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*Dissertation for the Degree of Doctor of Philosophy in Environmental Biology
presented at Sassari University in 2010, XXIII Cycle*

LEKKING IN FALLOW DEER (*Dama dama*):
A LONG WALK TO TERRITORIALITY

PH.D. CANDIDATE: ***Fabio De Cena***

DIRECTOR OF THE SCHOOL: ***Marco Apollonio***

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To all people that work with passion

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SUMMARY

Here I present results of a long-term study (1996-2010) performed in the lekking fallow deer population of San Rossore, Italy, where data were collected through radio-tracking and direct observations. New results on the behavioural ecology of the fallow deer, with special regard to mating strategies and success were reported. First, I showed that the actual position of the lek is handy with regards to female travel costs and predation risk avoidance, in accordance to the “female preference” and “predator avoidance” hypotheses. Second, I showed that males able to adopt risky but best foraging strategies are able to gain an optimal body condition before rut and thus to achieve a high mating success. Third, I showed that for all adult males, despite age and mating success, it is important to reach the lek well before the beginning of the rut to gain positions in the male hierarchy. However, I refused the hypothesis that that sooner a male arrives at the lek, higher will be its mating success. Finally, I refused the hypothesis that subadult males are supposed to leave the lek later than adult males in order to increase their possibility of mating when mating males are exhausted. For the first time, I showed the importance of experiences gained by subadult males in affecting the individual mating success, once they become adult males. The study of subadult males was possible due to the deploy of an hand-made expandable radiocollar created during this study.

RIASSUNTO

In questo elaborato vengono presentati i risultati ottenuti da uno studio condotto sulla popolazione di daino presente all'interno della Tenuta di San Rossore, Italia. I dati sono stati raccolti dal 1996 al 2010 per mezzo di tecniche radiotelemetriche e di osservazioni dirette effettuate su un ampio campione di femmine e maschi, marcati e radiocollari. Da questo studio sono emersi alcuni interessanti ed innovativi aspetti sull'ecologia comportamentale e sulle strategie riproduttive di questa specie. Facendo riferimento alle teorie sulla formazione del lek sono stati ottenuti risultati in accordo con le ipotesi di "female preference" e "predator avoidance". Inoltre, la posizione attuale del lek risulta essere funzionale rispetto sia alla riduzione dei costi di spostamento femminili sia a quella del rischio predatorio. Viene illustrata anche, l'importanza dell'uso da parte dei maschi adulti di un settore considerato di alto rischio-alto beneficio presente all'interno dell'area di studio, in relazione al loro successo riproduttivo ottenuto durante il periodo riproduttivo autunnale. Per quanto riguarda le strategie riproduttive, questa ricerca ha confermato l'importanza per i maschi di un precoce arrivo nei pressi del lek al fine di stabilire la scala gerarchica maschile per gli accoppiamenti in relazione all'età individuale, mentre sono state rifiutate le ipotesi secondo cui un arrivo precoce nei territori del lek comporterebbe un maggior successo riproduttivo per i maschi adulti, sia quella secondo cui i maschi subadulti abbandonerebbero i territori dell'arena riproduttiva tardivamente rispetto ai maschi adulti, per ottenere una maggior possibilità di accoppiamento. Inoltre, per la prima volta, vengono presentati risultati che dimostrano l'influenza delle esperienze giovanili acquisite dai maschi subadulti, sul loro futuro successo riproduttivo ottenuto tra i territori del lek, una volta, quindi, raggiunta l'età adulta e la giusta maturità sessuale e sociale necessaria per l'accoppiamento. Infine, viene illustrato il progetto di un radiocollare elastico per il monitoraggio tramite radiotelemetria, e la sua efficacia riscontrata nell'applicazione su un campione di maschi subadulti monitorati durante questa ricerca.

INTRODUCTION

The lek, a clump of displaying males that females attend primarily for the purpose of mating (Höglund and Alatalo, 1995), is a mating system that recur in a wide array of animal taxa (i.e., arthropods, fishes, amphibians, reptiles, birds, and mammals; see Höglund and Alatalo, 1995 for an extensive overview of the taxonomic occurrence of lekking). In mammals, lekking is rare and is found mainly in ungulates (Clutton-Brock et al., 1993; Höglund and Alatalo, 1995, Bartoš et al., 2003; Isvaran, 2005; Bro-Jørgensen, 2008; Buzzard et al., 2008). Leks in ungulates appear most similar to leks in birds: both show territoriality, have traditional mating sites, and exhibit pronounced variance in male mating success (Schaal and Bradbury, 1987; Wiley, 1991; Balmford et al., 1992; Höglund and Alatalo, 1995; Apollonio et al., 1992).

One of the most interesting aspects of leks is the spatial clustering of males at specific traditional sites that constitutes a still unsolved dilemma as a number of explanations has not proved fully comprehensive and sufficient to cover all cases. A plethora of possible hypotheses have been proposed and reviewed to explain it (Bradbury and Gibson, 1983; Balmford et al., 1993; Clutton-Brock et al., 1993; Stillman et al., 1993; Stillman et al., 1996; Höglund and Alatalo, 1995; Young et al., 2009), including both merely descriptive and explicit mathematical models. Indeed, researchers can rarely assist at the formation of a lek, but they usually describe a lek already existing. In the latter case only hypotheses that can be linked to the actual position of the lek can be tested with empirical data, unless with the help of theoretical approaches. For instance, the hotshot model (Arak, 1988; Beehler and Foster, 1988; Höglund and Robertson, 1990a, 1990b) implies that females prefer to mate with an attractive “hotshot” male which is joined by unattractive males with the aim of parasitize on his attractiveness, thus such a clustering of males leading to the generation of a new lek. This explanation of lek formation does not predict a specific site for the lek, and it cannot be evoked when the exact position of a lek is under scrutiny. Similarly, the black hole model (Stillman et al., 1993; a.k.a. the female harassment model, Clutton-Brock et al., 1992) predicts that the sexual harassment by young and inexperienced males towards females causes continuous female movements to escape their disturbance and, therefore, adult males have the highest possibility to retain more females when clustered in a lek, when females find shelter from the harassment irrespective from its position. Thus, only theories that contribute to the explanation of lek formation only (i.e. the above two mentioned models) and those that include also a specific reference for space, can be discriminated.

Taking into consideration these circumstances, I tested only three hypotheses on lek formation with empirical data to understand why males are clustered in given sites: i) the female preference model (Alatalo et al., 1992), ii) the hotspot model (Bradbury et al., 1986), and iii) the predator avoidance model (Wiley, 1991) (**Chapter 1**).

Males and females typically differ in the factors that limit their reproductive success, and this is especially the case for highly sexually dimorphic birds and mammals (Darwin, 1871; Andersson, 1994). In highly polygynous species, as is the case with many ungulates, females are limited mainly by their effort to raise young successfully (Clutton-Brock et al., 1982; Davies, 1991), while males are rather limited by the fierce fights they have in order to gain access to mates during the rutting season (Clutton-Brock et al., 1982; Geist, 1986; Festa-Bianchet et al., 1990; Komers et al., 1994). When two or more male mating strategies are found within the same population, evolutionary theory predicts that each male should choose the strategy that will confer him the greatest reproductive success, suggesting that a highly costly choice can lead to a high benefit. Such a huge reproductive effort in male ungulates originates from fighting with other males for access to females, patrolling territories, roaring and tending females (Mysterud et al., 2004, and references therein). High cost-high benefit mating strategies may entail huge weight loss (Leader-Williams and Ricketts, 1981; Pérez-Barbería et al., 1998; Mysterud et al., 2005), increased predation risk (Jakobson et al., 1995), antler wounding and fatal injuries during combats (Kitchen, 1974; Leslie and Jenkins, 1985; Geist, 1986; Bartos et al., 2007). Thus, during the rut males face a dilemma, the solution of which considerably depends on their body conditions (Apollonio et al., 1992; Balmford et al., 1992; McElligott and Hayden, 2000; McElligott et al., 2001): to adopt a high cost-high benefit mating strategy or to fall back on a low cost-low benefit mating strategy?

Surprisingly, little is known about the relation between male ungulates' ability to adopt a high cost-high benefit mating strategy during the rut and the behavioural strategy adopted before the mating season, when males are expected to enhance their condition and to invest in body size. Specifically, quantitative data on spatial and foraging strategies adopted by ungulate males before the mating season are lacking. In highly polygynous species such as many cervids, males are usually regarded as pure capital breeders, in that they allocate to reproduction the energy stored (mainly fat) in spring and summer (Stearns, 1992; Jönsson, 1997). These reserves are crucial to face the rut, especially for those ungulate males who experience feeding cessation (in fallow deer *Dama dama*: Apollonio and Di Vittorio, 2004; in red deer *Cervus elaphus*: Mysterud et al., 2008a). According to the reproductive strategy-predation risk hypothesis, optimal spatial and foraging strategies adopted before the rut may imply a risk, since males are supposed to exploit the best

feeding areas (even though characterized by higher predation risk) in order to invest in body size and fighting ability (Main et al., 1996; Bleich et al., 1997; Ruckstuhl and Neuhaus, 2000, 2002; Mooring et al., 2003). According to that, males may chose whether or not to exploit the best but risky foraging areas before the mating season. This choice, in turn, arguably plays a key role in affecting the chance to optimally invest in body size and the ability to adopt a successful mating strategy during the following rut. Fallow deer population of the San Rossore Estate (study area) represented a good study case in order to deeply investigate these aspects. In fact, a sector of the study area was characterized by the highest meadow productivity and the highest predation risk. Within this scenario, I tested the hypothesis that only those males that were able to exploit the best feeding areas (even though characterized by higher predation risk) and therefore to invest in body size and fighting ability before the rut, were consequently able to gain a higher mating success during the rut than males that were not as able to exploit the risky sector of the study area (**Chapter 2**).

However, other factors could affect male mating success among lek territories. On ungulates, male-male combats during the breeding season are decisive in hierarchy settlement (Mainguy and Coté, 2008; Taillon and Coté, 2007; Mysterud et al., 2005) as well as non-contact interactions (Jennings et al., 2002). Vocal communication can contribute to decrease the needs to fight, given that the acoustic structure of male vocalizations was showed to be individually distinctive and to contain information on male body size and/or dominance status (Reby et al., 1998; McElligott et al., 2006; Vannoni and McElligott, 2007, 2008, 2009; Wyman et al., 2008). At the same time, scent and visual marking activities are supposed to be important for male status signalling in male-male interaction as well as for mate choice by females (Stenström et al., 2000). Gosling (1990) proposed that the main function of scent marking by males should be status advertisement, providing a means of assessment to potential competitors, thereby reducing the cost of agonistic encounters.

In order to reproduce successfully, an ungulate male needs to be available for mating in the short time window in which the female is ready to conceive (in fallow deer about 36 h, Asher, 1985), and, above all, when the peak of oestrus females occurs (Apollonio et al., 1992). That means for an ungulate male to be in the right place at the right time, such as for a male fallow buck (*Dama dama*) defending a lek territory (Apollonio et al., 1992) or for a red lechwe (*Kobus leche leche*) defending a resource-based territory (Williamson, 1994). As a consequence, it is supposed to be an advantage for an ungulate male to gain a high rank before the beginning of the short period in which mating will occur, in order to maximize its own mating success (McElligott et al., 1998).

Young males are less likely to compete successfully in male–male combats, and paternity is highly skewed towards prime-aged males (e.g. Pemberton et al., 1992; Coltman et al., 2002). However, young males have a higher chance to sire later in the rut, when prime-aged males are exhausted (Preston et al., 2001; Mysterud et al., 2008b), and this explains why subadult males may begin to show interest towards mating activities at a later date during the rut than prime-aged males (Mysterud et al., 2004).

Hence, the timing of lek use by male fallow deer can be crucial in affecting their competitive ability and dominance rank, and, in turn, it can influence the ability to have access to females during the rut and finally mating success. In this context, I tested these starting predictions: (i) adult males (bucks aged > 4 y.o.) are supposed to arrive at the lek before subadult males (aged 2-4 y.o.). (ii) high ranked adult males (i.e. males achieving a high mating success) are predicted to arrive at the lek before than low ranked adult males. (iii) immature and less competitive males (i.e. subadult males and/or low ranked adult males) are predicted to leave the lek later than the more competitive ones, in the attempt to compensate for their scarce mating success in the main rut time (**Chapter 3**).

Within this picture, it's clear that many factors may contribute to individual reproductive success. Whether to participate actively or not in reproduction, because it is generally costly, is thus a recurrent decision that iteroparous animals must take every year, and males are thus expected to adjust their reproductive effort according to their age and body condition (Mainguy and Côté, 2008 and references therein). During the two last decades, male mating success has been studied extensively on ungulates according to body size and body mass, mating effort and mating investment, dominance rank, survival or age (e.g.; Kojola, 1991; Komers et al., 1997; McElligott et al., 2001; Forsyht et al., 2005; Saunders et al., 2005; Pelletier et al., 2006 ; Jennings et al., 2010). Nevertheless, no researches were conducted on the influence of the behavioural patterns adopted by males during subadult phases on their future individual mating success. In the long-term study described in **Chapter 4** I faced not only whether the animals participated actively or not in reproductive activities every year according to age, but also the causes that stand behind this choice. The idea arises from a research conducted by Pelabon et al. (1999) on fallow deer subadult males, in which authors hypothesized that young interactions may affect further reproductive success through both motor training for future interactions and/or competition for current resources that affect growth.

In details, formulated the following predictions to be verified with our data collected on males from the age of 1.5 y.o to the complete social maturation: 1) Experiences gained at the lek by subadult males are supposed to affect the future mating success once they become adult males. 2) Body mass

related to best foraging strategies of subadult males are supposed to affect the future mating success once they become adult males. 3) Subadult males that are leaving early female aggregations are supposed to escalate before the male hierarchy and to become successful once they become adult males 4) Subadult males early aggregating with adult male aggregations are supposed to escalate before the male hierarchy and to become successful once they become adult males.

Finally, in **Chapter 5**, I presented a design and its effectiveness of an expandable radiocollar applied on subadult males, during the researches period. The construction of these collars is simple as they are hand-made; moreover they are almost inexpensive (few euros), and they fall off the neck as the deer grow, thus not causing any injuries. Moreover, this collar design suggest a simple but truly effective methodological approach to be adopted by researchers aimed to perform long-term studies on ungulate species lacking information on the behavioural ecology of subadult males.

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Chapter 1



Evaluating competing hypotheses on lek formation looking at its position and timing of use: the evolution of the handy lek in fallow deer (*Dama dama*)

**Evaluating competing hypotheses on lek formation looking at its position and timing of use:
the evolution of the handy lek in fallow deer (*Dama dama*)**

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Abstract

We tested three hypotheses on lek formation in a fallow deer population using lek position relative to female and male seasonal and rut movements and the timing of its use by both sexes. We made use of observations on the leks and radiotelemetry data referred to 36 adult males and 31 adult females collected over 7 years and we put them in the frame of over 20 years study of fallow deer rutting behaviour in the study area. Females visited the lek only one lek and only once during the rut, their travel route to and from the lek was quite distinct from their usual foraging movements and the leks were more distant one female home range. Males kept on using the lek area quite early, i.e. more than one month before the rut and waited there the arrival of females. The lek was located outside the high predation risk area of the Estate. All these findings militate for the female preference hypothesis and the predator avoidance hypothesis of lek formation, however past observations suggests that formerly existing leks may have responded to hotspots logic.. Fallow deer lek position in San Rossore can be predicted following predator avoidance and female preference models, however out of all possibilities the present one is the most handy as it results the best possible with regards to female travel costs reduction and predation risk reduction.

Keywords

Dama dama, fallow deer, female preference model, Hotspot model, lek, predator avoidance model.

Introduction

The lek, a clump of displaying males that females attend primarily for the purpose of mating (Höglund and Alatalo, 1995), is a mating system that recur in a wide array of animal taxa (i.e., arthropods, fishes, amphibians, reptiles, birds, and mammals; see Höglund and Alatalo, 1995 for an extensive overview of the taxonomic occurrence of lekking). In mammals, lekking is rare and is found mainly in ungulates (Clutton-Brock et al., 1993; Höglund and Alatalo, 1995; Bartoš et al., 2003; Isvaran, 2005; Bro-Jørgensen, 2008; Buzzard et al., 2008). Leks in ungulates appear most similar to leks in birds: both show territoriality, have traditional mating sites, and exhibit pronounced variance in male mating success (Schaal & Bradbury, 1987; Wiley, 1991; Balmford et al., 1992; Höglund and Alatalo, 1995; Apollonio et al., 1992).

One of the most interesting aspects of leks is the spatial clustering of males at specific traditional sites that constitutes a still unsolved dilemma as a number of explanations has not proved fully comprehensive and sufficient to cover all cases. A plethora of possible hypotheses have been proposed and reviewed to explain it (Bradbury and Gibson, 1983; Balmford et al., 1993; Clutton-Brock et al., 1993; Stillman et al., 1993; Stillman et al., 1996; Höglund and Alatalo, 1995; Young et al., 2009), including both merely descriptive and explicit mathematical models. Indeed, researchers can rarely assist at the formation of a lek, but they usually describe a lek already existing. In the latter case only hypotheses that can be linked to the actual position of the lek can be tested with empirical data, unless with the help of theoretical approaches. For instance, the hotshot model (Arak, 1988; Beehler and Foster, 1988; Höglund and Robertson, 1990a; Höglund and Robertson, 1990b) implies that females prefer to mate with an attractive “hotshot” male which is joined by unattractive males with the aim of parasitize on his attractiveness, thus such a clustering of males leading to the generation of a new lek. This explanation of lek formation does not predict a specific site for the lek, and it cannot be evoked when the exact position of a lek is under scrutiny. Similarly, the black hole model (Stillman et al., 1993; a.k.a. the female harassment model, Clutton-Brock et al., 1992) predicts that the sexual harassment by young and inexperienced males towards females causes continuous female movements to escape their disturbance and, therefore, adult males have the highest possibility to retain more females when clustered in a lek, when females find shelter from the harassment irrespective from its position. So we can discriminate theories that contribute to the explanation of lek formation only (i.e. the above two mentioned models) and those that include also a specific reference for space.

Taking into consideration the latter, only three hypotheses on lek formation can be tested with empirical data to understand why males are clustered in given sites: i) the female preference model

(Alatalo et al., 1992), ii) the hotspot model (Bradbury et al., 1986), and iii) the predator avoidance model (Wiley, 1991). We tested these hypotheses considering a large set of data dealing with the lekking fallow deer (*Dama dama*) population of San Rossore (Italy) collected for 7 consecutive years. Lekking in this population has been documented since early 1980's (Apollonio et al., 1989; Apollonio et al., 1992). Males of this population could defend territories that were either single, clumped in leks, or satellite to leks (Apollonio et al., 1992), but the most highly successful males were repeatedly shown to occur in leks (Apollonio et al., 1992; Apollonio et al., 1989; Festa-Bianchet et al., 1990). Taking into consideration data collected in the field using the same methodologies from 1997 to 2003, when 2 leks were present in San Rossore, here we introduced the conceptual frame of each of the 3 models along with specific predictions that we tested in our study population.

- *The female preference model.*

Leks form because females prefer large clump of males that can give them high mate choice opportunities (Alexander, 1975; Bradbury, 1981; Beehler and Foster, 1988; Alatalo et al., 1992). As a consequence, almost all females in a given population should mate in a lek. The clustering of females is thus determined by the clustering of males (and not vice versa). To reach this male aggregation that can favour female choice (Höglund and Robertson, 1990a, 1990b), females could be forced to increase their home ranges to mate. Bradbury (1981) and Bradbury and Gibson (1983) suggested that female preference for larger leks would cause males to cluster until there was a single lek per population or per female home range. Leks should thus be spaced an average female home range diameter apart and each female should visit only one lek.

- *The hotspot model.*

Leks forms in those sites (namely hotspots) where the probability for males of encountering many females is high (Bradbury and Gibson, 1983; Bradbury et al., 1986). Such hotspots could arise from overlapping female home ranges (Bradbury et al., 1986). Males go there because of high female encounter rate, female go there because they have no travel costs. The clustering of males is thus determined by the clustering of females (and not vice versa). More in detail, the model predicts that females should visit more than one lek before breeding, and, as a consequence, there could be more than one lek within a female home range or, better, leks may be found less than one average female home range apart (Bradbury, 1981; Bradbury and Gibson, 1983). Thus, females are not expected to increase home range size to mate (Bradbury and Gibson, 1983). These predictions has been suggested to be used in discriminating between the hotspot model and models that assume female choice for lekking males (Bradbury, 1981; Bradbury and Gibson, 1983).

		Models' predictions			
		Field data (1997-2003)	Female preference model	Hotspot model	Predator avoidance model
LEK VISITS (OCCURRENCE AND TIMING)	1.1 – Percentage of females that visited the lek during the rut ^{1,3,4}	Almost all females	Almost all females	Only females that have at least a lek within their home range	Almost all females
	1.2 – Percentage of males that visited the lek during the rut ^{1,5}	Almost all males	Almost all males	<i>No prediction</i>	Almost all males
	1.3 - Number of visits to the lek per female during the rut ¹	1 (repeated if mating does not occur)	1 (repeated if mating does not occur)	Several visits	<i>No prediction</i>
	1.4 - Number of leks visited by each female during the rut ^{1,3,4}	1	1	More than 1	<i>No prediction</i>
	2 – Timing of male visits to the lek and marking behaviour of males before, during, and after the rut ^{1,5,6}	Males go to the lek in order to make visual and olfactory references for dominance well before the begin of the rut, i.e. well before the appearance of females	Males go to the lek in order to make visual and olfactory references for dominance well before the begin of the rut, when females already use or pass through this area	Males go to the lek in order to make visual and olfactory references for dominance well before the begin of the rut, when females already use or pass through this area	<i>No prediction</i>
RELATIONSHIP AMONG POSITION OF LEKS AND FEMALE HOME RANGES AND MOVEMENTS	3.1 - Number of leks within a female home range ⁴	1	1	More than 1	<i>No prediction</i>
	3.2 - Distance between two leks ⁴	Higher than a female home range diameter	Higher than a female home range diameter	Lower than a female home range diameter	<i>No prediction</i>
	4 - Home range sizes of females and their position with respect to the lek outside and during the rut ^{2,3,4}	Female home range sizes increase during the rut. Home range centers are far from the lek center	Female home range sizes increase during the rut. Home range centers are far from the lek center	Female home range sizes do not increase during the rut. Home range centers are close to the lek center	<i>No prediction</i>
	5.1 - Leks' location with respect to female deer movement outside the rut and during the rut ^{2,3,4}	Outside the area of higher female traffic and higher female home range overlap	Outside the area of higher female traffic and higher female home range overlap	In the area of higher female traffic and higher female home range overlap	All leks are located in the area of lowest predation risk
	5.2 - Usual daily movements of females before, during, and after the rut ³	Daily female movements do not cross through the lek	Daily female movements do not cross through the lek	Daily female movements cross through the lek	<i>No prediction</i>
	6 - Movements of females to the lek ³	Atypical if compared to usual daily movements	Atypical if compared to usual daily movements	Typical if compared to usual daily movements	Directed towards the area with low predation risk

¹ direct observations on leks; ² discontinuous radiotracking of females outside the rut; ³ continuous radiotracking of females before, during, and after the rut; ⁴ discontinuous radiotracking of females during the rut; ⁵ discontinuous radiotracking of males during and outside the rut; ⁶ marking activities collected around the lek before, during, and after the rut.

Table 1 – Field data typologies collected for 7 consecutive years in the lekking fallow deer population of San Rossore (white columns on the left). Accordingly, we reported the prediction of each model on lek formation for each related data typology (grey columns). Two leks were present (more than 15 active territories for each) during the period of study. Source of data typologies are reported by numbers in footnotes (see methods for major details).

- *The predator avoidance model.*

Leks form in areas where the predation risk is lower (Wiley, 1973; Wittenberger, 1978). Both sexes go there to minimize the risk of predation during mating activities.

Many authors have considered the benefit of mating in a lek because of reduced predation risk due to dilution effect (for extensive reviews see Höglund and Alatalo, 1995; Wiley, 1991), thus a lek should be used to mate by the majority of individuals of a given population, but few researches have taken into consideration the position of the lek with respect to predator home ranges or, more in general, to the differential predation risk among different areas. Among ungulates, in topi, leks are formed in places where the grass on the savannah is short and thus the risk of predations by lions may be low (Gosling and Petrie, 1990). The same has been suggested for the Uganda kob (Deutsch and Weeks, 1992). The female-initiated process (i.e. females moving towards large clumped male aggregations) described by the female preference model is strongly in contrast with the male-initiated process (i.e. males moving towards female hotspots) predicted by the hotspot model and, thus, resulting in two mutually exclusive set of predictions. Along with these two concepts, the predation avoidance model predicts a scenario that can be suitable for both the hotspot model and the female preference model. Accordingly, we selected the set of predictions to be tested in our fallow deer population (Table 1) combining a long-term set of observational and space use data collected on both adult males and females.

Methods

Study area - We carried out this study in the San Rossore Estate (4,650 ha), central Italy (43°43'N, 10°19'E). It was mainly covered by pine woods and mixed deciduous woods, and secondarily by wet deciduous woods, marshes, and meadows (Ciuti et al., 2006). Cultivated areas (946 ha) were fenced and not available to deer. Areas along the coast (dune vegetation, degraded coastal zone, and maritime pine woods) were unused areas by deer of the Estate (Ciuti et al., 2006; Ciuti and Apollonio, 2008). The eastern sector of the Estate (namely the disturbed sector, 466 ha) was characterized by high human disturbance during the period of the study (1997-2003) (Apollonio et al., 2005). Being the man the main predator of deer in this area (Ciuti et al., 2004), and given the differential response showed by sexes towards the predation risk (Main et al., 1996), the disturbed sector was mainly used by adult males and avoided by females with their fawns (Ciuti et al., 2004; Apollonio et al., 2005; Ciuti et al., 2006; Ciuti and Apollonio, 2008). Two traditional leks documented since 1980's and composed by at least 15 clustered territories were present during the

research, i.e. the lek of Stacca del Gatto (lek SG) and the lek of Fossacci (lek FO), located on the south and north side of the Estate, respectively. A third one disappeared in 1992.

Captures of deer - Deer randomly chosen for research were driven by 20-30 game keepers into circular corrals (Ciuti et al., 2004) during winter, from 1996 to 1999. Thirty-six bucks (> 4 y.o.) and 31 adult females (> 1 y.o.) were hand caught, blindfolded, aged by tooth wear (Chapman and Chapman, 1997), ear tagged, fitted with Televilt (Lindesberg, Sweden) radiocollars, and finally released.

Observation of lek activities during the mating season - Direct observations of activities dealing with 7 mating seasons (1997-2003) were performed from 2 hides located along the border of the lek SG, and from 1 located along that of the lek FO. At least 2 observers per hide carried out direct observations using binocular 10x and telescope 30-45x. Continuous observations on lek activities (every day from dawn to dusk) began when territorial defence was first detected (late September-early October), and ended when defence ended (late October) (Apollonio et. al., 1992). The rut (i.e. the core of the mating season) was defined as the time between the first (from 1997 to 2003: mean day \pm SE = October 5th \pm 0.5 days) and the last day (October 20th \pm 0.6 days) on which copulations were recorded each year. Accordingly, pre-rut and post-rut were defined as the periods preceding or following the rut, respectively. Only data of leks' activity dealing with collared deer (i.e. date of entrance and exit from the lek, and number of individual visits) were used in this work.

Discontinuous and continuous radiotracking of deer - From April 1997 to December 2003, both radiocollared males and females were monitored by discontinuous radiotracking (12-18 fixes per month homogeneously distributed over day and night). We calculated locations by triangulation (Ciuti et al., 2004). Seasons were defined as follows: winter (Dec.-Feb.), spring (Mar.-May), summer (Jun.-Aug.), and autumn (Sept.-Nov.). During autumn, i.e. the mating season, the monitoring effort was significantly increased (1 fix every 12 h for both sexes from early September to early November). From April 1997 to December 2003, by means of discontinuous radiotracking we collected 15,810 fixes for males and 12,451 fixes for females.

Moreover, during each mating season of the period 1997-2003, females were monitored at dawn and dusk (continuous radiotracking sessions) during their daily movements from night and day feeding areas and vice versa, respectively (Ciuti et al., 2004). During each session, we collected 1 fix every 15 minutes for a given female in the 5-hour period of dawn and dusk. Two or 3 different females per day were followed by 2-3 couples of operators, respectively. When a female route ended inside the lek (namely female route to the lek), a special session of continuous radiotracking (6-36 hours) was quickly organized to wait the female exit and to track the female movement from

the lek to the usual feeding areas (namely female route from the lek). Continuous sessions carried out at dawn and dusk were homogeneously distributed among all females in the pre-rut, the rut, and the post rut periods. At the end of this research, 943 female routes were recorded.

Observation of male marking activities (visual references for dominance) around the lek SG - In the period 1997-2003, from late August to late November, a 2,590 m path around the lek SG was walked by the same observer every 3-4 days. Each visual/olfactory reference for dominance (i.e. trashing on the vegetation or scraping on the ground made by bucks, Chapman and Chapman, 1997) observed along the path was mapped onto a digitized 1:2000 map of the lek area.

Data analyses – Data collection on lek activity (if not differently specified), on marked deer and related data analyses dealt with the south side (southern than the Morto river) of the Estate (Davini et al., 2004; Ciuti and Apollonio, 2008), i.e., where the lek SG was present. All data related to the north side (northern than the Morto river), i.e., where the lek FO was present, were considered testing predictions related to the occurrence in a given population of more than one lek. As showed for more than 600 deer (106 adult females, 79 yearling males, 48 sores, 263 bucks, and 118 juveniles) individually recognizable by numbered and coloured ear tags during the last 2 decades (Apollonio, *unpublished data*), the lek SG was commonly used by females using areas southern to the Morto river, while the lek FO was commonly used by females using areas northern to the Morto river. In contrast, males many times used the lek located in the opposite side of the sector they lived (Apollonio and Ciuti, *unpublished data*).

Through the combination of observational data collected on the lek with radiotracking data we computed the lek use by collared males and females (date of arrival and departure from the lek area for both sexes, number of different individual lek visits for females, number of different leks visited by females). We combined this dataset with the occurrence timing of marking activities around the lek.

Regarding the female spatial use, we computed the size of 369 female seasonal home ranges (winter, spring, summer, and autumn) using the Ranges VI software (Kenward et al., 2003) by means of the Kernel (Worton, 1989) method using the 90% of available locations (Börger et al., 2006). Coordinates of home range centres were assessed using the Kernel method (Worton, 1989), for which we computed the linear distances from the lek centre using ArcGIS 9.3.1 (© 2009 ESRI). Using the SPSS 13.0 (1989–2004 SPSS Inc.) program, we modelled the variation of log-transformed seasonal home range sizes by fitting a linear mixed model (LME, Pinheiro and Bates, 2000) with season included as fixed factor, and individuals repeated among seasons and years as random factor to avoid pseudoreplication of data (Machlis et al., 1985). We adopted the same LME

approach when we modelled the seasonal variation of the distance between female home range centres and lek centres. LME pairwise comparisons were run and adjusted with the Bonferroni method for multiple comparisons. Maximum overlap areas of female home ranges recorded during the autumnal mating season (namely hotspots) were computed using ArcGis 9.3.1, for which we determined the distance from the lek centre and, eventually, we assessed their overlap over the lek area. Every year, hotspots were computed if resulting from the overlap of at least home ranges of 3 females belonging to different social groups. Females were checked to belong to different social units by means of continuous radiotracking. By means of ArcGis 9.3.1 we assessed the number of lek included by female home ranges, and the average diameter of a female home range during the autumnal mating season.

Female routes collected at dawn and dusk by continuous radiotracking were analysed using the ArcView 3.2 extension Animal Movements SA v 2.04 beta (Hooge et al., 1999), which allowed us to determine the following set of variables for each route: (i) linear distance (meters) between the lek centre and the nearest fix of the route, (ii) total distance covered during the route (the sum of linear distances among consecutive fixes), and (iii) average speed m/min (total distance covered/time). The latter two variables were also computed for female routes to and from the lek. We modelled the variation of square-root-transformed linear distance between lek centre and the nearest fix of female routes by fitting a LME model with sub-period (i.e., pre-rut, rut, post-rut), and period of the day (dawn, dusk) included as fixed factor, and individuals repeated among sub-periods and years as random factor. This LME models were run first by including all main effects and two-way interactions. Then we removed the non-significant interaction terms and repeated the analysis in a stepwise fashion until all non-significant interaction terms were removed (Crawley, 2007). We repeated this procedures by fitting a LME with the log-transformed total distance covered during routes as the dependent variable. To compare usual female daily routes with those run to and from the lek, we fitted two LME models with log-transformed total distance covered and log-transformed speed of routes as dependent variables, respectively, and movement type (usual routes at dawn and dusk, routes to and from the lek) as fixed factors. Individuals repeated among years were considered as random factor.

Merging the costs of travel for females to reach the lek with the benefits of low predation risk. - The southern sector of the study site (i.e. where the lek SG was present) was subdivided into 300 x 300 squares (i.e. approximately the same dimension of the lek SG) using ArcGis 9.3.1. We computed the linear distance (i.e. the travel cost) required by females to reach each hypothetical lek included within each 300 x 300 m squares. In order to avoid a source of pseudoreplication, depending on the

different number of females monitored each year, we computed the female travel cost as the distances between female hotspots (and not single females) and each hypothetical lek within 300x300 m squares. In so doing, we classified hypothetical leks according to the travel cost required by females to reach them. At the same time, by means of ArcGis 9.3.1 we computed the linear distance between the eastern disturbed sector and each hypothetical lek within 300 x 300 m squares, thus classifying them according to the degree of predation risk (i.e., higher the distance from the disturbed sector, lower the predation risk perceived by deer *sensu* Ciuti et al., 2004). By means of ArcGis 9.3.1, we merged these two information of travel cost and predation risk (considering 50% of importance for each of the two benefits) in order to show the area of the Estate characterized by the best combination of low predation risk and travel cost. We then compared the actual position of the lek SG with respect to this area.

Results

Lek use by females and males (occurrence and timing) - Lek use by monitored females and males was reported on Table 2.

	The overall study period (1997-2003)	Rut 1997	Rut 1998	Rut 1999	Rut 2000	Rut 2001	Rut 2002	Rut 2003
1.1 - Percentage of females that visited the lek during the rut	89.0 % (female cases over total 81/91)	70% (7/10)	90% (9/10)	100% (8/8)	93% (14/15)	93% (14/15)	87% (13/15)	89% (16/18)
1.2 - Percentage of males that visited the lek during the rut	95.6 % (male cases over total 87/91)	100% (9/9)	100% (12/12)	87.5% (21/24)	100% (16/16)	100% (15/15)	90% (9/10)	100% (5/5)
1.3 - Number of visits to the lek per female ¹ during the rut	1.1 ± 0.3 visits (mean ± SD; female cases n = 81)	1.1 ± 0.4 (n = 7)	1.3 ± 0.5 (n = 9)	1.1 ± 0.4 (n = 8)	1.2 ± 0.4 (n = 14)	1.0 ± 0 (n = 14)	1.0 ± 0 (n = 13)	1.0 ± 0 (n = 16)
1.4 - Number of leks visited by each female during the rut	1.0 ± 0 lek visited (mean ± SD; female cases n = 81)	1.0 ± 0 (n = 7)	1.0 ± 0 (n = 9)	1.0 ± 0 (n = 8)	1.0 ± 0 (n = 14)	1.0 ± 0 (n = 14)	1.0 ± 0 (n = 13)	1.0 ± 0 (n = 16)

¹ Females that did not visit a lek were excluded.

Table 2 – Use of leks by male and female fallow deer in the San Rossore Estate (Italy) during 7 consecutive rutting periods. Data were collected by means of both direct observations on the lek and continuous/discontinuous radiotracking performed during the rut (see methods for major details).

The majority of females and males used the lek during the rut. Females commonly made only one visit to the lek each rut, while they seldom made two visits (only 6 out 81 cases from 1997 to 2003)

and never visited the lek more than two times during the same rut (Table 2). No collared females visited more than 1 lek during the same rut (Table 2).

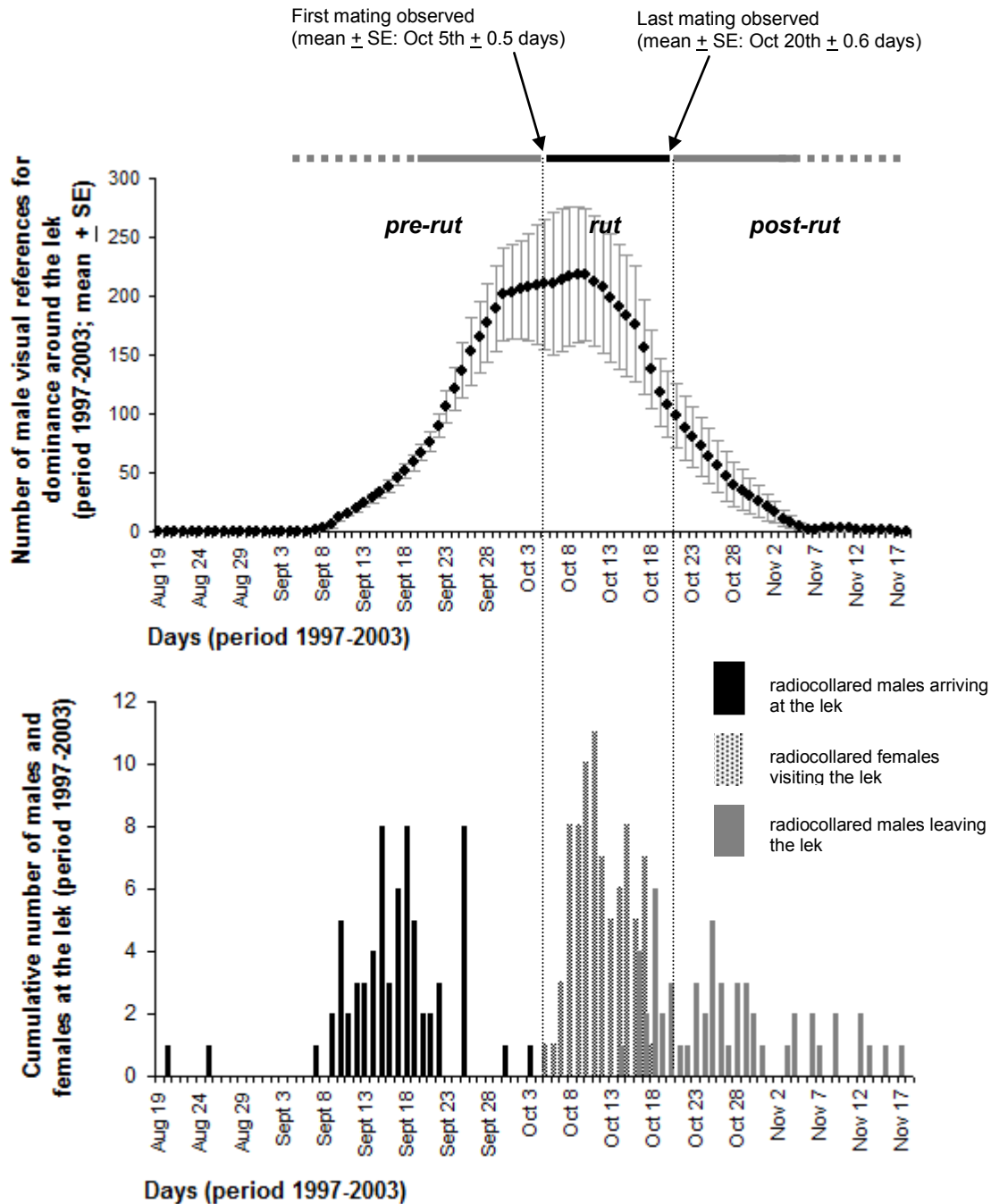


Fig. 1 – *Above* - Occurrence of male visual references for dominance (mean ± SE; period 1997-2003) recorded walking a 2.5-km path around the lek from late August to middle November. *Below* - Number of collared males arriving at (black bars) or leaving (grey bars) the lek, and number of collared females (shaded bars) visiting the lek (period 1997 – 2003). Nine males left the lek later than Nov 17th.

Adult males began to use the lek in early September, as documented by the beginning of marking activities recorded around the lek (Fig. 1 above), about one month before the first copulation observed in the mating arena. It was confirmed by radiotracking data (Fig. 1 below), which set the arrival of the majority of collared bucks in early September.

In contrast, females began to visit the lek only during early October (Fig. 1 below), i.e. one month later than the arrival of bucks in the area. Females stopped to visit the lek in the second half of October, when males began to gradually leave the mating area (Fig. 1 below).

Relationships among lek position and female home ranges and movements - Considering female home ranges recorded in autumn, which were computed considering all independent fixes including those recorded on the lek, no one included 2 leks (0 out 91 cases). Only 20 female autumnal home range (21 %) included 1 lek from 1997 to 2003 (in 1997 0 out 10 females, in 1998 0/10, in 1999 0/8, in 2000 4/15, in 2001 8/15, in 2002 5/15, and in 2003 3/18). The mean size of female home range recorded in autumn was 319.48 ha (SE = \pm 249.47 ha). Assuming a circular shape of a female home range (*sensu* Bradbury et al. 1986), the average home range diameter in autumn was 2017 m, more than 1 km shorter than the distance between the two leks of the San Rossore Estate, i.e. 3200 m. We recorded a significant variation among seasonal home range sizes of females (LME model, effect of season: $F_{3,374}=18,967$, $p < 0,001$). Female home range sizes were 147.37 ± 12.32 ha in winter, 191.25 ± 13.67 ha in spring, 138.50 ± 10.99 ha in summer, and significantly increased during the mating season in autumn (319.48 ± 26.30 ha; LME pairwise comparisons: autumn home ranges *vs* all the other seasonal home ranges: $p < 0.001$ in all cases). We found a significant seasonal variation of the linear distance between home range centres and lek centres (LME model, effect of season: $F_{3,374} = 6,482$ and $p < 0.001$). The lower distance was recorded in summer (1845.65 ± 71.17 m; LME pairwise comparisons: distances recorded in summer *vs*. distances recorded during other seasons: $p < 0.001$ in all cases) but not in the autumnal mating season (2254.43 ± 108.05 m), which did not differ to those recorded in winter (2387.13 ± 104.19 m) or spring (2187.51 ± 81.67 m) (LME pairwise comparisons between distances recorded in autumn *vs*. distances recorded during winter and spring were $p = 0.314$ and 0.601 , respectively).

The whole dataset of female locations collected from 1997 to 2003 was reported in Fig. 2. On the basis of Kernel 90% isopleths computed for female locations recorded in autumn, we identified the maximum overlap areas (namely hotspots) (Fig. 3). Each hotspot resulted from the overlap of at least 3 (and a maximum of 10) different autumnal home ranges of females not belonging to the same social unit.



Fig. 2 – Distribution of female fixes recorded during 7 consecutive years in the San Rossore Estate (all fixes: white dots; autumnal fixes: black dots). Localization of lek, fenced and other unused areas (i.e. maritime pine woods, degraded coastal zone, dune vegetation) by deer were indicated on the map.

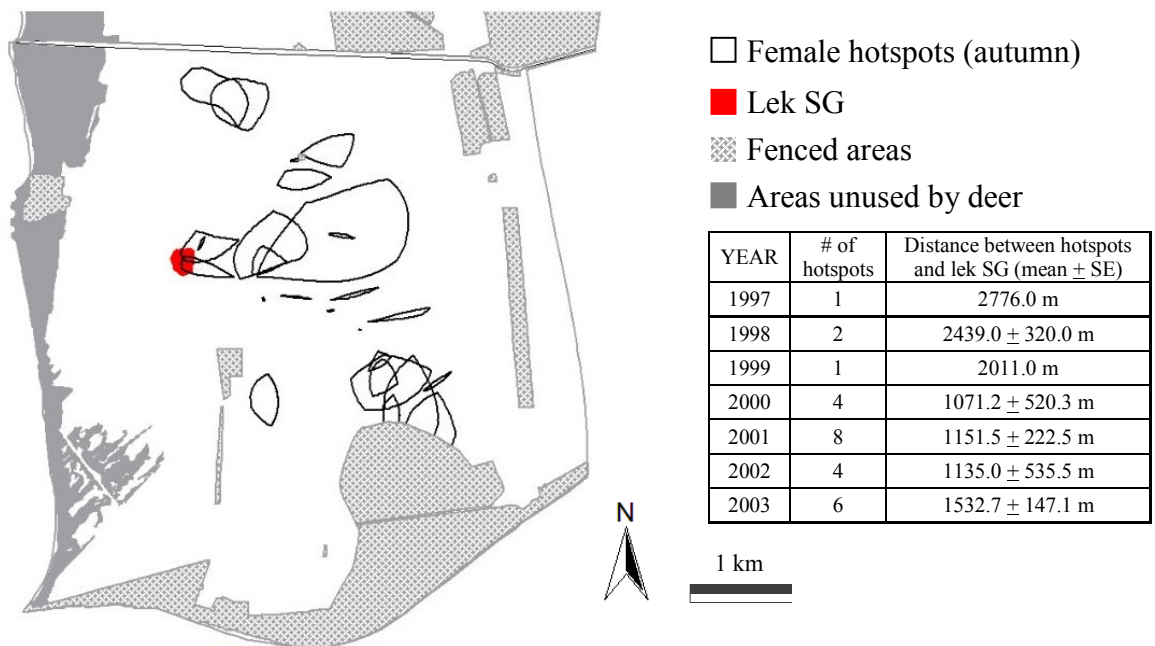


Fig. 3 – Localization of high female traffic areas (hotspots) in the San Rossore Estate. Hotspots were obtained by considering the maximum overlap areas of female home ranges (Kernel 90% isopleths) recorded in autumn from 1997 to 2003. Hotspots were computed considering at least overlapping home ranges of 3 females belonging to different social groups (see the text for major details). Localization of lek, fenced areas, and areas unused resources by deer were indicated on the map. Distances between hotspots centres and the lek centre were also reported in the small table.

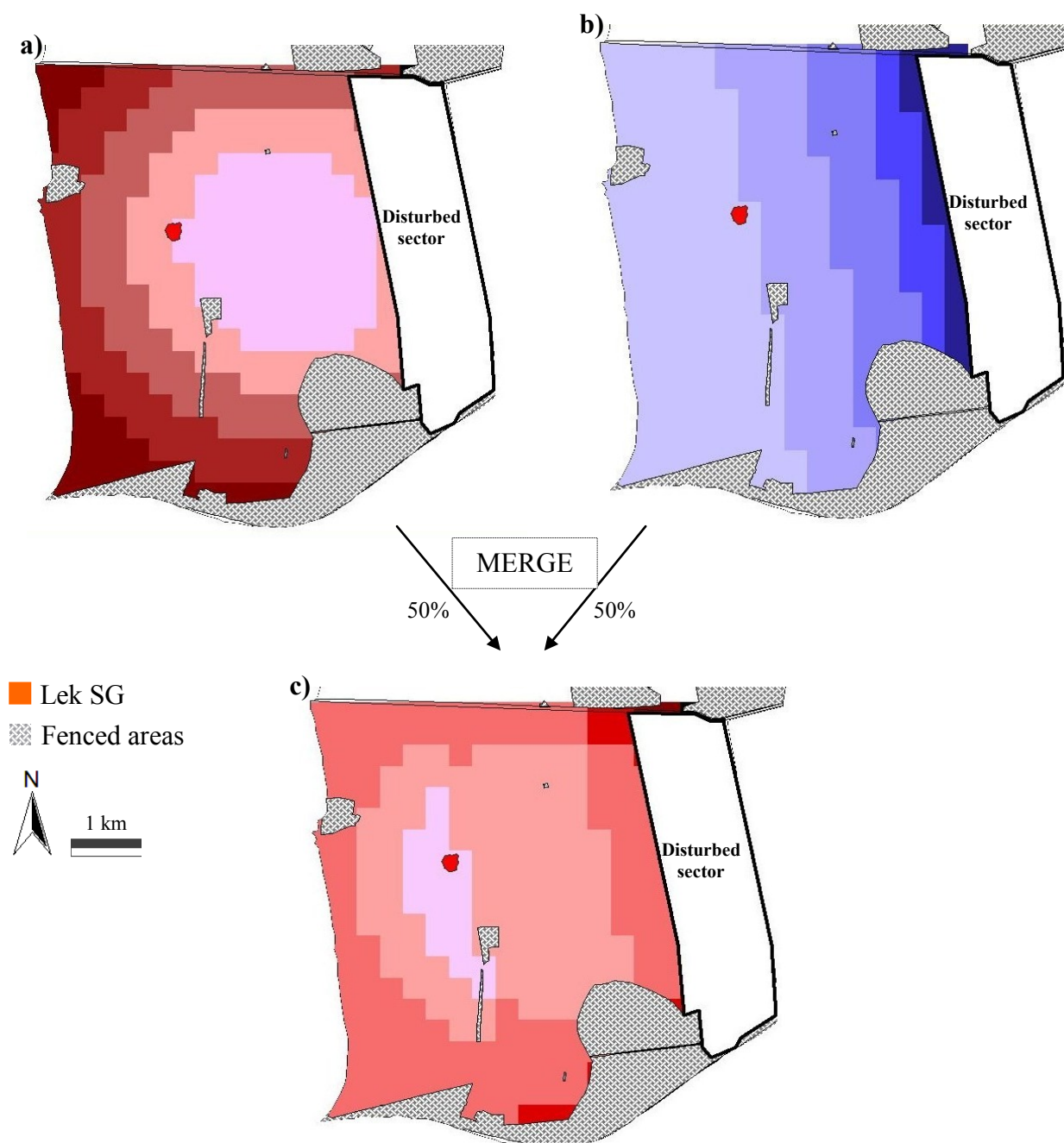


Fig. 4 – The southern side of the study area was subdivided into 300 x 300 m squares. We computed the travel cost required by females to move from hotspots to each hypothetical lek included within 300 x 300 squares (a). Lower the travel cost, lighter is the colour in the map. At the same time, we computed (b) the predation risk for each hypothetical lek considering the distance from the eastern disturbed sector. In this case, lower is the predation risk, lighter is the colour in the map. Finally, by means of ArcGis 9.3.1 we merged the two maps (c), considering the same contribution from travel costs (50%) and predation risk (50%), where the resulting lightest area represents the place of the Estate where we can find the best combination between low travel cost and low predation risk. The actual position of the lek SG was within this area.

Despite home ranges (and therefore hotspots) were computed with all independent autumnal fixes including those recorded in the lek, only 2 hotspots out of 26 overlapped the lek area (Fig. 3). It

happened in 2001, with a hotspot generated by 7 females, and in 2002, with a hotspot generated by 5 females (Fig. 3). With the exception of these two cases, hotspots commonly were more than 1 km far (mean \pm SE: 1537.0 \pm 146.41 m) from the lek centre (Fig. 3). Along with the previous analysis of hotspot position *vs* lek position, female traffic with respect the lek position can offer a more detailed point of view.

Considering the linear distance between the closest fix to the lek of female daily routes, no difference were found between routes recorded at dawn or dusk (LME model $F_{1,828} = 1.692$, $p = 0.194$), while we found a significant variation of such a distance among sub-periods (LME model, $F_{2,828} = 13.209$, $p < 0.001$).

Indeed, lower distances between the lek centre and the nearest fix of female routes were recorded during the rut (mean \pm SE 1510.66 \pm 55.75 m) if compared to the pre-rut (1675.03 \pm 44.21 m) and post-rut (1908.56 \pm 56.60 m) (LME pairwise comparisons: $p = 0.031$ and $p < 0.001$, respectively). Therefore, even if routes recorded during the rut were closest to the lek, the closest fix to the lek was distant more than 1.5 km. Indeed, if we excluded routes run to and from the lek by females to mate, no one route passed through the lek during pre-rut, rut, and post-rut.

We compared usual daily routes run by females at dawn or dusk with those run to go or to leave the lek. The total distance covered at dawn or dusk by females during usual daily movements (1403.78 \pm 31.29 m) was significantly lower to that covered in order to go (2783.63 \pm 241.22 m) or to leave the lek (2748.23 \pm 181.41 m) (LME model, $F_{2,913} = 51.138$ and $p < 0.001$; LME pairwise comparisons, $p < 0.001$ in both cases). Female routes to and from the lek were run at a different speed than that recorded during usual daily routes (LME analysis, effect of movement type: $F_{2,913} = 3.064$, $p = 0.047$). While routes run to go or to leave lek were travelled with an average speed of 12.0 \pm 1.04 m/min, daily routes were run at a slower speed, both at dawn (9.41 \pm 0.26 m/min) and dusk (9.20 \pm 0.31 m/min) (LME pairwise comparisons, $p = 0.032$ and $p = 0.014$, respectively).

Merging the costs of travel to the benefits of low predation risk - We reported in Fig. 4a the travel cost required by females to move from hotspots to each hypothetical lek included within 300 x 300 squares. We showed in Fig. 4b the degree of predation risk for each of the hypothetical leks, as a function of the distance from the disturbed sector. In both maps, lighter was the colour, lower was the travel cost or the predation risk, respectively. Considering the same contribution from travel costs (50%) and predation risk (50%), we merged information given by the two maps (Fig. 4c) in order to show the area (indicated by the lightest colour) where it is detectable the best combination of the two benefits. The actual position of the lek SG was within this particular area of the study area.

Discussion

Our data support the female preference and the predator avoidance models - but not the hotspot one - as the most likely candidates able to explain the actual lek position in San Rossore (Table 3). This is in accordance with the idea that leks are usually located over hotspots of high female density more in birds than in ungulates (Balmford et al., 1993; Clutton-Brock et al., 1993; Höglund et al.,

	Field data (1997-2003)	Models' predictions		
		Female preference model	Hotspot model	Predator avoidance model
LEK VISITS (OCCURRENCE AND TIMING)	1.1	SUPPORTED	NOT SUPPORTED	SUPPORTED
	1.2	SUPPORTED	-	SUPPORTED
	1.3	SUPPORTED	NOT SUPPORTED	-
	1.4	SUPPORTED	NOT SUPPORTED	-
	2	SUPPORTED	NOT SUPPORTED	-
RELATIONSHIP AMONG POSITION OF LEKS AND FEMALE HOME RANGES AND MOVEMENTS	3.1	SUPPORTED	NOT SUPPORTED	-
	3.2	SUPPORTED	NOT SUPPORTED	-
	4	SUPPORTED	NOT SUPPORTED	-
	5.1	SUPPORTED	NOT SUPPORTED	SUPPORTED
	5.2	SUPPORTED	NOT SUPPORTED	-
	6	SUPPORTED	NOT SUPPORTED	SUPPORTED

Table 3 – The table showed which predictions of models on lek formation were supported or not using empirical data collected for 7 consecutive years in the lekking fallow deer population of San Rossore. See Table 1 for correspondence and details on each prediction.

1993; Höglund and Alatalo, 1995; Ryder et al., 2006). In our study, the majority of females reached the lek during the rut, confirming how females strongly prefer large clumps of males that can give them high mate choice opportunities (Alatalo et al., 1992).

Also almost all males used the lek, being the place where the highest mating success can be achieved (Apollonio et al., 1992; Festa-Bianchet et al., 1990). In accordance with what predicted by the female preference model (Bradbury and Gibson, 1983; Alatalo et al., 1992; Höglund and Alatalo, 1995) females commonly visited only one lek once (or twice, if mating did not occur during the first visit). That almost all males and females used the lek to mate can be, in turn,

beneficial for both sexes from a predation risk point of view due to dilution effect (Wiley, 1991; Höglund and Alatalo, 1995). Both leks were located far from the disturbed sector, a sector where it was highest the perceived predation risk by deer (Ciuti and Apollonio, 2008). A lek located within the disturbed sector ought be likely continuously dispersed by human presence, given that human habituation did not occur in deer of this area (Ciuti et al., 2004, Apollonio et al., 2005, Ciuti and Apollonio, 2008).

As showed by the timing and occurrence of marking activities around the lek, males arrived at the lek well before the arrival of females, and not vice versa, in contrast with what predicted by the hotspot model (Höglund and Alatalo, 1995). During the month spent in the lek area before the arrival of females, males establish and mark territories within the lek (Chapman and Chapman, 1997), as well as they make scent marking stations around the lek to establish an individual reference for dominance (Chapman and Chapman, 1997; Stenström et al., 2000). As a matter of fact, dominance hierarchy among fallow bucks is mainly established through non-contact interactions, presumably occurring during the pre-rut period (Apollonio et al., 1989; McElligott et al., 1999). Visual/olfactory marking activities are supposed to be important for male status signaling in male-male interaction as well as for mate choice by females (Stenström et al., 2000).

The lek SG was not located over high female traffic areas (no one female routes passed through the lek, except for that walked by females to reach the lek to mate), and it was spaced more than an average female home range diameter apart from the other lek. It was in contrast with the scenario predicted by the hotspot model (Höglund and Alatalo, 1995). To reach the lek, being commonly an area far from those used by females, females enlarged their home range sizes during the mating season. Females were closest to the lek area in summer than in autumn, when they gave birth in suitable birth places located between the lek and the sea (Ciuti et al., 2003; Ciuti et al., 2006). Our data showed that females, when males were already clumped in the lek territories, reached the lek during the oestrus time leaving foraging areas. This was done with faster and more straight movement than routes of females recorded at dawn and dusk by females, showing a strong motivation. The latter ones were walked by females to move from night and day feeding sites, and vice versa (Ciuti et al., 2004). According to the hotspot model (Bradbury and Gibson, 1983; Bradbury et al., 1986), routes to the lek ought to be shorter than usual (i.e. females visiting leks located in the middle of their usual path). And yet, our data showed the opposite, with routes to and from the lek longer nearly two times than usual daily routes.

The evolution and maintenance of lek-breeding behaviour remain unclear and the subject of controversy (Carbone and Taborsky, 1996; Clutton-Brock et al., 1996) According to Höglund and

Alatalo (1995), it is not possible to find a unique explanation of lek evolution. Of all mating systems, leks are the most difficult to explain within an evolutionary framework (Wiley, 1991; Höglund and Alatalo, 1995). Given the differences in the ecology, life histories, and habitat used by different species, it should not be surprising if the occurrences of leks in different ecological contexts can be explained by different set of factors. For instance, the hotshot model is the best explanation of lek formation in marine iguanas (*Amblyrhynchus cristatus*) (Wikelski et al., 1996). More recently, Jones & Quinnell (2002) supported the hotspot model as a possible mechanism promoting lek formation in sandfly (*Lutzomyia longipalpis*). In a recent paper, Young et al. (2009) strongly supported the female preference model in bower-building cichlid fish (*Nyassachromis microcephalus*). Contrasting results were found also for ungulates. In a study dealing with three ungulate species, Balmford et al. (1993) suggested that while the hotspot model may help in explaining broad patterns of male dispersion, further mechanisms are needed to generate the extent of territory clustering seen at leks. Clutton-Brock et al. (1992) showed the importance of harassment in favouring lekking in fallow deer, at least at high densities, but the avoidance of harassment by females was considered unlikely to explain lek evolution in topi (*Damaliscus lunatus*) (Bro-Jørgensen, 2002; Bro-Jørgensen, 2003) and Kafue lechwe antelopes (Nefdt, 1995).

Indeed, it is important to distinguish among the formation of a lek and its maintenance, two phenomena that may evoke different models even if considering the same study species. The evolution of leks could be initially enhanced according to different explanations, e.g. according to the hotshot model (Beehler and Foster, 1988) or the hotspot model (Bradbury and Gibson, 1983; Bradbury et al., 1986), but their maintenance or the selection of the best and longer lasting ones can be the end results of different selective pressures. It's our thought that it could have stirred up the debate on hypotheses on lekking. Accordingly, Bradbury and Gibson (1983) asserted that leks may be initially spaced according to hotspot process, but a subsequent evolution of female choice between leks would lead to typical inter-lek spacing of female preference model by eliminating interstitial leks. Clutton-Brock et al. (1993) suggested that once clustered mating territories have established according to harassment avoidance, the additional costs of mate choice are likely to be low, and female preferences for particular male characteristics may be likely to develop. On this subject, a further lek (lek Macchia Capraia MC) was present till the end of 1980's in San Rossore (Apollonio et al., 1998), when lek FO and lek SG were already monitored. The lek MC, that was less than a female home range diameter apart east from lek SG, i.e. the two leks were located within 1 km within each other (Apollonio et al., 1998), was considered a high female traffic during the rut (Apollonio et al., 1998). As a consequence, the hotspot model was evoked in the past in San

Rossore as likely candidate in explaining lek position, at least for the lek MC. The ecological context of San Rossore was different at that time, about 20 years ago. The disturbance in the eastern sector was lower than today (Apollonio et al., 2005; Ciuti and Apollonio, 2008), given that it increased during late 1980's and early 1990's. Furthermore, logging operations affected in 1987 areas near the lek MC that were used by females as travel routes, and this lek disappeared within the 3 following years (Apollonio et al., 1998). Thus, more theories can be evoked for lek formation and its maintenance, even if we consider the same study area and the same study species such as for the fallow deer population of San Rossore. Indeed, we have no historical data before the 1980's, the pattern of leks was eventually different, and we cannot explain how the actual leks were formed. However, the actual position of the lek allowed us to understand which selective pressures are working for its persistence.

Indeed, the actual position of lek SG in San Rossore is maintained by two selective pressures: the female preference and the predator avoidance. Among the many hypothetical positions of the lek which can be assumed for a lek in our study site according to the predator avoidance (far from the eastern disturbed sector) and the female preference (a large clump of males visited by females even if not located over female high traffic), the actual position is that able to merge and to maximize these two benefits. Low travel cost for females and low predation risk are likely to be the selective pressures which allowed the maintenance of the lek on its actual position, which is a handy position for the whole female population using that lek. That a lek should be handy was predicted by Oring (1982) many years ago: 'males ought to display at the site having the lowest cumulative distance from the activity centres of all females of the population'. Males cluster in a site when is highest the chance to mate (Apollonio et al., 1992), females go there because prefer large clump of males that can give them high mate choice opportunities (Alexander, 1975; Bradbury, 1981; Beehler and Foster, 1988; Alatalo et al., 1992), and the position of such a handy cluster is favoured by low predation risk and travel cost for females.

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Chapter 2



Benefits of a risky life for fallow deer bucks (*Dama dama*) aspiring to patrol a lek territory

**Benefits of a risky life for fallow deer bucks (*Dama dama*)
aspiring to patrol a lek territory**

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Summary

Little is known about the relation between male ungulates' ability to adopt a successful mating strategy during the rut and certain foraging strategies before the rut. In highly polygynous species such as many cervids, males are regarded as pure capital breeders, in that they allocate the energy stored in spring and summer to reproduction. According to the reproductive strategy-predation risk hypothesis, optimal foraging strategies adopted before the rut may imply a risk because, in order to invest in body size, males exploit the best feeding areas, even though characterized by higher predation risk. We performed a 9-year research through monitoring 31 fallow bucks in the lekking population of San Rossore, Italy. Among the mating strategies adopted by males, defence of the lek territory was repeatedly shown to be the most successful one. A sector of the study area was characterized by the highest meadow productivity and the highest predation risk. We showed that only those males that were able to exploit the best feeding and yet risky areas before the rut, hereby adopting an optimal foraging strategy and investing in body size, were subsequently able to defend a lek territory and achieve a high mating success during the rut.

Keywords: lekking, fallow deer, reproductive strategy-predation risk hypothesis, mating success, territoriality, *Dama dama*.

Introduction

Males and females typically differ in the factors that limit their reproductive success, and this is especially the case for highly sexually dimorphic birds and mammals (Darwin, 1871; Andersson, 1994). In highly polygynous species, as is the case with many ungulates, females are limited mainly by their effort to raise young successfully (Clutton-Brock et al., 1982; Davies, 1991), while males are rather limited by the fierce fights they have in order to gain access to mates during the rutting season (Clutton-Brock et al., 1982; Geist, 1986; Festa-Bianchet et al., 1990; Komers et al., 1994). When two or more male mating strategies are found within the same population, evolutionary theory predicts that each male should choose the strategy that will confer him the greatest reproductive success, suggesting that a highly costly choice can lead to a high benefit. Such a huge reproductive effort in male ungulates originates from fighting with other males for access to females, patrolling territories, roaring and tending females (Mysterud et al., 2004, and references therein). High cost-high benefit mating strategies may entail huge weight loss (Leader-Williams & Ricketts, 1981; Pérez-Barbería et al., 1998; Mysterud et al., 2005), increased predation risk (Jakobson et al., 1995), antler wounding and fatal injuries during combats (Kitchen, 1974; Leslie & Jenkins, 1985; Geist, 1986; Bartos et al., 2007). Thus, during the rut males face a dilemma, the solution of which considerably depends on their body conditions (Apollonio et al., 1992; Balmford et al., 1992; McElligott & Hayden, 2000; McElligott et al., 2001): to adopt a high cost-high benefit mating strategy or to fall back on a low cost-low benefit mating strategy?

Surprisingly, little is known about the relation between male ungulates' ability to adopt a high cost-high benefit mating strategy during the rut and the behavioural strategy adopted before the mating season, when males are expected to enhance their condition and to invest in body size. Specifically, quantitative data on spatial and foraging strategies adopted by ungulate males before the mating season are lacking. In highly polygynous species such as many cervids, males are usually regarded as pure capital breeders, in that they allocate to reproduction the energy stored (mainly fat) in spring and summer (Stearns, 1992; Jönsson, 1997). These reserves are crucial to face the rut, especially for those ungulate males who experience feeding cessation (in fallow deer *Dama dama*: Apollonio & Di Vittorio, 2004; in red deer *Cervus elaphus*: Mysterud et al., 2008). According to the reproductive strategy-predation risk hypothesis, optimal spatial and foraging strategies adopted before the rut may imply a risk, since males are supposed to exploit the best feeding areas (even though characterized by higher predation risk) in order to invest in body size and fighting ability (Main et al., 1996; Bleich et al., 1997; Ruckstuhl & Neuhaus, 2000; Ruckstuhl & Neuhaus, 2002; Mooring et al., 2003). According to that, males may choose whether or not to exploit the best but risky foraging

areas before the mating season. This choice, in turn, arguably plays a key role in affecting the chance to optimally invest in body size and the ability to adopt a successful mating strategy during the following rut.

The fallow deer of San Rossore as a case of study

Within this scenario, we performed a 9-year research through monitoring 31 fallow bucks in the lekking population of San Rossore, Italy. In this study area, a long term process (1984-2003) has led the fallow deer population to show a marked large-scale spatial sexual segregation outside the rut (Ciuti et al., 2004; Apollonio et al., 2005; Ciuti & Apollonio, 2008). The study area (Figure 1) can be divided into two main sectors. The eastern sector (disturbed sector) was characterized by intense predation risk because affected by intense human presence (Apollonio et al., 2005), being the human-induced mortality the most important cause of death of fallow deer. The origin of the long-term process leading to large spatial sexual segregation was exactly the increase of human presence (perceived as predation risk) in the disturbed sector from 1984 onwards. Since 1984 females gradually abandoned the disturbed sector, where disturbance strongly increased, while males did not (Apollonio et al., 2005). Furthermore, Ciuti & Apollonio (2008) showed that while females increased their presence in the undisturbed sector, males gradually but significantly abandoned this area from 1989. In fact, contrary to the females' flow towards the undisturbed sector, males gradually increased their presence in the disturbed sector and avoided areas with high and constantly increasing female density, thus benefiting from a lower female density. As showed in Figure 1, there are only two large meadows in the study area, one each in the disturbed and undisturbed sector. On account of the over-browsing recorded in the undisturbed pasture, crowded with females, relative grass availability was assessed to be lower than in the disturbed sector (Ciuti & Apollonio, 2008). In short, males were not able to forage efficiently in the only large pasture of the undisturbed sector (Illius & Gordon, 1987), being this over-crowded by females that escaped from disturbance (Figure 1; Ciuti & Apollonio, 2008). The disturbed sector was characterized not only by a higher predation risk (Ciuti & Apollonio, 2008), but also by a higher predation rate when compared to the undisturbed sector. From 1996 to 2004, 394 deer were legally shot by game keepers using rifle guns in the 466 ha disturbed sector, while 244 deer were shot in the 2,640 ha undisturbed sector. Thus, the predation rate in the disturbed sector was 9.4 deer per 100 ha per year, more than 9 times higher than that recorded in the undisturbed sector: 1.0 deer per 100 ha per year (San Rossore game keepers, official data). A long-term consequence of this process was that males

living in the disturbed sector benefited from higher resource availability as well as lower female competition, even though being subject to the highest predation risk (Ciuti & Apollonio, 2008).

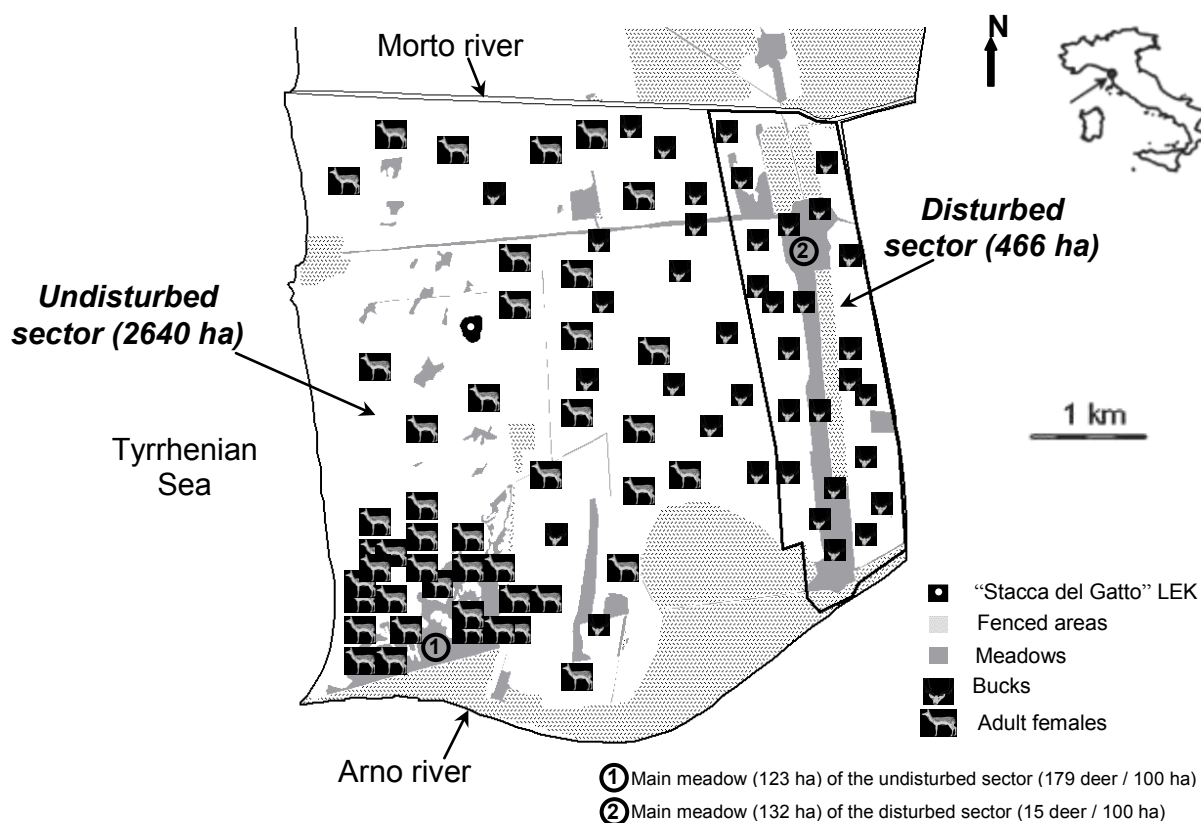


Figure 1 - Large scale spatial sexual segregation occurring before the rut in the San Rossore Estate, as showed in a concurrent study by Ciuti & Apollonio (2008). While males mainly occupied the eastern disturbed sector, females were present in the western undisturbed sector only, almost concentrated on its main meadow. During the rut, males usually moved from the disturbed sector to the lek, a traditional mating arena located in the undisturbed sector. Meadows and fenced areas where deer were not allowed are shown in the map. The two main meadows of the Estate (one each inside the disturbed and the undisturbed sectors) are indicated by numbers, along with corresponding deer density (Ciuti & Apollonio 2008).

Within such a peculiar ecological context, and given the existence of a risky but rich sector of the Estate, we aimed to show how spatial and foraging tactics adopted by fallow bucks in spring and summer (before the rut) may affect the adoption of a successful mating strategy during the rut in autumn. During the rut, males of this population could defend territories that were single, clumped in lek, or satellite to lek (Apollonio et al., 1992). The most successful males in terms of mating success were repeatedly shown to occur in lek (Apollonio et al., 1989, 1992), while males that adopted alternative strategies, such as the temporary defence of a single territory, were not as successful (Apollonio et al., 1992). Body condition appeared to be an important determinant of

male copulatory success, because only males in superior condition could defend a lek territory for up to 3 weeks, thus sustaining a high fighting rate (Apollonio et al., 1989; Festa-Bianchet et al., 1990).

Following the reproductive strategy-predation risk hypothesis' rationale (Main et al., 1996), we aimed to test the hypothesis that only those males that were able to exploit the best feeding areas of the disturbed sector (even though characterized by higher predation risk) and therefore to invest in body size and fighting ability before the rut, were consequently able to gain a higher mating success during the rut than males that were not as able to exploit the risky sector of the study area.

Material and methods

Study area

We performed this study in the 4,650-ha San Rossore Estate in central Italy (43° 43' N; 10° 19' E), a fenced area characterized by low elevation plains and a sub-Mediterranean climate (see Ciuti & Apollonio, 2008 for detailed habitat description). We collected data in the area between the Morto and the Arno rivers (Figure 1), where a traditional lek site, "Stacca del Gatto", has been monitored since the 1980's.

Captures of Bucks

During winter time, from 1996 to 2001, bucks (age > 4 y.o.; see Table 1 for yearly sample size) were driven by game keepers into 5 different corrals of the Estate, hand caught and blindfolded, aged by tooth eruption and wear (Chapman & Chapman, 1997), ear tagged, fitted with Televilt (Lindesberg, Sweden) radiocollars, and finally released. We enlarged the sample size when we captured more bucks (and re-captured 10 collared males; Table 1) in late October 1999 by means of vertical drop nets placed close to the lek. On this occasion males were also measured (shoulder height and hock length) and weighed.

Direct Observations of Lek Activities

From 1996 to 2004, we carried out daily observations on the lek (2,230 hours in total) from 2 fixed hides, from dawn to dusk (*sensu* Apollonio et al., 1989). Continuous observations began when territorial defense was first reported and ended when defense was no more reported. The rut occurred every year in October and was defined as the time between the first and the last recorded copulation. For each buck we collected the time of lek use, territory ownership, mating success

(number of copulations), and number of real and border fights in which they were involved, as descriptor variables of mating behaviour (Apollonio et al., 1989).

	rut 1996		rut 1997		rut 1998		rut 1999		rut 2000		rut 2001		rut 2002		rut 2003		rut 2004	
	age	mating strategy	age	mating strategy	age	mating strategy	age	mating strategy	age	mating strategy	age	mating strategy	age	mating strategy	age	mating strategy	age	mating strategy
male 305	9	T	10	NT	11	NT	12	NT*										
male 425	5	NT	6	NT	7	ST	8	ST	9	T	10	ST						
male 165	6	T	7	ST	8	T	9	T	10	T	11	T						
male 355	6	NT	7	NT	8	NT	9	ST	10	ST	11	NT	12	NT*	13	NT	14	NT
male 345	9	T	10	ST	11	T	12	NT	13	NT								
male 670	7	T	8	T	9	NT	10	NT*										
male 375	7	NT	8	T	9	T	10	T										
male 386	7	ST	8	ST	9	T	10	ST										
male 3951	?	T																
male 570			7	T	8	T	9	T	10	NT	11	ST	12	ST				
male 650						ST												
male 530					8	T	9	NT*	10	ST								
male 3651					?	NT												
male 1850							6	T										
male 175							4	NT	5	ST	6	T	7	T				
male 195							5	T	6	ST								
male 205							9	NT	10	NT								
male 215							7	NT	8	T	9	T						
male 225							5	NT	6	T	7	NT	8	ST				
male 285							4	NT	5	T	6	T	7	T				
male 395							12	NT	13	NT								
male 365							7	T	8	T	9	ST	10	T	11	NT	12	ST
male 3150							7	NT										
male 295							6	NT	7	T	8	ST	9	T	10	T	11	NT
male 235							10	NT										
male 265							9	NT										
male 145							7	NT	8	NT	9	ST	10	NT	11	NT	12	NT
male 315											9	NT						
male 3952											6	ST	7	T				
male 185											6	NT						
male 2051											5	NT	6	NT				
Sample Size	n = 31	n = 9	n = 9	n = 12	n = 24	n = 16	n = 15	n = 10	n = 4	n = 4								
Lek use		100%	100%	100%	87.50%	100%	100%	90%	100%	100%								

T = Territorial males; ST = Short-term Territorial males; NT = Non Territorial males (* if they were never observed inside the lek site)

Table 1 – Mating strategies adopted by 31 bucks from 1996 to 2004 according to direct observations performed on the lek. Individual age is reported along with mating strategy adopted each year, while yearly sample size and lek use are reported below.

During the rut, we daily searched and observed the males absent from the lek using predictive radio-tracking (White & Garrott, 1990) to ascertain any possible territory ownership outside the lek. Televilt RX-8910 HE receivers and four-element handheld Televilt Yagi antennas were used.

Radio-tracking during and before the mating season

From 1996 to 2002, during each mating season (from early September to late November), we located all males twice a day (1 fix every 12 hours). We calculated the locations (uniformly distributed over the day and the night) by triangulation (see Table 1 for yearly sample size). Before the mating season (i.e., in spring and summer, from 1996 to 2004), we made at least 18 monthly locations per animal, uniformly distributed over the day and the night, and always taken at least 12 h apart. In summer 2001 (n = 15 bucks) and summer 2002 (n = 10 bucks), we further performed

special 4-hour continuous radio-tracking sessions (1 fix every 15 minutes) to track male foraging routes ($n = 220$ routes) at dawn and dusk. By the end of this research, we collected 15,810 and 5,120 fixes through discontinuous and continuous radio-tracking, respectively.

Meadows productivity inside and outside the disturbed sector

Following Carranza & Valencia (1999), in spring-summer 2001-2004 we measured the absolute grass productivity in the two main meadows of the study site (inside and outside the disturbed sector, respectively; Figure 1). In both areas, all measurements were made along the same fixed linear transect, at five sampling points located within 10 m of each other. At each sampling point and in the area of approximately 1 m around it, we dropped a square of 30×30 cm and measured the percentage of grass cover inside it. The operation was carried out for four times for each sampling point and its outcomes proved to be strongly correlated to the biomass (in terms of dry mass) (Carranza & Valencia, 1999).

Data analyses

We used hierarchical cluster analysis to classify fallow bucks into 3 homogeneous groups according to the mating strategies adopted during the rut. For this analysis we used only the observational data collected on the lek (number of copulations, number of border fights, time of lek use). We adopted the between-groups linkage method and the squared Euclidean distance with a maximum of 3 clusters; the data were transformed into standardized values (z-scores) (Norusis 1998). As a general rule, the mating strategy assigned to each male by cluster analysis using observational data only was associated to the behavioural data collected by means of radio-tracking before (spring-summer) and during (autumn) the mating season.

Using ArcView 3.2, we defined the arrival date at the lek for each male as the day when the first fix was recorded within a 300-m diameter buffer zone around the lek center, while the departure date was assumed to be the day of the last recorded fix within the same area. Dates were standardized as number of days after August the 10th, i.e. the earliest arrival date of a male to be recorded from 1996 to 2004. Duration of the stay at the lek area (lek attendance period) was defined individually as the period between arrival and departure date.

We used Ranges VI software (Kenward et al., 2003) and the Kernel (Worton, 1989) method to evaluate the home range contour line. We computed the home ranges of lek attendance period (Kernel 95%; time interval as defined above), home ranges of rut (Kernel 25%, 50%, and 75%; time interval: between the first and the last copulation recorded on the lek), and spring (Mar.-May) and summer (June-Aug.) home ranges (Kernel 95%). Using ArcView 3.2, we computed the distances

between the lek center and the center of home ranges of lek attendance period, as well as the degree of overlap between seasonal home ranges and the disturbed sector of the Estate. Male foraging routes recorded in summer at dawn and dusk were processed in the GIS environment using the ArcView animal movement extension (v. 2.04 beta).

Given the asymmetric structure of our data, with several individuals repeatedly observed through different years (Table 1), we adopted a statistical approach designed to avoid pseudoreplication of data (Pinheiro & Bates, 2000). We modelled the variation of each dependent variable using Linear Mixed-Effects (LME, Pinheiro and Bates 2000) models, considering deer identity as repeated through years (random factor), the mating strategy as a fixed factor and the age of bucks as a covariate. In models with further time subdivisions, the random effect structure was modified accordingly. LME pairwise comparisons were used to test differences within each fixed factor of each model. Dependent variables were successfully tested for normality (Kolmogorov-Smirnov test) and homoscedasticity (Levene test) after data transformation, that was necessary for the following dependent variables: number of copulations observed on the lek (log-transformed), percentage degree of overlap between home range and the disturbed sector (arcsin-sqrt transformed), and seasonal home range sizes (log-transformed).

We computed the degree of overlap between seasonal home ranges and the disturbed sector of the Estate in males who changed mating strategy through the years. We tested for differences in such a variable according to varying mating strategies using the t-test for paired samples.

To assess seasonal habitat selection, we used compositional analysis (Aebischer et al., 1993). We examined the habitat use within the home range by comparing the proportion of fixes in each habitat with the proportion of the habitat in the Kernel 95% contour line (hence on a fine scale, level II of analysis, Aebischer et al., 1993). We computed the compositional analyses and statistics with an Excel macro (Smith, 2003), through which we also carried out the randomization procedure recommended by Aebischer et al., 1993. Habitat types were ranked in order of use from most to least selected. For each seasonal compositional analysis of male habitat selection, we reported Wilk's lambda (λ) and randomized p (p_r) values, and t statistic and p_r value for each significant difference among different ranks. We had no case of unused habitats in our database of resources used by monitored deer. Therefore, misclassified resource selection was avoided (Bingham et al., 2007). We tested for differences in habitat use among years, seasons, and mating strategies by adding these parameters as independent variables in the Wilk's log-ratio matrices, and analyzing these matrices by a MANOVA test (Aebischer et al., 1993). Post hoc comparisons were performed using the MANOVA Tukey post-hoc.

Body weights of males captured in late October 1999 either able or not to defend a lek territory were compared using the t-test for independent samples.

We modeled the variation of grass cover using a Generalized Linear Model (GLM; Gaussian distribution of the dependent variable). We considered sector of the Estate (disturbed/undisturbed), year (2001-2004) and month (March-August) as fixed factors in the model.

All correlations were fitted using the Pearson correlation coefficients. All analyses were run in SPSS 13.0. Means \pm SE are given.

Results

Mating behaviour of bucks during the rut

We classified bucks by means of hierarchical cluster analysis into 3 homogeneous groups (Table 1), namely Territorial (T) males, Short Term Territorial (ST) males, and Non Territorial (NT) males. We reported key descriptive statistics of male mating behaviours in Table 2. Males' mating success (log-copulations) differed according to the mating strategies adopted (LME model $F_{2,70} = 17.380$, $p < 0.001$). T males had higher mating success than ST males ($p < 0.001$) and NT males ($p < 0.001$), while ST males and NT males did not significantly differ in terms of number of copulations ($p = 0.476$). Males differed in the time spent (minutes) on the lek (LME model, effect of mating strategy $F_{2,70} = 67.583$, $p < 0.001$). ST males spent less time on the lek than T males ($p < 0.001$), and more than NT males ($p = 0.001$) (Table 2). We did not detect any significant effect of individual age in both models (LME model for number of copulation: $F_{1,70} = 0.411$, $p = 0.524$; LME model for minutes of lek use: $F_{1,70} = 0.195$, $p = 0.660$).

Spatial behaviour of bucks during lek attendance

The mean arrival date of bucks (who reached the lek every year despite their ability to defend a territory) to the lek was 15 September (36.8 ± 0.9 days after 10 August), well before the first mating observed on the lek (5 October ± 0.5 days), with no difference recorded among males adopting different mating strategies (LME model $F_{2,66} = 0.425$, $p = 0.655$). This also applied to the mean departure date from the lek (LME model $F_{2,61} = 0.465$, $p = 0.631$), which occurred around 31 October (82.7 ± 2.0 days after August 10th). The last copulation on the lek was observed around 20 October (± 0.6 days). Finally, the average duration of lek attendance period (46.1 ± 2.4 days) did not significantly differ among males (LME model: effect of mating strategy $F_{2,61} = 0.603$, $p = 0.550$). We did not detect any significant effect of individual age on the duration of lek use (LME

model for arrival date $F_{1,66} = 1.489$, $p = 0.227$; LME model for departure date: $F_{1,61} = 0.663$, $p = 0.419$; LME model for lek attendance period: $F_{1,61} = 0.128$, $p = 0.292$).

Mating strategy	Descriptor variables of mating behaviours (measure unit inside parentheses)	Sum	Mean	SE
Territorial males	Copulations (#)	197	3.6	1.1
	Border fights (#)	303	10.1	1.6
	Real fights (#)	183	6.1	0.9
	Days of lek use (days)	502	16.7	1.0
	Minutes of lek use (min)	222,547	7,418.2	593.2
Short term Territorial males	Copulations (#)	5	0.2	0.1
	Border fights (#)	47	2.2	0.5
	Real fights (#)	38	1.8	0.4
	Days of lek use (days)	218	10.3	1.0
	Minutes of lek use (min)	53,205	2,533.6	320.3
Non Territorial males	Copulations (#)	0	0	0
	Border fights (#)	0	0	0
	Real fights (#)	6	0.3	0.1
	Days of lek use (days)	51	2.4	0.7
	Minutes of lek use (min)	2,217	105.6	37.1

Table 2 – Descriptive statistics of the mating behaviours of 31 bucks from 1996 to 2004 (see Table 1 for yearly sample size). Males were grouped according to 3 mating strategies by means of cluster analysis (see the text for major details). Border fights were assumed to involve 2 males defending close lek territories, just to remark territory borders, for few seconds. Real fights were assumed to end with a loser and a winner, the latter preserving his own territory or gaining control of a new one.

We found significant differences in home range (Kernel 95%) sizes of lek attendance period (the period between arrival and departure date defined individually) among males adopting different mating strategies (LME model, $F_{2,67} = 8.199$, $p = 0.001$). T males occupied ranges (105.3 ± 21.3 ha) which did not differ from those recorded for ST males (131.5 ± 24.3 ha; $p = 0.574$), while NT males occupied larger home range sizes (222.1 ± 24.3 ha) than T males ($p < 0.001$) and ST males ($p = 0.003$).

The distance between the centre of the lek and that of the home ranges of lek attendance period significantly varied among males adopting different mating strategies (LME model $F_{2,67} = 20.457$, $p < 0.001$). The low distance recorded for T males (160.5 ± 27.6 m) and ST males (166.5 ± 25.9 m) did not differ ($p = 0.847$). In contrast, the home range centres of NT males were more distant from

the lek center (689.7 ± 115.3 m) than those of T and ST males ($p < 0.001$ in both cases). We did not detect any significant effect of age of bucks on spatial behaviour (LME model for home range of lek attendance period: $F_{1,67} = 2.505$, $p = 0.118$; LME model for distance between lek center and home range center: $F_{1,67} = 0.017$, $p = 0.896$).

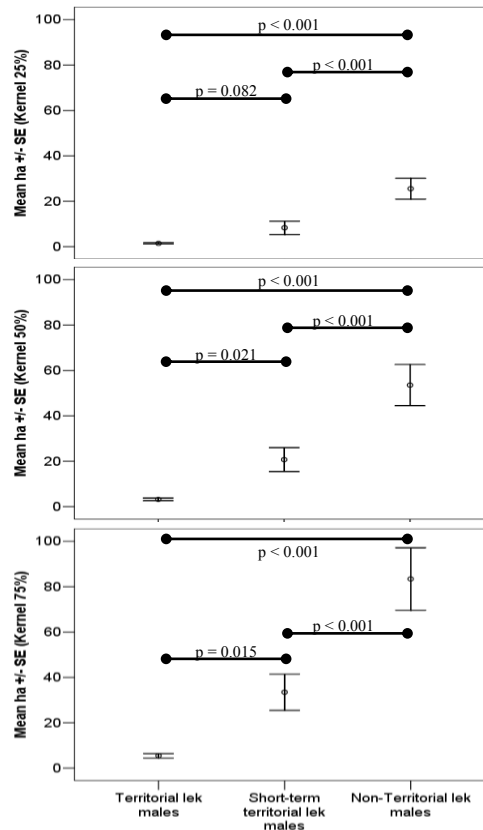


Figure 2 – Home range sizes of bucks during the rut (i.e., the period included between the 1st and the last copulation observed on the lek) computed with the Kernel 25% (top panel), the Kernel 50% (middle panel), and the Kernel 75% (down panel). Bucks were grouped according to the mating strategy adopted, as shown on the x axis. Differences among home range sizes of males adopting different mating strategies were reported on each graph (LME pairwise comparisons).

Home range recorded during the rut (Figure 2), i.e. the period of time between the first and the last copulation recorded on the lek, significantly varied among males adopting different mating strategies (LME models: K25%: $F_{2,70} = 16.901$, $p < 0.001$; K50%: $F_{2,70} = 19.591$, $p < 0.001$; K75%: $F_{2,70} = 20.014$, $p < 0.001$), regardless of the age of bucks (K25% $F_{1,70} = 0.131$, $p = 0.718$; K50%: $F_{1,70} = 0.072$, $p = 0.789$; K75%: $F_{1,70} = 0.188$, $p = 0.666$).

Spatial behaviour of bucks before the rut with respect to the disturbed sector

The overlap between spring and summer home ranges (Kernel 95%) and the disturbed sector differed among males adopting different mating strategies (LME model: $F_{2,159} = 8.166$, $p < 0.001$). Summer home range isopleths are shown in Figure 3. We did not detect any difference in the degree of overlap between spring and summer ranges and the disturbed sector between T males (71.7 ± 4.3 %) and ST males (61.3 ± 6.4 %) ($p = 0.221$). In contrast, NT males (43.3 ± 5.5 %) showed a lower use of the disturbed sector than T males ($p < 0.001$) and ST males ($p = 0.020$). Age did not significantly affect the degree of use of the disturbed sector by T and ST males (Pearson correlation coefficient: T males $n = 61$, $r_p = 0.215$, $p = 0.101$; ST males $n = 40$, $r_p = -0.086$, $p = 0.599$), while NT males use of the disturbed sector increased with increasing age ($n = 58$, $r_p = 0.351$, $p = 0.007$).

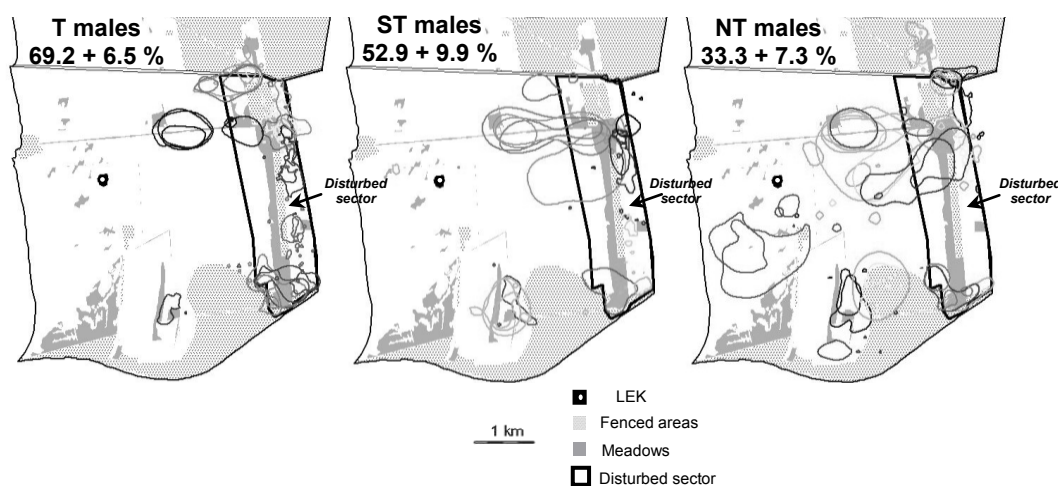


Figure 3 – Localization of home ranges (Kernel 95% isopleths; bucks $n = 26$, from 1996 to 2002) recorded in summer (thus before the rut) with respect to the Eastern disturbed sector. Males were grouped according to the mating strategy adopted during the following autumnal rut (Territorial males, left map; Short term Territorial males, central map; Non Territorial males, right map). Different grey tonalities correspond to different individuals. Average overlaps (\pm SE) of summer home ranges over the disturbed sector were reported on each map.

As regards the individual history of the bucks who changed mating strategy during the study period, T males that became ST males (or vice versa) did not significantly changed the degree of home range/ disturbed sector overlap (76.6 ± 4.9 % and 68.4 ± 5.8 %, respectively) (paired sample t-test: $n = 29$, $t = -0.677$, $p = 0.504$). This was also the case with ST males that became NT males (42.8 ± 6.6 %) and NT males that became ST males ($n = 18$, $t = 1.218$, $p = 0.240$). In contrast, T males that became NT males (and vice versa) significantly decreased their use of the disturbed sector ($n = 19$, $t = -3.109$, $p = 0.006$).

To verify whether territorial males were apart before the breeding season, we computed the yearly degree of overlap of spring and summer home ranges in the disturbed sector among those males that were observed to defend a lek territory in the following mating season (both ST and T males). This figure was always low (1996: $n = 5$, 2.0 ± 5.7 %; 1997: $n = 4$, 0 ± 0 %; 1998: $n = 8$, 8.4 ± 19.8 %; 1999: $n = 6$, 4.3 ± 17.9 %; 2000: $n = 10$, 3.4 ± 13.9 %; 2001: $n = 10$, 4.0 ± 16.7 %; 2002: $n = 6$, 1.2 ± 4.0 %).

Meadows productivity inside and outside the disturbed sector

In spring and summer, the grass cover of the main meadow (Figure 1) of the disturbed sector (75.7 ± 2.0 %) was higher than that of the main meadow of the undisturbed sector (56.7 ± 3.5 %) (GLM: effect of year $F_{3,48} = 0.869$, $p = 0.466$; effect of sector $F_{1,48} = 22.745$, $p < 0.001$; effect of month $F_{5,48} = 1.393$, $p = 0.249$).

Home range sizes and home range use of bucks before the rut

In spring and summer, we found significant differences in the home range size (Kernel 95%) of males adopting different mating strategies (LME model $F_{2,138} = 6.389$, $p = 0.002$), while no significant seasonal difference was found ($F_{1,138} = 1.472$, $p = 0.227$). NT males showed larger home range sizes (74.9 ± 14.4 ha) than T males (58.4 ± 10.3 ; $p = 0.029$) and ST males (50.9 ± 7.2 ha; $p = 0.027$), while T and ST males did not differ ($p = 0.843$). Age of bucks significantly affected home range sizes ($F_{1,138} = 6.672$, $p = 0.011$). Specifically, males adopting different mating strategies showed different home range sizes according to their age (combined effect age * mating strategy $F_{2,138} = 5.163$, $p = 0.007$). This was because age and home range sizes were significantly inversely correlated in NT males only (Pearson correlation coefficient NT males $n = 40$, $r_p = -0.615$, $p < 0.001$; T males $n = 58$, $r_p = -0.243$, $p = 0.067$; ST males $n = 40$, $r_p = 0.121$, $p = 0.456$). As regards the within summer home range use, the variables obtained from the foraging routes of males at dawn and dusk (total length, MCP area, speed, and maximum distance covered; Table 3) were significantly correlated ($r_p > 0.409$, $p < 0.004$).

Therefore, we modelled the variation of the best descriptor (the MCP area) according to mating strategy and age. Such a variable differed among males (LME model effect of strategy $F_{2,48} = 5.267$, $p = 0.009$) and according to the age of bucks ($F_{1,48} = 4.804$, $p = 0.033$), being the age inversely correlated to the area occupied along the routes ($n = 48$, $r_p = -0.337$, $p = 0.019$). NT males occupied larger areas along their routes than T males ($p = 0.009$) and ST males ($p = 0.004$); T males and ST males did not differ ($p = 0.602$).

Mating strategy	Descriptor variables of individual routes (measure unit inside parentheses)	Mean	SE
Territorial males	MPC area (ha)	2.6	0.5
	Total distance covered (m)	691.4	54.5
	Speed (m/min)	3.2	0.3
	Max distance among consecutive fixes (m)	206.1	32.1
Short term Territorial males	MPC area (ha)	1.6	0.3
	Total distance covered (m)	659.8	51.5
	Speed (m/min)	2.9	0.2
	Max distance among consecutive fixes (m)	189.9	35.9
Non Territorial males	MPC area (ha)	7.4	2.5
	Total distance covered (m)	942.5	172.2
	Speed (m/min)	4.1	0.7
	Max distance among consecutive fixes (m)	330.4	47.4

Table 3 - Descriptive statistics of foraging routes travelled at dawn and dusk by 15 bucks during summer 2001 and summer 2002. Males are split according to the strategy adopted during the following mating season.

Habitat selection and use by bucks before the rut

When the proportion of fixes in each habitat was compared with the proportion of the habitat in the Kernel 95% contour line, compositional analysis (1,000 interactions) revealed a significant departure from random use in spring and summer for all males (Table 4).

Season	Mating strategy	Wilk's λ	Randomized p	Ranked variable sequence (most to least used)
Spring	T males	0.0778	< 0.001	MDW > ME >>> PW > WMDW > O >>> MA
	ST males	0.2874	< 0.001	MDW > ME > PW > WMDW > O > MA
	NT males	0.1683	< 0.001	MDW > PW > ME > WMDW > O > MA
Summer	T males	0.3316	< 0.001	ME > MDW > WMDW > PW >>> O > MA
	ST males	0.2037	< 0.001	MDW > ME > WMDW > PW > O > MA
	NT males	0.3645	0.003	PW > MDW > ME > WMDW > O > MA

>>> denotes a significant difference between consecutively ranked variables. ME meadows; MDW mixed deciduous woods; PW pine woods; O oak plantation; WMDW wet mixed deciduous woods; MA marshes. T males: Territorial males, ST males: Short Term Territorial males; NT males: Non Territorial males.

Table 4 – Habitat selection of 26 bucks from 1996 to 2002 according to seasons (spring & summer) and the mating strategies adopted during each following rutting period (autumn), as revealed by compositional analysis after 1000 interactions.

The analysis of Wilk's log-ratio matrices using MANOVA did not reveal significant differences in habitat use recorded through the years (Wilk's $\lambda = 0.719$, $F_{6,142} = 1.334$, $p = 0.115$), and slight differences only between spring and summer seasons (Wilk's $\lambda = 0.919$, $F_{1,142} = 2.037$, $p = 0.078$). More in detail (Table 4), we detected major differences in the selection of meadows (ME), mixed deciduous woods (MDW) and pine woods (PW) among males adopting different mating strategies during the following rut. In spring, T males significantly selected MDW and ME over PW ($t = 2.577$, $p_r = 0.017$, and $t = 2.379$, $p_r = 0.027$, respectively), while selection of the same was slightly over the limit of significance for ST males ($t = 2.101$, $p_r = 0.064$, and $t = 2.324$, $p_r = 0.054$, respectively), and not significant for NT males ($t = 1.358$, $p_r = 0.216$, and $t = -0.347$, $p_r = 0.740$, respectively), that selected PW over ME (Table 4). In summer, T males significantly selected MDW and ME over PW ($t = 2.254$, $p_r = 0.041$, and $t = 3.452$, $p_r = 0.003$, respectively). The same applied to ST males ($t = 3.781$, $p_r = 0.004$, and $t = 2.492$, $p_r = 0.022$, respectively), but not to NT males ($t = -0.919$, $p_r = 0.337$, and $t = -1.724$, $p_r = 0.092$, respectively), that actually selected PW over both MDW and ME (Table 4).

The major differences found in habitat selection were confirmed by habitat use analysis: significant differences among males adopting different mating strategies were found (MANOVA Wilk's $\lambda = 0.829$, $F_{2,142} = 2.274$, $p = 0.015$). These differences were accounted for by differences in the use of meadows (tests of between-subjects effects $F_{1,142} = 6.862$, $p = 0.002$). Major differences were detected in the use of meadows between T males and NT males (Tukey post-hoc test: $p = 0.032$), while ST males showed an intermediate level of use when compared to T males ($p = 0.695$) or NT males ($p = 0.263$).

Body size of bucks during the rut

Age and body weight of males were not correlated (Spearman correlation coefficient $n = 22$, $r_p = -0.171$, $p = 0.447$), nor body weight and body size (hock length $n = 22$, $r_p = -0.032$, $p = 0.889$; shoulder height $n = 22$, $r_p = 0.005$, $p = 0.822$). Males that were able to defend a territory in the lek (T males and ST males: $n = 7$, 77.0 ± 2.4 kg) were heavier than NT males ($n = 15$, 70.0 ± 1.8 kg) (t-test for independent samples $t = 2.245$, $p = 0.036$).

Discussion

Regardless of the individual mating strategy adopted, every year fallow bucks moved to the lek at very much the same time in early September. Likewise, in a study conducted by Davini et al. (2004) in the same study site, males were reported to leave foraging areas and reach the lek as the summer

ends. A similar timing of mating activities was previously showed in fallow deer by Braza et al. (1986) in Spain. The fact that males move to the lek well before the first observed copulation was likely due to their need to establish and mark territories, as well as to make scent marking stations around the lek area to establish an individual reference for dominance. Dominance hierarchy among fallow deer bucks is mainly established through non-contact interactions, presumably occurring during the pre-rut period (Apollonio et al., 1989; McElligott et al., 1999). Marking activities are supposed to be important for male status signaling in male-male interaction as well as for mate choice by females (Stenström et al., 2000).

Territory defense ability, even though often lasting a short portion only of the rut period (e.g. ST males), did not seem to be a privilege of a few males in our study site. Among males sampled from 1996 to 2004 (Table 1), 22 out of 31 (71%) defended a lek territory at least once. The figure would raise to 86% (19/22) if we considered only the deer monitored for at least two consecutive years. Among them, however, the mating success was significantly skewed towards T males, i.e. those males that, according to previous studies on lekking as well as non-lekking populations, spend more time in defending the territory (Apollonio et al., 1992; McElligott & Hayden, 2000). The duration of lek territory defense was shown to be the major correlate of male copulatory success (Apollonio et al., 1989; San José & Braza, 1997) as reported for other lekking species (Gibson & Bradbury, 1985; Halliday, 1987). ST males were able to defend a lek territory for a short time and their mating success was scarce, like that recorded for NT males. Apollonio et al. (1992) showed a similarly skewed pattern of mating success in another lek in San Rossore in the 1980s, with only few territorial lekking males achieving nearly 40 copulations during a rut, while the rest of the males achieved less than 10 copulations (a similar figure was reported for many T males in our study), and even no copulation at all (like for most ST males and all the NT males in our study).

Males classified as NT in a given year were not able to establish and defend a lek territory, usually passing quickly through the lek, from where they were excluded by dominant males, and generally showing a high mobility during the whole mating season. As regards the period spent on the lek, ST and T males showed small home range sizes having the centre in the lek, while those of NT males were twice as large. During the rut, T and ST males occupied comparable ranges when involved in territory defense, as showed by the Kernel 25% use. By increasing the percentage of fixes used in such analytical approach, we documented the intermediate spatial pattern of ST males, as the consequence of the combination of lek territory defense and high mobility outside the mating arena. As confirmed by direct observations, the high mobility of NT and ST males outside the lek was due to the combination of a frenetic diversification of mating strategies, such as the temporary defense

of single territories and the following of females, even though this latter strategy seemed to be almost exclusively adopted by subadult males (Ciuti, personal observation). As confirmed by Thirgood et al. (1999), males that cannot defend lek territories often adopt a less successful mating strategy, one associated to correspondingly lower costs. Likewise, Apollonio et al. (1992) argued that males adopting alternative mating strategies in San Rossore were inferior competitors in that they selected a low-risk, low-benefit strategy. In fallow deer leks, males have to face high costs in terms of fighting rates. However, successful individuals are rewarded by higher mating rates than males adopting alternative strategies (Thirgood et al., 1999; Apollonio et al., 1992). As documented by Thirgood et al. (1999), combinations of alternative male mating strategies coexist in most fallow deer populations. In some populations a single mating strategy clearly was found to predominate over the others in that it accounted for most of the mating success achieved: like in other populations (Schaal & Bradbury, 1987; Clutton-Brock et al., 1988; Langbein & Thirgood, 1989), in the San Rossore population this strategy was the defense of lek territories (Apollonio et al., 1992). Research on strategy-switching by individual male fallow deer has focused on changes within individual breeding seasons because there are few data available on changes in reproductive behaviour during an individual male's lifetime (McElligott & Hayden, 2000; Thirgood et al., 1999 and reference therein). In our study, every male seemed to have the chance to defend a lek territory. As confirmed by Thirgood et al. (1999), individual male fallow deer are not necessarily all specialists and may switch from one mating strategy to another. In our study the choice among alternative mating strategies seemed to be significantly affected by the spatial and foraging strategies adopted before the rut (spring and summer), i.e. when males crucially invest in body size (Stearns, 1992; Jönsson, 1997). Moreover, in our study site the best foraging areas were characterized by higher predation risk, both perceived and actual (Ciuti et al., 2004; Ciuti & Apollonio, 2008). Contrary to what recorded for NT males, males that showed a higher use of the risky sector in spring and summer were able to defend a lek territory in the following mating season, validating our main prediction. The ability of each male to defend a lek territory in the rut could be predicted by looking at its use of the risky sector of the Estate in spring and summer, where, beside predation risk and rate, also forage availability was relatively (Ciuti & Apollonio, 2008) and absolutely (this study) higher than in the main pasture of the undisturbed sector. Such a pattern was confirmed by the analysis of yearly variation, e.g. by looking at the males that used to be territorial and subsequently showed a lower use of the risky sector in spring-summer eventually lost the status of territorial males during the rut. In such a risky/rich sector T and ST males limited their movements in spring-summer (low home range sizes) and probably also their energy

expenditure to levels lower than those recorded for NT males. The abundance and spatial arrangement of food resources influenced the deer's ability to forage efficiently (Kareiva, 1983; Cain, 1985). Evidence suggests that forage availability within a given home range size must meet energy and nutritional requirements, otherwise home range size will be increased to encompass additional resources. Accordingly, animals do range over larger areas when food is scarce or patchily distributed (Ford, 1983; O'Neill et al., 1988; Turner et al., 1993; Tufto et al., 1996; Relyea et al., 2000). Summer continuous radio-tracking sessions confirmed the higher mobility of NT males compared to that recorded for ST and T males. Arguably, the high energy expenditure hypothesized for NT males likely increase during the hot and dry Mediterranean summer. Interestingly, the second level of compositional analysis of habitat found ST males to show intermediate choices among T and NT males, thus displaying a wide range of behavioural choices. NT males also used areas outside the disturbed sector and showed a higher use of pine woods, i.e. an habitat with poor resource availability. In our study site, we had previously analyzed also the diet of fallow deer through the identification of the rumen content (Bruno & Apollonio, 1991), and male habitat selection, which was assessed by direct observation (Apollonio et al., 1998) and radiotracking (Ciuti & Apollonio, 2008). Following these results, PW proved to be very scarce in trophic resources used by deer and, as a consequence, it was poorly selected. The high mobility rates shown by NT males presumably were the end result of their continuous search for food in an area with low trophic availability and a shortage of large patch of meadows.

Males that used the risky sector optimally invested in body size through the exploitation of the best feeding areas. This was confirmed by our data on body weight collected on a sub-sample of 22 bucks in late October 1999, when T and ST males proved to be heavier than NT males. In a concurrent study, Ciuti & Apollonio (submitted) reported the antler growth rate (and final antler size) of territorial males to be faster (and larger) than that recorded for non territorial ones, and this was likely due to the optimal foraging strategies adopted before the rut. As showed by McElligott et al. (2001), body mass was related to pre-rut dominance rank which, in turn, was strongly related to rut dominance rank. Accordingly, an indirect relationship between mating success and body mass could be pointed out. McElligott et al. (2001) also found that mating success among mature males was unrelated to age. Likewise, we did not find any significant effect of age on mating behaviour or success. In fact, dominance rank influences male fallow deer participation in reproductive activities to a greater extent than age (Komers et al., 1997). Only a few males in our study population were older than 12 y.o. because of the high mortality rate recorded after the rut, which is likely connected to the adoption of such a costly mating strategy. In contrast, age seemed to affect the spatial

strategies adopted before the rut, with spatial use being reduced with increasing age. Age was shown to be inversely correlated to home range sizes in ungulates (McNab, 1963; Relyea et al., 2000; Cederlund & Sand, 1994; Rossi et al., 2003; Grignolio et al., 2004), and this is likely due to a better resource distribution knowledge. Indeed, this was marked for NT males, who reduced spatial use and increased the use of risky sector with increasing age. Arguably, age effect was not significant in T and ST males on account of already optimized spatial and foraging strategies, while this was significant for NT males, who optimized spatial strategies and lowered energy expenditure with increasing age.

ST and T males adopted risky choices in our study case, but a risky life does not necessarily entail a high mating success for all these males (i.e. higher for T males than ST ones): there is only a better chance for them to be able to defend a lek territory. According to Pelletier et al. (2006, and references therein), in polygynous species male mating success is largely dependent upon intra-sexual competition. Consequently, the benefits of a given allocation for males are more uncertain than its costs, and the correlation between mating effort and success is therefore much weaker in males than females.

In our study we detected only minor differences between the spatial and foraging strategies adopted by T and ST males. However, we think that such minor differences are probably not enough to explain the hugely different mating success between the two mating strategies. T and ST males gained a better body size (this study) and antler size (Ciuti & Apollonio, submitted) than NT before rut. Arguably, the combination of many other factors can contribute to the male individual success and to explain differences in success between T and ST males, such as the experience from previous mating seasons (McElligott and Hayden 2000), and that gained as subadult males (Pélabon et al., 1999). Furthermore, also the hierarchy established well before the beginning of the rut may play a role. Surprisingly, given the limited extension of the risky sector compared to male home range sizes (Davini et al., 2004), we found a very low degree of home range overlap among males using this area before rut, thus suggesting that males to become territorial in the autumnal rut already establish a “sort of territoriality” within spring-summer ranges. If this hypothesis were confirmed by future research, the low degree of overlap among male foraging areas and the exclusion of NT males from such a risky sector could also be explained by no-contact interactions.

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Chapter 3



**Timing of lek use by fallow deer (*Dama dama*) males according to age
and mating success: first-come first-served?**

**Timing of lek use by fallow deer (*Dama dama*) males according to age and mating success:
first-come first-served?**

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Abstract

During 13 consecutive mating seasons, we studied the timing of lek use by 84 fallow deer males monitored through radio-tracking and direct observations to test the hypotheses that timing of lek use may affect individual mating success in the lek. Males able to achieve copulations in the lek (≥ 5 y.o), were ranked according to lek territory occupancy and mating success. Thus, we analyzed the timing of lek use of males according to both age and rank. While males older than 5 y.o. arrived at the lek well before the first copulation observed there, younger males showed up just few days before the beginning of mating activities. This confirmed the early arrival importance for an adult male in order to gain positions in the male hierarchy. However, among males older than 5 y.o., high ranked males did not arrive at the lek before low ranked ones. Thus, the hypothesis predicting that sooner a male arrives at the lek, higher will be its mating success was rejected. Finally our data militated against the hypothesis that sub-adult males leave the lek later than adult males in order to increase the copulation chance when mating males were exhausted.

Keywords

Dama dama, fallow deer, lek, marking activities, mating rank, radio-tracking.

Introduction

Male dominance rank plays a key role on male reproductive success during the breeding season in many vertebrate species (e.g. McGhee and Travis, 2010; Romero and Castellanos, 2010; Rodriguez-Llanes et al., 2009; Lovari et al., 2009; Kruczek and Zatorska, 2008). Male intra-sexual interactions for dominance rank settlement are established by means of direct contacts (e.g. Reaney and Whiting, 2002; Foster et al., 2009; Wegge et al., 2005), acoustic (e.g. Christie et al., 2004; Fisher et al., 2004; Reby and McComb, 2003), visual (e.g. Lovari et al., 2009; Bokony et al., 2006), or scent signals (Setchell et al., 2010; Muller and Manser, 2008). As regards to ungulates, male-male combats during the breeding season are decisive in hierarchy settlement (Mainguy and Coté, 2008; Taillon and Coté, 2007; Mysterud et al., 2005) as well as non-contact interactions (Festa-Bianchet et al. 1990; Jennings et al., 2002). Vocal communication can contribute to decrease the needs to fight, given that the acoustic structure of male vocalizations was showed to be individually distinctive and to contain information on male body size and/or dominance status (Reby et al., 1998; McElligott et al., 2006; Vannoni and McElligott, 2007, 2008, 2009; Wyman et al., 2008). At the same time, scent and visual marking activities are supposed to be important for male status signalling in male-male interaction as well as for mate choice by females (Stenström et al., 2000). Gosling (1990) proposed that the main function of scent marking by males should be status advertisement, providing a means of assessment to potential competitors, thereby reducing the cost of agonistic encounters.

Male dominance rank and related reproductive success of ungulate males are mostly associated with their competitive ability, where larger males are supposed to have an advantage in acquiring and defending access to females (Andersson, 1994; Hogg and Forbes, 1997; Coltman et al., 2002). In order to reproduce successfully, an ungulate male needs to be available for mating in the short time window in which the female is ready to conceive (in fallow deer about 36 h, Asher 1985), and, above all, when the peak of oestrus females occurs (Apollonio et al., 1992). However, to gain access to females during this short time window is not an easy task, because it may involve fighting with other males for access (Geist, 1974; Clutton-Brock et al., 1979), patrolling territories (Alvarez 1993), and tending females (Hogg, 1984; Hogg and Forbes, 1997; Pelletier et al., 2006). That means for an ungulate male to be in the right place at the right time, such as for a male fallow buck (*Dama dama*) defending a lek territory (Apollonio et al., 1992) or for a red lechwe (*Kobus leche leche*) defending a resource-based territory (Williamson, 1994). In the two latter cases, it's crucial for a male to be a territory owner at the peak of the rut. As a consequence, it is supposed to be an

advantage for an ungulate male to gain a high rank before the beginning of the short period in which mating will occur, in order to maximize its own mating success (McElligott et al., 1998).

In this context, where the access to oestrous females depends on the competition among males, young males are expected to delay their reproductive effort until they can participate efficiently in this competition (Clutton-Brock, 1988; Roff, 1992). Young males are less likely to compete successfully in male–male combats, and paternity is highly skewed towards prime-aged males (e.g. Pemberton et al., 1992; Coltman et al., 2002). However, young males have a higher chance to sire later in the rut, when prime-aged males are exhausted (Preston et al., 2001; Mysterud et al., 2008), and this explains why subadult males may begin to show interest towards mating activities at a later date during the rut than prime-aged males (Mysterud et al., 2004).

All these aspects of the behavioural ecology of ungulates are markedly pronounced in the case of fallow deer. In this deer, the short seasonal rut involves intense intra-sexual competition leading to a markedly skewed male reproductive success (Clutton-Brock et al., 1988; Apollonio et al., 1989; 1992; Ciuti and Apollonio, *in press*). Only bucks (older than 4 years) are able to successfully participate to the mating activities (Chapman and Chapman, 1997; Apollonio et al., 1992), while younger males, despite they can potentially display proper rutting behaviours (Chapman and Chapman, 1997), postpone their reproductive effort in the presence of older and bigger individuals (Komers et al., 1997). The highest level of competition is recorded when fallow deer males defend clustered territories resulting in a traditional mating site as the lek (Apollonio, 1992; Hoglund and Alatalo, 1995). Lekking is a high cost-high benefit strategy given that the majority of copulations within a population takes place at leks (Apollonio et al., 1992; Clutton-Brock et al., 1988; Apollonio et al., 1990).

Given such scenario, the timing of lek use by male fallow deer can be crucial in affecting their competitive ability and dominance rank, and, in turn, it can influence the ability to have access to females during the rut and finally males mating success. Indeed, the study of the timing of lek use by males can be an indirect measure of the importance to be present in the lek area well before the beginning of the rut in order to establish hierarchies and establish territories. In this context, we studied the timing of lek use by fallow deer males according to age classes and mating rank in the San Rossore fallow deer population during 13 consecutive mating seasons. Our predictions were: (i) adult males (bucks aged > 4 y.o.) are supposed to arrive at the lek before subadult males (aged 2–4 y.o.). (ii) high ranked adult males (i.e. males achieving a high mating success) are predicted to arrive at the lek before than low ranked adult males. (iii) immature and less competitive males (i.e.

subadult males and/or low ranked adult males) are predicted to leave the lek later than the more competitive ones, in the attempt to compensate for their scarce mating success in the main rut time.

Material and methods

We carried out this study in the San Rossore Estate (4,650 ha), central Italy (43°43'N, 10°19'E: see Ciuti et al., 2006 for details on vegetation). Two traditional leks (documented since 1980's; Apollonio et al., 2003; Ciuti and Apollonio, *in press*) were active during this research, i.e., the lek of Stacca del Gatto (lek SG) and the lek of Fossacci (lek FO), located on the south and on the north side of the Estate, respectively.

Since 1996, bucks (males aged more than 4 y.o.; Chapman and Chapman, 1997) were driven by 20-30 game keepers into circular corrals during winter time (see for major details Ciuti et al., 2004; Ciuti and Apollonio, 2008). Thirty-six bucks were hand caught, blindfolded, aged by tooth eruption and wear (Chapman and Chapman, 1997), ear tagged, fitted with Televilt (Lindesberg, Sweden) radiocollars, and finally released. The age was accurately confirmed post-mortem on lower jaws (Chapman and Chapman, 1997; Ciuti and Apollonio, *in press*), given that all males died for natural causes (commonly after the autumnal rut due to fighting injuries) before the end of this research. Using the same methodology, since 2003 we fitted with radio-collars 48 prickets (males aged 1 y.o., Chapman and Chapman, 1997) during winter time. In this case, we fitted them with Televilt transmitters adapted to flexible collars. This was done to avoid injuries due to neck growth. Such flexible collars were automatically lost by deer between 1-3 years after their first capture with no injuries to the neck (De Cena et al., *in prep.*), and we replaced them with new collars when recapture events occurred during winter time. Given that prickets aged between 1 and 2 y.o. were captured during winter time, such males monitored during the following rut (autumn) were belonging to the following age class, i.e., sores (2-3 y.o.). As a consequence, we grouped deer according to the age at the time of the rut into 10 age classes as follows: sores (S) 2-3 y.o., S 3-4 y.o., bucks (B) 4-5 y.o., 5-6 y.o., 6-7 y.o., 7-8 y.o., 8-9 y.o., 9-10 y.o., 10-11 y.o., and bucks older than 11 y.o.

We performed direct observations of mating activities during 13 consecutive mating seasons (1996-2008) from 3 fixed hides located along the border of the 2 leks. At least 2 observers per fixed hide carried out direct observations using binocular 10x and telescope 30-45x. Continuous observations on lek activities (every day from dawn to dusk) began when territorial defence was first detected (late September-early October), and ceased when defence ended (late October) (*sensu* Apollonio et al., 1992; Ciuti and Apollonio, *in press*). The days in which we observed the first copulation (from

1996 to 2008: mean day \pm SE = October 5th \pm 0.5 days) and the last copulation (from 1996 to 2008: mean day \pm SE = October 20th \pm 0.6 days) were markedly constant during the time span covered by this research, in accordance to previous findings in the same study site (Ciuti and Apollonio, *in press*). By means of such direct observations, we collected for each buck present in the lek the time spent in defending a territory and the mating success (number of copulations observed).

During the same years, from late August to late November (i.e., during a period large enough to include the whole mating season; Chapman and Chapman, 1997; Apollonio et al., 1992), we monitored the radio-collared males by discontinuous radio-tracking (1 fix every 12 h, homogeneously distributed over day and night) in order to detect both the arrival date at the lek and the departure date from there for each radio-collared male. This monitoring schedule allowed us to determine the arrival or the departure dates from the lek with a bias lower than 12 h. We calculated locations by means of triangulation (Ciuti et al., 2004). Radio-tracking data were supported and verified by direct observations of radiocollared males in the lek. We defined the male arrival date at the lek as the first day of presence within a 300-m diameter buffer area around the lek centre. The departure date from the lek was the last day in which a fix was recorded within this buffer zone. All spatial analyses were performed using 1:10,000 digitized maps of the study area using Quantum GIS (v1.4.0-Enceladus - © QGIS 2010). At the end of this research, we recorded 120 arrival dates at the lek and 113 departure dates from the lek. The number of arrival dates at the lek was lower than the number of departure ones, given that during the rut 4 males lost their radio-transmitter (flexible collars), 2 males died due fighting injuries, and only 1 ceased transmitting due to low battery.

We standardized the arrival dates at the lek as the number of days before (negative values) and after (positive values) the first copulation (October 5th = 0) observed there. The departure dates from the lek was standardized as the number of days before (negative values) and after (positive values) the last copulation (October 20th = 0) observed at leks.

Using the SPSS 13.0 (1989–2004 SPSS Inc.) program, we modelled the variation of the arrival date (dependent variable) of monitored males using a Linear Mixed Effects model (LME, Pinheiro and Bates, 2000). In this model, we considered age class (as defined above) and lek used by males (lek SG or lek FO) as fixed factors. Deer identity repeated among years was included as a random term in the model in order to avoid pseudo-replication of data (Machlis et al., 1985). The same approach was applied in modelling the variation of departure dates as the dependent variable.

By means of data collected during continuous observations of mating activities of leks, only bucks older than 5 y.o. were observed able to mate at least once from 1996 to 2008 (namely mating

males), while bucks 4-5 y.o. or sores 2-4 y.o (namely non-mating males) were never observed to mate in the lek. Thus, we fitted two further LME models with the arrival and the departure dates as dependent variables, respectively. This time, for both models, we considered the ability to achieve copulations in the lek according to age (i.e., mating and non-mating males, as defined above) and lek used as fixed factors. Again, deer identity repeated among years was included as a random term in the model. In these cases, we did not consider the age class as fixed factor in the models due to patent collinearity with the ability of mating in the lek (mating/non-mating males).

Given the high skewness of data dealing with the mating success, as typical for a fallow deer lek, with only few males able to achieve almost the matings recorded in a lek (Apollonio et al., 1992), we selected the time spent defending a lek territory as the continuous variable able to express the individual mating rank (see also Ciuti and Apollonio, *in press*). Mating males (i.e., bucks older than 5 y.o.) were ranked every year according to the time spent in the lek (minutes spent defending a territory in the lek). The rank 1 was assigned to the male who defended a lek territory for longer time than other males in the lek that year. Obviously, the yearly individual rank was correlated to the individual mating success, i.e., the number of copulation achieved in the lek (Pearson correlation coefficient, $n = 67$, $r_p = -0.366$, $p = 0.002$). The measure of male mating success was based on the number of directly observed copulations for each fallow deer male, and this provides a very good estimator of reproductive success in cervids as shown for both fallow deer (Say et al., 2003) and red deer (Pemberton et al., 1992).

Considering only the subset of males older than 5 y.o. (i.e., mating males), we modelled the variation of the arrival date at the lek by fitting a LME model with age and lek used as fixed factors, individual rank as a covariate and deer identity repeated among years as a random term. As a starting point, we fitted this model by including all main effects and two-way interactions. Subsequently we removed the interaction terms which did not prove to be significant in a stepwise fashion (Crawley, 2007). We adopted the same approach when we modelled the departure dates from the lek as the dependent variable. All data were successfully tested for homoscedasticity (Levene test) and normality (Kolmogorov-Smirnov test).

Results

We found a significant difference among the arrival dates at the lek of males according to age (Table A, 1st model). According to 95% confidence interval differences (Fig. A.1), sores aged 2-3 y.o. and 3-4. y.o, and, surprisingly, bucks aged 4-5 y.o. reached the lek later than males older than 5 y.o. We obtained the same result considering the ability to mate of males according to age (i.e.

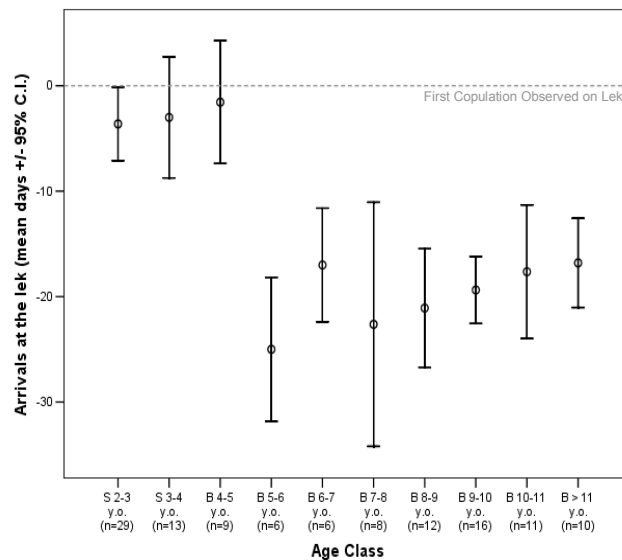
mating males aged ≥ 5 y.o., and non-mating males aged < 5 y.o) (Table A, 2nd model). Non-mating males reached the mating arena only 3.2 days (CI 95%; lower bound = -6.0, upper bound = -0.4) before the first copulation observed in the lek, whereas mating males reached this place nearly 3 weeks before, i.e., 19.8 days (Confidence interval 95%; lower bound = -22.6, upper bound = -17.1) before the first observed copulation. We did not detect significant differences in the timing of lek use among males using different leks (Table A; 1st and 2nd model).

Dependent variable	Factors	DF (numerator, denominator)	F	P
Arrival dates	Intercept	1,109	146.370	< 0.001
	Age class	9,109	12.525	< 0.001
	Lek SG/Lek FO	1,109	0.008	0.931
	Intercept	1,117	99.747	< 0.001
	Mating/Non-mating males	1,117	108.219	< 0.001
	Lek SG/Lek FO	1,117	0.028	0.867
Departure dates	Intercept	1,102	13.220	< 0.001
	Age class	9,102	3.943	< 0.001
	Lek SG/Lek FO	1,102	0.485	0.488
	Intercept	1,110	8.024	0.005
	Mating/Non-mating males	1,110	26.071	< 0.001
	Lek SG/Lek FO	1,110	0.594	0.442

Table A – Four Linear Mixed Effect (LME) models explaining the variation of the arrival date (two models above) at the lek and that of the departure date (two models below) from the lek of fallow deer males monitored from 1996 to 2008 in the San Rossore Estate, Italy. Arrival dates at the lek were standardized as the number of days before (negative values) or after (positive values) the first copulation observed on the lek (5th October). Departure dates from the lek were standardized as the number of days before (negative values) or after (positive values) the last copulation observed on the lek (20th October) (see the text for details on factors included in the model).

As regards to the departure dates from lek, we found significant differences among males according to age (Table A; 3rd model). Bucks aged 8-9 y.o, 9-10 y.o, and 10-11 y.o leaved the lek later than does 3-4 y.o and bucks 4-5 y.o (Fig. A.2). Accordingly, we found significant differences between the departure dates from the lek when we considered the sample split into mating and non-mating males (Table A, 4th model).

A.1



A.2

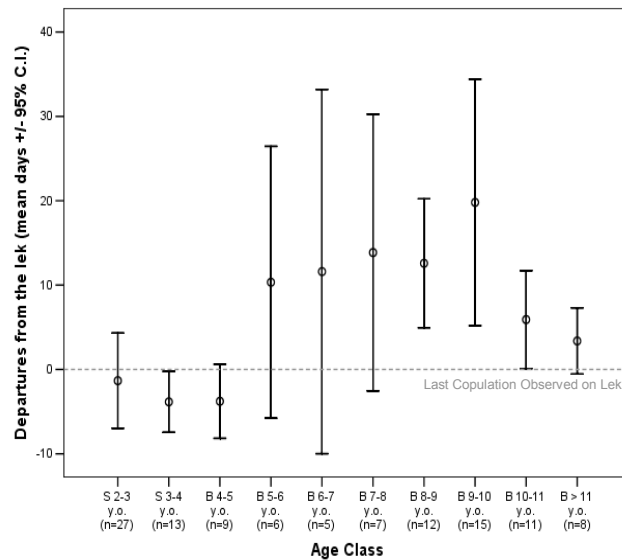


Fig. A.1 - Arrival dates (mean days \pm 95% Confidence Interval) at the lek of radiocollared fallow deer males according to age class (S = sores, B = bucks) from 1996 to 2008 in the San Rossore Estate, Italy. Individual arrival dates were standardized as the number of days before (negative values) or after (positive values) the first copulation observed on the lek (5th October).

Fig. A.2 - Departure dates (mean days \pm 95% CI) from the lek of males according to age class from 1996 to 2008. Individual departure dates were standardized as the number of days before (negative values) or after (positive values) the last copulation observed on the lek (20th October).

Non-mating males left the lek before the end of mating activities, i.e. 1.4 days (Confidence interval 95%; lower bound = -6.4, upper bound = 3.5) before the last copulation observed the lek. In contrast, mating males left the lek 13.1 days (Confidence interval 95%; lower bound = 8.1, upper bound = 18.1) after the last copulation observed on the mating arena. We did not detect significant differences of timing of lek use among males using different leks (Table A; 3rd and 4th model).

Dependent variable	Factors	DF (numerator, denominator)	F	P
dates	Intercept	1,58	55.363	< 0.001
	Age class	6,58	0.752	0.611
Arrival	Rank	1,58	1.154	0.287
	Lek SG/Lek FO	1,58	2.208	0.143
Departure dates	Intercept	1,53	0.977	0.327
	Age class	6,53	1.246	0.298
	Rank	1,53	0.930	0.339
	Lek SG/Lek FO	1,53	0.336	0.565

Table B – Two Linear Mixed Effect (LME) models explaining the variation of the arrival date at the lek (model above) and the variation of departure date from the lek (model below) of males able to achieve copulations in the lek (i.e., bucks older than 5 y.o.). (Period: 1996 - 2008, San Rossore Estate, Italy). Arrival dates at the lek were standardized as the number of days before (negative values) or after (positive values) the first copulation observed on the lek (5th October). Departure dates from the lek were standardized as the number of days before (negative values) or after (positive values) the last copulation observed on the lek (20th October). (see the text for details on factors included in the model).

However when we considered the subset of males older than 5 y.o. (mating males), we did not find a significant effect of age and mating rank in affecting the arrival dates at the lek (Table B, 1st model; Fig. B.1) or departure dates from the lek (Table B, 2nd model; Fig. B.2). In both cases, we did not find behavioural differences in the timing of lek use among males using a different lek (Table B).

We summarized in Fig. C the timing of lek use shown for monitored males from 1996 to 2008 according to age classes. Indeed, following results obtained in the previous paragraphs (no differences in the timing of lek use among mating males of different rank) males were grouped into sores, non-mating bucks, i.e. aged 4-5 y.o., and mating bucks, i.e. aged more than 5 y.o. The timing of lek use by males was shown in comparison with the first and the last copulation observed in the lek, as well as in comparison with the timing of occurrence of marking activities recorded around the lek (Ciuti et al., unpublished data; Ghiandai et al., 2004), Marking activities around the lek begun around September 8th, exactly when monitored males older than 5 y.o. begun to arrive at the lek.

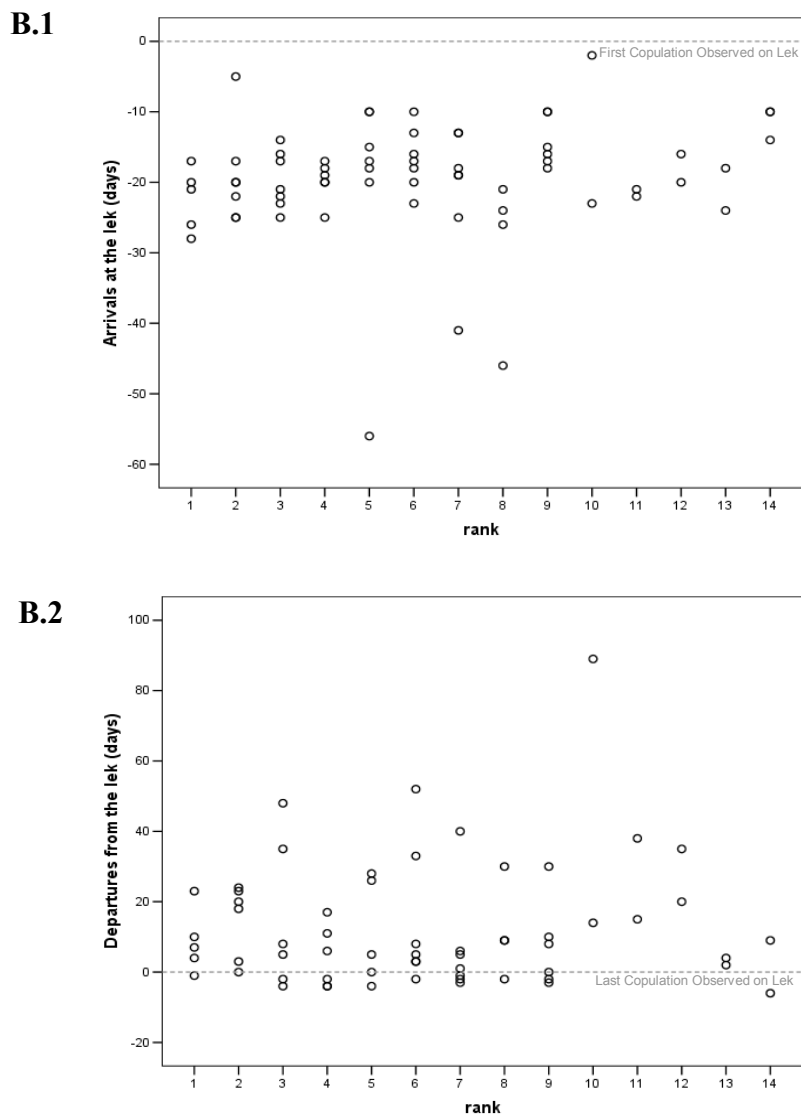


Fig. B.1 – Arrival dates at the lek of radiocollared fallow deer bucks (older than 5 y.o., i.e. the only able to achieve copulations in the lek) according to individual lek rank from 1996 to 2008 in the San Rossore Estate, Italy. Arrival dates were standardized as the number of days before (negative values) or after (positive values) the first copulation observed on the lek (5th October). All bucks older than 5 y.o. arrived at the lek before the first copulation observed.

Fig. B.2 – Individual departure dates from the lek of fallow deer bucks (older than 5 y.o.) according to individual lek rank from 1996 to 2008. Departure dates were standardized as the number of days before (negative values) or after (positive values) the last copulation observed on the lek (20th October).

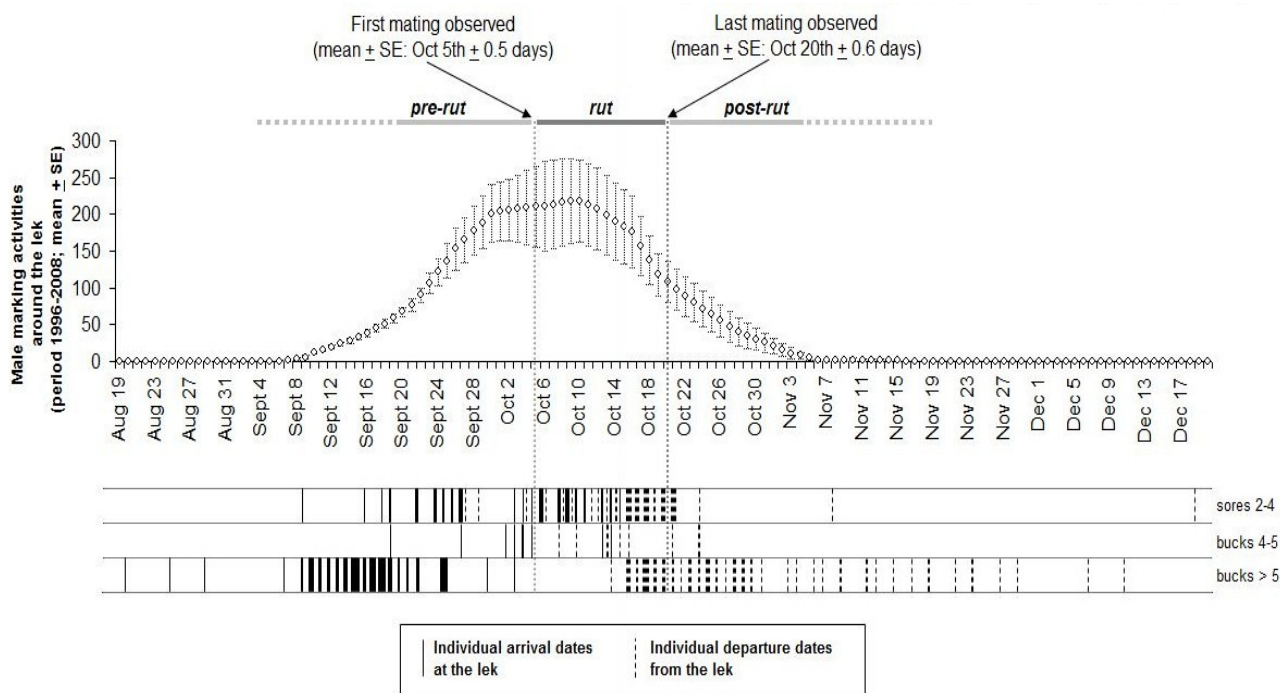


Fig. C - Marking activities of fallow deer males (top graph) recorded around the lek (Ciuti, unpublished data; Ghiandai et al. 2004) from 1996 to 2008 in the San Rossore Estate, Italy. Visual marks on the ground and vegetation were counted every 3-4 days walking a 2,590 m-trail around the lek. Individual arrival dates (solid vertical bars) at the lek and departure dates (broken vertical bars) from the lek of males (sores aged 2-4 y.o., bucks aged 4-5 y.o., and bucks aged > 5 y.o.) were reported below the graph. The pre-rut, rut, and post-rut periods (defined according to copulations observed in the lek) were reported above the graph. One male aged > 5 y.o. arrived at the lek on August 10th, while one male aged > 5 y.o. left the lek on January 17th (both males were not included in the figure).

Discussion

The timing of lek use by fallow deer males is crucial to understand if and how can be important for a male to be there well before the beginning of the rut. We firstly predicted that adult males were supposed to reach the mating arena before than younger ones, and this was only partially confirmed. Indeed, males older than 5 y.o. reached the lek significantly before younger males, but this was not true for bucks aged 4-5 y.o. Bucks aged 4-5 y.o. are commonly considered adult males (Chapman and Chapman, 1997), but they reached the lek at the same time of younger males, i.e. few days before the beginning of the rut. Thus, given that no copulations were not recorded for bucks aged 4-5 y.o. in San Rossore during the mentioned study period, arguably they are inferior competitor with respect to older bucks for the access to females. That males aged 4-5 y.o. can be excluded from the competition for females in a lek is in accordance with the fact that sexual selection is expected to be stronger in lekking species than in other species (Darwin, 1871) and, thus, young bucks cannot

arguably compete with larger and more experienced males. Komers et al. (1997) already showed how young bucks aged 4-5 y.o. were commonly excluded from mating activities in six captive non-lekking fallow deer populations in south-central Sweden (Langbein and Thirgood, 1989). Hence, such results were confirmed in our lekking population, where the intense intra-sexual competition are supposed to evoke a markedly skewed male reproductive success (Clutton-Brock et al., 1988; Apollonio et al., 1989, 1992). In such cases, non-mating males (i.e. immature and less competitive males) appear to resort to alternative mating strategies (Clutton-Brock et al., 1988; Apollonio et al., 1992). The presence of non-mating males (both bucks 4-5 y.o. and sores) in the lek during the breeding season could be the consequence of the following of females until lek territories (Clutton-Brock et al., 1988; Apollonio et al., 1992). As a matter of fact, they arrived at the lek almost simultaneously with the arrive of females, i.e. when the first copulation was observed. The presence of these males can be considered for them a chance for acquiring experience of mating activities fundamental during reproductive seasons of the following years (Bekoff, 1977; Byers, 1980; Rothstein and Griswold, 1991; Pelabon et al., 1999).

We secondly predicted that high ranked males were supposed to arrive at the lek before than low ranked males. This was not the case. All bucks older than 5 y.o. arrived at the lek well before the beginning of the rut, irrespective to the rank occupied. That almost all the fully grown males of this population arrived at the lek about one month before that the first copulation was recorded was confirmed by the simultaneous occurrence of marking activities around the lek that are crucial for male status signalling (Stenström et al., 2000). As a consequence, it is arguable that all potentially mating males arrived at the lek well before the beginning of the rut in the attempt to begin the escalation of male hierarchy. Indeed, in polygynous mating systems with high levels of male competition and low levels of paternal care, high-ranking dominant males obtain more copulations than do low-ranking males (Choe, 1994; Katano, 1990; Appleby, 1982; Hoelzel et al., 1999; Cowlshaw and Dunbar, 1991), thus it appears crucial to occupy high ranked position from the beginning. Social dominance may reduce the costs of conflict by terminating an interaction before physical engagement (Gosling et al., 1996), avoiding the loss of females from territories, injury or death (Clutton-Brock et al., 1988; Apollonio et al., 1989). As regards to fallow deer, McElligott et al. (1998) showed that males established dominance rank largely by non-contact agonistic interactions during the pre-rut period and this rank was substantial carry-over to the rut, when it was correlated with mating success. Vannoni and McElligott (2009) also indicated that higher ranked fallow bucks start groaning several weeks before that the first mating takes place (McElligott and Hayden, 1999; McElligott et al., 1999). According to these results, it appears that the month before

the beginning of the rut is a fundamental period of time in which fallow deer bucks build a part of their oncoming success in the lek, but this seems not to be a function of the time of arrival at the lekking site, as all the adult males being arrived simultaneously in our study case.

Finally, we predicted that immature and/or less competitive males (i.e. subadult and low ranked adult males) were supposed to leave the lek later than successful males, in the attempt to mate when dominant males were exhausted (Preston et al., 2001; Mysterud et al., 2008). During the last part of the rut, male-male competition can be lower due to fatigue (Stevenson and Bancroft, 1995; Pelabon et al., 1999), and this is true in the final part of lekking when it is lower the number of females and males in the lek (Apollonio et al., 1992). However, our prediction was completely falsified by our results. Namely, sores and bucks aged 4-5 y.o left the lek well before than adult males, while low ranked males left the lek at the same time (but not later) than high ranked males. This result for the first time suggests that in a fallow deer lek young or low ranked males do not try to compensate their scarce mating success leaving the lek later than dominant males. This could be expected as a consequence of the fatigue of dominant males, who spent almost 1 month in defending a lek territory without feeding (Apollonio and Di Vittorio, 2004). Thus, the alternative strategy of these unsuccessful males can be to leave the lek following the females that are leaving this area as well (Clutton-Brock et al., 1988), but further researches are needed to disentangle the mating tactics adopted by low ranked males. On the contrary successful males seems to be very lek-faithful as already shown in a females removal experiment from the one of the leks that were studied. On that occasion, high ranking males stayed in their territories from days even if they were deprived from females by artificial disturbance, showing a remarkable site fidelity possible due to the previous successful experience linked to the specific area, represented by the lek itself (Apollonio et al., 2003).

Conclusions

For the first time, thanks to the combination of radiotracking and direct observation data, we documented the lek use by fallow deer males according to age and rank. Our results open new scenarios for future research aimed to understand on which mechanisms the lekking behaviour relies. Particularly, as regards to the month spent by adult males (irrespective to their rank) in the lek area before the beginning of the rut, it remains unknown how marking activities and combats may affect the possibility to occupy a high rank in the lekking hierarchy. It is a fact that larger males with larger antlers are more likely to achieve a high mating success during the rut (Ciuti and

Apollonio, *in press*) but differences in the mating success between same-sized antlered males probably relies in what happened before the arrival of females in the lek area.

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Chapter 4



Lekking in fallow deer (*Dama dama*): a long walk to territoriality

Lekking in fallow deer (*Dama dama*): a long walk to territoriality

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Abstract

Experiences gained by subadult male ungulates are supposed to be an important step in the long-term process leading to social maturity. This could be especially true in lekking species, such as the fallow deer. In this particular case of study, the experiences gained by subadult fallow deer males are considered crucial in the ability to defend a territory in the lek, once they become adult individuals. However, this important aspect of fallow deer behavioural ecology was never studied in the past. Thus, the aim of this work is to fill this gap, assessing the determinants of the process leading males to acquire a territory in a lek. Thus, we tested for correlations between experiences gained by subadult fallow deer and reproductive success achieved many years later, once they become prime-aged males. Data were collected from 2004 to 2010 in the lekking fallow deer population of San Rossore, Italy. We monitored individuals from the age of 1 y.o to the complete social maturation (7 y.o). For the first time, we showed how it is important for a subadult male to attend to lekking activities (observing, fighting, moving along borders of the territory defended by adult males), thus acquiring experiences on how the system works, being this positively correlated with the individual mating success achieved as adult males. Moreover, we showed that also experiences gained by subadult males outside the mating season are important in the ontogenesis of the territorial behaviour (and related success), given that intra-sexual interactions among subadult males and mature bucks within male aggregation were related to the gain of a high rank in the social and complex hierarchy established among adult fallow deer males.

Keywords

Dama dama, fallow deer, lek, territoriality, reproductive success.

Introduction

Many factors may contribute to individual reproductive success. In most dimorphic mammals this depends on fighting with other males for access to mates (Clutton-Brock et al., 1982; Geist 1986; Gosling et al., 1987; Festa-Bianchet et al., 1990; Komers et al., 1994) with a consequent energy consumption. Many species of large mammals are thought to rely heavily on accumulated body reserves to satisfy the energy needs of reproduction and survival (Festa-Bianchet et al., 1998) being thus considered capital breeders (Stearns, 1992; Jönsson, 1997). Capital breeders should thus adjust their reproductive effort according to their phenotypic condition (Festa-Bianchet et al. 1998; Shine and Mason 2005) because the energy allocated to reproduction is not available for body growth or maintenance (Green and Rothstein 1991; San José et al. 1999). This leads to trade-offs between investment in current reproduction or in other fitness components such as survival (Descamps et al. 2006; Moyes et al. 2006). Whether to participate actively or not in reproduction, because it is generally costly, is thus a recurrent decision that iteroparous animals must take every year, and males are thus expected to adjust their reproductive effort according to their age and body condition (Mainguy and Côté, 2008 and references therein).

Given such intriguing scenario, we are not surprised that, during the two last decades, male mating success has been studied extensively on ungulates according to body size and body mass, mating effort and mating investment, dominance rank, survival or age (e.g.; Kojola, 1991; Komers et al., 1997; McElligott et al., 2001; Forsyht et al., 2005; Saunders et al., 2005; Pelletier et al., 2006 ; Jennings et al., 2010). Nevertheless, on our knowledge, any research was focused on the influence of the behavioural strategies adopted by males during subadult phases on their future individual mating success. Experiences gained by subadult male cervids are supposed to be an important step in the long-term process leading to social maturity. This could be especially true in lekking species, such as the fallow deer. In this particular case of study, the experiences gained by subadult fallow deer males are considered crucial in the ability to defend a territory in the lek, once they become adult individuals. However, this important aspect of fallow deer behavioural ecology was never studied in the past. Thus, the aim of this work is to fill this gap, in the attempt what is going on in the process leading to territoriality in this lekking cervid. In the long-term study described in this paper, we evaluated not only whether the animals actively participated in reproductive activities every year according to age, but also the causes that stood behind this choice. This was triggered by a research conducted by Pelabon et al. (1999) on fallow deer subadult males, in which authors hypothesized that young interactions may affect further reproductive success through both motor training for future interactions and/or competition for current resources that affect growth. In

details, we conducted the research on fallow deer males monitoring individuals, by means of radio-tracking technique and direct observations, from early stage of social maturation (1.5 years of age) until their adulthood (6-7 years of age). Data collected from 2004 to 2010 allowed us to investigate choices and behavioural strategies adopted by young males that could affect their future chance to obtain high mating success in a lek arena. We started from our previous results on the consequences of different behavioural and spatial patterns adopted by adult fallow deer males during and outside the mating season to test a similar frame for subadults. In fact, adult males showed a differential use of risky but rich areas of the study site (rich in food availability, but characterized by the higher predation risk), with respect to their mating success (higher the risk taken before the rut to adopt better foraging strategies, higher the mating success) and to female use of this sector (Apollonio et al., 2005; Ciuti et al., 2004; Ciuti et al., 2008; Ciuti et al., *submitted*).

We formulated the following predictions to be verified with our data collected on males from the age of 1.5 y.o to the complete social maturation:

- 1) Experiences gained at the lek by subadult males are supposed to affect the future mating success once they become adult males.
- 2) Body mass related to best foraging strategies of subadult males are supposed to affect the future mating success once they become adult males.
- 3) Subadult males that are leaving early female aggregations are supposed to escalate before the male hierarchy and to become successful once they become adult males
- 4) Subadult males early aggregating with adult male aggregations are supposed to escalate before the male hierarchy and to become successful once they become adult males.

Predictions 3 and 4 are not mutually exclusive, given that males that leave early female aggregations may not aggregate to adult male aggregations as a result, thus forming same-age aggregations as an alternative strategy (Apollonio et al. 1998).

Material and methods

We carried out this study in the San Rossore Estate (4,650 ha), central Italy (43°43'N, 10°19'E: see Ciuti et al., 2006 for details on vegetation). The study area is subdivided into two main sectors (Fig.1). The eastern sector (disturbed sector, DS) is characterized by intense predation risk and affected by intense human disturbance (Apollonio et al. 2005; Ciuti et al. 2004; Ciuti and Apollonio 2008): human-induced mortality is the most important cause of death of fallow deer (i.e., yearly culling and capture program) (Ciuti et al. 2004; Ciuti et al., *submitted*). The human disturbance is present in DS only during the day, being closed to the public at night (Ciuti et al. 2004; Ciuti and

Apollonio 2008). Based on previous researches (see Ciuti and Apollonio 2008 and reference therein) DS proved to be richer in food availability because of the presence of larger pastures and high productive deciduous woods. In contrast, the western sector (undisturbed sector, US) is not affected by human disturbance and characterized by a lower food availability and by an high utilization and presence of females that selected this area for fawning (Apollonio et al. 2005; Ciuti et al. 2004; Ciuti et al. 2006; Ciuti and Apollonio 2008).

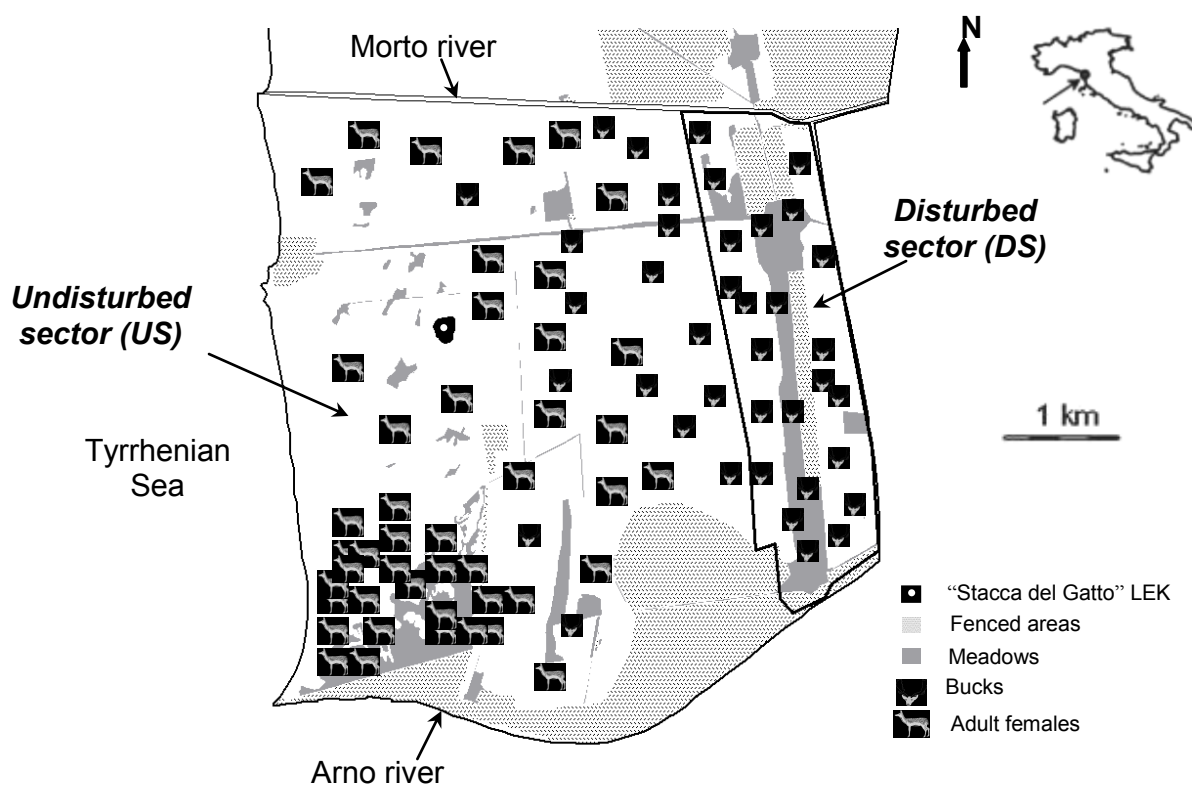


Fig.1 – Large scale spatial sexual segregation occurring before the rut in the San Rossore Estate (modified from Ciuti and Apollonio, 2008). While males mainly occupy the eastern disturbed sector, females are present in the western undisturbed sector only, almost concentrated on its main meadow. During the rut, males usually move from the disturbed sector to the lek, a traditional mating arena located almost in the geographical centre of the undisturbed sector. Meadows and fenced areas where deer are not allowed are shown in the map.

From 2004 to 2010, during winter time, deer selected for research were driven into corrals by game keeper (see for major details Ciuti and Apollonio, 2008), hand caught, blindfolded, ear tagged, fitted with expandable radiocollars and released. We fitted with radio-collars 49 prickets (males aged 1 y.o., Chapman and Chapman, 1997). We fitted them with Televilt transmitters adapted to flexible collars. This was done to avoid injuries due to neck growth. Such flexible collars were automatically lost by deer between 1-3 years after their first capture with no injuries to the neck (De

Cena et al., *in prep.*), and we replaced them with new collars when re-capture events occurred during following winter time. From January 2004 to November 2008 we collected 7,154 locations calculated by triangulation and plotted them onto a 1:10,000-scale digitized map of the study area (Ciuti et al., 2004). Seasonal distances of locations from the DS for each individual was computed by means of ArcGIS v9.3.1 software. Radio-tracking data were supported by direct observations of radiocollared males outside the rutting period. We collected 1,202 direct observations from 2004 to 2009 in order to identify the composition of social group for each individual.

From 2004 to 2010, we also performed direct observations of mating activities from 2 fixed hides, from dawn to dusk (*sensu* Apollonio et al., 1989). At least 2 observers per fixed hide carried out direct observations using binocular 10x and telescope 30-45x. Continuous observations began when territorial defense was first reported and ended when defense was no more reported. The rut occurred every year in October and was defined as the time between the first and the last recorded copulation. By means of such direct observations, we collected for each buck present in the mating arena the time of lek use, territory ownership, the mating success (number of copulations observed) and number of real and border fights in which they were involved, as descriptor variables of mating behaviour (Apollonio et al., 1989). Moreover, thanks to ear tags and radiocollars applied on prickets during capture sessions, we were able to identify individuals previously captured and monitored with radio-tracking and to check their presence each year at the lek, collecting individual data during the whole process of social maturation. When these males were adult males, we collected the same descriptor variables of mating behaviour described above for bucks. Instead, when they were subadult males we collected only their time of the lek use and fights if these occurred.

In that way, we collected a large set of descriptor variables from the age 1 to the adult age for each of the individual monitored in this long term research. We tested the data for correlation using the Spearman correlation coefficient given that data were not normally distributed, as verified by conventional normality tests. We further analyzed the relation between the minutes of permanence at the lek of bucks aged 5-6 y.o. and the time spent at the lek when these individuals were aged 2 y.o. using linear regression analysis. With the same methodology we analyzed the relation between the minutes of permanence at the lek of sores aged 2-3 y.o. with the percentage of bucks observed in their social units observed during their previous winter. All statistical analyses were performed with the software R v2.10.1 (R Development Core Team, 2009); in all tests significance level was set at $p < 0.05$.

Results

Prediction 1) Experiences gained at the lek by subadult males are supposed to affect the future mating success once they become adult males.

Significant correlations found among the times of lek permanence according to individual age class were reported in Fig.2.

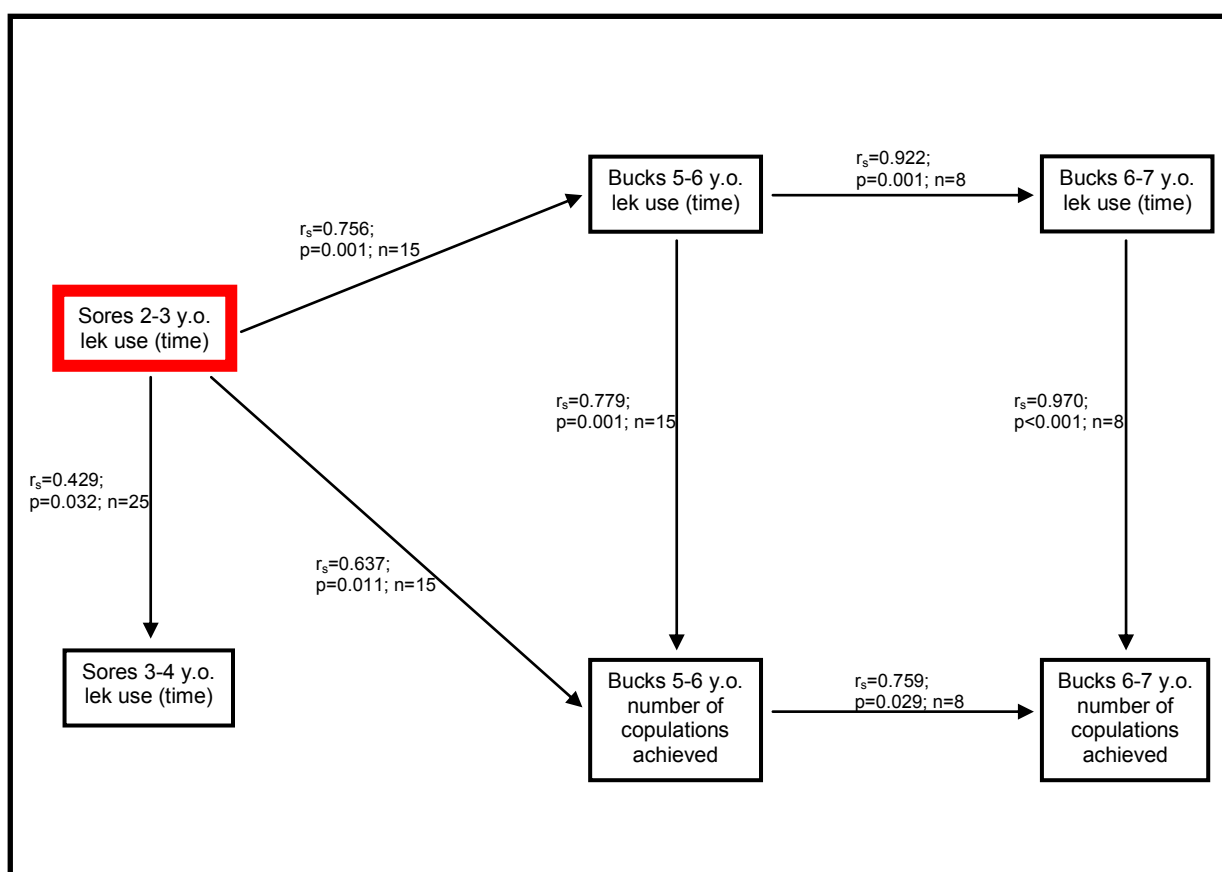


Fig.2 - Map of significant correlations among permanence at the lek (recorded for each individual according to age) and copulations achieved in the lek once they become adult males. Arrows indicate significant correlations founded between variables. We reported sample size (n), Spearman correlation coefficient (r_s) and p values for each significant correlation computed.

The time spent by sores aged 2-3 y.o. was the crucial variable in our correlation map: higher was the time spent in the lek at that time, higher was the mating success once these males became adult males. In details, we found that permanence (minutes at the lek) at the lek of sores aged 2-3 y.o. was positively correlated with permanence in the lek when individuals were sores aged 3-4 y.o. ($r_s = 0.429$; $p = 0.032$; $n = 25$) or bucks aged 5-6 y.o. ($r_s = 0.756$; $p = 0.001$; $n = 15$). Moreover,

performing linear regression between permanence at the lek of sores aged 2-3 y.o. and permanence at the lek of bucks aged 5-6 y.o. we found that the 44.2% of variability of the latter was explained by the variability of the former (linear regression analysis: $F_{1,13} = 10.3$; $R^2 = 0.442$; $\beta = 0.665$; $p = 0.007$) (Fig.3).

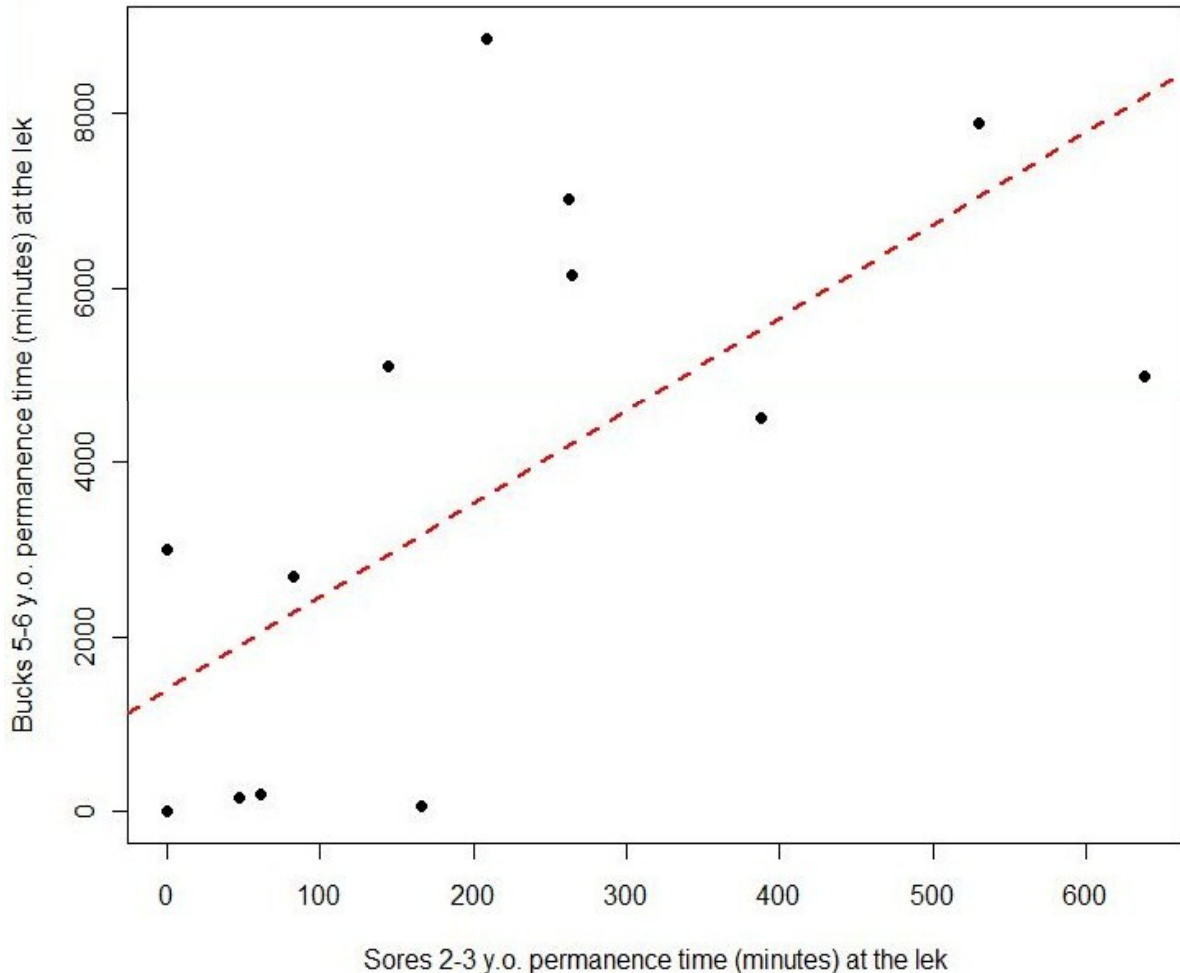


Fig.3 - Linear Regression analysis: x-axis: permanence at the lek of sores aged 2 y.o.; y-axis: permanence at the lek bucks aged 5-6 y.o. R^2 and p values are reported in the figure.

On the contrary, we did not detect significant correlations among the time spent at the mating arena by sores aged 2-3 y.o. and the time spent at the lek both by bucks aged 4-5 y.o. ($r_s = 0.411$; $p = 0.072$; $n = 20$) and by bucks aged 6-7 y.o. ($r_s = 0.403$; $p = 0.323$; $n = 8$). We found significant correlations among permanence at the lek of bucks aged 5-6 y.o. and of the same bucks aged 6-7 y.o. ($r_s = 0.922$; $p = 0.001$; $n = 8$) as well as among the number of copulations achieved during the rut in the mating arena by individuals in the two mentioned age classes ($r_s = 0.759$; $p = 0.029$; $n =$

8) (Fig.2). Permanence at the lek was a good estimator of mating success given that this variable was directly correlated with the number of observed copulations both for bucks aged 5-6 y.o. and bucks aged 6-7 y.o. (Fig.2).

Prediction 2) Body mass related to best foraging strategies of subadult males are supposed to affect the future mating success once they become adult males.

We did not detect any significant correlations among the time of lek permanence of sores aged 2-3 y.o. and biometric measures (corrected body mass and antler sizes) both of prickets and sores aged 2-3 y.o. ($p > 0.05$ in all cases).

Prediction 3) Subadult males that are leaving early female aggregations are supposed to escalate before the male hierarchy and to become successful once they become adult males

The time spent in the lek by males 2-3 y.o in the lek resulted the key variable: higher was the time spent at the lek at that time, higher was the mating success recorded once they became adult males. As a consequence, variable able to affect the time spent in the lek at the age of 2-3 y.o were at the same time able to affect the future individual mating success.

Permanence at the lek of sores aged 2-3 y.o. resulted inversely correlated with distance from the DS (male areas) before the rutting period, both during spring and summer (i.e. mean distance from the DS; spring: $r_s = -0.519$; $p = 0.001$; $n = 36$; summer: $r_s = -0.465$; $p = 0.013$; $n = 28$) (Fig.3). Higher was the distance from DS, lower was the use of male areas, lower was the lek attendance as sores 2-3 y.o. Higher was the distance from DS, higher was time spent in female aggregations ($r_s = 0.446$; $p = 0.009$; $n = 33$) and mixed herds ($r_s = 0.568$; $p = 0.001$; $n = 33$), lower was the time spent with males ($r_s = -0.453$; $p = 0.008$; $n = 33$) observed in their social groups during this season (Fig.4).

Prediction 4) Subadult males early aggregating with adult male aggregations are supposed to escalate before the male hierarchy and to become successful once they become adult males.

We found that minutes of permanence at the lek of sores aged 2-3-y.o. was inversely correlated only with the joining to adult male groups during the winter before the rut (% of bucks observed; $r_s = 0.642$; $p = 0.005$; $n = 17$). However, distance from DS during spring and summer of these individuals were inversely correlated with the frequentation of adult males (% of bucks observed in spring: $r_s = -0.470$; $p = 0.008$; $n = 31$; % of bucks observed in summer: $r_s = -0.439$; $p = 0.036$; $n = 23$) during the respective seasons (Fig.4). Finally, looking at the linear regression between the permanence at the lek of sores aged 2-3 y.o. and joining to adult males (% of bucks in the social

group) during the previous winter, we found that the 32.5% of the variability of the latter was explained by the variability of the former variable (linear regression analysis: $F_{1,15} = 7.232$; $R^2 = 0.325$; $\beta = 0.570$; $p = 0.017$).

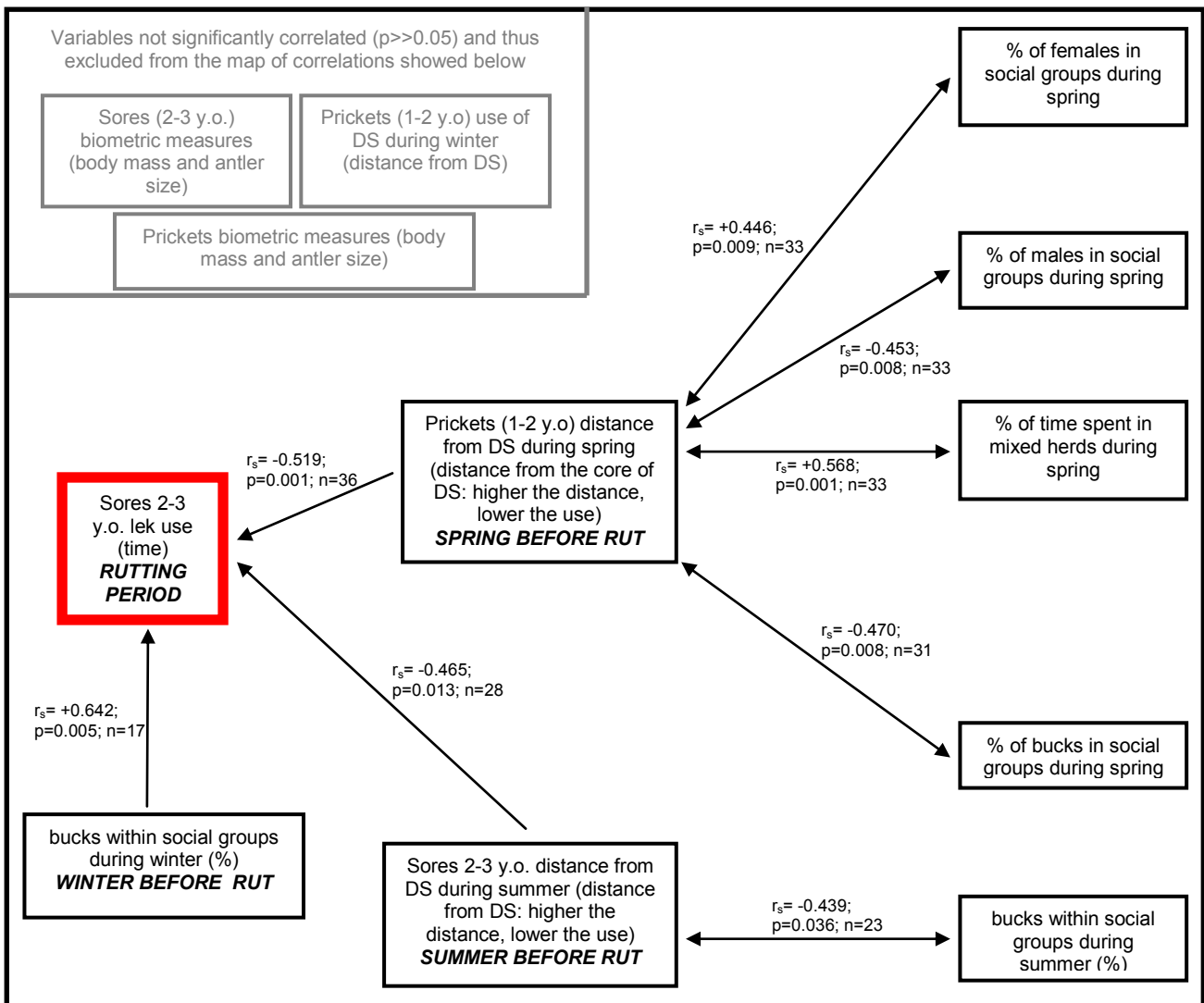


Fig.4 – Map of correlations (Spearman correlation coefficient, n, p and r_s are reported on the figure) documenting how the behaviour recorded outside the rut for subadult males (use of specific areas of the study site, ability to join specific male aggregations) is able to affect the ability of subadult males to actively attend to lek activities (as a mere observer, but acquiring experience) during early phase of social maturation. This, in turn, is able to affect the future mating success (see map of correlations of Fig. 2). See the text for major details and descriptions on single variables included in the map of correlations.

Discussion

Predictions 1, 3 and 4 were fully verified, while prediction 2 was fully refused. It is important how this work showed which is the most important period of the social maturation of fallow deer males

during their long walk to territoriality. The areas used before the first rutting period experienced as sores 2,5 y.o, the social aggregations selected before that rut, and the time spent in the lek that year were crucial steps to the achievement of a high mating success when subadults become adult males. For the first time, this work showed the importance of experience gained as subadults in determining the future mating success in male ungulates. Nobody showed these behavioural patterns before, leading to the creation of new scenarios for future researches dealing with the behavioural ecology of ungulates.

Prediction 1) Experiences gained at the lek by subadult males are supposed to affect the future mating success once they become adult males.

Verified. Time spent at the lek by males aged 2-3 y.o. resulted to be a crucial step for their future access to females among lek territories during the rut. On our knowledge this is the first time that juvenile experiences gained during the mating season was directly related to the future reproductive success on deer. Mating success, thus, seems not only linked directly to the mating strategy (Pelletier et al., 2006 and references therein), body mass (Mainguy and Côté, 2008) or survival (McElligott and Hayden, 2000) of males as many studies on ungulates species have already showed. Surprisingly, only the time spent at the mating arena by males 2-3 y.o. resulted directly correlated with their reproductive success observed at 5-6 year of age. Our interpretation is that older individuals (3-4 y.o. and 4-5 y.o.) have to deal with an high rate of aggression during the rut by dominant males when approaching the females (Komers et al. 1997). Indeed, because of their smaller size, sores aged 2-3 y.o. probably could stand relatively easily among females and thus among lek territories, as already hypothesized by Pelabon et al. (1999) for fallow deer yearlings. In that way, they can gain crucial experience during that rutting period, observing the behaviour of adult males, moving along territory borders, fighting with same-aged males. Moreover, De Cena et al. (*in prep.*) showed that males aged 4-5 y.o. were outcompeted from female access among lek territories, despite their already reached sexual and social maturity. Hence, behavioural development during early stages may affect the reproductive success through both a easier access to resources and a motor training function of the behaviours (Bekoff, 1977; Byers 1980; Rothstein and Griswold, 1991). This suggests that early growth in addition to its effect on the adult phenotype (Pelabon and Komers, 1997; Birgersson and Ekvall, 1997) may influence reproductive behaviours and ultimately reproductive success via its effect on behavioural development (Pelabon et al., 1999).

Prediction 2) Body mass related to best foraging strategies of subadult males are supposed to affect the future mating success once they become adult males.

Not verified. Ciuti et al. (*submitted*) recently showed that only those males that were able to exploit the best feeding areas of the disturbed sector (characterized by higher predation risk) and therefore to invest in body size and fighting ability before the rut, were consequently able to gain a higher mating success during the rut than males that were not as able to exploit the risky sector of the study area. This was true in affecting the possibility of an adult male to gain a high mating success, but this was not the case of subadult males. Our results showed that time spent at the lek of sores 2-3 y.o. was not directly correlated with body conditions (body mass, antler sizes) either of prickets (1-2 y.o.) or of sores aged 2-3 y.o. This results are clearly in contrast with the hypothesis formulated by Pelabon et al. (1999) predicting that early body growth was presumed to be able to affect behavioural development on young stages and, in turn, reproductive success. So, we are able to disentangle the 2 main factors able to affect the mating success of male fallow deer: i) the experiences gained as subadult males, both before and during the rut (this work) and ii) the foraging strategies adopted by bucks before the rut (Ciuti et al. *submitted*), thus able to guarantee the proper body condition to face the long and harsh mating season.

Prediction 3) Subadult males that are leaving early female aggregations are supposed to escalate before the male hierarchy and to become successful once they become adult males

Verified. As previously described, the eastern sector (DS) of the study area is characterized by an high utilization and presence of adult males, while the western sector (US) is characterized by an high utilization and presence of females that selected this area for fawning (Apollonio et al. 2005; Ciuti et al. 2004; Ciuti et al. 2008; Ciuti et al., *submitted*). We recorded that the time spent at the lek by sores 2-3- y.o. was inversely correlated to the distance from DS before the rutting period of these males during spring and summer. Thus the use of male areas was crucial in affecting lek attendance of sores 2-3 y.o. Higher the distance from the DS, lower the permanence at the lek of sores.

Prickets during winter are in general still a member of the mother's social group (Apollonio et al. 1998, Apollonio et al. 2005, Ciuti et al. 2004). This was confirmed by results obtained, only during spring (when they abandoned female aggregations) the distance of prickets from DS resulted directly correlated with time spent within female or mixed aggregations, thus indicating that males that showed an high frequentation of the DS didn't joined female groups.

Prediction 4) Subadult males early aggregating with adult male aggregations are supposed to escalate before the male hierarchy and to become successful once they become adult males.

Verified. Percentage of bucks within male aggregations frequented before the rut was positively correlated with time spent in the lek by sores 2-3 y.o. .

So, we conclude that there are 2 main factors able to affect the mating success of male fallow deer: i) the experiences gained as subadult males, both before and during the rut (this work) and ii) the foraging strategies adopted by bucks before the rut (Ciuti et al. submitted), thus able to guarantee the proper body condition to face the long and harsh mating season. For the first time, we showed how it is important for a subadult male to actively attend to lekking activities (observing, fighting, moving along borders of the territory defended by adult males), thus acquiring experiences on how the system works, being this positively correlated with the individual mating success achieved as adult males. Moreover, we showed that also experiences gained by subadult males outside the mating season are important in the development of the successful mating strategy, given that intra-sexual interactions among subadult males and mature bucks within male aggregations were related to the gain of a high rank in the social and complex hierarchy established among adult fallow deer males.

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Chapter 5



Effectiveness of an expandable collar for subadult male cervids

Effectiveness of an expandable collar for subadult male cervids.

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Abstract

We designed and tested an expandable radiocollar for fallow deer subadult males. The construction of these collars is simple as they are hand-made; moreover they are almost inexpensive (few euros), and are lost by deer as their neck grows without causing any injuries. This is possible thanks to the use of an elastic rubber bands covered by a leather layer which protect them from an early consumption caused by mechanic friction against the vegetation. Eventually, the collar drop-off as the elastic rubber bands break due to neck growth. Using Kaplan-Meier survival analysis, we estimated the life length of 37 hand-made flexible collars deployed on prickets (1-2 y.o.). Average duration of collars from their deployment to the natural drop-off was almost 2 years (mean \pm SE, 91.7 ± 6.4 weeks). This simple methodological approach should be adopted by researchers aimed to perform long-term studies on ungulate species as quite often, a lack of information on the behavioural ecology of subadult males is evident. Due to its effectiveness, this expandable collar should be considered especially when the re-capture of the deer is possible, making possible the substitution with a new device before the estimated natural drop-off of the expansible collar.

Keywords

Dama dama, fallow deer, radiocollar, long term, subadult males.

Introduction

In order to investigate properly the ecology and life-history of wildlife species, long-term studies of individually marked animals are strongly required (Jorgenson et al., 1993, 1997; Sarno et al., 1999; Bank et al., 2000). As regard with elusive or forest-dwelling species, several studies require necessarily the use of radio-collars in order to record data on a long-term on an individual (White and Garrott, 1990). Radio-telemetry has enhanced the study of animals, being materials, methodologies and costs required to fit radiocollars to wildlife inevitably vary among species (Strathearn et al., 1984 and references therein). The first collars deployed in large mammals was fixed in size, and colour coded for identification (Progulske, 1957). Expandable collars for subadult individuals were later introduced to allow for the natural body growth (Hamilton, 1962; Beale, 1966). The evolution and evaluation of expandable radiocollars has continued until today (e.g. Diefenbach et al., 2003) in order to find the best compromise between avoiding injuries to wildlife and being effective in the collection of long-term data. Many researchers pointed out the importance of long-term projects in behavioural ecology (e.g. Mysterud et al., 2005), population dynamics (e.g. Bonenfant et al., 2005) and survival (e.g. Ueno et al., 2010) studies on ungulates.

In this paper, we designed and tested an expandable radiocollar for fallow deer subadult males. These collars are simple as are hand-made, are almost inexpensive, and are lost by deer as their neck grows causing no injuries. Our aim is to suggest a simple but truly effective methodological approach to be adopted by researchers aimed to perform long-term studies on ungulate species lacking information on the behavioural ecology of subadult males.

Material and Methods

Expandable collars: We showed materials used to build expandable collars in the Fig.1. We did cut Televilt collars, TXV-10 model (Fig 1 B), the broken piece of collar measuring 11cm and 16 cm, respectively, the longer cut being done where the VHF antenna occurred (Fig 1 I). Then we deployed 3 perfectly overlapping pieces of elastic acrylic tissue (1mm thick, 30 cm length) (Fig 1 A) and fixed them in the internal side of the plastic broken piece of collars (Fig 1 H) with 3 pop rivets (Fig 1 C) per side by means of a riveter (Fig 1 E). A punch pincher (Fig 1 F) easily allowed us to place and fix the pop rivets. Moreover, spacing washers (Fig 1 D) were inserted between the pop rivets head and the collar plastic material in order to ensure the right grip of rivets. The 3 layers of elastic acrylic tissue were covered by a layer of leather (Fig 1 G) which has the role to protect the expandable tissue from the friction and wear with the vegetation once deployed in free-ranging animals (Fig 1 K).



Fig. 1 – *Materials deployed to build expandable radiocollars: A) Layers of elastic acrylic tissue. B) Televilt radiocollar TXV-10. C) Pop rivets. D) Spacing washers. E) Riveter. F) Punch pincers. G) leather layer. Assemblage stages: H) Detail of riveted layers on collar. I) Cut collar. J) Collar with acrylic layers assembled. K) Final stage of the device with all parts assembled. See text for major details.*

Deployment of expandable collars: This study was performed in the San Rossore Estate, Italy (see Ciuti et al., 2004 for characteristics of the study site). Starting from November 2004 to November

2008, we captured fallow deer males every winter (see Ciuti and Apollonio, 2008 for details). During such operations we hand caught, blindfolded, ear tagged, fitted with expandable radiocollars, and finally released 37 prickets (males aged 1-2 y.o.) that represented our sample in this study. . When re-capture events occurred, we re-placed the flexible radiocollars (n=13) with a new definitive one. In order to take into account the natural neck growth of males during the rutting period (Chapman & Chapman 1997), definitive devices were fitted on each individual leaving enough room (four fingers) between the neck and the radiocollar in order to avoid damages on animals.

Analyses of data: Statistical analyses were performed using R v.2.10.1 (R Development Core Team, 2009). The “survival” R package was used to establish the life length of expandable radiocollars using the Kaplan-Meier method survival analysis (Crawley, 2007). Censored events were considered in the analysis in order to include collars that did not drop-off naturally, i.e. the replacement of expandable collars during re-capture events (n=13), individual dispersal and related lost of contact (n=4) or death (n=6). All deceases registered during the study period were consequent on annual culling program (n=5) or on natural causes (n=1). Time interval of duration curves was considered from animals release until the latest breakaway or censored event, i.e. after 132 weeks from release.

Results

After one year from the deployment of expandable collars, the survival rate was 0.874 (95% C.I.: 0.76-0.99), while after two years this figure was 0.339 (95% C.I.: 0.085-0.59) (Fig.2). The quartiles analysis of the duration curve estimation showed that these devices (n=37) have a probability of 75%, 50% and 25% of being still worn by subadult males until the 65th week, the 101st week and the 115th week after release, respectively (Kaplan-Meier; quartile estimate \pm standard error: 1st quartile 65 ± 6.9 weeks, median 101 ± 7 weeks, 3rd quartile 115 ± 8.4 weeks). Thanks to the replacement of expandable collars in recapture events, we were able to monitor until the end of the study period (i.e. until November 2008) those individuals at whom we replaced the radiocollar at least once during their first 3 years of age (n=13) with a definitive one. This was the case with the exception of missing dispersal individuals (n=4) and in case of decease (n=6). We verified the deaths within the day after the event occurred and in all cases we did not observe any signs of neck injury due to the presence of expandable collars. At the same time, we verified the neck in all animals at whom we changed the expandable collar during re-capture events.

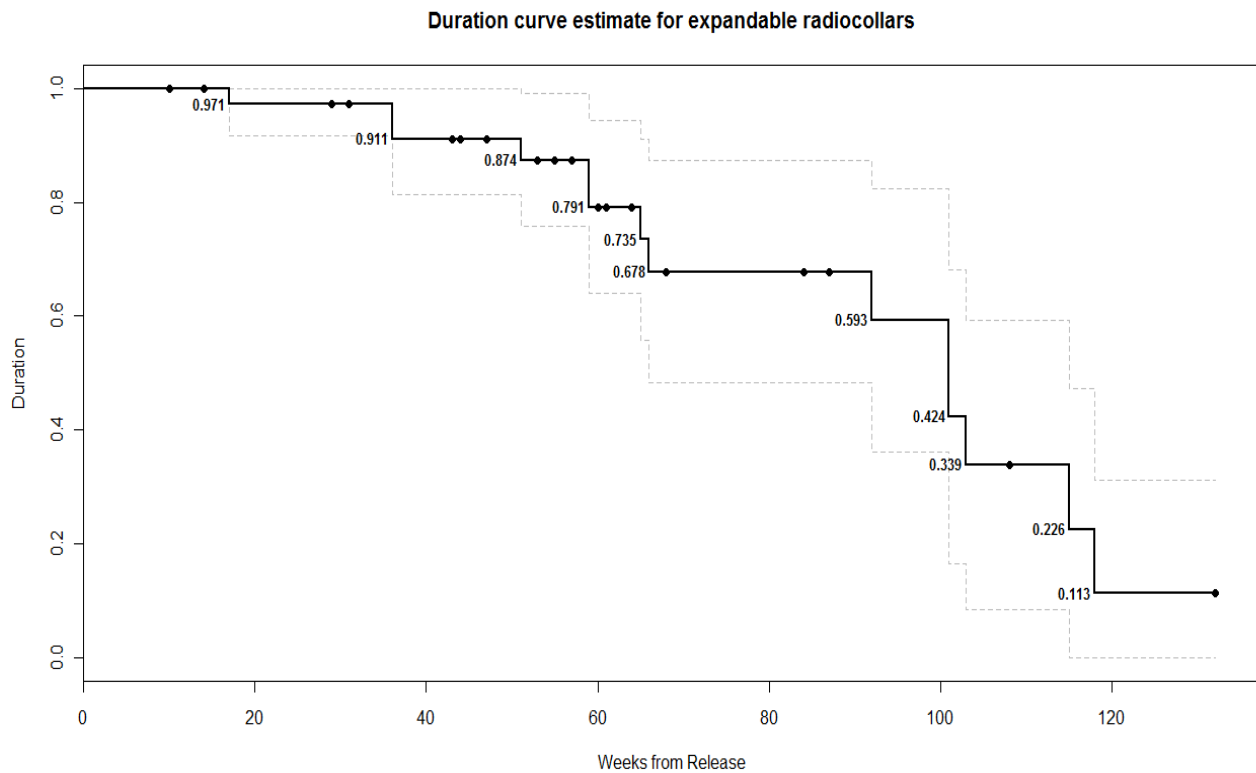


Fig. 2 – Duration of expandable radiocollars (bold line) deployed in fallow deer prickets (1-2 y.o. males) and confidence intervals (dotted lines) (sample size $n=37$). Black dots indicate the censored events ($n=23$) in the Kaplan-Meier survival analysis. Time interval for the survival analysis was considered from the release of prickets until the latest breakaway or censored event recorded in our study (132nd week).



Fig. 3 – Examples of expandable collars deployed in this study. The presence of injuries or lack of fur was carefully evaluated during each re-capture events.

Usually the lack of fur below collars is the first sign of friction due to collar presence, but, in our case, we didn't find any sign of fur loss (Fig.3). This study complies with all provincial, regional and national Italian laws.

Discussion

Long-term studies are important to deeply investigate population dynamics and life histories of ungulates (e.g. Lingle et al., 2008; Rodriguez-Hidalgo et al., 2010). However, long-term studies implies increasing difficulties when the monitoring of young males is required. In our study case, the adoption of the expandable collar described in this research was crucial in the long-term study we performed dealing with the fallow deer behavioural ecology (De Cena et al., *in prep*) that included the juvenile phase of males. To reach our research goal, it was important to monitor deer by means of radio-tracking from early stage of social maturation to the full complete sexual maturation (De Cena et al., *in prep.*). Estimated life length of our devices showed that this design of expandable radiocollars was useful to monitor subadult males during their growth, in particular in a study area where recapture probability of the same individuals is high (37%) and thus high is the chance to replace expandable collar with a new definitive one, especially when large sample size are monitored. Expansible collars resulted not harmful to monitored deer. We verified the health conditions of animals, as suggested by Bank et al. (2000) and we investigated cause of death of individuals we lost during the research. Only 6 deceases were recorded, one due to wolf predation, the other deer being shot by game keepers in the study site. To further increase the probability to monitor for a long time subadult males, along with the use of the expandable collars we designed, we strongly suggest researchers to deploy time-delayed radio-ear-tags. Indeed, ear-tags should provide a further help for researchers to find, recognize and, eventually, re-capture individuals who lost their expandable device. .

In conclusion, these expansible radiocollars were effective, easy to produce and deploy, inexpensive and lasting on average 2 years on the deer before the natural drop-off. Thus, they allowed us to monitor deer in the period in which the neck growth occurs (Chapman & Chapman 1997) and the use of permanent collars should be not considered in order to avoid neck injuries to monitored animals.

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CONCLUSIONS

I described how results obtained support the female preference and the predator avoidance models - but not the hotspot one - as the most likely candidates able to explain the actual lek position in San Rossore Estate (**Chapter 1**). To reach the lek, being commonly an area far from those used by females, females enlarged their home range sizes during the mating season. Females were closest to the lek area in summer than in autumn, when they gave birth in suitable birth places located between the lek and the sea (Ciuti et al., 2003; Ciuti et al., 2006). Data analyses showed that females, when males were already clumped in the lek territories, reached the lek during the oestrus time leaving foraging areas. However, according to Höglund and Alatalo (1995), it is not possible to find an unique explanation of lek evolution but its actual position allowed us to understand which selective pressures are working for its persistence. Indeed, the actual position of lek in San Rossore is maintained by two selective pressures: the female preference and the predator avoidance. Among the many hypothetical positions of the lek which can be assumed for a lek in our study site according to the predator avoidance (far from the eastern disturbed sector) and the female preference (a large clump of males visited by females even if not located over female high traffic), the actual position is that able to merge and to maximize these two benefits. Low travel cost for females and low predation risk are likely to be the selective pressures which allowed the maintenance of the lek on its actual position, which is a handy position for the whole female population using that lek.

Apart from the lek position, I observed that foraging strategy adopted by adult males before the rutting period can affect their mating strategy and, in turn, their reproductive success gained among lek territories (**Chapter 2**). In some populations a single mating strategy clearly was found to predominate over the others in that it accounted for most of the mating success achieved: like in other populations (Schaal and Bradbury, 1987; Clutton-Brock et al., 1988; Langbein and Thirgood, 1989), in the San Rossore population this strategy was the defense of lek territories (Apollonio et al., 1992). This choice resulted to be significantly affected by the spatial and foraging strategies adopted before the rut (spring and summer), i.e. when males crucially invest in body size (Stearns, 1992; Jönsson, 1997). Moreover, in the study site the best foraging areas were characterized by higher predation risk (Ciuti et al., 2004; Ciuti and Apollonio, 2008) and males that showed a higher use of the risky sector in spring and summer were able to defend a lek territory in the following mating season. Hence, the ability of each male to defend a lek territory in the rut could be predicted

by looking at its use of the risky sector of the Estate in spring and summer, that allowed an optimal investment in body size through the exploitation of this feeding area.

I continued to investigate which factors or behavioural patterns can contribute to reach a successful mating strategy and, in turn, an high reproductive success by males among lek territories. In details, I try to clarify if the timing of lek use by fallow deer males is crucial to understand if and how can be important for a male to be there well before the beginning of the rut, in particular according to their age and mating success (**Chapter 3**). The findings of this work suggested that males younger than 5 y.o. (non-mating males) cannot compete with larger and more experienced males. The presence of non-mating males (both bucks 4-5 y.o and sores) in the lek during the breeding season could be the consequence of the following of females until lek territories (Clutton-Brock et al., 1988; Apollonio et al., 1992) or alternatively can be considered for them a chance for acquiring experience of mating activities fundamental during reproductive seasons of the following years (Bekoff, 1977; Byers, 1980; Rothstein and Griswold, 1991; Pelabon et al., 1999). As a matter of fact, they arrived at the lek almost simultaneously with the arrive of females, i.e. when the first copulation was observed, while older males (mating males) reached the lek well before the beginning of the rut. I supposed that this choice in timing by mating males could be related with the attempt to begin the escalation of male hierarchy and thus those males that starting this escalation before, could occupy high ranked position from the beginning. But, from results obtained, it appears that the month before the beginning of the rut is a fundamental period of time in which fallow deer bucks build a part of their oncoming success in the lek, but this is not a function of the time of arrival at the lekking site, all the adult males being arrived simultaneously in our study case. Moreover, I evaluate that young or low ranked males do not try to compensate their scarce mating success leaving the lek later than dominant males. This could be expected as a consequence of the fatigue of dominant males, who spent almost 1 months in defending a lek territory without feeding (Apollonio and Di Vittorio, 2004).

Others factors that can affect mating success achieved by adult males among lek territories, were showed in **Chapter 4** in which I presented innovative and intriguing results on the behavioural ecology of ungulates. Here I showed the importance of experience gained as subadult males in affecting the future individual mating success. It is important how this work showed which is the most important period of the social maturation of fallow deer males during their long walk to territoriality. The areas used before the first rutting period experienced as sores 2,5 y.o, the kind of aggregations they joined before that rut, and the time spend in the lek that year are a crucial step in the possibility to achieve a high mating success when they become adult males. In details, I verified

the following predictions: i) Experiences gained at the lek by subadult males are supposed to affect the future mating success once they become adult males. ii) Subadult males that are leaving early female aggregations are supposed to escalate before the male hierarchy and to become successful once they become adult males iii) Subadult males early aggregating with adult male aggregations are supposed to escalate before the male hierarchy and to become successful once they become adult males. On the contrary, I rejected the prediction assessing that body mass related to best foraging strategies of subadult males are supposed to affect the future mating success once they become adult males.

Finally, from this thesis appeared clear that in order to investigate properly the ecology and life-history of wildlife species, long-term studies of individually marked animals are strongly required (Jorgenson et al., 1993, 1997; Sarno et al., 1999; Bank et al., 2000). As regard with elusive or forest-dwelling species, several studies require necessarily the use of radio-collars in order to record data on a long-term on an individual (White and Garrott, 1990). Thus, I presented the design of the expandable radiocollar deployed on fallow deer subadult males during the study period (**Chapter 5**). I estimated life length of those devices using the Kaplan-Meier method survival analysis (Crawley, 2007). Results obtained showed that this design of expandable radiocollars was useful to monitor subadult males during their growth, in particular in a study area where recapture probability of the same individuals is high (37%) and thus high is the chance to replace expandable collar with a new definitive one, especially when large sample size are monitored. Moreover, expansible collars resulted not harmful to monitored deer. I verified the health conditions of animals, as suggested by Bank et al. (2000) and I investigated cause of death of individuals lost during the research. Only 6 deceases were recorded, one due to wolf predation, the other deer being shot by game keepers in the study site.

Hence, these expansible radiocollars were effective, easy to produce and deploy, inexpensive and lasting on average 2 years on the deer before the natural drop-off. Thus, these devices allowed to monitor deer in the period in which the neck growth occurs (Chapman & Chapman 1997) and the use of permanent collars should be not considered in order to avoid neck injuries to monitored animals.

In conclusions, I reported new results on the behavioural ecology of the fallow deer, with special regard to mating strategies and success.

First, I showed that the actual position of the lek is handy with regards to female travel costs and predation risk avoidance, in accordance to the “female preference” and “predator avoidance” hypotheses.

Second, I showed that males able to adopt risky but best foraging strategies are able to gain an optimal body condition before rut and thus to achieve a high mating success. Third, I showed that for all adult males, despite age and mating success, it is important to reach the lek well before the beginning of the rut to gain positions in the male hierarchy. However, I refused the hypothesis that sooner a male arrives at the lek, higher will be its mating success and the hypothesis that subadult males are supposed to leave the lek later than adult males in order to increase their possibility of mating when mating males are exhausted.

Finally, for the first time, I showed the importance of experiences gained by subadult males in affecting the individual mating success, once they become adult males.

The study of subadult males was possible due to the deploy of an hand-made expandable radiocollar created during this study.

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