belong to the common form (Harrison 1968), while the original distribution of the Mesopotamian deer ranged from southeastern Turkey and the Levant to eastern Persia (Uerpmann 1987).

Archaeozoological evidence suggests that translocations of fallow deer began early in the Pre-Neolithic Cyprus and in the Neolithic of continental Greece and several Aegean islands (Masseti and Vernesi 2014). Translocations increased during the Bronze Age when this species also began to spread into the western Mediterranean (Masseti and Vernesi 2014). The artificial occurrence of the genus *Dama* in northern Africa, as reported by Chapman and Chapman (1980) and Kitagawa (2008), is questionable.

The Mesopotamian fallow deer qualify as Endangered (EN) in the IUCN Red List under criterion D, due to very small and restricted population numbers in Iran and in Israel. However, the population trend seems to be increasing (www.iucnredlist.org). Reintroduction projects have been undertaken in different Iranian locations and in Israel (Fernández-García 2012; Saltz et al. 2011) and today are still ongoing.

Current Distribution

The common fallow deer are the most widespread deer species in the world (Chapman and Chapman 1997). From as early as the Pre-Neolithic period, the species was exported around the Mediterranean, later to central and northern Europe and, more recently, to the rest of the world. Free-living herds have been established in North and South America, South Africa, New Zealand, and Australia. Fallow deer were introduced on small and medium-sized islands in different parts of the world. Many fallow deer are also maintained in captivity for exhibition, commercial production of meat and antler velvet, or hunting. The distribution of the common fallow deer is, therefore, a direct consequence of human activity, to the point that it can provide information on past patterns of human migration and trade (Masseti 1996, 2002; Sykes et al. 2011).

The common fallow deer are also one of the most widespread introduced mammals in Europe (as it has been established in over 10 countries; Genovesi et al. 2009). At present it is difficult to define in detail the distribution of the species because of many introductions and re-introductions over the course of centuries. Distributional data which has been published in some European countries are poor, especially for free-ranging populations, often referring to different spatial and temporal scales and sometimes conflicting. Hence the distribution map of the species reported in Fig. 2 can be affected by the heterogeneity of the data sources.

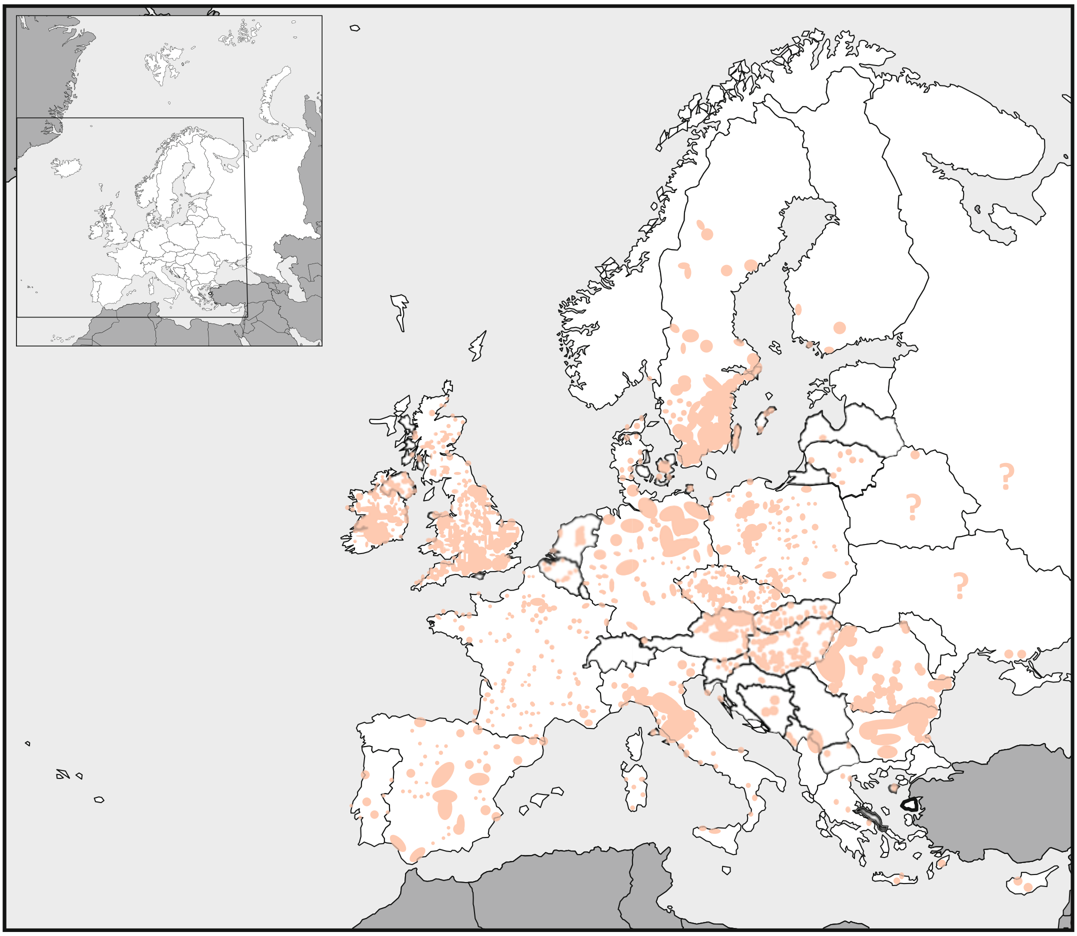
The only geographical area where common fallow deer have persisted as a native form is southern Anatolia (Masseti 2002; Masseti et al. 2008). Here its historical range extended from the Marmara region through the coastal mountains to the southeast till the first half of the twentieth century (Borovali 1986; Danford and Alston 1880). This range has drastically decreased during the second half of the last century, when the species was reported only from Antalya and Adana provinces (see Durmuş 2019). Illegal hunting and environmental changes caused by human activities and increasing urbanization have led to the progressive disappearance of the fallow deer from Anatolia. Today a small number of deer have survived in a single site in Düzlerçamı Wildlife Development Area (Antalya province).

Description

Size and Morphology

The common fallow deer is a medium-sized deer. Adult males can reach more than 100 kg while adult females more than 50 kg. As the mass ratio of males to females is between 1.7 and 2.4 (McElligott et al. 2001), this deer is probably the most sexually dimorphic cervid (see Table 1).

Body mass varies throughout the year in relation to reproductive activity. Male body mass changes dramatically during the rutting period, decreasing by 15–30% (Berlioz et al. 2017). In females, body mass changes during gestation and lactation are related to higher energy requirements which in female ungulates are *c.* 40% during late gestation and 150% during peak lactation, compared to maintenance (Loudon 1985). Body mass



Map template: © Getty Images/iStockphoto

Fig. 2 Distribution map of the common fallow deer in Europe based on the IUCN Red List of Threatened Species. Version 2021–2 modified according to Chapman NG and Chapman DI 1980, Chapman DI and Chapman NG 1997, Masseti 1999, 2012, Apollonio 1999, Long 2003, Apollonio et al. 2010, Ilie and Enescu 2018, and data available from https://species.biodiversityireland.ie/profile.php?taxonId=119294&taxonDesignationGroupId=25, https://www.bds.org.uk/index.php/research/deer-distribution-survey; https://ias.biodiversity.be/species/show/25, https://globalspecies.org/ntaxa/901536#cite_1, https://www.gbif.org/species/5220136 ? = Country with data deficiency (Map template: © Copyright Getty Images/iStockphoto)

Table 1 Body and skull measurements of adult males and females of the common fallow deer

Measurement	Females				Males			
	n	Mean	Min	Max	*n*	Mean	Min	Max
HBL (cm)	9	141	114	167	11	159	138	177
SH (cm)	8	81	67	95	11	94	87	101
CBL (mm)	46	247	231	267	47	263	241	283
ZW (mm)	54	109	102	118	69	127	115	140
ML (mm)	49	191	175	203	68	200	185	216

Data from Ueckermann and Hansen (1994) for body measurements of free-ranging deer (8–10 years old) from Germany, and Feldhamer et al. (1988) for skull measurements of free-ranging and park deer (2 years old and over) from England and Scotland

n sample size, *mean* mean value, *min* minimum value, *max* maximum value, *HBL* head-body length, *SH* shoulder height, *CBL* condylobasal length, *ZW* zygomatic width, *ML* mandible length varies also from year to year depending on food availability, local density, habitat, presence of other ungulates, and management strategies, especially in park deer (Putman and Langbein 2003). Interpopulation variation can be very marked, considering that the species was introduced throughout the world. Insular populations show a reduction in size in comparison to their mainland source population; body size shifts are more pronounced for populations with longer residence times on the islands (van der Geer et al. 2018).

Pelage

The common fallow deer have the most variable pelage coloration of any deer species because of a long history of semi-domestication. Four main color variants (common, black, white, and menil; Fig. 3) and many intermediate color variants have been described (Chapman and Chapman 1997).

The common color variant has a rich yellow-brown summer coat with many white spots on the back and flanks, and a dull gray-brown winter coat with spots indistinct or absent. Through the year, a black dorsal stripe extends from the nape to the tip of the tail; the lower flanks and the belly are whitish; the rump patch is white bordered by a black curved line and the tail is white with a central black stripe. The menil variant is paler, retains spots in winter, and lacks the black border on the rump patch and the black on the tail, the upper surface of which is light reddish-brown. The black variant is usually slightly dappled, especially in summer, and has no white at all. True albinos with pink eyes and pink nostrils are very rare, while individuals with white or off-white coats are common. The velvet color

Fig. 3 Color variants of pelage in the common fallow deer: common (upper left), black (upper right), white (bottom left), menil (bottom right, file n. 505984862, www.istock.com, all other photographs by A. M. De Marinis)

tends to match the pelage. Coat colors are alike in both sexes. The fawn coat is similar to the summer coat of the adults except for fawns of white fallow deer which are sandy colored without any spotting at birth and become white in a period of one to several years (Chapman and Chapman 1997). Selection for or against color variants is often practiced in parks (Chapman and Chapman 1997). All the color variants can interbreed, and the offspring are sometimes different from either parent. Spots are dominant over no spots, and white coat color is controlled by a recessive allele. However, the genetics of coat color in fallow deer remains a wide and complex field of research.

A rare variation concerning the hair length was observed in Mortimer Forest (Shropshire, England) where both sexes have unusually long and curly hairs that are the expression of a dominant, autosomal gene. No similar polymorphism in hair length has been reported in any other species of deer (Chapman and Putman 1991).

Males have a prominent brush of hairs from the penis sheath visible from *c.* 3 months while females have a tuft of long hairs (*c.* 12 cm) below the vulva (Chapman and Putman 1991).

The dorsal guard hairs are shielded. A dichotomous key based on macroscopic and microscopic features of the dorsal guard hairs (De Marinis and Asprea 2006) allows the identification of the species and the age class (young prior to the first molt and adults). These data can be used in feeding ecology studies of large predators.

Molt takes place twice a year in spring (April–June) and in autumn (late September–November). The molt period varies in relation to body condition, sex, age, and population, while the sequence of molt changes in relation to the individual (Chapman and Chapman 1997). The fawn coat is retained until the first winter coat develops. Small birds as finches can collect tufts of hair as nesting material (Chapman and Chapman 1997).

The summer coat of Mesopotamian fallow deer has spots blending together to form a continuous line along each side of the brown dorsal stripe, and a white rump patch not completely bordered by a dark curved line with a white tail. It is difficult to find substantial differences in the coats of the common and Mesopotamian fallow deer because of the extremely wide range of the pelage colors of the common fallow deer (Chapman and Chapman 1997).

Skull

The fallow deer skull, as that of other cervids, shows numerous adaptations to support an herbivorous diet, such as a long rostrum providing solid anchorage for masseter muscles, a thin and long mandible, and a dentition able to grind herbaceous as well as woody materials. This species has a slender skull whose width is usually less than one half of the length (see Shackleton 1999). Nasal bones are considerably longer than the upper teethrow with anterior ends showing deep notches and posterior ends reaching and even surpassing the line of the forward edges of the orbita; size and shape of nasal bones are species-specific in cervids. The premaxillary bones articulate with the nasals, as observed only in some deer species. Rostral fenestrae are large and distinctive as in cervids generally. Orbits protrude to either side of the skull and are larger than in *Cervus*. Zygomatic arches protrude less than the orbits, as in other cervids. The braincase is large, rounded, and convex with developed occipital crests. The palate is somewhat wider than the length of the row of the upper molars and equal in females and males. Posterior nares are not divided by the vomer. Pterygoid processes are weakly bent forward and the hooks of the pterygoid bone lie behind the posterior processes of the superior jaw. The auditory bullae are small, inflated, and rounded with short auditory tubes. The foramen magnum has stout occipital condyles. The mandible is long and slender with a high and recurved coronoid process, a small condyle well above the tooth rows, and a large and rounded angular process not projecting behind the condyle. Most of the cranial measurements of adult males exceed those of females by 4–14% (Feldhamer et al. 1988), as reported in Table 1.

Skulls of the common and Mesopotamian fallow deer show some minor differences: the Mesopotamian fallow deer have different sutures between zygomatic and maxilla bones, nasal bones with blunt and much broader anterior ends and a more strongly convex lateral profile (Harrison 1968).

Antlers

As in all cervids, antlers develop from permanent outgrowths of frontal bones called pedicles. When fully grown, fallow deer antlers show a broad flattened “palm” and have only two frontal tines, the well-developed brow tine, just above the coronet, and the small trez tine, just below the palm; the upper and rear edges of the palm end in a series of points or spellers, directed posteriorly, with the longest at the bottom of the palm (Chapman and Chapman 1997). Antlers of the Mesopotamian fallow deer differ distinctly from those of the common fallow deer, being flattened in their basal part, immediately above the short brow tine, and not at all or only slightly palmated in their distal part (Harrison 1968).

Antler size, mass, and complexity are very variable, depending on age, body condition, habitat quality, and genotype and seem to be negatively associated to the degree of teeth wear (De Marinis 2015). The maximum average antler size occurs before 10 years of age (Chapman and Chapman 1997).

The growing antlers are covered with velvet, a specialized skin transformed from pedicle integument, most likely due to a mix of chemical and mechanical induction (e.g., Li 2013). Velvet is thickened in comparison to pedicle epidermis, contains hair follicles without arrector pili muscles, and is connected to extremely large sebaceous glands, but lacks sweat glands. Velvet is richly supplied with arteries and veins and, hence, is the main nutritional source for antler formation.

The antler cycle is closely associated with the photoperiodic regulation of the reproductive activity. Antlers grow during the late spring and early summer, they mineralize before the rut and are cast thereafter. A cascade of events involving several hormones such as melatonin, prolactin, luteinizing hormone, and testosterone mediates the primary effect of the photoperiod. Histogenesis and ossification of antlers were described by Kierdorf H. et al. (1995) and Kierdorf U. et al. (2003), and the mechanism of casting by Goss et al. (1992). In Mediterranean habitats, that are the native environments of the species, velvet shedding occurs in mid-August while antler casting occurs between mid-March and mid-April, with older bucks losing antlers 2 or 3 weeks earlier than younger ones (Ciuti and Apollonio 2011).

Pedicles usually start to develop from 5 to 7 months. First antlers vary from small knobs to spikes and are clean of velvet by about 15 months of age. Some second and third sets of antlers have porous tips because the velvet is shed before mineralization of the antler is complete. Antler growth is faster during the velvet period in territorial males (about 10 g/day per antler) than in non-territorial males (3.6–5.2 g/day per antler), likely because the first adopt better foraging strategies (Ciuti and Apollonio 2011). When the antlers are growing, the diet of males should be richer both in species diversity and nutritive value with increased protein content due to a higher energy requirement (Robbins 2013). Males can be grouped in age classes in relation to antler development. In Mediterranean habitats males show spike antlers when younger than 23 months, branched antlers between 29 and 34 months of age, and palmate antlers when older than 41 months (De Marinis 2015).

Antlers, as other secondary sexual characters, should reflect the condition of their possessors; in particular the symmetrical development of antlers should signal male quality. Fluctuating asymmetry (random difference in size observed between bilateral structures, FA) should reflect the individual capacity to cope with stressful situations (Palmer and Strobeck 1986). Therefore, FA could be used as a measure of ecological stress and give useful information on individual quality. It is this visual asymmetry that would be assessed by potential mates and rivals. Antlers are hypothesized to demonstrate decreasing levels of FA with increasing trait size and decreasing level of FA with increasing age. The studies of FA patterns in fallow deer reported conflicting results: some studies have found a relationship between asymmetry and measures of individual quality while others have not (e.g., Ciuti and Apollonio 2011; Putman et al. 2000). However, the studies of FA pattern in fallow deer, carried out mainly in enclosed populations, could probably be biased by the small sample size and the use of linear measurements to quantify asymmetry of complex structures like antlers. On the contrary, directional asymmetry, DA, which occurs when the character on one side is larger than on the other, is not considered a signal of developmental instability and hence of individual quality (Palmer 1996). In fallow deer DA toward the right side has been reported in several antler measurements (Alvarez 1995; Pélabon and Joly 2000).

Abnormal antlers in size and shape occur due to genetic or physiologic causes or injuries to pedicles, growing antlers, contralateral hind limb, or same-side front limb (Chapman and Chapman 1997). Double-head antlers have been observed in the common fallow deer as in other deer species; this malformation is the result of a new antler growth without the previous casting of the old antler; the double-head's second antler generation develops as a periosteal exostosis of the distal pedicle bone (Kierdorf U. et al. 1994). Antlerless or perruque heads (i.e., with antlers that continue to grow year after year without casting) are rare (Chapman and Chapman 1997).

Dentition

Fallow deer dentition is 0.0.3.0/3.1.3.0 for deciduous teeth and 0.0.3.3/3.1.3.3 for permanent teeth. Incisors and incisiform canines are spatulate; the first permanent incisor is twice as wide as others. There is a thick pad of fibrous connective tissue instead of upper incisors. Several dental eruption sequences were recorded (see De Marinis 2015, Bowen et al. 2016) according to the different criteria adopted to describe the eruption pattern. Teeth wear rate changes in relation to sex, as shown by the variation of I_1 crown height with the age class (De Marinis 2015). Male tooth row length is not significantly different from that of female (Chapman and Chapman 1970) contrary to what one might expect considering that the fallow deer is a strongly dimorphic species. Males consume a higher amount of food compared to females, even of lesser quality, hence the male wear rate is higher. The relatively early depletion of male teeth could be associated to a sex-specific strategy of dentine depletion, as already observed in red deer (Carranza et al. 2008).

Morphological characters for the discrimination between red and fallow deer teeth from archaeological and paleontological remains were described on permanent dentition by Lister (1996).

Dental anomalies have been found very occasionally, except in the population of Richmond Park (England), where the following incidence values were recorded for congenital dental anomalies: absence of one or two lower incisiform teeth in 19% of fawns and 18% of adults and presence of one or two upper canines in 25% of fawns (Chapman and Chapman 1997).

Age Determination

A protocol for estimating the age till 8 years was developed recording the epiphyseal sutural states in known-age deer of an enclosed population (Carden and Hayden 2006). Skeletal development in terms of epiphyseal fusion can be delayed by malnutrition, diseases, and trauma.

The chronology of mandibular tooth eruption varies in relation to the population due to environmental and genetic factors as well as material and methods adopted to study the eruption process. The following data identify the eruption times in months of each mandibular tooth according to several authors (see De Marinis 2015): 4–7 (M_1), 7–12 (I_1), 13–20 (M_2, I_2), 15–20 (I_3, C), 18–28 (M_3, P_4, P_3), 20–30 (P_2).

Scoring schemes were developed from known-age specimens coming from park deer population. A first scheme, based on radiographs of developing permanent molariform teeth, allows age estimation up to 3 years (Brown and Chapman 1990). A second scheme, based on eruption and wear stage of the fourth premolar and molars, should allow age estimation up to 10 years, but there is considerable overlap among wear stages at the upper end of the age spectrum (Bowen et al. 2016). Photographic reference systems and dichotomous keys were developed separately for males and females from known-age specimens coming from a Mediterranean free-ranging population. Taking into account that teeth wear rate depend on sex and habitat, these systems and keys can be used to age estimation of males and females living only in Mediterranean habitats (De Marinis 2015).

Glands

Fallow deer have several scent glands (areas of specialized skin rich in secretory cells) which play an important role in communication among members of the species. Males have preputial glands associated with the penis sheath. They consist of modified sebaceous glands. In fallow deer these glands are associated to sweat glands, unlike in other deer (Odend'hal et al. 1996). The preputial glands become active during the rut, and their secretion is responsible of the strong rutty smell of the urine during this period. Urine scattering, attained by a series of vigorous side-to-side penile movements, is used by fallow deer bucks for habitat and self-marking. Urine odor provides specific information about reproductive state, physical condition, and energy level that is important for both sexes to assess the social and physical status of bucks (Apollonio and Di Vittorio 2004). The pungent smell is believed to help synchronize female estrus (Chapman et al. 1981). Morphological changes in the preputial gland of immature fallow deer start at about 9–12 months of age (hypertrophy of the epidermis of the transition zone, together with some keratosis) and then recommences at about 15 months (hyperkeratosis). Eversion of the transition zone, which is a rutting characteristic of the adult, occurs for the first time when the deer are about 17 months old (Chapman et al. 1981). Accessory glands of reproduction were described by Chapman and Chapman (1979) in male fallow deer; these glands undergo an annual cycle of growth and regression, reaching their maximum development at the time of the rut.

Both sexes have suborbital, rear interdigital, and metatarsal glands. The suborbital glands are situated just below the corner of each eye and consist of pockets of skin, which fit into depressions of the skull (lacrimal fossae) next to the eye sockets. Lawson et al. (2000) highlighted the total lack of detectable volatiles in suborbital gland secretions between November and March, unlike what has been observed in other cervids. Considering that the presence of particular volatiles has been related to the possibility to carry information about individual identity, suborbital gland secretions of fallow deer do not seem to be individually characteristic outside the reproductive period. Rear interdigital glands are situated in pockets of skin between the two cleaves of the hoof. They start their activity within 2–3 weeks of birth and remain active throughout life. The glucidic content of their secretions does not change in relation to sex and age, suggesting that the interdigital glands may play only an accessory role in the production of odoriferous signals in fallow deer (Parillo and Diverio 2009). The metatarsal glands are located on the hock. Changes in their activity are documented in rut and post-rut periods only in adult males (Apollonio and Vailati 1996). Fallow deer have more complex gas chromatographic profiles of volatiles in metatarsal secretions than in suborbital secretions (Lawson et al. 2000). Only metatarsal gland secretions contain coded information about the individual identity of the signaler, and this information remains consistent over time, as shown in individuals sampled in successive years (Lawson et al. 2000). The scent profile of metatarsal gland secretions of cervids seems to change as a function of habitat type and sociality. Species habitually associated with open habitats and living in social groups, like fallow deer, show more complex scent profiles in metatarsal than in suborbital secretions (Lawson et al. 2000).

Physiology

Fallow deer can live in many different habitats showing great adaptability; for this reason, this species does not have any particular physiological adaptation to a specific environment. Body temperature depends on health, season, and activity patterns. The average tympanic temperature is 38.6 ± 0.7 °C, range 37.4–40.8 °C and the average rectal temperature is 40.1 ± 0.8 °C, range 37.5–42.0 °C (Drew 1998). Tympanic temperature seems to be superior to rectal temperature as an indicator of normothermia in fallow deer and may be a better method to assess the individual health status during capture and handling (Drew 1998). Heart and respiratory rates are 24–52 beats/min and 6–28 breaths/min, respectively (Galka et al. 1999).

Different values of blood parameters were recorded in relation to sex and age, as well as genetic, environmental, nutritional, and physiological factors (e.g., Poljičak-Milas et al. 2009). Management practices, capture methods, and blood sampling techniques also result in differences in blood parameters values (e.g., Vengušt et al. 2006): for example, variations in leucocyte count and serum proteins were recorded in relation to transport stress (English and Lepherd 1981). The relative proportions of fetal and adult hemoglobins were recorded in fawns captured during their first week of life in a free-living population of fallow deer in Coto Doñana National Park, southwestern Spain (Schreiber et al. 1992). The percentage of adult hemoglobin at birth seems to be correlated with the survival rate of the fawns. The exact age when the transition to adult hemoglobin is completed remains unresolved. The relative amount of persisting fetal hemoglobin is an indicator of the age of fawns. Blood coagulation parameters were reported by Siroka et al. (2011). A significant difference was found in the average activated partial thromboplastin time between males and females. It may be hypothesized that the differences in clotting times represent a physiological advantage for females to deal with delivery-associated bleeding but a physiological disadvantage for males to deal with injuries (e.g., due to fighting in the rut period).

The male and female reproductive cycle depends on seasonal variation in day length through the hypothalamus and pituitary control. The importance of light in determining the breeding season is confirmed by the fact that in the southern hemisphere fallow deer mate 6 months later than in the northern hemisphere. The male reproductive cycle is characterized by a variation in testes mass. The first stages of spermatogenesis occur at about 7 months of age, while the appearance of spermatozoa is only at about 14–16 months when the testes and epididymes are ten times larger than those of fawns (Chapman and Chapman 1997). Adult deer appear to be in breeding condition over a period of about 6 months with a peak in spermatogenic activity in October/November and are fertile as late as February or March (Chapman and Chapman 1997). There is no apparent age effect on the seasonality of testes and epididymes size fluctuations (Gosch and Fischer 1989). These cyclical changes are positively associated with changes in body mass (Chapman and Chapman 1997). Velvet shedding and antler casting occurred at about 80% and 25%, respectively, of maximal testis volume (Gosch and Fischer 1989). The male sexual activity is dependent not only on spermatogenesis but also on seasonal changes in hormone secretion. Testosterone induces rutting activity, but it is of short duration compared with the length of spermatogenic activity. Thus, high testosterone levels are not essential for fertilization to occur.

The ovaries of fawns are inactive and small and increase in size gradually until the females reach puberty that is at about 16 months of age. The length of the estrus cycle is 20–27 days. The highest percentage of fertilization occurs generally during October in the northern hemisphere, although females are receptive between September and January. Females are polyestrous and, in the absence of pregnancy, may cycle up to six times (Asher 2007). Most of females conceive during their first cycle. The absence of mature, high ranking, older bucks, or even the larger representation of younger bucks can prolong the fertile period of females (Komers et al. 1999). The reproductive state of females is assessed by males through the behavior known as *flehmen*. Multiple successive silent ovulations and short-lived (8–10 days) *corpora lutea* leading up to the start of the breeding season have been observed.

The transient nature of the preliminary *corpora lutea* may serve to promote within-herd synchrony of the first estrus of the season (Asher 2007).

The mammary glands undergo an annual cycle of growth and regression. The mass of these glands at the time of parturition is about 400 to 800 g (Chapman and Chapman 1997). Lactogenesis is strongly influenced by prevailing photoperiod during the last few months of pregnancy (Asher 2007). The energy requirements of lactation exceed those of pregnancy (Loudon 1985). The chemical composition of milk (Malacarne et al. 2015, Wang et al. 2017) changes over the lactation period, as found in other ruminants, and may also change among populations living in different habitats and having different diets.

Genetics

Chromosomes

The diploid number of chromosomes in *Dama dama* is $2n = 68$, and the number of chromosomal arms is $FN = 70$ (Rubini et al. 1990 and reference therein).

The karyotype of the fallow deer was described by studying various captive or introduced populations (Arslan and Zima 2014 and reference therein). It includes 32 acrocentric autosomal pairs of diminishing size and one medium-sized metacentric autosomal pair. The sex chromosomes are acrocentric (X) and metacentric (Y); X is the largest chromosome and Y is one of the smallest. There are significant amounts of heterochromatin at all autosomal centromeres as well as at X-chromosome, while the metacentric autosome pair shows only slight C-bands and the whole Y chromosome is relatively heterochromatic. The C-banding pattern is apparently rather uniform in the Cervidae family (Arslan and Zima 2014 and reference therein).

The results of the karyotype comparison between red and fallow deer are surprising because their karyotypes differ much less than those of red and sika deer, two easily interbreeding species (e.g., Herzog 1990). This means that the reproductive barrier between red and fallow deer may not primarily be caused by karyological incompatibility but by other physiological (e.g., immunological) or behavioral factors.

The localization of the nucleolus organizer regions (NOR) at the telomeric position in the two largest acrocentric autosomes was described by Mayr et al. (1987). A similar number and distribution of the NORs were reported in other deer species.

Fontana and Rubini (1990) discussed the chromosomal evolution of the Cervidae, pointing out that Robertsonian fusions took part in the karyotypic differentiation of Cervinae.

Phylogeny and Phylogeography

Baker et al. (2017) studied the relative influence of natural as well as anthropogenic processes in shaping the evolution of genetic diversity among European populations using microsatellite and mitochondrial DNA loci. The results confirmed very low levels of diversity within regional populations and revealed a high degree of differentiation among them. These data are consistent with populations being founded by low numbers of individuals and affected by strong genetic drift. The northern and central populations could descend from animals captured in Anatolia and translocated in Europe, while the southern populations could descend from animals forced into Italian, Iberian, and Anatolian peninsulas during the last glacial period. However, the origin of the Iberian lineage and the identification of refugia remain open questions. Marchesini et al. (2021) criticized the methodological approach adopted by Baker et al. (2017) with particular reference to sampling scheme, mitochondrial DNA, and microsatellite dataset, and contested that the genetic “signature reflecting postglacial refugia can still be detected” in the extant populations. By means of a reanalysis of the data, they concluded that the genetic expectations of the glacial refugia hypothesis cannot be found in current fallow deer populations which derive from extensive human-mediated translocations. Baker et al. (2021) revisited the study published in 2017, taking into account the comments by Marchesini et al. (2021). Some further analyses reinforced the original conclusions of the earlier paper: the low levels of diversity within populations and the strong structure among populations due to a combination of natural and anthropogenic processes, and the conservation implications of these data.

Genetic Diversity and Population Structure

Despite the wide distribution of the species and the availability of the samples, fallow deer genetic studies are very few. Initially, enzyme electrophoretic analyses revealed a very low level of genetic variation in British, German, and Italian populations (Hartl et al. 1986; Pemberton and Smith 1985; Randi and Apollonio 1988).

Subsequently, DNA variation analyses confirmed very low levels of diversity within populations and showed a high degree of differentiation among them (Ludwig et al. 2012; Masseti et al. 1997, 2008).

In particular, the analysis performed using the RAPD fingerprinting technique by Masseti et al. (1997) on two historical stocks that still survive in Central Italy showed that a fairly high percentage of the variability is due to differences between populations (75.54%). The Castelporziano stock revealed a higher level of genetic variability in contrast to San Rossore stock. The higher rate of within population genetic variability of the Castelporziano stock may be the result of multiple introductions even in very recent historical times. San Rossore stock generated populations with a low level of genetic variation (e.g., Maremma Regional Park, Central Italy; Scandura et al. 1998).

Moreover, Masseti et al. (2008) analyzing mitochondrial DNA sequences revealed that the Rhodian fallow deer population, founded by humans in Neolithic times, possesses a set of mitochondrial lineages, never found in any other population. Two highly distinct groups of haplotypes can be identified with a divergence time of at least 31 kya. The presence of these haplotypes could be due to translocation from Anatolia to Rhodes of two groups, already well differentiated in the mainland. Rhodian fallow deer are distinct even from the extant deer surviving in Düzlerçamı. The persistence of these haplotypes is particularly significant because human-mediated processes (e.g., domestication) usually result in genetic depletion and erosion of an ancestral genetic pool. Masseti et al. (2008) hypothesized that humans unknowingly preserved a remarkable portion of the original genetic diversity of the source population in the Rhodian fallow deer.

Hybridization

In captivity, the common fallow deer hybridized with the Mesopotamian fallow deer and produced fertile offspring (Zuckerman 1952; Gray 1972).

Hybridization between two different genera of deer is rare. In captivity, the hybridization between the common fallow deer and *Axis porcinus* has been recorded, but it is unknown if the offspring was fertile or how long it survived.

Life History

Growth

As in other cervids, maternal condition plays a determining role in prenatal growth (Pélabon 1997). Fetal body mass is linearly and negatively related to maternal kidney-fat-index and body mass during pregnancy (Ács and Lanszki 2017). Prenatal growth is faster for males (Birgersson and Ekvall 1997). Thus, male fawns appear to have higher body mass at birth than females (4.7 kg vs. 4.3 kg, Putman and Langbein 2003). However, the literature data on body mass by sex are quite different. Significant birth mass differences were recorded between fawns born to yearlings, around 3.5 kg, and those born to adult females, around 4.5 kg (Putman and Langbein 2003). Males grow faster than females, but male fawns of primiparous mothers have a slower growth rate than male fawns of multiparous mothers, whereas no such difference exists for female fawns (Birgersson and Ekvall 1997). According to Braza et al. (2000), male-biased maternal investment exists in fallow deer and it is affected by the environmental conditions such as the earliness of autumn rainfall, and the level of extra-investment made by mother in male fawns during the previous breeding season.

Average birth mass was revealed greater in the middle of the fawning period in a free-ranging population (Ács and Lanszki 2017), but it turned out greater at the beginning of this period in a fenced population (Birgersson and Ekvall 1997). According to Putman and Langbein (2003), the mass of fawns that were born in the first week of June were significantly greater at the beginning of winter than those that were born later. Moreover, pre-winter body mass was constantly greater and more strongly correlated to subadult body mass in males than in females and was positively related to maternal body mass (Birgersson and Ekvall 1997). Fallow deer seem to quadruple their birth mass by 3 to 4 months. Females attain the maximum body mass when about 3 years old while males continue to increase in mass, not reaching their maximum until at least 6 years old; the greatest body length (from head to rump) is not reached until 7–8 years in both sexes, and the shoulder height shows a similar growth pattern (Chapman and Chapman 1997). Mandibles are fully grown by about 2.5–3 years in females and 5 years in males (Langbein 1991).

Reproduction

Puberty occurs in males between about 7 and 14–16 months. Although yearlings are physiologically capable of breeding, males generally do not breed until they are about 4 years old, except in heavily hunted populations (McElligott et al. 2001). The complex social structure of the herds appears to preclude matings until a male reaches social maturity when it can actively compete for reproductive opportunities. Fallow bucks usually get most of the matings between 5 and 8 years of age (Farrell et al. 2011), when males are considered prime-aged (McElligott et al. 2003). Unlike males, females reproduce for the first time when they reach puberty (at around 16 months of age). To date, reproduction in females has been reported until 23 years of age (Farrell et al. 2011).

The gestation period is 225–237 days long; there is no embryonic diapause (Harrison and Hyett 1954). The development goes slowly until the embryo establishes a placental circulation (between 3 and 4 weeks of age). The common fallow deer give birth to a single fawn, twins occur in <1% of births, and, even if a doe carries twins, there is no guarantee that both will survive to term (Chapman and Chapman 1997). The neonatal sex ratio is 1:1 (Asher and Adam 1985). The sex ratio of adults depends on several factors, including the management regime.

In deer park populations yearling does have a fecundity consistently lower than that of adults, mate and give birth later, and produce fawns lighter at birth (Putman and Langbein 2003). The mean winter live body mass at which 50% of yearling does give birth to fawns was estimated at 32 kg (Putman and Langbein 2003). The average fawning rate varies a lot in yearlings (from 12 to more than 90%) and less in adult females (>80%). The pattern of rearing success reflects that of fawning success with yearlings achieving lower rates than adults (Putman and Langbein 2003). The rearing ability of old females declines with age due to a loss in grazing efficiency causing insufficient milk production.

The effects of age and body condition on female reproductive success have been studied in several fallow deer park populations (Putman and Langbein 2003). In general, the reproductive success is consistently lower in parks that have extensive public access and where are present mixed herds with red deer. A higher level of postnatal mortality could probably explain this low reproductive success. Disturbed does may leave neonates immediately after parturition before they have a chance to establish the mother-infant bond.

Survival

Prenatal mortality is around 10% (Chapman and Chapman 1997). The highest mortality is recorded among neonates. Kjellander et al. (2012) found a death rate of 23.6% without significant differences between sexes in a free-ranging population of southern Sweden. The survival probability of adult females is relatively high until old age. Survival probabilities of males resulted highly variable with age, and have been described in a park deer population using a model incorporating four phases: yearling, pre-reproductive, prime-age, and senescent (McElligott et al. 2002). Yearlings had a survival rate of 70–75%. Pre-reproductive males (2–3 years old) had the highest survival rate (85%) compared to all other males. Prime-aged males (4–9 years old) had a slightly lower rate (between 70 and 80%) due to the intense intrasexual competition, and this rate remained stable up to 9 years of age. Considering reproducing and non-reproducing males separately, there were differences in the survival probabilities, with reproducers consistently surviving better than non-reproducers. The higher survival probabilities of reproducing males could indicate their generally higher phenotypic quality. Survival probabilities declined sharply after 9 years of age. The decrease also in reproduction probabilities, body condition, and antler size indicates that senescence had begun (McElligott et al. 2002).

The lifespan recorded in the fenced populations of Castelporziano estate (Rome, Italy) and Phoenix Park (Dublin, Ireland) is respectively 11.5–13 years for males and 19–23 years for females (see De Marinis 2015). The lifespan in captivity is over 20 years.

Natural mortality is mainly determined by climatic conditions. Severe drought and heavy snowfall can induce abrupt variations in population density; high rainfall can affect the fawn survival in summer when they are more easily chilled and risk hypothermia (Putman et al. 1996). Overwinter losses represent a considerable proportion of the annual mortality among wild populations (Putman and Langbein 2003). Length of the growing season of the previous year, days of snow, late winter temperature, and mean body mass in autumn are significantly correlated with winter losses in park deer populations (Putman and Langbein 2003). A threshold dressed body mass in autumn of 24 kg for adult females and yearling males is suggested as critical for overwinter survival (Putman and Langbein 2003). Mortality due to carnivore predation is low. The vigilance behavior and herding help to protect deer from predation. The contribution of fallow deer (mainly fawns and youngs) is less than 5% to the diet of Iberian lynx *Lynx pardinus* (Coto Doñana National Park, southwestern Spain, Delibes 1980) and less than 3% to that of wolf *Canis lupus* (the Apennines, central Italy, Mattioli et al. 2011; central and western Poland, Nowak et al. 2011). Foxes *Vulpes vulpes* may sometimes predate neonates; eagle *Aquila* sp. and golden jackal *Canis aureus* should be mentioned as other potential predators of fawns. During an experimental evaluation of predator avoidance in Sweden, fallow deer completely avoided areas with bear scent (Sahlen et al. 2016). Hunting, poaching, and to a lesser extent road accidents are other causes of mortality. Few individuals may die for injuries from conspecific during the rut or other accidents (e.g., entanglement of antlers in fences); chases by free-ranging and feral dogs may cause injuries and deaths (Langbein and Putman 1992), especially in those countries where these potential predators can reach high numbers.

Habitat and Diet

Habitat Use

Fallow deer live in a variety of climates ranging from cool-humid to hot-dry areas. However, most populations are found in a hot-humid climate. The most suitable habitats are plains and slightly rugged or hilly areas with a combination of vegetation types. Fallow deer prefer deciduous or mixed mature woodland with established understory, interspersed with grassy and brushy open areas, but can live in a wide variety of environments from Mediterranean forests to conifer plantations (Feldhamer et al. 1988). Fallow deer do not commonly live in high-altitude areas or regions with long snowy winters. Populations are currently expanding into areas composed of a mosaic of housing, gardens, orchards, parks, farmland, and pastures. Deer may be attracted to human environments because of the lack of predators and hunting threats as well as the availability of edge habitats where find food supply and tree cover. In such habitats, human activity may greatly affect the distribution, dynamics, and behavior of deer (Duarte et al. 2016). Habitat use changes seasonally with food availability (deer can feed mainly in open areas during spring and summer and in woods during autumn and winter, Thirgood 1995), differs between daytime and nighttime (woodland are used more by day while open areas more at night, Borkowski and Pudelko 2007), and varies strongly according to sex and age classes (Apollonio et al. 2005).

Sexual segregation is widespread among sexually dimorphic ruminants. Several hypotheses have been formulated to explain this phenomenon. Recent studies have provided evidence that only more hypotheses simultaneously may explain sexual segregation because they account for factors operating at different spatial and temporal scales. Ciuti and Apollonio (2008) analyzed a long-term dataset using a multitemporal (among years and between night and day) and multispatial (among and within habitats) approach to investigate sexual segregation in a fenced population of fallow deer. The predation risk hypothesis (females select safer areas to reduce predation risk even at the expense of nutrient intake) and the indirect competition hypothesis (males are forced into suboptimal foraging habitats through indirect competition by females) can explain segregation on large spatial and temporal scales. The forage selection hypothesis (differences in foraging efficiency and hence food selection between sexes) provides a general explanation of small scale sex differences in habitat use. The predation risk hypothesis and the indirect competition hypothesis give a valid interpretation of the sexual segregation on small temporal and large spatial scales and large temporal and small spatial scales, respectively. The influence of human activities could be a strong drive to sexual segregation, forcing the more vulnerable or sensitive sex into suboptimal habitats. This, in turn, may lead to a not natural browsing pressure on environments, causing habitat deterioration (Apollonio et al. 2005). Contrasting results were found in parks subjected to high public visitor pressure, where human disturbance increased levels of vigilance mainly in females, without changing patterns of habitat use and overall daily time budgets (Langbein and Putman 1992).

Home Range

Fallow deer do not establish territories except males during the rut. Home range size can vary a lot among populations and within the same population among seasons in relation to the availability and distribution of food and shelter, climatic factors, density of animals, and degree of disturbance. Home ranges can overlap extensively. In general, males have home ranges larger than females due to higher energy demands. Female home ranges are usually smaller during summer (e.g., Ciuti et al. 2003) because their movement patterns are restricted by the presence of fawns (Ciuti et al. 2006). As in other cervids, mothers seldom move further than 400 m away from their fawns in the first 2–3 months following parturition (Kjellander et al. 2012). Males have usually larger home ranges during the rutting period (e.g., Davini et al. 2004) due to the movements between breeding and non-breeding grounds. As in other deer, inter-seasonal home range fidelity proved to be remarkably high (Ciuti et al. 2003; Davini et al. 2004).

In Mediterranean habitats, that are the native environments of the species, the mean size of annual home range resulted larger (some hundreds of hectares, e.g., Ciuti et al. 2003, Davini et al. 2004) than those reported in northern Europe (some tens of hectares, e.g., Chapman and Chapman 1997, Putman 1996), mainly because these Mediterranean environments are characterized by a fragmented distribution of trophic resources.

Spatial Movements

The common fallow deer seem to be one of the least dispersive deer species. Large-scale one-directional movements that could be classed as dispersal are unusual. Most dispersal movements tend to be of juvenile males leaving family groups, before the birth of the next fawn. For this reason, the proportion of males among juveniles killed in road accidents is very high. This species is tolerant of very high local densities and hence colonization of new areas is gradual.

This cervid is not noted for any migratory behavior. Erratic movement may occur up to 15 km or more and on these occasions, fallow deer can cross large rivers. Bucks are often responsible of wide movements during the rut and may visit more than one lek or rutting stands. Females move from their home ranges to lek and can travel also more than 8 km, as recorded in a Mediterranean habitat (Imperio et al. 2020). It seems to be a distance threshold over which females are no longer able to compensate travel costs; this distance should change with population, depending in a complex way on topography, vegetation type, physical barriers (roads, channels), presence of predators, hunting, and human disturbance.

Diet

Anatomical considerations based on the ratio of small to large intestines suggest that the common fallow deer is an unselective bulk-feeder (sensu Hofmann 1985). Field studies confirm that this deer is both browser and grazer. Fallow deer show morphological adaptations in the mouth, teeth, and salivary glands for processing and digesting the chemical compounds of the plant cell wall (Pérez-Barbería 2020). Herbaceous monocots contribute to more than 60% of forage intake from March to September, and more than 20% even in winter (e.g., Caldwell et al. 1983). The browsing of young broadleaved trees gives a significant contribution to the diet in autumn and winter. Acorns, chestnuts, beech mast, and other fruits are characteristic food through autumn and early winter. Increasing amounts of dwarf brushes, sedges, rushes, brambles, forbs, mosses, and conifer browse are mainly consumed in winter, if graze material is limited (e.g., Caldwell et al. 1983). The barking of trees occurs in winter; bark is stripped using incisiform teeth and dental pad (Chapman and Chapman 1997). Fallow deer appear to drink rarely, taking water from dew and vegetation.

The quality of the diet and the nutrient composition (protein, digestible fiber, and lignin) depend on food resources, change with the season, year, and habitat, and vary across age and gender classes. Bucks have a higher quality diet in autumn and winter whereas does have a higher quality diet in spring and summer (Putman et al. 1993). Sex-related differences in the diet can be explained because of different metabolic demands (Barboza and Bowyer 2000). In the rutting season, a low diet similarity was found between nonreproductive males and females despite the sex spatial overlap (Azorit et al. 2012).

Food choice is based on constant sampling and evaluation of the variety of food available as recorded in cafeteria (multiple-choice) experiments (Bergvall and Leimar 2005). Deer seem to be more selective when food types are limited in number, occur relatively close to each other, and are characterized by distinct tastes or other cues used for food selection. Therefore, fallow deer should be more or less selective based on the spatial distribution of food resources (Bergvall et al. 2007).

Behavior

Foraging Behavior

Fallow deer tend to lie up by day in cover, where they drowse and ruminate, and to move by night in open areas where they graze. The movements from forestry to foraging areas are usually along well-marked tracks. Peak feeding periods are generally at dusk and dawn. This activity pattern is influenced by many factors, such as cyclical changes in the environment, food availability, foraging efficiency, predation risk, mating activity, intraspecific and interspecific interactions, and last but not least human disturbance. In little disturbed areas fallow deer graze and ruminate in open areas at all hours, with a pattern of alternation between feeding and rumination roughly every 3–4 h (Caravaggi et al. 2018).

Foraging decisions are conditioned by the tradeoff between the benefits of gaining more food and the costs of reduced vigilance or increased toxin ingestion. This trade-off reflects personality dimensions such as boldness (Bergvall et al. 2011). Bold females will raise heavier fawns but these females, and their fawns, will be more prone to predation. On the opposite, shy females and their offspring will be less prone to predation, even though the fawns will be lighter and at greater risk of starvation. Different personality types coexist in a population. Selection pressures on boldness should depend on environmental variation and predator density (Bergvall et al. 2011).

For group-living animals as fallow deer, foraging decisions are probably taken at the hierarchical level: at the higher level the group chooses where to forage, at the lower level the individual chooses what to eat (Stutz et al. 2018), becoming less selective due to the competition for food especially in large groups (Bergvall et al. 2006). Group foraging may prioritize other critical needs such as the management of predation risk rather than foraging efficiency (Stutz et al. 2018). The protection against predators and foraging interference decreases from the center to the periphery of the group. The conflicting requirements among group members can determine the instability of large groups (Focardi and Pecchioli 2005).

Social Behavior

The common fallow deer present a very flexible social organization strongly influenced by environmental context and closely linked to the annual cycle.

Adult females spend most of their time in family groups mainly composed of five or fewer individuals with one or two adult females with their current and sometimes previous year’s offspring (e.g., Thirgood 1996). Males may remain in the family group up to 20 months of age. These groups are very stable in time and space and are generally led by a dominant doe (Apollonio et al. 1998). Female groups tend to be two to four times larger in more open habitats than in woodland and larger in winter/spring than in summer/autumn (e.g., Thirgood 1996). When living in heterogeneous environments, group sizes frequently change as animals move between closed and more open habitats, thus few permanent social associations develop. In more homogeneous environments, changes in group size are less apparent and more permanent groupings may persist, developing dominance hierarchies. The groups can reach the size of several hundred individuals where food resources are abundant, but such large aggregations are mostly transient. In general size of herds and social dynamics depend on habitat type/quality, deer density, food resources, degree of disturbance, time of year, and weather conditions. Males are solitary or form unstable groups with unrelated individuals (“bachelor groups”). Groups of adult males and females are separated for much of the year in most populations. The degree of social and spatial segregation shows great variability in relation to habitat, population density, and sex ratio (e.g., Thirgood 1996, Apollonio et al. 2005, Focardi and Pecchioli 2005). For example, where male density is high, bucks tend to remain in single-sexed groups; where it is lower, they tend to form mixed-sex groups; these groups have a high probability of splitting up into single-sex groups (Villerette et al. 2006).

Social interactions such as mutual grooming are relatively rare, except between does and their fawns. Play behavior, such as sudden chases and jumps, is common among young fawns in summer, and sometimes adult females join in.

Inter-male mounting is restricted to the first 3 months of antler regrowth (Holečková et al. 2000). It is typical for young animals and significantly decreases with age, suggesting that the animal needs the experience to cope with changing hormonal states or that the behavior is a form of learning. There is no evidence of bonding between individuals involved in mounting and no apparent dependence of mounting activity on testosterone levels. Inter-male mounting cannot be clearly linked to the roles of a dominant actor and a subordinate recipient. Female-female and female-male mounts are very rarely observed (Holečková et al. 2000).

Mating Behavior

The common fallow deer is a polygynous breeding species. The mating season occurs in October in the northern hemisphere and in April in the southern hemisphere (Chapman and Chapman 1997). The rut period changes with location and latitude as the photoperiod is the key stimulus controlling the deer reproductive processes by neurohormonal changes. The rut lasts approximately 135 days. The time of the mating season is influenced by several factors such as the sex ratio, population structure and density, spatial distribution of animals, and weather conditions (Sándor et al. 2014).

At the beginning of the mating season males start to scrape the ground, mark trees, thrash bushes, and groan. The buck vocalization may serve for threatening males and attracting females. McElligott et al. (1999) identified a strong correlation between the time invested in vocal display and mating success. Bucks use acoustic cues such as call rate and overall call structure to gain information on the dominance rank, motivation, and condition (fatigue) of competitors (Pitcher et al. 2015). Therefore, groans are the product of sexual selection driving the buck vocalizations to transmit multiple data on the caller quality (Pitcher et al. 2015). Since bucks have individually distinctive vocalizations, it was proposed that they may call repeatedly to familiarize females with their vocal characteristics (McElligott et al. 1999). However, the familiarization hypothesis has yet to be tested in fallow deer. Groaning is not fixed over time but is modified dynamically according to male age and rank. Therefore, groans are individually distinctive only within each breeding season (Briefer et al. 2010). However, changes in the structure of groans and groaning rate occur also during the same breeding season and are associated with the declining body condition of males and variation in the availability of mating opportunities (Vannoni and McElligott 2009). The bucks who achieved most of the matings are those who had initiated vocal activity early in the season (also more than 3 weeks before any matings occur) and who had remained vocal on most days. Dominance relationships are established during this pre-rut period, largely by non-contact agonistic interactions depending on body size and body mass. These relationships are in turn tested and modified by fights during the rut to produce the dominance ranks that influence mating success (McElligott et al. 1998, Moore et al. 1995). In summary, the number of matings gained by males is highly variable and is related to factors such as age, body size and mass, vocal display, social dominance rank, fighting success, and spatial strategies together with the experience from previous mating seasons, and that gained as subadult males (see McElligott et al. 2003). Mating success peaks between the ages of 6 and 7 years, when males usually have the highest numbers of matings (McElligott and Hayden 2000, McElligott et al. 2002). Successful males do not appear to suffer a decrease in survival probabilities or a reduction in fecundity, despite the high investment required to gain matings (McElligott et al. 2002).

Rutting activities are linked to pronounced hypophagia among adult males, starting weeks before the mating period and resulting in an important mass loss. Hypophagia and scent urination occur at the same time. The physiological processes inducing preputial gland activity and scent-urination may be the same as for appetite suppression (Apollonio and Di Vittorio 2004). These processes are possibly linked to hormonal changes recorded during the breeding season. Prime-aged males (5–8 years old) lose on average 26% of their body mass. This mass loss is positively correlated with initial mass and not with mating success or activities associated with mating success (McElligott et al. 2003). Foraging strategies adopted before the mating season affect mass loss. All other age and sex classes are unaffected in their feeding behavior by the rutting season. Females and young males even show a marked increase in grazing in response to a higher forage quality from summer to autumn.

Mating System

Langbein and Thirgood (1989) distinguished three main mating strategies: single male territorial strategy (classic rutting stands and temporary stands), multi-male territorial strategy (multiple stands and leks), and non-territorial strategy (dominance within mixed-sex herds, harem holding, and rowing males). Lekking is by far the most demanding mating strategy for males but is also the most successful strategy in terms of matings achieved within the population (e.g., Ciuti et al. 2011). A lek is a communal male display area that females visit for the sole purpose of mating and leave soon after mating. Many different models have been proposed to explain how leks initially form (Beehler and Foster 1988; Bradbury and Gibson 1983; Höglund and Alatalo 2014; Stillman et al. 1993). Leks are usually located in the same area year after year, and multiple factors are thought to be responsible for the persistence of a lek in a specific location, the combination of which depends on local ecological conditions (Apollonio et al. 2014). Therefore, habitat manipulations can affect the use of these traditional mating sites (Apollonio et al. 1998).

The mating system of a population can be single or mixed. The density of bucks and breeding females, as well as habitat structure (environmental heterogeneity, resource distribution, and tree cover) exert the greatest influence on the dominant mating strategy within a population or during a year. A greater variety of concurrent mating strategies was observed in the wild compared to park populations (Thirgood et al. 1999). The mating system adopted by a male appears to be determined primarily by the male's age and dominance status, the density and degree of aggregation of females, and the degree of competition experienced from other breeding males (Langbein and Thirgood 1989).

Individual male reproductive success is highly skewed in all systems (e.g., each year three males accounted for 60–90% of copulations in a lek, Apollonio et al. 1989) as confirmed by paternity assessment based on genetic data (Say et al. 2003). The asymmetry in copulatory success may be associated with male dominance rank and/or female choice. High skew in male reproductive success may contribute to the low genetic diversity recorded in fallow deer, mainly in enclosed populations. Assortative mating can help explain the persistence of genetic variation for male traits associated with reproductive success (Farrell et al. 2011). A small but consistent proportion of females (mainly yearlings) do not mate with the most successful males each year. Yearling females mate later in the rut than older ones and hence they are more likely to mate with younger and low ranking males. The timing of matings by young males coincides with the peak of yearling female matings, while low ranking males attempt to mate at a later stage when highly successful competitors show fatigue. Alternatively, yearling females may not be able to pay the potential costs associated with mating with high quality males or could be less experienced at discriminating between males of differing quality or at avoiding mating with young and low ranking males. Therefore, there is a strong behavioral difference between young and adult females in mate choice (Imperio et al. 2020).

Different reproductive strategies have been reported in female fallow deer. During 10 years of study in a large urban park in Dublin, Ireland, polyandrous and monandrous multiple-mating females as well as single-mating females were observed in a non-lekking population (Briefer et al. 2013). Each year, on average, 12% of all females were polyandrous females. This small but consistent proportion suggests that monandry and polyandry are alternative female strategies in fallow deer. Polyandry was not related to female age, stage of the rut, dominance rank of mates, or number of matings achieved by males during the rut and did not increase offspring viability and quality. The hypothesis of fertility insurance, where females remating if fertilization from the first mating is uncertain due to the possible sperm depletion, could explain polyandry in fallow deer. This strategy is more costly in terms of increased predation risk, energy and time spent searching for mates, selecting mates, and copulating and involves a complex trade-off between fertility success, preferences for high-quality males, and potential costs (Briefer et al. 2013).

Aggression

Studies on the aggressive behavior of territorial males were carried out primarily in enclosed parks where live lekking or non-lekking populations. Before the start of the rut, males become more and more intolerant to the presence of rivals resulting in a marked increase in aggression.

Many agonistic interactions are non-contact displays (such as groaning, parallel walk, antler displaying, or thrashing against vegetation) to avoid combat situations that may result in physical injuries (Bartoš et al. 2007). Nevertheless, direct fights are not uncommon between animals of comparable size and can last several minutes (Festa-Bianchet et al. 1990). There is no evidence that body mass and antler length are important factors in either the duration or intensity of fighting (Jennings et al. 2004). Fights are longer when at least one of the males had previously experienced a victory (Jennings et al. 2004). Lateral palm presentation serves to de-escalate fighting between mature bucks (Jennings et al. 2002). Damage likelihood is associated with dominance status and not with fight duration/number or mating success (Jennings et al. 2017). Chapman and Chapman (1997) described a thickening of the integument of the forehead of fallow bucks (dermal shield) during the rut that gives resilience against knocks, preventing severe damages to the skull. However, death and serious injuries can occur, especially toward later stages of the rut when the most actively rutting bucks lose their strength (e.g., Festa-Bianchet et al. 1990, Moore et al. 1995). As the number of estrus females increases during the rut, there is an increase in fighting (e.g., Jennings et al. 2013). The resulting hierarchy of dominance is linear (see Jennings et al. 2010), and mating success is highly skewed in favor of high ranking males (Moore et al. 1995).

Although most fights tend to involve only pairs of males, approximately 10% of contests are disrupted by the intervention of a third-party male, as recorded in a large enclosed city park in Ireland (Jennings et al. 2009). High ranking males engage in these triadic interactions against lower ranked individuals to prevent the advancing of subordinates in the hierarchy and at the same time to achieve a limited increase in dominance rank (Jennings et al. 2018). Suffering third-party interventions during fighting may reduce the probability of mating during the day on which the interventions occur. Therefore, intervention and suffering intervention might represent an interrelated strategy for which males that suffered an intervention are also highly likely to engage in third-party interventions (Jennings et al. 2017). This kind of behavior is highly variable between and within individuals over days and between years. However, further studies are needed to provide a more complete understanding of the evolution of third-party intervention behavior in fallow deer.

Parental Care

Fawns are born from mid-May to July with a peak in June (Chapman and Chapman 1997). Occasionally fawns can be born as late as November, but they are lighter and have higher mortality rates compared to early-born fawns (Ács and Lanszki 2017). As maternal age increases, fawns are born earlier in the breeding season. After parturition, the doe eats the afterbirth to prevent the attraction of predators.

The fawn is active within few minutes of birth, and suckling occurs within an hour or so. The doe establishes a mother-infant bond immediately after the birth, cleaning and drying the newborn by licking it. After parturition, the females do not return to the herd for 2 to 10 days. The type of mother-infant relationship can be categorized as "hider" type where the mother and the infant stay separated and out of contact for long periods, during which the infant stays hidden in the vegetation, near where it was born. Although the change of hiding place is typically initiated by the female, the exact position of the bed-site is chosen by the fawn. Selected bed-sites show significantly lower visibility and a higher amount of canopy cover than random sites. Fawns seem to select these two bed-site variables independently, perhaps for thermoregulatory reasons (see Kjellander et al. 2012). The newborns generally rest most of the time; the dappled coat provides excellent camouflage. If disturbed, the fawn "freezes"; after a period varying from an individual to the other, the "freezing" behavior changes in "fleeing" behavior. The doe remains separate from the fawn for much of the day but within hearing distance of a fawn distress call. At least for the few days after the birth, the mother recognizes the fawn apparently by smell, later it seems that the recognition is by the mother as well as by the fawn. The doe nurses the fawn on average once every 4 h until it is at least 4 months of age. Fawns to primiparous mothers suckled relatively longer, with no corresponding increase in mass, compared to multiparous mothers (Birgersson and Ekvall 1994). However, during the first 2 weeks, it seems that the transfer of milk is poorly reflected by suckling time since the inexperienced mothers do not terminate the lactation when the udder is empty. Grasses may be eaten a few days after the birth, but rumination does not begin until 2 to 3 weeks of age (Chapman and Chapman 1997). After about a month from birth, youngs and their mothers form small groups. The fawns may be left in the care of few adults while the other does feed. The mother begins weaning the fawn when it is around 20 days old, but weaning continues until the fawn is about 7 months old and can be prolonged up to January–February, even if sporadically. Mothers begin decreasing maternal care by decreasing the duration of tactile contacts (Chapman and Chapman 1997).

Allosuckling (i.e., suckling from a female other than the mother) was observed in captive and wild populations. The onset of allosuckling behavior seems to be related to the increasing ability of the fawns to move around after the first 2 weeks of life. Birth date affects allosuckling, with late-born fawns performing fewer and shorter allosuckling bouts. No difference was found between sexes (Pélabon et al. 1998). Allosuckling was positively correlated with the age of the females and negatively correlated with the rate of their aggressive behavior and it was common between related members in a stable social unit (Ekvall 1998). Allosuckling could be a result of kin selection and/or reciprocal altruism (Ekvall 1998) or could be a mean for offspring to gain important immunological benefits by acquiring antibodies from various lactating females (Roulin and Heeb 1999).

Senses and Communication

The common fallow deer have an acute sense of smell as would be expected in a species well endowed with scent glands and a good sense of hearing. The large ears can be swiveled together or separately through circa 180 degrees, picking up sound from any direction without turning the head.

The eyes, set on the side of the head, give a wide field of vision but poor depth perception. Discrimination of distant stationary objects is very poor, but any movement is quickly detected. Dissection of the eye reveals that deer do not appear to possess a UV filter, suggesting that they may be sensitive to ultraviolet light. Two classes of cone pigments together with a high concentration of rod pigments are present in the retina, with sensitivity in the blue-green part of the electromagnetic spectrum (Jacobs et al. 1994). Fallow deer possess a *tapetum lucidum*, common to all nocturnal mammals. These cells reflect light that would otherwise be lost when it passes through the retina back into the eye, increasing the amount of available light. This combination of adaptations allows a good dichromatic vision both by day and by night. Fallow deer can discriminate colors in the blue-green part of the spectrum (Birgersson et al. 2001). This dichromatic color vision may allow distinguishing between different plant species or different parts of plants that might be of variable nutritional (or toxic) value.

Communication and recognition make use of whole-body odor as well as vocal and visual cues. Tactile signals such as touching, licking, pawning, nipping, and butting occur mainly between mothers and their fawn, but also between adults.

Fallow deer use different types of vocalizations in mother-offspring interactions, during the rut and in a situation of danger: bleating is a short medium-high pitched sound produced by females close to parturition or with their young; peeping is a high pitched sound produced by fawns when are in distress or to establish contact with their mothers; wailing is an intense distress sound produced by a fawn older than 2 days; barking is a short, loud, and explosive alarm call used by females, sometimes repeated several times; mewing is a higher pitched sound given by any deer during submission postures; and groaning is a low belch like the sound produced by rutting males [rarely by subadults $(2<\text{years}<4)$ and yearlings] composed by a series of single events up to more than 3000 vocalizations per hour, lasting 0.35/0.5 s and ranging from about 100 to 8000 Hz (Stachowicz et al. 2014).

Visual communication is essentially based on body posture as well as on the position and movement of the tail and the appearance of the rump patch (Alvarez et al. 1976). Alarm signals are one of the most common visual cues and pronking is a characteristic alarm gait of fallow deer as of other ungulates. Pronking is also a signal of the animal's fitness which should deter any pursuit by a predator as well as a play that may prepare young animals for adult life.

Parasites and Diseases

Current knowledge of the common fallow deer diseases is likely to be biased in favor of those pathogens and host populations viewed as important by interest groups as for other deer species. Moreover, the European countries hardly have systematic national disease surveillance for wild ungulates except for epidemic diseases (Putman et al. 2011). Data available are not suitable for the assessment of the possible long-term effects of pathogen infection on deer population dynamics (East et al. 2011).

Ectoparasites

The most common ectoparasites reported for this deer species in Europe (Chapman and Chapman 1997; Pavlásek and Minár 2014; Sleeman 1983; Szczurek and Kadulski 2004) include: lice (*Solenopotes burmeisteri*, *Bovicola tibialis*, and *Damalinia* sp.), keds (*Lipoptena cervi*), warble flies *Hypoderma diana,* flies (*Cephenemyia multispinosa* and *C. auribarbis*), ticks (*Ixodes ricinus, Haemaphysalis punctata, H. concinna*, and *Dermacentor reticulatus*), fleas (*Paraceras melis*), and mites (*Sarcoptes scabiei, Chorioptes texanus*, and *Demodex kutzeri*).

The percentage of deer infested varies with locality and times of the year. For example, the percentage is high in late winter, spring, and early summer for *Damalinia tibialis*, and from August to December for *L. cervi* (Chapman and Chapman 1997). The extent of the infestation is species-dependent. For example, in Poland, the highest percentages were reported for *L. cervi* (76%) and *I. ricinus* (29%), while the lowest for *C. texanus* (<1%); despite the percentage value, the infestations were symptomless (Szczurek and Kadulski 2004).

Fallow deer are among the most widespread ungulates in the world and so are their parasites. Mertins et al. (2011) described the impact on native species of deer of *Bovicola tibialis*, a chewing louse brought to North America with fallow deer. This louse causes a pathologic hair loss syndrome that is most evident in winter and spring. The most severe cases may progress to morbidity and mortality, mainly in young deer.

In the last decades, an increasing incidence of tick-borne zoonoses has been reported in Europe. This trend regards in particular pathogens (viruses, bacteria and protozoa) transmitted by *Ixodes* ticks. Like other deer species, the common fallow deer are becoming more and more important as a tick maintenance host. This deer can reach high density in potential tick habitats such as deciduous and mixed forests or green periurban and urban areas (Jaenson et al. 2018). However, at high density, fallow deer can destroy the ground vegetation to such an extent to reduce tick abundance (van Wieren and Hofmeester 2016). Hence the relationship between deer density and tick abundance is complex, due to a large number of climatic and environmental factors acting simultaneously, and still unclear (Gray et al. 2021).

Lyme borreliosis and tick-borne encephalitis are the two tick-borne diseases with the largest impact on human health (Hönig et al. 2019). Lyme borreliosis is caused by spirochetes of the *Borrelia burgdorferi* sensu lato complex, while encephalitis is caused by the tick-borne encephalitis virus (*Flavivirus*, Flaviviridae) (Hönig et al. 2019). Deer are not reservoirs for *B. burgdorferi* s.l. and encephalitis virus (Gray et al. 2021; Michelitsch et al. 2019). The presence of the zoonotic bacterium *Anaplasma phagocytophilum*, the causative agent of granulocytic anaplasmosis in both humans and animals, has frequently been reported in fallow deer from different regions of Europe with infection rates ranging between 1.5 and 95.4% (see Kazimírová et al. 2018). This variation is mainly due to the locality, examined tissue, and the sensitivity of the detection method used. The fallow deer may act as reservoir host for *A. phagocytophilum* (Kazimírová et al. 2018). Piroplasms are tick-borne protozoa, infecting red and white blood cells of their hosts. The common fallow deer have been identified as susceptible to *Theileria* and *Babesia* infections (e.g., Kazimírová et al. 2018, Yabsley and Shock 2013).

Endoparasites

Chapman and Chapman (1997), Kowal et al. (2012), Rehbein et al. (2014), and Vengušt and Bidovec (2003) provide a review of internal parasites (mainly nematodes, cestodes, and trematodes) affecting fallow deer. These parasites have different prevalence and intensity of invasion in relation to a different susceptibility of fallow deer to infection. The presence of eggs, larvae, and oocysts of gastrointestinal and pulmonary endoparasites was investigated in fecal samples of fawns and yearlings of farmed fallow deer by Rehbein and Bienoschek (1995). Outbreaks of parasitic diseases are rare (Vengušt and Bidovec 2003).

Ashworthius sidemi, an abomasum nematode of Asiatic cervids introduced in many European countries via sika deer, was observed in fallow deer from Poland, Sweden, the Czech Republic, and Russia (Kowal et al. 2012; Kuznetsov 2021; Magdalek et al. 2017). This parasite can cause chronic abomasitis and infection can have health consequences, especially in young animals (Kowal et al. 2012). This nematode may be able to infect cattle and sheep feeding together with deer on the same meadows or pastures (Kornacka et al. 2020).

Even not showing any significant clinical sign if not a moderate decline of physical conditions, fallow deer may be affected by the following trematodes: the common liver flukes *Fasciola hepatica*, a native European endoparasite and the giant liver fluke, *Fascioloides magna*, an alien endoparasite of American origin introduced in Europe in the nineteenth century, probably together with North American elk (e.g., Nagy et al. 2018). The giant liver fluke has established in three permanent natural foci: northern Italy, floodplain forests along the river Danube, and the Czech Republic with southwestern Poland (see Králová-Hromadová et al. 2016). However, the European distribution of *F. magna* is permanently growing and its emergence is expected in new areas (Nagy et al. 2018). This alien species has already replaced the endemic one in some areas (Houszka et al. 2016). Fallow deer is a definitive host of the liver flukes (Malcicka 2015). Fasciolosis is an emerging/re-emerging zoonosis in many countries as a consequence of environmental changes as well as anthropogenic modifications (Mas-Coma et al. 2005). The strong dependence of liver fluke's incidence on weather factors (such as high rainfall) indicates that climate change may have a remarkable influence on the future evolution of this disease (Iglódyová et al. 2017).

Neosporosis caused by *Neospora caninum* is among the main causes of abortion in cattle nowadays. However, many aspects of the life cycle of this protozoan parasite are unknown, and the role of wildlife as reservoirs in this cycle is still not completely explained. The seroprevalence of *N. caninum* in wild and farmed fallow deer varies greatly: from 1% (Bartova et al. 2007) to 13% (Moskwa et al. 2018). Seronegative results were obtained in Spain (Almería et al. 2007) and in Belgium (De Craeye et al. 2011). A fatal case of meningoencephalomyelitis caused by *N. caninum* was diagnosed in a 3 weeks fallow deer in a zoo in Switzerland (Soldati et al. 2004). A study conducted at a fallow deer farm (Cabaj et al. 2017) revealed that the mean vertical transmission ratio of *N. caninum* in naturally infected deer seems to be comparable to those observed in cattle and showed a significant reduction in birth rate. Bucks naturally infected by *N. caninum* cannot transmit the infection to females by natural fertilization.

Toxoplasmosis and sarcosporidiosis (sarcocystosis) are other protozoal diseases causing abortion. The seroprevalence of *Toxoplasma gondii* varies from 10% (Moskwa et al. 2018) to 24% (Bartova et al. 2007). Seronegative results were obtained in the Czech Republic and Belgium (De Craeye et al. 2011; Hejlícek et al. 1999). Coinfections with *N. caninum* seem to be rare (Moskwa et al. 2018). Compared to sheep and goats, fallow deer appear to be at less risk of infection by *T. gondii* and *N. caninum* through the ingestion of food contaminated with oocysts excreted with feces because of the different feeding habits (Moskwa et al. 2018).

The prevalence of *Sarcocystis* infection in fallow deer is very high (>90%, e.g., Poli et al. 1988) and comparable to the prevalence reported in other cervids in Europe (see Prakas et al. 2016). No significant difference between fawns and adults was recorded (Poli et al. 1988). The clinical disease is rare. A detailed microscopic investigation of the ultrastructure of the cyst wall morphology of *Sarcocystis* sp. was carried out by Poli et al. (1988).

Viral Diseases

Foot and mouth disease FMD affects even-toed ungulates, both domesticated and wild. The virus responsible for FMD is a non-enveloped RNA *Aphthovirus*, belonging to the Picornaviridae family. The common fallow deer are susceptible to natural and experimental infection with FMD virus. The disease is mild or inapparent and is characterized by the formation of vesicles and ulcers in the mouth, nose, teats, and feet. Fallow deer are unlikely to play a significant role in the maintenance and transmission of FMD in the long term in the absence of FMD infection in domestic ungulate populations (Weaver et al. 2013). To date, the European countries are recognized as free from FMD without vaccination (https://www.oie.int/en/disease/foot-and-mouth-disease/).

Rabies is a fatal viral infection that causes encephalitis in warm-blooded animals. In deer rabies occurred infrequently. Only one case is reported for fallow deer: an outbreak affecting more than 20 fallow deer in a farm of Mongolia, caused by rabid dog bites (Zhu et al. 2015).

Bacterial Diseases

According to EFSA and ECDC report (2021), in European Union the first and second most reported zoonoses in humans are campylobacteriosis and salmonellosis, respectively. No *Campylobacter* or *Salmonella* species were isolated from wild or farmed fallow deer (Carbonero et al. 2014). Shiga toxin-producing *Escherichia coli* (STEC) infection, yersiniosis, and listeriosis are the other most reported zoonoses in humans (EFSA and ECDC report 2021). *Yersinia* (Syczyło et al. 2018) and *Listeria* (Pomilio 2016) species and Shiga toxin-producing *Escherichia coli* (STEC) strains (Sánchez et al. 2008) were isolated from fallow deer.

Tuberculosis (TB) is a worldwide disease caused by members of the *Mycobacterium tuberculosis* complex. It may cause zoonotic disease in humans; to date, it is a rare zoonosis in the European Union (EFSA and ECDC 2021). Bovine tuberculosis (bTB) has complex epidemiology, which may involve multiple hosts. For example, in Doñana National Park (DNP) in southern Spain, wild boar *Sus scrofa*, red and fallow deer, domestic cattle, and to a lesser extent carnivores as Iberian lynx contribute to the maintaining of *M. bovis* circulation (Gortázar et al. 2008). Infection prevalence in DNP was 13.0% in fallow deer, lower than that recorded in red deer. Differences in grazing patterns and feeding areas as well as use and aggregation around watering areas, especially during summertime, could determine a different exposition to mycobacteria (Gortázar et al. 2008). Deer may be long-lived reservoirs of infection having the potential to initiate new outbreaks well outside currently infected areas or to reinitiate infection after bTB has been eliminated through selective culling of all positively tested animals (Gortázar et al. 2008). bTB may contribute to the periodic die-offs that occur among deer during severe droughts (Gortázar et al. 2008). The importance of wildlife in the epidemiology of *M. bovis* infection in domestic animals may continue to grow in the near future (Gortázar et al. 2010).

Mycobacterium avium subspecies *paratuberculosis* is the etiological agent of paratuberculosis. It is one of the most serious diseases affecting dairy cattle worldwide. The frequency of detection in fallow deer reported in different areas of Europe (see Álvarez et al. 2005) is low, suggesting that free-ranging deer populations are rarely infected by the pathogen, unlike farmed animals. However, deer might contribute to the persistence and spread of the pathogen, particularly where higher densities of animals occur (such as at drinking points and in dens and shelters).

Brucellosis is an infectious disease caused by bacteria of the genus *Brucella*, being considered one of the most important zoonosis worldwide. The fallow deer like other deer have not been identified as a significant brucellosis reservoir for livestock in Spain (Muñoz et al. 2010).

Prion Diseases

Chronic wasting disease (CWD) is the most contagious prion disease affecting wild and farmed cervids; it is a neurodegenerative disease that is always fatal once the clinical signs appear. CWD is enzootic in some areas of North America. The first cases of CWD in Europe were documented in a wild moose and a wild reindeer in Norway (Ricci et al. 2017). In addition to its increased geographic distribution, the known host range of CWD is also expanding (Ricci et al. 2017). The fallow deer seem to have reduced susceptibility to CWD. The absence of clinical disease in individuals exposed to a contaminated environment and infected mule deer for 7 years suggests that a relatively strong species barrier against CWD infection may exist in fallow deer (Rhyan et al. 2011).

Population Ecology

Population Dynamics

Size fluctuations of a population are a result of temporal variation in survival, fecundity, and dispersal rates. This variation can be associated with density-dependent and -independent processes, which primarily affect recruitment rates and levels of mortality within a population (Putman et al. 1996). For example, analyzing the performance of park populations of fallow deer in Great Britain, the first response to density-resource limitation seems to be an increased age at first breeding and a reduction in the proportion of yearlings ovulating and subsequently maintaining pregnancy. Neonate mortality is directly related to weather conditions in the first week of life (Putman et al. 1996).

The importance of each density-dependent and -independent process may vary with latitude and habitat.

In northern/central Europe, resources are scarce in winter because vegetation stops growing, and snow cover renders food inaccessible. The scarcity of resources, combined with high thermoregulation costs, high costs of movement in deep snow, shorter length of growing season, and high susceptibility to predation, constitutes limiting factors for survival. Therefore, the combination of these density-independent factors should represent a crucial determinant of fluctuations of population size. To date, the population dynamics of fallow deer has received poor attention in northern/central Europe.

Some insights in Mediterranean areas come from a fenced estate of central Italy, where a combination of density-dependent and climatic factors plays a relevant role in regulating fallow deer population (Imperio et al. 2012). The intraspecific density-dependent factors are stronger than interspecific ones. The fallow deer appear not to be much influenced by the other herbivores occurring in the same area, probably due to its trophic position (between intermediate and roughage eaters, Hofmann 1989). In Mediterranean environments, the only important climatic factor is presumably associated with spring and summer precipitation. For example, very wet conditions in May–June appear to play a negative role in fawn survival, probably due to the insurgence of thermoregulatory problems (Van Moorter et al. 2009). On the contrary, water availability during the spring of the previous year has a positive effect on fallow deer population size. It improves body conditions in young females and their fecundity, presumably through the increase of primary productivity (Imperio et al. 2012).

Studying fallow deer population dynamics for nearly two decades in two enclosed game reserves of southern Spain allowed a better assessment of the effects of density and hunting pressure in the same climatic regime (López-Montoya et al. 2017). Density-dependent mechanisms have a stronger effect than hunting and climatic factors whereas the populations are close to their carrying capacity. Density-dependent mechanisms compensate for harvest extractions. Hunting causes a reduction in population that in turn relieves intraspecific forage competition, increases performance and reproduction, and leads to subsequent rapid population growth. The weather effect is more important the more abundant the deer are.

Effects of Climate Change

There is a growing concern about the potential negative effects of climate change on the behavior and ecology of deer populations (Root et al. 2003; Parmesan 2006, for reviews).

The Mediterranean Basin is facing the effects of climate change more than ever. During the twenty-first century temperature will warm 20% more than the global average and warming will be particularly large in summer, approximately 50% larger than the global average (Lionello and Scarascia 2018). Fallow deer populations with densities far from their carrying capacity and less competition for resources could take advantage of these climatic changes to reach autumn in better body condition. The worst effects of climatic constraints have been detected when populations are closer to their carrying capacity. The importance of weather factors could become much greater if both densities of fallow deer and aridity increase. Therefore, population densities must be well controlled to modulate the negative effects of climatic constraints on fallow deer condition (López-Montoya et al. 2017).

Furthermore, climatic changes could increase the ecological overlap between deer species, emphasizing the negative effects of interspecific competition, for example between fallow and roe deer (Ferretti and Fattorini 2021).

Competition with Other Ungulates

Several studies suggested a potential interspecific competition among the common fallow deer and native/introduced deer species based on behavioral interferences and/or overlapping in habitat and resource use (e.g., Ferretti et al. 2012, Putman 1996). A few studies analyzed changes in deer population density to look for evidence of actual competition among deer. Inverse numerical trends were recorded for fallow and roe deer populations in the New Forest (southern England) over more than 30 years. These changes in deer population density appear to be, for the most part, independent of one another and hence cannot be considered an uncontroversial effect of competition (Putman 1996). On the contrary, the decline of the endemic subspecies of roe deer *Capreolus capreolus italicus* observed in a Mediterranean area can be mainly explained by the increased numbers of fallow deer (Focardi et al. 2006). This species could have changed the vegetative cover in the long term and fragmented the distribution of suitable habitats for roe deer, contributing to the variations in home range size and phenotypic performance of the endemic subspecies. Only when the fallow deer density has increased above some threshold, is it possible to detect the effects of this density increase on roe deer population. These results provide evidence of the real existence of interspecific competition between fallow and roe deer. Evidence was also collected in the State Nature Reserve of Bosco della Mesola, northern Italy, where occurs the only native red deer population of peninsular Italy, recently recognized as a distinct subspecies (*Cervus elaphus italicus*) by Zachos et al. (2014). Modest body size, simplified antlers, and a low reproductive performance characterize Mesola red deer. The common fallow deer was reintroduced in the same area after the Second World War and in the following decades outnumbered the red deer, decreasing the availability of habitat and food resources. In the last decades, actions were conducted to reduce the population size of fallow deer by capture and culling with positive consequences on the Mesola red deer population (Mattioli et al. 2003). However, additional efforts are required to eradicate fallow deer (Lovari and Nobili 2010).

Conservation Status

The common fallow deer are not globally threatened and is categorized as Least Concern (LC) in the IUCN Red List. However, the last autochthonous population in Anatolia and the Rodhian population, the oldest still surviving on a Mediterranean island, are of the utmost importance.

To conserve the Anatolian population, in the 1960s the Turkish government began a breeding program at Düzlerçamı. In 1964 an area of 1750 ha, in which seven individuals were living, was designated as Fallow Deer Conservation Area (see Arslangündoğdu et al. 2010). In the following decades, the conservation area was gradually expanded until when the Düzlerçamı Wildlife Development Area was designated in 2005 (Arslangündoğdu et al. 2010) with a surface of more than 28,000 ha. The fallow deer number of the last autochthonous stock, reported by Arslangündoğdu et al. (2010) from 1966 to 2009, shows strong fluctuations throughout the years. A combination of several factors (increasing human pressure due to urbanization and recreational activities, poaching, poisoning by local people, as well as the presence of shepherds and stray dogs) may have had a negative impact on the fallow deer number (Arslangündoğdu et al. 2010). As far as we know, the latest study carried out in the breeding station using camera traps (Ünala and Çulhacıa 2018), identified 80 adult individuals on the base of spot distribution and antler structure, and estimated a population density of 20.1 deer per km^2. Attempts to reintroduce fallow deer in the former ranges of the species (Gökova and Adaköy, Muğla province; Ayvalık, Balıkesir province and Pos-Çatalan, Adana province), translocating animals from the Düzlerçamı Breeding Station in the 1980s and 1990s, have not been successful (Masseti 1999, 2002). Reintroduction projects, carried out in the second decade of twenty-first century, have instead successfully translocated fallow deer in the National Park of Dilek Peninsula and Büyük Menderes Delta, Aydın province, and in the Köyceğiz Dalyan Special Environmental Protection Area, Muğla Province (Durmuş 2019). Reintroductions result to be an important tool for the conservation of the Asia Minor population.

The number of fallow deer on the island of Rhodes is reputed that today do not exceed a few hundred. Spotlight counts, carried out in the northcentral part of the island, gave a mean value of Kilometric Abundance index of 1.4 deer/km (De Marinis and Masseti 2021). The Rodhian fallow deer appear to be seriously threatened by poaching and by the continual habitat reduction.

Management

Introductions

Movements of fallow deer by humans, including introductions/translocations and release/escape of animals from fenced areas, were a common practice in past centuries and determined the establishment of the populations currently living in Europe and in other countries. The Romans introduced the common fallow deer to most of Europe, from the Iberian Peninsula to Britain (Baker et al. 2017 and references therein). Medieval introductions gave rise to many of the extant populations today. There is historical evidence confirming that, during the 1400s, common fallow deer were still captured in Anatolia and taken to western Europe to embellish palaces and game parks (Masseti 1996). Still today, humans contribute to change the distribution of this species all over the world.

Impact on Human Activities and Collisions

An analysis of methods and systems for assessment, prevention, and control of deer damage in different European countries is reported in Apollonio et al. (2010). This analysis reveals that an ecosystem management approach, instead of a single species approach, become more and more necessary to manage conflicts among relevant stakeholder groups in reaching decisions about the use and conservation of biological resources (Kviberg and Craig 2006).

Fallow deer-vehicle collisions are not distributed randomly in space and time and show daily and seasonal peaks (Langbein et al. 2011; Valente et al. 2020). Deer cross the roads during daily movements to or from foraging areas within their home range, especially at dusk and dawn when they are more active. These movements are rather regular and distributed throughout the year. In addition, there are peaks in road-crossing coinciding with larger-scale dispersal movements of juveniles in late spring and early summer and mating movements of adults in autumn.

The common fallow deer have a rather patchy distribution and therefore might be less vulnerable to traffic than other ungulates. Moreover, major roads or railways seem to be recognized as barriers to movement; the boundaries of home ranges appear to coincide with these major routes. Vehicle collisions involving fallow deer represent only a low percentage of all collisions involving ungulates reported per country. Traffic mortality rates are low in relation to the fallow deer population size. In the UK, the total mortality due to vehicle collisions is estimated to lie between 7 and 13% as a proportion of the spring population size of fallow deer (Langbein et al. 2011). In Finland collision and traffic mortality rates are 3.2% and 2.1% of the winter population, respectively (Niemi et al. 2015). The behavioral responses of fallow deer when crossing roads to some mitigation measures are reported in Langbein et al. (2011). Fallow deer seem to use underpasses more frequently than overpasses and begin using the underpasses a few months after their construction. The ratio between the size of the aperture and the total length of an underpass appears critical: fallow deer seem to avoid the underpasses with a ratio of less than 1.5. Wildlife warning reflectors and auditory deterrents seem ineffective at modifying fallow deer behavior due to habituation. However, the potential effectiveness of these deterrents would be expected to be quite different in different contexts.

Farming

The common fallow deer have become one of the most commonly farmed deer in Europe to the point that its farming significantly contributes to the meat industry (Ward et al. 2014). The ratio of lean meat produced per kg of live mass is high and the meat is highly nutritious, and with a low cholesterol content (e.g., Daszkiewicz et al. 2015).

Velvet antler is regarded as a by-product of fallow deer farming, used in traditional Chinese medicine, and in some countries as a dietary supplement.

Hunting

The legislation regarding hunting (organization, methods, seasons and management objectives), the effectiveness and problems of the current strategies, and the monitoring techniques in different European countries are summarized in Apollonio et al. (2010). However, a brief comparative review of some of these issues based on available data is reported in Table 2 for most of the European countries.

The meat quality of hunted animals is quite different in relation to different hunting methods like dog-driven hunting and harvest culling, which imply different animal stresses before shooting (Cifuni et al. 2014). The value of the carcasses is also influenced by the age of the deer shot. Carcasses of young fallow deer (18–30 months), compared to older animals, are characterized, for example, by a higher dressing proportion, a higher percentage of the most valuable commercial cuts (the saddle, haunch, and shoulder), a high meat yield with the lowest percentage of bones and a lower percentage of skin and head (Żochowska-Kujawska et al. 2019).

Fallow deer are also a popular trophy hunting species because of their “exotic” antlers.

Future Challenges for Research and Management

The common fallow deer are a species capable of rapid population growth, although its spatial dispersal rate is low. This species can reach a high density in suitable habitats where it can have an impact on forestry, crops, and native vegetation. Fallow deer are potential competitors for native ungulates. The attendance of urban areas can result in increasing the likelihood of vehicle collisions and disease transmission to humans, livestock, and pets. This can lead to increased human-deer

Table 2 Hunting bags, use of artificial feeding, monitoring types and techniques, hunting methods, and seasons in different European countries

Country	Number of culled animals[a]	Artificial feeding	Monitoring	Hunting methods	Hunting plans	Hunting period
Austria	2	Obligatory	Estimation based on hunting records	Hunting from high seats; stalking; rarely driving (hunting dogs allowed in most provinces)	Minimum and maximum number to be culled	Buck: 01–08/31–12; doe-fawn: 01–08/15–01
Belgium	1	Sporadic	Estimated spring population (no rules exist concerning methods)	All hunting methods	Escaped individuals	01–10/31–12
Czech R.	4	Obligatory	Visual survey	Hunting from high seats; stalking, usually with dogs	Shooting plans	16–08/31–12
Croatia	2	Obligatory	Counts at feeding sites; vantage point counts	Stalking; tracking; hunting from high seats or from the ground	Shooting plans	Buck: 16–09/14–01; doe-fawn: 01–10/31–12
Denmark	4	Sporadic	Estimation based on hunting records and hunters questionnaires	Driving; stalking	Suggested hunting quotas	Buck: 01–09/31–01; doe-fawn: 01–10/31–01
Estonia	0					
Finland	1	Common	Counts at feeding sites; estimation based on hunting records	Hunting at feeding sites, agricultural fields or flushing by beaters	No shooting plans; number of hunting licenses based on estimated numbers	25–09/31–01
France	3	Usually not used for this species	Total or partial drives	Hunting drives with dogs; stalking; hunting from high seats	Minimum and maximum number to be culled, in some departments no shooting plans according to	01–06/28–02

(continued)

Table 2 (continued)

Country	Number of culled animals[a]	Artificial feeding	Monitoring	Hunting methods	Hunting plans	Hunting period
					the attempt to eradicate this species	
Germany	5	Obligatory (part); common (part)	Estimation based on hunting records and on amount of damage to forest regrowth and forest stand	All hunting methods, even night hunting	Shooting plans	Buck and doe: 10–08/31–12; yearling female: 10–06/31–12; yearling male: 10–06/31–01; fawn: 10–08/31–01
Greece	0					
Hungary	5	Common	No standardized methods (usually vantage point counts; counts at feeding sites; roadside counts)	Stalking on foot or by horse cart; hunting from high seats; females and fawns also in drives without dogs	Shooting plans	Prime-aged male: 01–10/31–12; male yearling and low quality buck: 01–10/31–01; doe, female yearling, fawn: 01–10/28–02
Ireland	3	Sporadic	No standardized methods (drive censuses; vantage point counts; pellet surveys)	Hunting from high seats; stalking	Shooting plans prepared by some landowners on voluntary basis	Northern Ireland = male: 01–08/30–04, female: 01–11/31–03; Ireland = male: 01–09/31–12, female: 01–11/28–02
Italy	3	Usually not used for this species	No standardized methods (usually vantage points counts, drive censuses, spotlight counts in 45% of provinces)	Stalking	Shooting plans	Two months, usually 01–10/30–11, but also 60 days before and after this period, exceptions in Eastern Alps and Emilia Romagna region (longer periods)
Latvia	0					
Lithuania	0					
Luxembourg	2	Not available	Not available	Not available	Not available	15–08/15–12
Macedonia	1	Not available	No censuses performed, only fenced animals	Not available	No shooting plans; no harvest data exist	16–09/31–01
Netherland	2	Forbidden	Drive counts; vantage point counts	Hunting from fixed places	3 types: (1) no management; (2) culled only for public health, public safety,	01–09/15–02

(continued)

Table 2 (continued)

Country	Number of culled animals[a]	Artificial feeding	Monitoring	Hunting methods	Hunting plans	Hunting period
					safety of air traffic, to prevent damage to crops, cattle, forests; (3) shooting plans	
Norway	0					
Poland	4	Obligatory	No standardized methods	Stalking; hunting at high seats or blinds; silent drives	Shooting plans	Male: 01–10/31–01; female and fawn: 01–10/15–01
Portugal	2	Sporadic	Estimation based on hunting records; censuses in few areas (usually open hill counts, drive counts, pellet surveys)	Stalking; sit and wait hunting; spear hunting; drive hunting (only from October to February)	Shooting plans	01–06/31–05 (but usually 01–09/28–02)
Romania	2	Common	Counts of footprints in the snow and other complementary methods (vantage points counts; counts at feeding sites)	Stalking; hunting from high seats	Shooting plans	Buck: 10–10/01–12; cull buck: 01–09/15–12; doe and fawn: 01–09/15–02
Serbia	1	Not available	Estimation, methodology not very scientific	Not available	Shooting plans	Male: 01–02/15–09; female and fawn: 01–02/30–09
Slovakia	4	Obligatory	Transects; vantage point counts; counts at feeding sites	Stalking; hunting from high seats	Shooting plans	01–09/31–12
Slovenia	2	Common	Estimation based on hunting records	Hunting from high seats	Shooting plans	Bucks: 16–08/31–12; does and fawns: 01–09/31–12; yearling: 01–07/31–12
Spain	5	Sporadic	Linear transects; counts at feeding sites	Stalking; Montería (Spanish system)	Shooting plans, except for Montería system based on hunting records	01–10/28–02

(continued)

Table 2 (continued)

Country	Number of culled animals[a]	Artificial feeding	Monitoring	Hunting methods	Hunting plans	Hunting period
Sweden	5	Common	No censuses performed	Drive hunting; stalking even with dogs; hunting from high seats (small hunting grounds)	Minimal management plans	Changes from year to year and between different areas of the country
Switzerland	0					
UK	5	Sporadic	No standardized methods (drive censuses; vantage point counts; pellet surveys)	Hunting from high seats; stalking	Shooting plans prepared by some landowners on voluntary basis	England, Wales = male: 01–08/30–04, female: 01–11/31–03; Scotland = male: 01–08/30–04, female: 21–10/15–02

The hunting bags refer to the last 5 years. Data from Apollonio et al. (2010) and Putman et al. (2011)
Note:
[a]Number of culled animals: 0 = 0; 1 = 1–100; 2 = 101–1,000; 3 = 1,001–5,000; 4 = 5,001–10,000; 5 > 10,001

conflicts. Further introductions, translocations, and escapes from fenced areas should be avoided.

This species needs a broader consideration that allows developing a countrywide standardized system to monitor population densities, damages to ecosystem and human activities, vehicle collisions, and disease impacts.

Actions to contrast factors threatening the conservation of the native population in Turkey should be considered a priority. Other introductions should be carried out to establish new stable nuclei in Turkish territory, avoiding interbreeding of different genetic lineages.

Further interdisciplinary researches, based on ecological, genetic, morphometric, historical, archaeological, and archaeozoological data, are needed to increase the knowledge of the origin, history, genetic variability, and status of the most ancient populations present in some southern European areas such as Castelporziano and San Rossore (central Italy) and in the Aegean island of Rhodes to ensure their conservation.

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