THE NUTRITIONAL CARRYING CAPACITY OF
FOUR MEDITERRANEAN HABITATS
FOR FALLOW DEER (*DAMA DAMA*)

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Information on carrying capacity of natural ecosystems is essential for the development of sound management procedures. The ecology of Mediterranean wild ruminants is yet poorly understood and reliable estimates of carrying capacity for Mediterranean ecosystems are not available. For wild ruminants there are several studies on diet selection and impact on vegetation (Venero, 1984 ; Bruno & Apollonio, 1991 ; Focardi *et al.,* 1991b ; Garcia-Gonzales & Cuartas, 1992) but the information about the trophic value of typical Mediterranean plant species is yet scarce (Meuret & Giger-Reverdin, 1990). In the few studies on food digestibility in fallow deer (Putman & Hemmings, 1986 ; Duranti *et al.,* 1986 ; Poli *et al.,* 1989 ; Poli *et al.,* 1990) forage items of natural Mediterranean ecosystems have not been analysed.

Fallow deer (*Dama dama*) is characterized by a natural distribution limited to warm areas of the Central-east Mediterranean basin (Chapman & Chapman, 1975 ; Masseti & Rustioni, 1988) ; now it is largely present and represents an important component of the community of ungulates in many coastal ecosystems in Italy (Perco, 1987) as well as in other Mediterranean countries. A rationale for the management and exploitation of these environments is extremely necessary because many wild Mediterranean ecosystems are at risk of destruction and degradation (Naveh & Lieberman, 1984).

The aim of the present paper is to assess the nutritional carrying capacity of four different habitats for fallow deer using the model proposed by Hobbs & Swift (1985). This method is based on optimal foraging arguments (Stephens & Krebs, 1986) in that it assumes that animals should select higher quality forage items in preference of lower quality ones ; more specifically, available feeds are ranked in decreased order of concentration of a limiting nutrient and progressively included in diet. The model yields more realistic estimates of carrying capacity than traditional methods based on range-supply/animal-demand procedures.

MATERIALS AND METHODS

THE MODEL

The algorhythm of Hobbs & Swift (1985) is based on the calculation of the minimal necessary concentration, C^*, of the limiting nutrient. In this study, we

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assume that the metabolizable energy of forage (Kcal/Kg of dry matter) is a critical nutrient for fallow deer. To compute C^* we divide the mean energy requirement (Kcal per day), E_{ave}, by the maximal daily intake of forage, I_{ave} (Kg of dry matter). In order to express the carrying capacity in terms of number of « average » fallow deer we have to take into account the actual structure of the population. Let E_j and N_j be the mean daily energy requirements and number of individuals, respectively, of the j-th class of age and sex — young and adult females, young males, prickets, sores and bucks (cf. Chapman & Chapman, 1975 for definitions) — then

$$E_{ave} = \Sigma E_j N_j / \Sigma N_j .$$

Moreover let the energy concentration of each food item be C_i and B_i be its biomass available to the foragers. The M feeds have to be ranked in order of decreasing concentration of the nutrient (i.e. $C_1 > C_2 > \cdots > C_M$). Then we can write the recursive equation :

$$A_N = \Sigma C_i B_i / \Sigma B_i , \quad i = 1, ..., N \quad N = 1, ..., M .$$

A_N is the concentration of the critical nutrient in the mixing used by the forager when it exploit N items. The value of A_N decreases monotonously with N, i.e. with the number of feed included in the diet. Subject to the constraint $C^* < C_1$, we find that $A_{N-1} < C^* < A_N$, for some N. Thus N represents the last feed to be included in the diet ; all feed with a rank larger than N should be ignored by the foragers. Then the edible biomass is

$$B_e = \Sigma B_i + U , \quad i = 1, ..., N - 1$$

where $U < B_N$ is the amount of biomass of the last feed to be included in the diet. The equation for U is reported by Hobbs & Swift (1985). The carrying capacity is simply B_e/I_{ave}. In summary, to compute the carrying capacity it is necessary to estimate the following parameters : the critical concentration C^* in the mixing, using animal's energy requirement and intake, the concentration of the nutrient in the feed, C_i, and the available biomass of feed, B_i.

STUDY AREA AND PARAMETER ESTIMATES

This study was carried on in the 43 km^2 Preserve of Castelporziano near Rome, Italy. The area represents one of the most important relict Mediterranean forests in Italy ; it mainly consists of an oak wood where 300 years-old trees are relatively common. Fallow deer are usually culled in autumn and winter. The climate is Mediterranean, both winter and summer are dry seasons. Mean temperature and rainfall for the period 1981-91 yield values of the Mitrakos' (1982) index of 75.5 in summer and of 50.4 units in winter (Guerrini, pers. com.) suggesting that the summer stress is greater than the winter stress.

The detailed structure of the ecosystem has been described elsewhere (Focardi *et al.*, 1991a). In this study we are concerned with four habitats heavily

exploited by fallow deer : (i) the *Viburno-Quercetum ilicis* (evergreen oak forest) dominated by *Q. ilex* and, to a lesser extent, *Q. suber.* The understory is usually dense with a prevalence of *Myrtus communis, Phyllirea latifolia, Pistacia lentiscus* and, where the cover is reduced, by *Rubus ulmifolius* ; (ii) the scrub is characterized by a reduced overstory and by a dense understory of *P. latifolia, P. lentiscus, Erica arborea* and *Arbutus unedo* ; (iii) mixed plantations of *P. pinea* and *Q. ilex* with an understory very similar to the one described for habitat (i), and (iv) open pastures, characterized by a widespread presence of *Asphodelus microcarpus* and by the presence of scattered oak trees, wild pear (*Pyrus pyraster*) and *Prunus spinosa.* Graminoids and forbs are very abundant. *Lolium perenne, Phleum pratense, Anthoxanthum odoratum, Avena barbata, Lamarckia aurea* and *Stipa capensis* are the more common graminoids. Habitat (i) is representative of the natural Mediterranean forest, the scrub is a degradated formation, on account of antropogenic action, very common along the Mediterranean coast. Even pastures are a degradated habitat, produced by heavy cattle grazing in the past.

Vegetation sampling occurred each three months between December 1990 and February 1992. Thus, six seasons have been studied from autumn 1990 to winter 1991. The vegetation sampling was performed using the point intercept method described in detail by Focardi *et al.* (1991a). Two sampling areas were established in habitat (i), one area in habitat (ii), two areas in habitat (iii) and one in habitat (iv). Each area was sampled by four transects.

The foraging impact of ungulates at Castelporziano is concentrated on four species of shrubs (*Rubus ulmifolius, Cistus salvifolius, Phyllirea latifolia, Quercus ilex*) and on graminoids (Focardi *et al.,* 1991a) ; the other available items are used with a frequency lower than 5 % and only the more important feed shall be considered for this study.

Focardi *et al.* (1993) have showed that the number of pin contacts is a good predictor of vegetation biomass. The equations which link the number of pin contacts and biomass, for the five food items considered here, are :

$$\text{dry matter} = 0.33 \text{ intercepts} - 1.39 \quad \text{for } P.\ latifolia$$
$$\text{dry matter} = 0.22 \text{ intercepts} - 6.5 \quad \text{for } C.\ salvifolius$$
$$\text{dry matter} = 0.27 \text{ intercepts} - 6.7 \quad \text{for } R.\ ulmifolius$$
$$\text{dry matter} = 0.82 \text{ intercepts} - 45.6 \quad \text{for } Q.\ ilex$$
$$\text{dry matter} = 0.28 \text{ intercepts} - 29.2 \quad \text{for graminoids}$$

Using these equations it is possible to translate the number of pin contacts to dry matter. The independent variable in the equation is the mean number of pin contacts per sampling unit. The equations yield a biomass value in gr of dry matter per square meter. The adoption of the point intercept method to non-destructively estimate plant biomass allowed us to use the same sampling areas for the whole study period. When plant biomass is measured by mowing samples, an uncontrollable spatial variability (which in natural habitats may be also very large) is introduced because sampling areas have to be moved at each season.

Structure and size of population is assessed each year by counts made in spring and autumn using the methods described by Focardi *et al.* (1991b).

To estimate digestibility traits and the nutritive value of the collected plants for fallow deer in the different seasons, *in vitro* digestibility trials were performed.

The two-stage *in vitro* assay, according to Tilley & Terry (1963) and modified by Alexander (1969), is recognized as the most accurate and practical laboratory method available for predicting digestibility data for ruminants (Goldman *et al.*, 1987). The reliability of the method was improved using inocula provided by fallow deer culled in the study area in the same season of vegetation sampling (Ward, 1971 ; Robbins *et al.*, 1975 ; Blankenship *et al.*, 1982 ; Poli *et al.*, 1989). Five hundred mg of each sample were tested in triplicate for *in vitro* organic matter digestibility (OMD) ; by using standard feed (for fallow deer) of known *in vivo* OMD, the *in vivo* OMD of the studied plants was also estimated. Metabolizable energy of samples was calculated from the *in vivo* OMD percentages according to INRA (1988) method.

Information on food intake in fallow deer is scarce, but seasonal variations have been reported in other ruminants (Kay & Staines, 1981 ; Van Wieren, 1992). To estimate food intake of fallow deer, we used data collected on groups of 2-5 does reared outdoors during 20 *in vivo* digestibility trials, distributed in different seasons (Poli, pers. obs., Poli *et al.*, 1989 ; Giorgetti *et al.*, 1990).

The energy requirements of the different age and sex classes, E_i, were taken from Hartfiel (1990) and corrected for the mean weight of each sex and age class from a sample of 50 culled animals.

RESULTS

The structure of fallow deer population in spring 1991, mean weights and energy requirements for each sex and age class are reported in Table I. The spring counts yield a correct structure of the populations in terms of relative aboundance of the different sex and age classes, however the estimate of population size is subject to sampling error. The analysis of 5 years spring counts (1990-1994) showed that these censuses are characterized by large fluctuations in the estimate of population size ; during the 5-years period the standard error has been 238 animals (Focardi *et al.*, in prep.). Because in 1991 we have estimated a population of 537 fallow deer, the upper 95 % confidence limit of this value is 1 001 animals. Thus the actual population density lies in the range 12.5-23 deer/100 ha.

The mean weight of fallow deer at Castelporziano was 43.2 kg. The mean energy requirement, E_{ave}, was 3 478 Kcal/day.

In order to compute the critical concentration of metabolizable energy, C^*, in Table II we have reported the amount of dry matter ingested by female fallow deer. Note that the amount of ingested food is lower in autumn and winter than in spring and summer (Kruskall-Wallis ANOVA, $\chi^2_3 = 8.0$, $P < 0.05$). The seasonal mean intake, I_{ave}, is obtained by the coefficients of Table II times the mean weight.

The value of metabolizable energy which deer may get from the studied feed is reported in Table III. It is interesting to note that there are no seasonal difference in the amount of energy which can be extracted by this set of feed (Kruskal-Wallis ANOVA $\chi^2_3 = 0.28$, $P > 0.05$) but there is a strong between-feed difference Kruskal-Wallis ANOVA $\chi^2_4 = 14.6$, $P < 0.01$). In each season *R. ulmifolius* exhibits the best and *Q. ilex* the worst nutritional traits ; the nutritional value of graminoids are characterized by a sharp variation which peaks in summer.

TABLE I

Living weights (Kg), energy requirements (Kcal/day) of each age and sex class and structure of population during March 1991 count.

Class	weight	E_i	N_i
Females			
Yearlings	27.9	2 057	33
Does	46.6	2 924	97
Males			
Yearlings	31.3	2 242	42
Prickets	49.4	3 442	18
Sores	59.5	3 812	70
Bucks	81.1	4 804	98
Undetermined			
Yearlings			32
Other			
Undetermined			147
TOTAL			537

TABLE II

Seasonal average per-day food intake of female fallow deer expressed in percent of living weight.

Season	No trials	Intake	95 % confidence limits
Spring	8	3.28	0.65
Summer	4	3.25	0.68
Autumn	3	2.89	1.37
Winter	5	2.39	0.33

TABLE III

Metabolic energy (kcal per kg of dry matter) of food items as a function of season.

	C. salvifolius	R. ulmifolius	P. latifolia	Q. ilex	Graminoids
Spring	1 641.3	2 392.7	1 920.4	1 354.9	1 557.6
Summer	1 686.8	1 962.0	1 736.7	1 327.3	1 809.7
Autumn	2 009.0	2 091.7	1 541.7	1 440.2	1 483.8
Winter	1 868.6	1 884.7	1 860.8	1 325.2	1 375.6

For management and conservation purposes the computation of the carrying capacity depends on the *a priori* decision of how much fraction of available

vegetal biomass has to be exploited by a population of herbivores. We have assumed that, at most, only the annual productivity should be available to fallow deer ; a larger exploitation rate involves overgrazing and consequently habitat deterioration in the long-term, in other words we try to assess the ecological carrying capacity (Bainley, 1984) based on sustainable production. In Table IV we have reported the average productivity of the studied feed in the four habitats. Graminoids may be exploited at a large extent, three species of shrubs, *R. ulmifolius, P. latifolia* and *Q. ilex* present a productivity around 30 % while *C. salvifolius* is characterized by the lowest productivity.

TABLE IV

Average maximum standing biomass of five forage items. The productivity of feed is given by the difference between maximum and minimum biomass observed during the year expressed as the fraction of the maximum (relative productivity).

Feed	Maximum	Productivity	Relative Productivity
Graminoids	12.19	10.93	0.90
Q. ilex	9.15	3.00	0.33
R. ulmifolius	5.25	1.72	0.33
P. latifolia	4.51	1.10	0.24
C. salvifolius	3.48	0.40	0.11

The results of the application of the algorhythm proposed by Hobbs & Swift (1985) to the studied population of fallow deer are reported in Fig. 1. Mixed plantations and scrub are characterized by a sharp increases of carrying capacity in spring with respect to the other seasons. For open pastures the increase of carrying capacity in spring is smaller than for the previous habitats and the highest peak is observed in autumn. The carrying capacity of the ever-green oak wood does not exhibit the strong phenological variations which characterize the other habitats, but only by a small spike in spring. The observed differences of carrying capacity are explained by seasons (Friedman's two-way ANOVA, $F = 3.5$, $P < 0.05$) but not by habitats (Friedman's two-way ANOVA, $F = 2.5$, $P > 0.05$) ; the maximal seasonal difference is between summer and autumn (Bonferroni multiple t-test, $P < 0.05$). Interestingly, mixed plantations and scrub exhibit a phenology which is complementary with respect to the one of pastures : the former two habitats are characterized by a very high carrying capacity in spring, while the latter one in autumn and winter.

From our data it appears clear that summer is the most critical season for fallow deer ; during this period all studied habitats exhibit a reduced carrying capacity. If we compare the size of the studied population with the calculated capacities we observe that it is close to the capacity of the most productive habitats in summer.
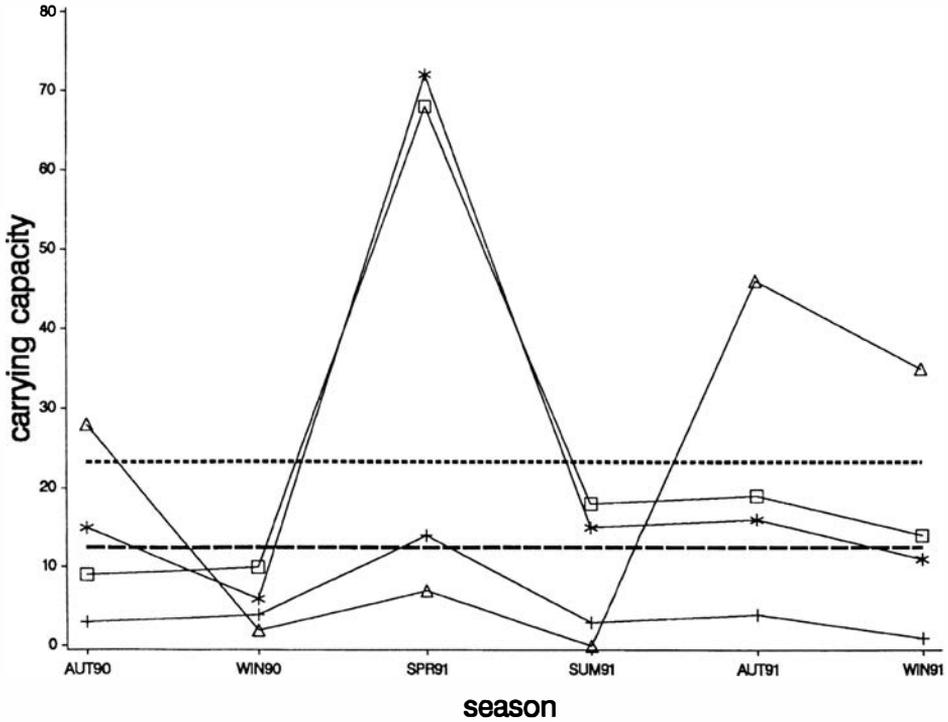
Figure 1. — Phenological variations of carrying capacity (specimen per 100 ha) during the study period in the evergreen oak wood (cross), pastures (triangle), scrub (square) and mixed plantations (star). The broken line represents the population density in spring 1991, the dotted line its upper 95 % confidende limit.

DISCUSSION

To our knowledge, this is the first paper where it is possible to give figures of carrying capacity of Mediterranean habitats for wild ruminants. The method which has been used (Hobbs and Swift, 1985) is based on more realistic assumptions than traditional methods in that it takes into account the interactions between quality and quantity of forage ; as a matter of fact forage quality is often inversely related to its aboundance (e.g. White 1978). Thompson's (1990) study on moose supports this point : without taking into account nutritional constraints, carrying capacity should be substantially overestimated.

A comparison between the carrying capacities of the different habitats can not be based on the study of habitat use by animals. In fact, Hobbs & Hanley (1990) and Hanley (1990) have showed by simulation that habitat use reflects carrying capacity only under specific circumstances : a positive relation is expected when population size is not far from the equilibrium with its resources while for lower population sizes, individuals behave in such a way to hide any positive correlation between habitat use and carrying capacity. For instance, in our study case, we

might expect a positive correlation in summer but not in spring and autumn. A comparison between the carrying capacity estimated for Mediterranean habitats and the values which characterizes the populations of fallow deer living elsewhere is difficult because specific studies are scarce. Ueckermann & Hansen (1983) report sustainable densities lower than 10 deer/100 ha in Germany. Perhaps the carrying capacity is usually higher in Mediterranean countries than in Central Europe because in the former environment the winter carrying capacity is similar to the autumn and summer ones, while in Central Europe there are more severe winter conditions. Little understory of some German forests may also contribute to reduce the figures of carrying capacity.

In the interpretation of our results it is necessary to be aware that our figures of carrying capacity represent the relative importance of each habitat, their absolute importance depends on their surface areas. For istance in our case the surface area covered by mixed plantations and scrub is lower than the one of the evergreen oak wood.

The results of this study are yet preliminary because it is based on a small number of sampling areas (no more than eight transects have been used in each habitat) so that the calculated carrying capacity may reflect more local conditions than average values. Moreover, our estimates of the carrying capacity might be influenced by the heterogeneity of the data used to evaluate the parameters of Hobbs & Swift's (1985) model ; in particular, it might be questionable to use observation of tamed animals to estimate energy requirement and intake for wild ones.

Despite these limitations, we have presented a consistent application of one method which is potentially very useful for range evaluation. Our results suggest that in the Mediterranean environment, summer more than winter is the limiting season for fallow deer ; the importance of summer food as a determinant of carrying capacity has been also assessed by Denis (1991) for roe deer. The climatic factors most influencing Mediterranean evergreens have been reviewed by Mooney (1981) : in general temperature optimum of photosynthesis is around 20 °C : in summer, the average monthly temperature at Castelporziano is 23 °C (with maximum values usually less than 30 °C) so that temperature may not be the cause of the observed reduction in forage productivity and quality which is probably due to the intensity of summer drought (12.2 mm of rain in July) which may determine a quite low water potential for most of shrub vegetation.

Natural forested habitats are less important for wildlife than the ones modified by human activity ; in particular a degradated habitat like the scrub, not very important for commercial forestry, may be very productive for wild ungulates. This observation suggests that unproductive areas dominated by the scrub (which are quite common along Mediterranean coasts), might be exploited for recreation and hunting. Moreover, our study suggests that a certain degree of habitat variability is necessary in order to improve forage availability through the year. Open areas and clearings are especially important in autumn and winter.

In our estimates of carrying capacity we have not considered the trophic contribution of acorn, especially relevant in winter. In Mediterranean areas exploitation of acorns by deer is dominated by competition with the wild boar for this resource. Some preliminary assays have shown that acorns have a high *in vitro* digestibility (*Q. ilex* 82.7 %, *Q. suber* 70.8 %, *Q. frainetto* 68.6 % and *Q. cerris* 65.4 %).

Finally, our results show that the population size in the Preserve of Castelporziano conforms to our estimate of carrying capacity. The good balance between population size and resources is also suggested by the healthy conditions of the fallow deer population (Faggioli 1992), and by the apparent good condition of the understory in most of the preserve.

SUMMARY

The assessment of the trophic value of the most consumed feed by fallow deer in a coastal mediterranean landscape (*Rubus ulmifolius, Cistus salvifolius, Phyllirea latifolia, Quercus ilex* and graminoids) was based on *in vitro* digestibility trials, performed throughout the year (1 set of samples per season) using rumen inocula from wild fallow deer from the Preserve of Castelporziano, collected simultaneously with the vegetal samples. Moreover, *in vivo* digestibility coefficients have been estimated by using standard feed (for fallow deer) of known *in vivo* digestibility.

Using the digestibility coefficients, the metabolizable energy yield of studied forage items was computed. Information about plant biomass, structure of fallow deer population, metabolizable energy yields, estimates of forage intake and energy requirements were combined using the model presented by Hobbs & Swift (1985) to evaluate the nutritional carrying capacity of four typical mediterranean habitats (natural evergreen oak wood, scrub, mixed plantations of *Quercus ilex* and *Pinus pinea,* open pastures).

Spring represents the most favourable situation, while summer, autumn and winter exhibit similar values of carrying capacity of about 15-20 deer/100 ha. Mixed plantations of *Pinus pinea* and *Q. ilex* seem to be the most productive condition for fallow deer.

RÉSUMÉ

Une évaluation de la valeur trophique des aliments les plus consommés par le daim dans un paysage côtier méditerranéen (*Rubus ulmifolius, Cistus salvifolius, Phyllirea latifolia, Quercus ilex* et graminoïdes) a été menée, basée sur des essais de digestibilité *in vitro* effectués tout au long de l'année (un jeu d'échantillons par saison) à l'aide d'inocula de rumen de daims sauvages de la Réserve de Castelporziano, prélevés en même temps que les échantillons végétaux. En outre, des coefficients de digestibilité *in vivo* ont été estimés à l'aide d'aliments standards pour daim de digestibilité *in vivo* connue.

Ces coefficients de digestibilité ont permis de calculer le rendement en énergie métabolisable des items alimentaires. Les informations sur les biomasses végétales, la structure des populations de daim, les rendements en énergie métabolisable, les estimations de prises alimentaires et les besoins énergétiques, ont été combinées pour utiliser le modèle de Hobbs & Swift (1985) et estimer la capacité limite alimentaire de quatre habitats méditerranéens typiques (boisements sempervirents naturels de chênes, maquis, plantations mixtes de *Quercus ilex* et *Pinus pinea,* pâturages).

Les situations les plus favorables se présentent au printemps alors qu'en été, automne et hiver, les capacités limites ne sont que de 15-20 daims/100 ha. Les plantations mixtes de *Pinus pinea* et *Quercus ilex* réuniraient les conditions les plus productives pour le daim.

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