

Boitani, L. and Ciucci, P. (1995). Comparative social ecology of feral dogs and wolves. *Ethology Ecology & Evolution* 7: 49-72.

Keywords: activity pattern/behaviour/*Canis familiaris*/*Canis lupus*/comparative/demography/domestication/ecology/evolution/feral dog/group composition/Malme/predation/reproduction/social ecology/space use/wolf

Abstract: In this paper we compare some socio-ecological traits of feral dogs and wolves in order to assess the social ecology of feral dogs in terms of its adaptive value in the natural environment, and to evaluate to what extent the domestication process altered the wolf's socio-ecological patterns. Referring to feral dogs as those dogs living in a wild state with no food and shelter intentionally provided by humans, and showing a continuous and strong avoidance of direct human contacts, we review the currently available information on feral dog ecology, and particular reference is made to a 3-year term project on feral dog ecology in Abruzzo, Italy. Through comparison of relevant behavioural and ecological features of both wolves and feral dogs, we hypothesize that some aspects of the feral dogs' ecology, having escaped natural selection pressures, represent primarily expression of "evolutionary inertia" or an epiphenomena of artificial selection. Fitness-related measures of sociality, demography, reproduction, space-use, activity patterns, and feeding ecology in feral dogs tend to support our original hypothesis: feral dogs are not reproductively self-sustaining, suffer from high rates of juvenile mortality, depend indirectly upon humans for food, co-optable individuals, and space, and their demography appears dominated by unpredictable mechanisms. However, further research is needed, especially concerning different ecological conditions and multi-generational time-scales, as well as the role that dominant breed-types and cross-breeding history within feral dog groups might play in the expression of the analyzed socio-ecological features.

Comparative social ecology of feral dogs and wolves

L. BOITANI and P. CIUCCI

*Dipartimento di Biologia Animale e dell'Uomo, Università di Roma "La Sapienza",
Viale dell'Università 32, 00185 Roma, Italy*

Received 26 August 1994, accepted 29 November 1994

In this paper we compare some socio-ecological traits of feral dogs and wolves in order to assess the social ecology of feral dogs in terms of its adaptive value in the natural environment, and to evaluate to what extent the domestication process altered the wolf's socio-ecological patterns. Referring to feral dogs as those dogs living in a wild state with no food and shelter intentionally provided by humans, and showing a continuous and strong avoidance of direct human contacts, we review the currently available information on feral dog ecology, and particular reference is made to a 3-year term project on feral dog ecology in Abruzzo, Italy. Through comparison of relevant behavioural and ecological features of both wolves and feral dogs, we hypothesize that some aspects of the feral dogs' ecology, having escaped natural selection pressures, represent primarily expression of "evolutionary inertia" or an epiphenomena of artificial selection. Fitness-related measures of sociality, demography, reproduction, space-use, activity patterns, and feeding ecology in feral dogs tend to support our original hypothesis: feral dogs are not reproductively self-sustaining, suffer from high rates of juvenile mortality, depend indirectly upon humans for food, co-optable individuals, and space, and their demography appears dominated by unpredictable mechanisms. However, further research is needed, especially concerning different ecological conditions and multi-generational time-scales, as well as the role that dominant breed-types and cross-breeding history within feral dog groups might play in the expression of the analyzed socio-ecological features.

KEY WORDS: *Canis*, wolf, canid evolution, social ecology, feralization, domestication.

Introduction	50
Feral dogs and the feralization model	51
Demography and group composition	53
Social system	53
Social unit	54
Group size and density	54
Reproduction and life histories	56
Breeding	56
Denning and parental care	57
Litter size and pup survival	58
Sex ratio	59

Space use patterns	60
Home-range	60
Territoriality	61
Activity patterns	62
Food sources and predation	63
Concluding remarks	65
Acknowledgments	67
References	67

INTRODUCTION

Feral dogs probably existed in Eurasia soon after the beginning of dog domestication, as a result of the high integration of Mesolithic human cultures and the natural environment, and of the many opportunities the dogs had to move in and out of human settlements. Also on the North American continent feral dogs are believed to have existed well before European contact (MCKNIGHT 1964). There are at least two notable examples showing that the feralization process was already going on several millennia ago: the dingo in Australia and its likely ancestor the pariah dogs of all southern Eurasia (ZEUNER 1963; BRISBIN 1974, 1977; CLUTTON-BROCK in press). In the 18th century, stray and feral dogs roaming many of the large cities of the Mediterranean basin (Istanbul, Alexandria) were consistently reported by many authors, and indeed described almost as separate subspecies (cf. BREHM 1893). Warm climates and plenty of food resources have probably favoured the subsistence of dog populations around villages and towns, shifting through the house-stray-feral conditions. In particular, Mediterranean lifestyles and environmental conditions appear very favourable to the support of stray and feral dog populations (relatively warm climate, small game, free-ranging livestock, garbage dumps, loose interests and controls on the “commons”) (BOITANI & FABBRI 1983). In a nation-wide dog census conducted in Italy in 1981, BOITANI & FABBRI (1983) revealed that feral dogs, i.e. those domestic dogs that live without any direct contact with and dependence on humans, were estimated to be about 80,000, representing about 10% of the total free-ranging dog population, which includes also stray dogs and all those left by their owner to move freely in and out of villages into the surrounding areas. In spite of their significant impact on human and natural environments, free-ranging dogs have rarely been investigated until recently and few studies of their ecology have been reported (BECK 1973; SCOTT & CAUSEY 1973; NESBITT 1975; CAUSEY & CUDE 1980; BARNETT & RUDD 1983; DANIELS 1983a, 1983b; GIPSON 1983; DANIELS & BEKOFF 1989a, 1989b; BOITANI et al. in press).

Wolves and dogs are often given separate names (i.e., *Canis lupus* for the wolf, and *Canis familiaris* for the dogs), but they are, by all taxonomic criteria, the same species, and it is now widely accepted that the wolf is the ancestor of all dog types. Almost 12,000 years of selection by humans has amplified the phenotype diversity of the dogs, as a result of natural and artificial selection. While the dog's fitness appears high when tested in its “natural” human context, little is known of the dog's performance when matched by natural selection forces alone.

In this paper we compare ecological and life-history traits of feral dogs and wolves; analysis of their differences and similarities might help understand to what extent the domestication process altered the wild progenitors' behavioural and ecological patterns, and affected the dog's fitness in a natural environment. We focus

primarily on feral dog groups whose existence in the wild is recent (i.e., a few generations) and who do not belong to populations which have completed a de-domestication process in an evolutionary perspective (PRICE 1984). Dingoes and pariah dogs are therefore excluded from the analysis having been exposed to natural selection for a number of generations significant enough to attain a rather stable "wild" phenotype: dingoes, having totally lost any domesticity, are often no longer considered feral (PRICE 1984). However, given (i) relatively brief (in terms of generations) exposure of feral dog groups to natural selection forces, and (ii) the degree of both intra- and inter-group individual variability due to differences in breed-types and cross-breeding history, we believe that one cannot reasonably expect any adaptive value of feral dog socio-ecological traits. It is also obvious that the great variability observed in the 350 and more different dog breeds might play a substantial role in determining the degree of expression of some socio-ecological traits (e.g., social attitudes, territorialism, etc.). However, even though information on breed influence on feral dogs' biology is not yet available, "pure" modern breeds are rarely found in well-established feral dog groups, where one might assume extreme breed tendencies to be selected against.

The perceived differences in ecological strategies as revealed by feral dog groups and wolf packs living in the natural environment, might be viewed as a test of our understanding of the evolutionary and adaptive values of the ecological traits in the wolf, as well as in other social, wild canids. Our underlying hypothesis is that many aspects of feral dog ecology, being the results of relaxed natural selection forces, represent primarily expressions of "evolutionary inertia" and/or results and epiphenomena of artificial selection in the dog.

In our comparative approach, we focus on those behavioural and ecological features of both wolves and feral dogs for which data are available and for which similar methodologies have been adopted. Particular reference is made to a research programme carried out on a group of feral dogs from 1984 to 1988 by means of radio-tracking in a mountainous area of the central Apennines (Abruzzo, Italy) (ANDREOLI 1987, CIUCCI 1987, FRANCISCI et al. 1991), and whose results are comprehensively reported by BOITANI et al. (in press). In particular we analyze parameters such as demography and sociality, reproduction and life-history, space-use patterns, activity patterns and feeding habits.

Although limited data on feral dog ecology are currently available, we have attempted a critical review of the existing literature. However, the same problems found in the study of domestication such as the geographic variation in biological characteristics and the choice of what constitutes a "representative" study population (PRICE 1984) might apply in our case, therefore limiting the generalization of our conclusions.

FERAL DOGS AND THE FERALIZATION MODEL

Feral dogs are not a homogeneous category of animals. One of the critical difficulties encountered in conducting feral dog research is the determination of the true status of the dog being investigated, and several different definitions have been proposed (CAUSEY & CUDE 1980; BOITANI & FABBRI 1983; DANIELS & BEKOFF 1989a, 1989b). The distinction among feral, stray, and other free-ranging dogs is sometimes a matter of degree (NESBITT 1975). Dogs categories have been classified on

the basis of behavioural or ecological traits (SCOTT & CAUSEY 1973, CAUSEY & CUDE 1980); the dog's origins (DANIELS & BEKOFF 1989a, 1989b); the dog's main type of range (rural vs urban free-ranging; BERMAN & DUNBAR 1983; those having unrestricted access to public property: BECK 1973); the dog's kind and level of human dependency (WHO 1988). BOITANI et al. (in press) defined feral dogs as those living in a wild and free state with no direct food or shelter intentionally supplied by humans (CAUSEY & CUDE 1980), and that did not show any evidence of socialization to humans (DANIELS & BEKOFF 1989a), but rather a strong continuous avoidance of direct human contacts. Visual and radiotracking observations were used to distinguish feral dogs from other free-ranging dogs. This diversity of definitions contributes to the difficulties of comparing results from different studies. Further complexity arises from considering feralization from the evolutionary perspective, where it has been viewed as the domestication process in reverse (HALE 1969, BRISBIN 1974, PRICE 1984), or as a behavioural ontogenetic (developmental) process (DANIELS & BEKOFF 1989c): the two interpretations focus on different levels (population and individual) and imply different temporal scales as well as different theoretical and research approaches (DANIELS & BEKOFF 1989c).

Indeed, most authors agree that "owned", "stray" and "feral" dogs are not closed categories and that dogs may change their status throughout their life (SCOTT & CAUSEY 1973, NESBITT 1975, HIRATA et al. 1987, DANIELS 1988, DANIELS & BEKOFF 1989a), supporting DANIELS & BEKOFF (1989c) view of feralization as a behavioural ontogenetic process, sometime occurring within an individual lifetime. Only three dogs out of the 11 adults studied by BOITANI et al. (in press) were certainly born in the wild, while the others were recruited from the village populations, shifting from a stray to a feral condition. Shifting status may depend upon several natural and artificial causes (Fig. 1): a dog can become stray by escaping human control, by abandonment or simply by being born to a stray mother (BECK 1975). A stray dog can become feral when forced out of a human environment or when co-opted or simply accepted by a feral group existing nearby (DANIELS 1988; DANIELS & BEKOFF 1989a, 1989c), like the majority of group members studied by BOITANI et al. (in press). In the same study, it was found that some free-ranging dogs could display behaviours and attitudes intermediate to those expected on the basis of the proposed categories. This suggests that change of status in dogs is not always radical and abrupt, but rather, depending on local stimuli and conditions, might require a

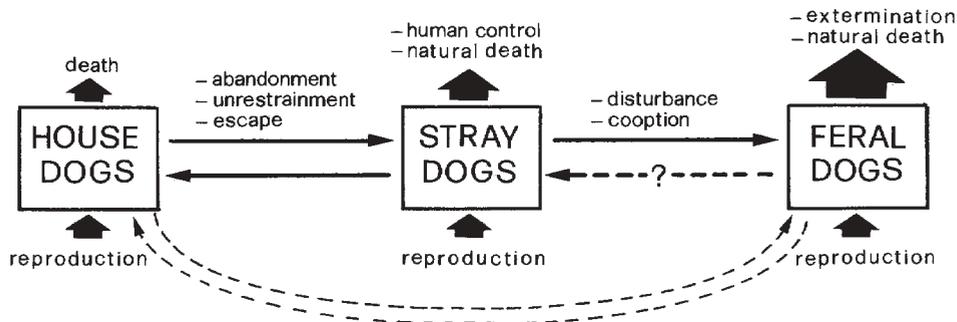


Fig. 1. — The feralization model.

significant portion of an individual life-span. A change in local conditions might force an individual dog to reverse its tendencies. The way back (i.e., toward the "house" category) may be observed when a stray dog is adopted by humans. The further step (i.e., from feral to stray or even owned condition), although generally unlikely, has been observed by BOITANI et al. (in press), and more recently experimentally demonstrated by one of us (P. CIUCCI unpubl.) by rehabilitating a feral dog to a domestic status (both cases referring to individuals who, although living as feral dogs, were not born in the wild). However, the evidence so far collected suggests that, when feral dogs live in socially independent units (i.e., they are socially bonded with other dogs), and in the absence of interference from humans, it is highly unlikely for them to reverse their status (i.e., the feralization process is reinforced through new generations). From this perspective, our definition of feral dogs (cf. BOITANI et al. in press) matches DANIELS & BEKOFF (1989c) view that feralization occurs through the development of a fear response to humans, and does not necessarily involve a significant genetic divergence from their domestic ancestors.

DEMOGRAPHY AND GROUP COMPOSITION

Social system

The typical social system found in wolves is a linear hierarchy structure extended to all members of the social unit (males and females), where dominant-subordinate distances are regulated on the basis of individual agonistic behaviour (MECH 1970, ZIMEN 1982). The wolf social structure, where dominance is reflected both in terms of privilege (e.g., "peck order") and initiative (travelling, hunting, territorial defence, reproduction, etc.) appears to allow for a higher functional integration among individual members than the mere aggregation of individual behaviours. Indeed, forms of social control might affect individual tendencies to increase the group's functionality and survival. For example, social control on reproduction (i.e., deferred reproduction, PACKARD et al. 1983) regulates the number of reproducing individuals within the group and, at the same time, might increase the chances of pup survival through availability of non-reproducing adults (HARRINGTON et al. 1983).

In the case of feral dogs the social structure appears to be essentially an aggregation of monogamous breeding pairs and their associates (pups and/or subadults of pair members). Agonistic behaviour, which has been observed in ritualized forms similar to those of wolves (L. BOITANI et al. unpubl. data), does not seem to extend over the individual level and does not seem to translate into a higher social structure (i.e., the hierarchical scale of wolves) that includes all individuals and exerts forms of social control on group activity (e.g., in reproduction). It is not clear if the lack of a higher social organization is related to the nature, the intensity and the frequency of agonistic confrontations among individuals in feral dog group, or rather to the lack in the dog of the same social susceptibility, in terms of behaviour and physiology, which appears to be critical in wolf sociality, or to all these. Indeed, in the case of feral dogs the observed intraspecific social behaviour might simply reflect the influence of human contacts during its early phases (SCOTT & FULLER 1965). This is even more important in dogs living under feral conditions but who have been recruited from the house and/or stray categories. If this were true we would expect, as the

number of generations under feral conditions increases, for social attitudes in feral dogs to resemble more closely those of wolves. Also, the extent different breeds influence the social behaviour should be carefully considered.

Social unit

Among canids, packs are social units that hunt, rear young and protect a communal territory as a stable group (MECH 1970); and their members are usually related individuals (BEKOFF et al. 1984).

Wolves, in particular, live in packs that are basically one-family units (MECH 1970, HABER 1977, PETERSON 1977) that form when two adults of opposite sex meet on a vacant territory, and reproduce (ROTHMAN & MECH 1979, FRITTS & MECH 1981). Formation and persistence of the pack as a functional unit is based on the social bond among its members, or what has been referred to, in human terms, as a sort of "affectional tie" (MECH 1970: 46). Although there are also cases of "non-family" packs reported in the wild, all have in common a male-female pair (MECH & NELSON 1990).

Feral dogs in Italy showed characteristics of the wolf pack only to a limited extent and, most notably, members of the same social unit were not generally related (BOITANI et al. in press), as in most cases of stray and feral dogs studied elsewhere (SCOTT & CAUSEY 1973; NESBITT 1975; CAUSEY & CUDE 1980; BERMAN & DUNBAR 1983; DANIELS & BEKOFF 1989a, 1989b). However, even though the whole social unit centred around stable breeding-pairs, the kinds of association and social bond among feral dogs did not reflect the precise rules of pack living, as known for other canids (KLEIMAN & EISENBERG 1973, BEKOFF et al. 1984, GITTLEMAN 1989). Therefore, we propose the term "group" as more appropriate for a feral dogs' social unit rather than pack.

Group size and density

Group size was 2-5 individuals in SCOTT & CAUSEY (1973) and 2-6 individuals in 14 groups in CAUSEY & CUDE (1980), both in Alabama. DANIELS & BEKOFF (1989b) report 2-4 animals per pack in their feral population in Arizona. NESBITT (1975), in his 5-years study of feral dogs in Illinois, found a mean group size of 5-6 animals. BOITANI & RACANA (1984) also report feral dogs in Basilicata (southern Italy) seen mostly in pairs. BOITANI et al. (in press) found group size ranging 3-6 adults. Urban free-ranging dog studies report a majority of animals being seen alone or in pairs (BECK 1975, BERMAN & DUNBAR 1983, DANIELS 1983a, HIRATA et al. 1986, DANIELS & BEKOFF 1989b, MACDONALD & CARR in press). It is possible that the smaller group sizes in urban and rural areas are due to the little advantage conferred on group-living when food resources are scarce (BECK 1973, DANIELS & BEKOFF 1989b), or, alternatively, to the fact that in urban areas food resources are plentiful and co-operative "hunting" is not an advantage (BERMAN & DUNBAR 1983). Unfortunately neither of these considerations are supported by accurate estimates of food resources, in both spatial and temporal terms.

Pack size in wolves varies greatly, generally ranging from two to 15 individuals per pack in winter (MECH 1986), and packs of up to 36 individuals have been reported from Alaska (RAUSCH 1967). However, average pack size from different

areas appears to be seven or less (MECH 1970). Although information regarding pack dynamics in wolves has been obtained both in captivity and in the wild (e.g. ZIMEN 1982; MECH 1977a, 1986), the factors through which pack size are regulated have not been clearly defined. Pack size is a function of mortality and recruitment rates, as well as time of dispersal by pack members (PACKARD & MECH 1980). However, the ultimate and most important factor affecting pack size appears to be prey abundance, as changes in prey availability correspond to proportional changes in pack size: MECH (1977a) reported a decrease in mean pack size (midwinter) from 5.7-8.6 to 3.7 during a period of deer decline in Minnesota, and MESSIER (1985) reported a mean pack size of 5.7 and 3.7, respectively in areas of high and low prey density in Quebec. Pack size is not to be expected to be stationary year-round (MECH 1977a, 1986), and major fluctuations (up to 12%) have been observed from December through March in areas of low prey density (MESSIER 1985).

The group composition of feral dogs was found to be rather stable by BOITANI et al. (in press), although in the absence of any apparent, intrinsic regulatory mechanism. In the 1984-1987 period, all events reducing or increasing the group numbers appeared to be related to external factors (human persecution and the availability of stray dogs), and without any predictable adaptive value. All deaths of sexually mature individuals were accidental and caused by human interference, while the newborn from feral parents contributed almost nil to the long term group stability. Only by recruitment of new members from the village stray population was the feral group able to maintain its size: at the end of the study, all but one dog in the group were of stray origin. The accidental disruption of the breeding pair appeared essential to trigger the recruitment mechanism: as a pair-bonded adult died the adult left alone managed to co-opt a sexually mature individual of the opposite sex. This new member became in turn socially accepted by the whole feral group. Breeding periods in canids are accompanied by extensive social interactions which, in turn, may contribute to stronger pair bonds (KLEIMAN & EISENBERG 1973). Increased social interactions may facilitate co-option of external adults (most interactions with dogs from the villages were observed during these periods), while a strong pair bond may be the major cause of preventing further co-options. Although these speculations might be a promising hypothesis, they do not foresee any self-regulating mechanism for group size, and are weakened by the lack of data on the behavioural responses of in-group individuals to the attempts of external dogs to approach and join the group.

Quantity and distribution of food resources are often called as primary causes of social groups and determinants of group size (MACDONALD 1983, VON SCHANTZ 1984, MACDONALD & CARR 1989 and in press). BOITANI et al. (in press) discussed the role of the dumps at their study area, which provided a food supply in excess during all seasons: group size was then referred more to social factors rather than ecological ones. It is interesting to note that the marked philopatry of those dogs would meet the general premises of the Territory Inheritance Hypothesis (LINDSTROM 1986): this hypothesis on the evolution of group-living in carnivores gives stronger importance to the attachment of individuals to the parents' territories, and it predicts an optimal group size which fits the results obtained by BOITANI et al. (in press). The same authors, however, failed to report differential measures of fitness of philopatric sub-adults versus dispersers, which are critical to assess LINDSTROM's hypothesis. The feral dog ecology must undergo deeper and longer term research in order to be reasonably tested against these theoretical generalizations. In addition, we believe that theoretical analysis of canid evolutionary strategies (BEKOFF et al.

1984) are of limited value when carried out on animals which have been living under artificial and natural selection pressures.

It seems reasonable to assume that the lack of social structure and social bonds, that is typical of the wolf pack, poses an upper limit to the number of feral dogs that can effectively cooperate as a functional unit (in hunting, territorial defence, offspring care, etc.). This might in part explain the smaller size of feral dog groups (SCOTT & CAUSEY 1973, NESBITT 1975, CAUSEY & CUDE 1980, DANIELS & BEKOFF 1989b, BOITANI et al. in press) as compared to wolf packs. However, the situation appears obscured in Italy where, for both wolves and feral dogs, even though to a different extent, human persecution and interference is perhaps the most important (and unpredictable) factor affecting, directly and indirectly, the pack and group demography. This could also explain the lower density values observed for wolves in Italy (1.25/100 km², ZIMEN & BOITANI 1975) and in Spain (1.5-2/100 km², VILA et al. 1993) as compared to those at the same latitudes in North-America, even in periods of population decline (3.4/100 km², MECH 1986). A conservative density estimate for the feral dogs studied through intense field research by BOITANI et al. (in press) accounts for 1.3-2.0 feral dogs/100 km², which appears closer to the wolf density in Italy (ZIMEN & BOITANI 1975). This could suggest that feral dog groups in Abruzzo tend to be regulated by the same ecological factors (including human persecution) that operate on wolves, although through very different mechanisms (see BOITANI et al. in press).

Conversely, wolf densities in North-America appear to be regulated essentially by the availability of the ungulate biomass (KEITH 1983) which, through the wolves' social behaviour, has an effect on their numerical and functional responses.

REPRODUCTION AND LIFE HISTORIES

Breeding

Domestic dogs usually breed twice a year, although without seasonal patterns. In feral dogs, BOITANI et al. (in press) found an average 7.3 months (range 6.5-10 months) between oestrus. As 50% of the parturitions occurred during the period February-May, they indicate a breeding increase in spring, whereas the others were scattered during the rest of the year. Although the spring concentration was significant, it has not yet been possible to determine any real synchrony of breeding among females. MACDONALD & CARR (in press) report a much more synchronized breeding in their dogs and refer this to a period of group stability: this hypothesis is consistent with data by BOITANI et al. (in press), and it deserves further observation. Increase in breeding in spring and fall was reported by GIPSON (1972) and suggested as possible by DANIELS & BEKOFF (1989b). Time of the year breeding occurs has a critical adaptive value, in terms of pup survival rates, and wild canids in Italy generally give birth in April (*Vulpes vulpes*) and in April-May (*Canis lupus*) (BOITANI 1981). In this regard, however, it is quite unlikely that the observed concentration in spring of oestrus cycles in feral dogs might indicate a converging strategy, even at a very early degree, with other wild canids. The life spans and poor viability of the dog population would not allow sufficient time for a strategy to be successfully attained. It might rather represent the remnant of an ancestral condition, i.e. the physiological potential to synchronize endogenous reproductive rhythms to the photoperiod cycle, as can be inferred from wolves (SEAL & MECH 1983, SEAL et al. 1987) and Cape hunting dogs

(CUNNINGHAM 1905). On the other hand, the lack of synchronicity among the breeding females of the studied group (BOITANI et al. in press), as well as the casual distribution throughout the year of the off-spring oestrus cycles, might be expression of modifications of the ancestral reproductive traits due to artificial selection: the loss of susceptibility to a social control on reproduction and an escape from photoperiod synchronization (PACKARD et al. 1985).

Although there are cases of two litters being raised successfully within the same pack of wolves (MURIE 1944, VAN BALLEMBERGHE 1983, MECH & NELSON 1989), restriction of breeding to a single dominant female appears to be the general rule (e.g. RABB et al. 1967, MECH 1970, ZIMEN 1976, PACKARD & MECH 1980, HARRINGTON et al. 1982), and it is achieved through deferred reproduction of the subordinates (PACKARD et al. 1983, 1985). Within the feral dog group studied in Italy (BOITANI et al. in press) no indication was gathered of any form of social control on the sexual behaviour of the (subordinate) adults. All females reproduced, giving the group its full potential for demographic increase.

Denning and parental care

Only one case of group splitting was observed by BOITANI et al. (in press) when denning and pup rearing by one of the feral dog females was observed to last more than 5 months. In all other denning activities, females always reared their pups without any care or threats by other group members, and located their dens within or in close proximity to the group's traditional core areas. Denning females spent most of the time at the den, with frequent visits to the closest feeding sources. Denning females who reared offspring within the group's traditional home-range were often visited by other group members, although there was no indication of communal care of the litters (BOITANI et al. in press). Pups in their first weeks of life were often left unattended at the den while the mother was feeding, and this might indeed account for a significant rate of infant mortality due to predation (BOITANI et al. in press). Denning and rearing pups apart from the group has been reported in feral dogs by DANIELS (1988) and DANIELS & BEKOFF (1989b). Group splitting during denning has been suggested as an adaptive strategy for pack-living canids as a way to reduce the burden of alloparental care on the pack, and to reduce the threats of infanticide by the dominant female (DANIELS & BEKOFF 1989b); on the other hand, group participation in rearing is adaptive for just the opposite reasons, i.e. it relieves the female from the burden of caring alone for her pups, and it provides more protection for the young from other predators (KLEIMAN & EISENBERG 1973). In absence of a selective pressure for pack splitting, denning within the group's territory increases protection from intruders and potential predators.

In wolves, dens are generally located within the pack territory (LOWHEAD 1983, CIUCCI & MECH 1992), and all the pack movements during denning periods are influenced by the den location, where the adults and the yearlings return periodically to regurgitate and attend the pups (MURIE 1944, MECH 1970, CARBYN 1974, VAN BALLEMBERGHE et al. 1975, HARRINGTON & MECH 1982). In wolves, the role of auxiliaries (non-breeding adults and yearlings) in the communal rearing of the relatives' offspring has recently been interpreted in terms of individual selection (PACKARD & MECH 1980, HARRINGTON & MECH 1982, HARRINGTON et al. 1983) where, rather than a form of altruism, it is viewed as part of the optimal reproductive strategy of those individuals who temporarily defer reproduction (PACKARD et al. 1983).

In feral dogs, rearing pups without male assistance might be due to the domestication process, where humans have provided assistance. In fact, dogs stand alone, among all canids, for a total lack of paternal care (KLEIMAN & MALCOM 1981). This could also explain the apparent lack of auxiliaries of any sex in feral dog groups, even though it is mostly the absence of deferred reproduction in the adults, i.e. absence of social control on subordinates' sexual behaviour (PACKARD et al. 1985), that seems to affect the availability of potential helpers.

Litter size and pup survival

Dogs are known to have litter sizes up to 17, although up to 10 is the most usual range (KLEIMAN 1968, KLEIMAN & EISENBERG 1973). For feral dogs, a litter of five and a total of eight for two other litters have been reported by NESBITT (1975), and DANIELS & BEKOFF (1989b) report a total of 10 pups from two litters. However, estimates of litter size rely on pups first sightings, which rarely occur before they are mobile (2-4 weeks old), when natal and post-natal mortality might have already contributed to lower estimates. BOITANI et al. (in press) report a lower mean litter size (3.63 pups/litter, $n = 11$) than previously reported for feral dogs elsewhere, and also lower than the figure (5.5 pups/litter, $n = 17$) obtained by MACDONALD & CARR (in press) in the same study area for a different period and group composition. Along with factors such as nutritional status of the bitches, occurrence of epizootics and competition among pups, and predation, the different litter size values might be explained by the great variability in age-related fecundity in different breeds, as well as by different age-structures of the groups studied.

Wolf average litter sizes in the wild range from 4.0 to 6.5 (MECH 1970), estimates being mostly based on the first observation of the litters after parturition, as for the dogs. Based on active nipple counts of lactating females, and on mid-summer and winter pups observations, MECH (1977a) reported an average litter size from 3.0 to 3.4 pups/litter, relating the lower than average estimate to the considerable nutritional stress that the population was facing. It remains unclear, however, if food availability affects the natality rates of the breeding females or rather pup survival rates during the early post-natal period, or both.

Survival rates for wolf pups are generally low in conditions of malnutrition (MECH 1970, VAN BALLEMBERGHE & MECH 1975, SEAL et al. 1975), and appear positively correlated with the number of in-group auxiliaries (HARRINGTON et al. 1983). Survival rates are generally low in feral dogs as compared with wolves: BOITANI et al. (in press) found that out of 40 pups, 28 (70%) died within 70 days of birth, 9 (22.5 %) died within 120 days, 1 (2.5%) within one year, and only 2 (5%) survived the age of one year. These values compare with similar ones found by NESBITT (1975), SCOTT & CAUSEY (1973), DANIELS & BEKOFF (1989b), MACDONALD & CARR (in press). The low survival rate at 4 months of age (7.5%) found by BOITANI et al. (in press) is a clear indication that the majority of mortality occurs during this period of early independence, and may be due to four factors relevant for the purpose of this paper: a) in the absence of communal helping, pups are often left at the den unattended, thus increasing the risks of predation; b) from about 6-8 weeks of age the pups begin to explore, without adult supervision, increasing portions of range surrounding the den site and this, again, increases risks of predation; c) as their mother enters her new oestrus cycle, she is most likely to lower her interest in her offspring, and d) irregular breeding cycles occurring twice a year cause many a lit-

ter to be born in periods of inclement weather. Thus, although early mortality deserves further study, low efficiency in reproduction in feral dogs appears to be mostly affected by two relevant aspects of their breeding biology: (i) the social environment of the group which does not provide auxiliaries for the communal care of the offspring, and (ii) the reproductive physiology of the females in terms of number and timing of their oestrus cycles. Such conditions, when transferred to natural environment, determine high rates of reproductive failures and offspring/juvenile mortality.

From a demographic standpoint, survival rates of only 5% to one year of age contribute to understanding why free-ranging dogs are not able to maintain their population levels. This was already stressed by urban dog studies (BECK 1973, DANIELS 1983a) and it was left unanswered by DANIELS & BEKOFF (1989b) for feral dogs in Arizona. In the area investigated by BOITANI et al. (in press), the feral dog group could not have maintained the observed population level without a continuous recruitment of new group members from outside (i.e., free-ranging and stray dogs).

Sex ratio

A critical component of the set of parameters contributing to the negative demographic balance observed by BOITANI et al. (in press) in feral dogs is the skewed sex ratio. Urban and rural/suburban dog populations generally show a skewed sex ratio for males, ranging from 1.6:1 to 5:1 in favour of males (BECK 1973, DANIELS 1983a, BOITANI & RACANA 1984, DANIELS & BEKOFF 1989b, WHO 1988). MACDONALD & CARR (in press) found ratios of 4:1 and 2.6:1 in favour of males in the villages of the same Italian study area where BOITANI et al. (in press) reported a sex ratio of from 2:1 to 1.5:1 (group composition at various stages, and considering only the adult members of the group) in favour of females. Possible reasons for these findings have already been discussed (BECK 1973, DANIELS & BEKOFF 1989b): the sex ratios of urban dogs result from the direct selection of males as pets and from selective removal of females from the population, either temporarily to avoid unwanted pregnancies, or permanently by killing them as newborn. However, a differential mortality rate for the two sexes is not likely to occur outside artificial human interference. DANIELS & BEKOFF (1989b) also reported a sex ratio of 3.5:1 in favour of females in a feral dog population in Arizona, in an area adjacent to the previously cited urban areas: they explained the result by suggesting that an important source of feral dogs was the abandonment of females removed from urban and rural areas. This appeared the only logical, though weak, explanation since no evidence could be obtained either on skewed sex ratios of new-borns, or on differential survival between sexes.

These results are even more difficult to discuss when considering that overall litter composition was found by BOITANI et al (in press), highly skewed in favour of males (3.2:1). In wolves, MECH (1975) found a male biased pup sex ratio in condition of marginal nutrition or intense food competition among adults suggesting this might contribute to the population regulation process. While the dog litter sex ratio in favour of males might suggest retention in feral dogs of the similar, though unknown, physiological mechanism (MECH 1975), higher female survival rates appear the only explanation when litter sex ratio is compared to adult sex-ratio: it might possibly be related to a) a stronger tendency of male pups to explore the

areas surrounding the den site, and b) differential maternal care of pups of different sexes. Further research is needed on the relation between survival rates of the two sexes to nutritional status, philopatry tendencies and maternal care.

SPACE USE PATTERNS

Home-range

Space use in feral dogs is not dissimilar from most other wild canids, in that for their life-history activities they utilize definite and traditional areas (home-ranges) which, to a varying extent, intensity and variability, tend to be defended against intruders (i.e., territory) (SCOTT & CAUSEY 1973, CAUSEY & CUDE 1980, GIPSON 1983, DANIELS & BEKOFF 1989a, BOITANI et al. in press). In addition to the several environmental factors which determine home-range size and configuration, human activities can play a powerful role in affecting the biological answers of canids (KLEIMAN & BRADY 1978), and of dogs in particular.

Within the overall home-range of 57.8 km², BOITANI et al. (in press) found that the dog group used smaller portions at a time, shifting core areas in response to several factors: the finding of new food resources (i.e., a large livestock carrion), disturbance by human presence, denning activities, previous spatial-use patterns of newly recruited dogs, unpredictable fluctuation in food availability at dumps, possible interference by wolves. These factors had no seasonal predictability, and they appeared randomly in the group history. DANIELS & BEKOFF (1989a) reported seasonal variations related to the presence of dependent pups for one of the two groups studied, while the other did not show any change in its core area use. Differential energetic requirements were suggested as a possible reason for the two groups behaviour (DANIELS & BEKOFF 1989a). SCOTT & CAUSEY (1973) also found a change of core areas depending on the presence of pups.

Drifting ranges have been recorded for urban foxes as a consequence of social instability entailed by abrupt changes to population structure and food availability (DONCASTER & MACDONALD 1991). BOITANI et al. (in press) suggest that drifting of seasonal ranges reflect not only direct environmental changes, but also the influence of previous knowledge of the area by a new member of the group. The random changing of core areas was maintained within three main alternate areas, and within the same long term boundaries, indicating that a tradition of area use prevented more random movements.

Home-range estimates can yield very different results as a consequence of the methods being adopted, and this should be taken into account when interpreting data from different studies (MACDONALD et al. 1980). Furthermore, telemetry techniques produce sets of data hardly comparable with other type of information (i.e., visual observation, tracks in snow, etc.) in assessing the extent of range and habitat utilization. These considerations might explain a great part of the variability in home-range sizes reported so far for feral dogs (see BOITANI et al. in press, for a review). Limited to radio-telemetry studies, home-range sizes reported for feral dogs range from 4.44-10.4 km² for three different groups in east-central Alabama (SCOTT & CAUSEY 1973), to 18.72 km² in Alabama (CAUSEY & CUDE 1980) and 70 km² in Alaska (GIPSON 1983). BOITANI et al. (in press) discussed the factors believed to play a significant role in determining home range size, namely the relative distances of dens, dumps and resting (refuge) sites, that are largely independent of group size.

Urban and suburban dogs are reported to have much smaller home-ranges (from 2-11 up to 61 ha) (BECK 1973, FOX et al. 1975, DANIELS 1983a, BERMAN & DUNBAR 1983, SANTAMARIA et al. 1990). Food availability patterns, small group sizes and reduced social contacts are probably the determinants of such behaviour, confirming the mechanism being suggested for the feral dog data.

Average wolf territory sizes may range from 78 km², in areas where wolves prey primarily on white-tailed deer (*Odocoileus virginianus*) (FULLER 1989), to 2.541 km² at higher latitudes with moose (*Alces alces*) and caribou (*Rangifer tarandus*) as the main prey (BALLARD et al. 1987). Much of the observed variation in territory size has been interpreted as dependent on several factors among which the most relevant appear to be pack size (PETERSON et al. 1984, MESSIER 1985, BALLARD et al. 1987), prey density (MESSIER 1985), and wolf population density (FRITTS & MECH 1981). The influence of all these factors on territory size appears to depend also on the level of human exploitation of the local wolf populations (PETERSON et al. 1984, BALLARD et al. 1987). Shifts in the use of the internal parts of wolf territories have been reported: in summer as a result of pup presence at the den and at rendezvous sites, and in winter to increase effectiveness of prey exploitation (FRITTS & MECH 1981, MESSIER 1985). Thus, it seems reasonable to assume that the flexibility observed in space use by feral dogs might substantially be the same strategy of their wild ancestors where, depending on local conditions, territory utilization tend to optimize resource utilization and survival. In fact, in the same area where feral dogs have been studied by BOITANI et al. (in press), radiocollared wolves exhibited a similar pattern of territory use (CIUCCI 1994).

Territoriality

Territorial behaviour in feral dogs was observed by BOITANI et al. (in press) more consistently than previously reported (SCOTT & FULLER 1965, BEKOFF 1979, DANIELS & BEKOFF 1989a, BERMAN & DUNBAR 1983, BOITANI & RACANA 1984), as it was displayed not only in the vicinity of den sites, but within the entire core areas and during the whole year; this pattern is also reported by MACDONALD & CARR (in press) for the same area. Territorial defence could be inferred through observation of direct encounters (chasing and/or facing conspecific intruders), vocal advertisement (barking), and the absence for the study time-span of other stable groups of dogs in the same territory. Even though there were signs of scent-marking activities, no attempt was made to clarify the role of such marking in territory maintenance, as it has been done for wolves (PETERS & MECH 1975, ROTHMAN & MECH 1979).

The higher frequency of territorial behaviour reported by BOITANI et al. (in press) might be related to a higher level of integration within the group, a higher degree of isolation from other dogs, and to the food resources being concentrated mostly in localized patches at the dumps. Also, the partial overlap with two wolf pack territories in the same study area might have increased the dogs' general alertness and territorial behaviour. In addition, breed influence on territorial behaviour needs to be contemplated, since it is likely that the observed degree of territoriality in part reflected the typical traits of the Maremma dog, one of the dominant types in the feral group breeding history.

Although in the absence of any evidence for direct competition between feral dogs and wolves (apart from one dog most probably being killed by wolves), partial overlap of territories and the almost identical niche that they share in central Italy

(BOITANI 1983) make competition for food and space highly likely. Thus, the presence of wolves might have been an important component in shaping the dogs' home-range, and in determining its location and maintainance. The fact that feral dogs' core-areas were closer to human settlements than the wolves' core-areas, and located in the interstice between two neighbouring wolf territories (CIUCCI 1987, BOITANI et al. in press), might indicate that the dog group was not competing efficiently enough to succeed independently from human presence.

Territorial behaviour in wolves has been investigated (e.g., PETERS & MECH 1975, HARRINGTON & MECH 1979), related to intraspecific density and prey abundance (e.g., MECH 1977a, 1986), and interpreted as a mechanism of population regulation (PACKARD & MECH 1980). Although the proximate causation of territorial behaviour might be similar in dogs and wolves (i.e., the defence of resources within the territory), it seems unlikely that in feral dogs it might work as a mechanism of population regulation; in fact, for this to be true, one would expect feral dog populations to appear reproductively self-sustaining and their in-group sexual behaviour susceptible to social control (PACKARD & MECH 1980). However, both these conditions have not been met in the group studied by BOITANI et al. (in press). It would be intriguing to investigate further the evolution of territorial patterns and mechanisms in feral dogs, searching for the rules that minimize inter-group encounters typical of saturated wolf populations (e.g., PETERS & MECH 1975, HARRINGTON & MECH 1979). This would contribute to our understanding of the evolution scent-marking and vocal behaviours, and the role that natural and artificial selection plays in their shaping.

ACTIVITY PATTERNS

A tendency for nocturnal and crepuscular activity was first reported by BECK (1973) for urban dogs: during the summer months, it was mainly restricted to two periods, 07:00-10:00 p.m. and 05:00-08:00 a.m. A similar bimodal model of activity distributions was found by BERMAN & DUNBAR (1983) for the dogs of Berkeley, California. HIRATA et al. (1986) reported that dogs of several Japanese towns were most active from 00:00 to 06:00 a.m., with a peak just before and around 06:00 a.m. The predominant dawn peak had already been observed in free-ranging rural dogs in Virginia (PERRY & GILES 1971), while the bimodal distribution was confirmed by several studies on feral dogs (SCOTT & CAUSEY 1973, CAUSEY & CUDE 1980, BOITANI & RACANA 1984, DANIELS & BEKOFF 1989a). NESBITT (1975), discussing similar temporal patterns, suggested that feral dogs could be active and travel all day but were restricted to nocturnal and crepuscular hours in the attempt to avoid human contact. BOITANI et al. (in press) presented similar results which seem to confirm NESBITT's hypothesis: when the human presence was low, a female dog moved mostly during daytime, while she later resumed nocturnal habits when visiting the more "dangerous" dumps close to the villages. Avoiding humans may provide an explanation for nocturnal activities, but it does not explain the bimodal pattern found for all dogs and for all seasons. Nine out of 17 canids are strictly nocturnal (cf. BEKOFF et al. 1981); bimodal activity regimes are known for a great variety of carnivores (*Vulpes fulva*: ABLES 1975; *Crocuta crocuta*: KRUUK 1972; *Chrysocyon brachyurus*: DIETZ 1984) and they are a common biological pattern. ASCHOFF (1966) called it the "bigeminus pattern" and suggested that it is an innate behavioural trait, indepen-

dent from any environmental pressure. ASCHOFF (1966) also pointed out that the second (dawn) peak is usually lower, but this is not the case in the study by BOITANI et al. (in press), where maximum activity levels have been always observed at dawn.

Wolf activity patterns are extremely influenced by different environmental conditions, including human interference. Activity in wolves in North-America has been studied primarily through direct observation, and therefore most of data are essentially limited to daylight hours. However, available radiotelemetry data (KOLENOSKY & JOHNSTON 1967, BALLARD et al. 1991) and other direct observations (MURIE 1944, JOSLIN 1966, BALLARD et al. 1991) tend to confirm the nocturnal activity pattern of wolves, with crepuscular times (dawn and sunset) being the most likely periods of arrival at, and departure from, the den- and rendezvous-sites. Nevertheless, other authors reported that wolves tend to be active also during the daylight hours, and that this proportion of activity (moving, travelling, hunting) tend to be higher in winter months, as well as indirectly correlated with the nutritional status of the wolves (MECH 1977b, PETERSON et al. 1984). West-European studies, based on 24-hr monitoring cycles, depict wolf activity as being almost nil during daylight hours, with the wolves being primarily active from sunset to dawn (BOITANI 1982, URIOS et al. 1993, VILA et al. 1993, CIUCCI 1994). In Spain, an analysis of wolf activity confirmed a nocturnal, bimodal pattern (URIOS et al. 1993, VILA et al. 1993), whereas in highly populated areas of Italy nocturnal activity was mostly unimodal, lacking periods of decreased activity in the night hours (CIUCCI 1994). This has to be expected if the innate bimodal pattern (ASCHOFF 1966) has been selected against: in areas of high anthropic interference, activity peaks at dawn and sunset would increase the chance of wolf-human encounters, especially where the location of wolf refuge-sites and feeding-sites appear to be interspersed with human settlements (CIUCCI 1994).

Although the present studies on feral dog 24-hr activity patterns have been essentially descriptive, and environmental correlates of activity (food abundance, intra- and interspecific interferences, climatic and physiological factors, etc.) deserve deeper investigation, they tend to confirm that the canids' innate rhythmicity has not been altered to a great extent through artificial selection, and that feral dog activity patterns may just reflect their ancestors' flexibility.

FOOD SOURCES AND PREDATION

Potential predation on wildlife and livestock has been the instigation for feral dog studies: feral dogs have long been accused by the popular press of predation on deer in North-America and on livestock in Italy, although with little supporting evidence (cf. BOITANI 1983, for a short review on wolf-dog competition). BOITANI et al. (in press) and SCOTT & CAUSEY (1973) did not find any evidence of predation on livestock. NESBITT (1975) was unable to document a single case of livestock depredation in his 5-years study. This last situation resembles that found by BOITANI et al. (in press), where cattle were free-ranging over most of the area, yet no interference was ever observed. On the other hand NESBITT (1975) reported that free-ranging pet dogs killed three calves in that area during his study. This again compares with severe damage by free-ranging owned dogs on livestock that one of us was able to document in other areas of Italy (L. BOITANI unpubl.). Thus, some evidence

would suggest that it is essentially free-ranging owned and stray dogs that are primarily responsible for livestock depredation, although more research is needed on this subject. As for predation on wildlife, BOITANI et al. (in press) report that wild boar (*Sus scrofa*), the only ungulate significantly present in the area, was rarely found in dogs' faeces and, as yet, no evidence has been gathered for predation on a live wild boar. Feral dogs have been reported to have little impact on wildlife by all previous research on their feeding ecology (PERRY & GILES 1971, SCOTT & CAUSEY 1973, GIPSON & SEALANDER 1977, CAUSEY & CUDE 1980). Different experimental hunting with radio-marked and trained dogs failed to prove successful hunting on deer (PROGULSKE & BASKETT 1958, CORBETT et al. 1971, SWEENEY et al. 1971, OLSON 1974). On the other hand, HAWKINS et al. (1970) and LOWRY & MACARTHUR (1978) reported a small percentage of successful hunting in Illinois and in Idaho, respectively. Most importantly, DENNEY (1974) in Colorado and GAVITT et al. (1974) in Virginia reported deer being killed by feral dogs. As for livestock, these apparently contradictory results are probably best explained by local conditions in terms of the presence of alternate food resources (and their stability and predictability), dog group size and breed-types, foraging tradition, livestock husbandry techniques, wildlife distribution and density, and level of human persecution. It seems reasonable to assume that all these factors somehow modulate to different extents an innate propensity for predation, which also depends strongly on the attitude of the dominant breed-types in the group (i.e., an effect of artificial selection). Other casual factors, such as the previous experience of some individual in the group, might influence the feeding habits of the whole group (i.e., cultural tradition): exposure to prey, successful predatory trials and cultural transmission are important components in determining hunting techniques, attitudes and prey-type preference.

SCOTT & CAUSEY (1973) and BOITANI et al. (in press) reported brief, apparently uncoordinated, and unsuccessful hunting chases during which the dogs were constantly barking: one might assume that predatory tendencies in a feral dog group are lowered in the long term by unsuccessful attempts due to lack of a coordinated and effective hunting technique. If this were true, one might expect, in the presence of alternative food sources, dog groups to have a more flexible diet, and to incorporate in their diet items easier for single individuals to catch. Alternatively, their diet might just be more stable and predictable. This has been reported by several authors who found that feral dogs hunt and feed on rodents, rabbits, and other small game, although the details are not reported. Detailed accounts of a special predatory situation were given for feral dogs on the Galapagos Islands who feeding on marine iguanas (*Amblyrhynchus cristatus*) (KRUUK & SNELL 1981, BARNETT & RUDD 1983), and for feral and semi-feral dogs predating capybaras (*Hydrochoerus hydrochaeris*) in Venezuela's llanos (MACDONALD 1981). BOITANI et al. (in press) and MACDONALD & CARR (in press) stressed the importance for the feral dogs of refuse found at the several garbage dumps located within the dogs' home range.

The importance of parental-teaching, exposure to prey, and successful experience for the development of hunting efficiency in wolf pups has long since been documented (MECH 1970). The same group-living in wolves has been interpreted as a way to overcome prey with a larger body mass (MECH 1970), as also suggested for other predators (e.g., hyenas: KRUUK 1972). Indeed, it is the same social structure of wolf packs that allows each individual to be integrated within an efficient hunting unit. In feral dog groups, however, where leadership is more questionable and social bonds among individuals are more flexible, one would expect predatory tendencies, if any, to be less effective, mostly uncoordinated, and with severe limita-

tions (e.g., kill rate, prey type and size, energetic cost and benefit balance, time to functional response, etc.). Hence, given the feral dogs' social structure, it seems reasonable to expect diversified food habits which include smaller and easier-to-catch items (see above). It is noteworthy to report that this also appears to be the case for the dingo in Australia (CORBETT 1989). However, for those dog groups that prey on wildlife (DENNEY 1974, GAVITT et al. 1974), the same mechanisms that regulate most wolf-prey systems (MECH 1977a, 1977b; PETERSON 1977; NELSON & MECH 1981; MESSIER 1985) cannot be expected to be effective, for the feral dog ecology seems to be dictated by non self-regulating biological traits (e.g., productivity and survival). Further research is especially needed in areas where dogs are known to prey on wildlife and in the absence of more predictable food sources (i.e., garbage dumps).

CONCLUDING REMARKS

The ecology of feral dogs, dominated by their behavioural tendency to avoid contact with humans, appears to be shaped by a complex of biological traits which, on the one hand, still resemble their ancestors' flexibility, but on the other fail to meet their original fitness requirements.

Feral dogs' survival strategies still maintain, to some extent, some ancestral traits, namely group-living tendencies, territorialism, predatory instincts, and a large degree of ecological flexibility. Even though most of these traits appear void of their adaptive value (just as "evolutionary inertia" or artificial selection phenomena, as our hypothesis postulated), the dog's ancestor flexibility seems to be reflected mostly by food habits, space-use patterns, and activity patterns.

The dog flexibility, in both behavioural and morphological traits was enhanced by the domestication process: in particular, the retention of juvenile characters into adulthood (i.e., neoteny), having a significant adaptive value in domesticated environments (e.g., lower aggressiveness, more dependence on humans, early sexual maturation, easier submission), also provided greater plasticity in behavioural development (GINSBURG & SCHOTTE 1978, FRANK 1980, FRANK & FRANK 1982, PRICE 1984). By escaping the full pressure of natural selection, dogs attained greater plasticity also through relaxed selection. This enhanced flexibility of the dogs as compared to wolves appears to be the critical mechanism which partly allow the dogs to overcome the toll of natural selection and to survive in the natural environments. On the other hand, the domestication process is largely responsible for a loss of fitness through altering the response thresholds of several behavioural traits, lowering the observational capability and affecting the cognitive mechanisms, and reducing the overall responsiveness to environmental change due to living for generations in "safe" environments (PRICE 1984). Feral dogs still show variable degrees of these quantitative changes.

The limited data currently available on feral dogs do not allow for a thorough testing of our original hypothesis, even though they tend to confirm the lack of adaptive value of the most relevant socio-ecological traits: feral dogs are not reproductively self-sustaining, suffer from high rates of juvenile mortality, depend indirectly upon humans for food, co-optable individuals, and space, and their demography appears dominated by stochastic and unpredictable mechanisms (BOITANI et al. in press). It is noteworthy that feral dogs which are still dependent on humans for

some aspects of their biology, may still be affected by some form of selection connected to human activities (BECK 1973, BRISBIN 1977, DANIELS & BEKOFF 1989c). Therefore, the feral dog ecology may be significantly different in various habitats and ecological conditions (i.e., different levels of dependency of the dogs on humans). In addition to this, the lack of an operational definition of feral status, based on consistent criteria and referring to a definite temporal scale, makes the comparison among different studies difficult. However, at a general level of analysis, the characteristics of feral dogs and the adaptive value that they fail to match, can be classified in terms of three main biological aspects:

Sociality. Feral dogs social units do not function as wolf packs, namely for the lack of clear dominant-subordinate relationships throughout and of firm social bonds among all group members. This directly affects the potential groups size, the breeding system, the group's efficiency as a functional unit (hunting, territory defence, communal pup rearing, etc.). The most relevant consequences in terms of fitness are: (i) potential limits in the social unit's efficiency and functionality as group size increases (i.e., potential upper limit to group size); (ii) potentially drastic population fluctuations. The social structure and its expression in feral dog groups does not allow for an efficient mechanism of population regulation in relation to environmental and ecological conditions; (iii) unavailability of potential non-reproducing 'auxiliaries'; (iv) negative energetic balance of breeding females; (v) high pup/juvenile mortality rates; (vi) low recruitment rates.

Physiology. Among the main traits to be affected by artificial selection, reproduction in the dog, as well as in most other domestic species, has been strongly influenced to increase reproductive potential and to shorten generation time. Consequences of this process on physiology are obvious and may be inferred from the frequency of breeding cycles in the females, the apparent escape from photo period synchronization and social-control (i.e., deferred reproduction). In addition it has been suggested, though without good evidence, that the immunodefence system of the domestic dog appears limited in a natural environment, accounting for high mortality rates among pups and subadults (FRANCISCI et al. 1991). All this directly affects reproduction, survival and recruitment in feral dogs, and the most relevant consequences in terms of fitness are: (i) negative energetic balance of breeding females; (ii) high pup/juvenile mortality; (iii) low recruitment rates.

Behaviour. Both in terms of individual and social behaviour, the effectiveness of group activities such as hunting, territorial defence, cultural transmission, and reproduction appear limited to some extent. The most relevant consequences in terms of fitness are: (i) low predatory attitude; (ii) low kill rate (efficiency of predation); (iii) potential limits in prey size; (iv) indirect food-dependency upon humans; (v) indirect space-dependency upon humans; (vi) low efficiency or absence of alloparental care of pups.

In conclusion, we believe the present discussion offers a general framework for an assessment of the effects of artificial selection on the dog as it returns to live in the wild, analyzing the adaptive values of the most relevant socio-ecological features of the wolf is natural history. The ultimate goal of assessing the adaptive value of traits which are the results of a mixture of ancient and recent natural and artificial selective pressure might prove impossible to achieve. It is also important to emphasize that our discussion mostly applies to those feral dogs living in the wild for a few generations: our conclusions, then, might not be valid for feral dog populations which have been living under the effects of natural selection forces for

hundreds of years (e.g., pariah dogs and dingoes), where longer reproductive isolation from their domestic ancestors might result in lower phenotypic variability and in behavioural differences which could be genetically determined.

An investigation of feral dog biology under different ecological conditions and longer, multi-generational time-scales, might offer a deeper insight into the issues herein discussed. Future research should also address the role that different dominant breed-types in feral dog groups, as well as the cross-breeding history within them, might play in the expression (nature, quantity, frequency) of the analyzed socio-ecological traits. In this regard, we hope that future studies will benefit from some of the working hypotheses highlighted by our discussion.

ACKNOWLEDGMENTS

We are greatly indebted to F. Francisci and G. Andreoli who contributed to the work on the feral dogs in Central Italy. We are also grateful to F. Dessi-Fulgheri, J. Clutton-Brock and an anonymous referee for substantial comments on an earlier version of this manuscript. The work was partly supported by a grant from the Regione Toscana.

REFERENCES

- ABLES E.D. 1975. Ecology of the red fox in North America, pp. 216-236. In: Fox M.W., Edit. The wild canids. *New York: Van Nostrand Reinhold*.
- ANDREOLI G. 1987. Analisi dei modelli di attività di un gruppo di cani inselvatichiti in Abruzzo. *Laurea Thesis, University of Roma, Rome*.
- ASCHOFF J. 1966. Circadian activity patterns with two peaks. *Ecology* 47: 657-702.
- BALLARD W.B., AYERS L.A., GARDNER C.L. & FOSTER J.W. 1991. Den site activity patterns of gray wolves, *Canis lupus*, in South-Central Alaska. *Canadian Field Naturalist* 105: 497-504.
- BALLARD W.B., WITHMAN J.S. & GARDNER C.L. 1987. Ecology of an exploited wolf population in South-Central Alaska. *Wildlife Monograph* 98: 1-54.
- BARNETT B.D. & RUDD R.L. 1983. Feral dogs of the Galapagos Islands: impact and control. *International Journal of Studies on Animal Problems* 4: 44-58.
- BECK A.M. 1973. The ecology of stray dogs: a study of free-ranging urban animals. *Baltimore: York Press*.
- BECK A.M. 1975. The ecology of "feral" and free-roving dogs in Baltimore, pp. 380-390. In: Fox M.W., Edit. The wild canids. *New York: Van Nostrand Reinhold*.
- BEKOFF M. 1979. Scent-marking by free-ranging domestic dogs. *Biological Behaviour* 4: 123-139.
- BEKOFF M., DANIELS T.J. & GITTLEMAN J.L. 1984. Life history patterns and the comparative social ecology of carnivores. *Annual Review of Ecology and Systematics* 15: 191-232.
- BEKOFF M., DIAMOND J. & MITTON J.B. 1981. Life history patterns and sociality in canids: body size, reproduction, and behaviour. *Oecologia* 50: 388-390.
- BERMAN M. & DUNBAR I. 1983. The social behaviour of free-ranging suburban dogs. *Applied Animal Ethology* 10: 5-17.
- BOITANI L. 1981. Lupo, *Canis lupus*, pp. 61-67. In: Pavan M., Edit. Distribuzione e biologia di 22 specie di mammiferi in Italia. *Roma: Consiglio Nazionale delle Ricerche*.
- BOITANI L. 1982. Wolf management in intensively used areas of Italy, pp. 158-172. In: Harrington F.H. & Paquet P.C., Edits. Wolves of the world. Perspectives of behavior, ecology and conservation. *New Jersey: Noyes*.
- BOITANI L. 1983. Wolf and dog competition in Italy. *Acta Zoologica Fennica* 174: 259-264.
- BOITANI L. & FABBRI M.L. 1983. Censimento dei cani in Italia con particolare riguardo al fenomeno del randagismo. *Ricerche di Biologia della Selvaggina, INBS, Bologna* 73: 1-51.

- BOITANI L., FRANCISCI F., CIUCCI P. & ANDREOLI, G. (in press). Population biology and ecology of feral dogs in central Italy. In: Serpell J., Edit. The dog: its ecology, behaviour and evolution. *Cambridge: Cambridge University Press*.
- BOITANI L. & RACANA A. 1984. Indagine eco-etologica sulla popolazione di cani domestici e randagi di due comuni della Basilicata. *Silva Lucana, Bari* 3: 1-86.
- BREHM A. 1893. Tierleben. *Liepzig-Wien*, 4 vols.
- BRISBIN I.L. JR 1974. The ecology of animal domestication: its relevance to man's environmental crises - past, present and future. *Association of Southeastern Biologists Bulletin* 21: 3-8.
- BRISBIN I.L. JR 1977. The pariah. Its ecology and importance to the origin, development and study of pure-bred dogs. *Pure-bred Dogs American Kennel Gazette* 94: 22-29.
- CARBYN L.N. 1974. Wolf predation and behavioral interactions with elk and other ungulates in an area of high prey density. *Ph.D. Thesis, University of Toronto, Edmonton*.
- CAUSEY M.K. & CUDE C.A. 1980. Feral dog and white-tailed deer interactions in Alabama. *Journal of Wildlife Management* 44: 481-484.
- CIUCCI P. 1987. Uso dello spazio e dell'habitat in una popolazione di cani inselvatichiti nell'Appennino abruzzese. *Laurea Thesis, University of Roma, Rome*.
- CIUCCI P. 1994. Movimenti, attività e risorse del lupo (*Canis lupus*) in due aree dell'Appennino centro-settentrionale. *Ph.D. Thesis, University of Roma, Rome*.
- CIUCCI P. & MECH L.D. 1992. Selection of wolf dens in relation to winter territories in North-eastern Minnesota. *Journal of Mammalogy* 73: 899-905.
- CLUTTON-BROCK J. (in press). Origins of the dog: domestication and early history. In: Serpell J., Edit. The dog: its ecology, behaviour and evolution. *Cambridge: Cambridge University Press*.
- CORBETT L.K. 1989. Assessing the diet of dingoes from feces: a comparison of 3 methods. *Journal of Wildlife Management* 53: 343-346.
- CORBETT R.L., MARCHINTON R.L. & HILL C.L. 1971. Preliminary study of the effects of dogs on radio-equipped deer in mountainous habitat. *Proceedings of the Annual Conference of the Southeastern Association of State Game and Fish Commissioners* 25: 69-77.
- CUNNINGHAM D.J. 1905. Cape hunting dog (*Lycaon pictus*) in the gardens of Royal Zoological Society of Ireland. *Proceedings of the Royal Society of Edinburgh* 25: 843-848.
- DANIELS T.J. 1983a. The social organization of free-ranging urban dogs: I. Non-estrous social behaviour. *Applied Animal Ethology* 10: 341-363.
- DANIELS T.J. 1983b. The social organization of free-ranging urban dogs: II. Estrous groups and the mating system. *Applied Animal Ethology* 10: 365-373.
- DANIELS T.J. 1988. Down in the dumps. *Natural History* 97: 8-12.
- DANIELS T.J. & BEKOFF M. 1989a. Spatial and temporal resource use by feral and abandoned dogs. *Ethology* 81: 300-312.
- DANIELS T.J. & BEKOFF M. 1989b. Population and social biology of free-ranging dogs, *Canis familiaris*. *Journal of Mammalogy* 70: 754-762.
- DANIELS T.J. & BEKOFF M. 1989c. Feralization: the making of wild domestic animals. *Behavioural Processes* 19: 79-94.
- DENNEY R.N. 1974. Impact of uncontrolled dogs on wildlife and livestock. *Transactions of the North-American Wildlife and Natural Resources Conference* 39: 257-291.
- DIETZ J.M. 1984. Ecology and social organization of the maned wolf (*Chrysocyon brachiurus*). *Smithsonian Contributions to Zoology* 392: 1-51.
- DONCASTER C.P. & MACDONALD D.W. 1991. Drifting territoriality in the red fox *Vulpes vulpes*. *Journal of Animal Ecology* 60: 423-439.
- FOX M.W., BECK A.M. & BLACKMAN E. 1975. Behaviour and ecology of a small group of urban dogs (*Canis familiaris*). *Applied Animal Ethology* 1: 119-137.
- FRANCISCI F., CIUCCI P., ANDREOLI G. & BOITANI L. 1991. Storia naturale di un gruppo di cani inselvatichiti residenti nell'areale del lupo in Marsica (AQ). *Final Report to the Italian Institute of Wildlife Biology (INFS), Bologna*.
- FRANK H. 1980. Evolution of canine information processing under conditions of natural and artificial selection. *Zeitschrift für Tierpsychologie* 53: 389-399.

- FRANK H. & FRANK M.G. 1982. On the effects of domestication on canine social development and behaviour. *Applied Animal Ethology* 8: 507-525.
- FRITTS S.H. & MECH L.D. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildlife Monograph* 80: 1-79.
- FULLER T.K. 1989. Population dynamics of wolves in North-Central Minnesota. *Wildlife Monograph* 105: 1- 41.
- GAVITT J.D., DOWNING R.L. & MCGINNES B.S. 1974. Effects of dogs on deer reproduction in Virginia. *Proceedings of the Annual Conference of the Southeastern Association of State Game and Fish Commissioners* 28: 532-539.
- GINSBURG B. E. & SCHOTTE C.S. 1978. Genetic differences determining the capacities for social behaviour among wolves and dogs. *Behavioural Genetics* 8: 94 (abstract).
- GIPSON P.S. 1972. The taxonomy, reproductive biology, food habits, and range of wild *Canis* (Canidae) in Arkansas. *Ph.D. Dissertation, University of Arkansas, Fayetteville*.
- GIPSON P.S. 1983. Evaluation and control implications of behaviour of feral dogs in Interior Alaska, pp. 78-92. In: Kaukeinen D.E., Edit. Vertebrate pest control and management materials: 4th Symposium. *Philadelphia: ASTM Special Technical Publication*.
- GIPSON P.S. & SEALANDER J.A. 1977. Ecological relationships of white-tailed deer and dogs in Arkansas, pp. 3-16. In: Philips R.L. & Jonkel C., Edits. Proceedings of 1975 Predator Symposium. Bulletin of Montana Forest Conservation Experimental Station. *Missoula: University of Montana*.
- GITTLEMAN J.L. 1989. Carnivore behaviour, ecology and evolution. *London: Chapman & Hall*.
- HABER G.C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. *Ph.D. Thesis, University of British Columbia, Vancouver*.
- HALE E.B. 1969. Domestication and the evolution of behaviour, pp. 22-42. In: Hafez E.S.E., Edit. The behaviour of domestic animals. *London: Bailliere Tindall*.
- HARRINGTON F.H. & MECH L.D. 1979. Wolf howling and its role in territory maintenance. *Behaviour* 68: 207-249.
- HARRINGTON F.H. & MECH L.D. 1982. Patterns of homesite attendance in two Minnesota wolf packs, pp. 81-105. In: Harrington F.H. & Paquet P.C., Edits. Wolves of the world: perspectives of behavior, ecology and conservation. *New Jersey: Noyes*.
- HARRINGTON F.H., MECH L.D. & FRITTS S.H. 1983. Pack size and wolf pup survival: their relationship under varying ecological conditions. *Behavioral Ecology and Sociobiology* 13: 19-26.
- HARRINGTON F.H., PAQUET P.C., RYON J. & FENTRESS J.C. 1982. Monogamy in wolves: a review of the evidence, pp. 209-222. In: Harrington F.H. & Paquet P.C., Edits. Wolves of the world: perspectives of behavior, ecology and conservation. *New Jersey: Noyes*.
- HAWKINS R.E., KLIMSTRA W.D. & ANTRY D.C. 1970. Significant mortality factors of deer on Crab Orchard National Wildlife Refuge. *Transactions Illinois State Academy of Sciences* 63: 202-206.
- HIRATA H., OKUZAKI M. & OBARA H. 1986. Characteristics of urban dogs and cats, pp. 163-175. In: Obara H., Edit. Integrated studies in urban ecosystems as the basis of urban planning, I. Special research project on environmental science (B276-R15-3). *Tokyo: Ministry of Education*.
- HIRATA H., OKUZAKI M. & OBARA, H. 1987. Relationships between men and dogs in urban ecosystem, pp. 113-120. In: Obara H., Edit. Integrated studies in urban ecosystems as the basis of urban planning, II. Special research project on environmental science (B334-R15-3). *Tokyo: Ministry of Education*.
- JOSLIN P.W.B. 1966. Summer activities of two timber wolf (*Canis lupus*) packs in Algoquin Park. *M.A. Thesis, University of Toronto, Toronto*.
- KEITH L.B. 1983. Population dynamics of wolves, pp. 66-77. In: Carbyn L.N., Edit. Wolves in Canada and Alaska. Their status biology and management. *Canadian Wildlife Service Report Series* No. 45.
- KLEIMAN D.G. 1968. Reproduction in the Canidae. *International Zoo Yearbook* 8: 1-7.
- KLEIMAN D.G. & BRADY C.A. 1978. Coyote behaviour in the context of recent canid research: problems and perspectives, pp. 163-188. In: Bekoff M., Edit. Coyotes. *New York: Academic Press*.

- KLEIMAN D.G. & EISENBERG J.F. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. *Animal Behaviour* 21: 637-659.
- KLEIMAN D.G. & MALCOM J.R. 1981. The evolution of male parental investment in mammals, pp. 347-387. In: Gubernik D.J. & Klopfer P.H., Edits. Parental care in mammals. *New York: Plenum*.
- KOLENOSKY G.B. & JOHNSTON D.H. 1967. Radio-tracking in timberwolves in Ontario. *American Zoologist* 7: 289-303.
- KRUUK H. 1972. The spotted hyena: a study of predation and social behaviour. *Chicago: University of Chicago Press*.
- KRUUK H. & SNELL H. 1981. Prey selection by feral dogs from a population of marine iguanas (*Amblyrhynchus cristatus*). *Journal of Applied Ecology* 18: 197-204.
- LINDSTROM E. 1986. Territory inheritance and the evolution of group living in carnivore. *Animal Behaviour* 34: 1825-1835.
- LOWHEAD B.D. 1983. Wolf den site characteristics in the Nelchina Basin, Alaska. *MS Thesis, University of Alaska, Fairbanks*.
- LOWRY D.A. & MACARTHUR K.L. 1978. Domestic dogs as predators on deer. *Wildlife Society Bulletin* 6: 38-39.
- MACDONALD D.W. 1981. Dwindling resources and the social behaviour of Capybaras, (*Hydrochoerus hydrochaeris*). *Journal of Zoology* 194: 371-391.
- MACDONALD D.W. 1983. The ecology of carnivore social behaviour. *Nature* 301: 379-384.
- MACDONALD D.W., BALL F.G. & HOUGH N.G. 1980. Evaluation of home range size and configuration, pp. 405-424. In: Amlaner C.J. & Macdonald D.W., Edits. A handbook on biotelemetry and radio-tracking. *Oxford: Pergamon Press*.
- MACDONALD D.W. & CARR G.M. 1989. Food security and the rewards of tolerance, pp. 75-99. In: Standen V. & Foley R.A., Edits. Comparative socioecology: the behavioural ecology of humans and other mammals. *Oxford: Blackwell Scientific Publications*.
- MACDONALD D.W. & CARR G.M. (in press). Variation in dog society: between resource dispersion and social flux. In: Serpell J., Edit. The dog: its ecology, behaviour and evolution. *Cambridge: Cambridge University Press*.
- MCKNIGHT T. 1964. Feral livestock in Anglo-America. *Berkeley: University of California Press*.
- MECH L.D. 1970. The wolf: the ecology and behaviour of an endangered species. *New York: Natural History Press*.
- MECH L.D. 1975. Disproportionate sex ratios of wolf pups. *Journal of Wildlife Management* 39: 737-740.
- MECH L.D. 1977a. Productivity, mortality and population trends of wolves in North-Eastern Minnesota. *Journal of Mammalogy* 58: 559-574.
- MECH L.D. 1977b. Population trend and winter deer consumption in a Minnesota wolf pack, pp. 55-83. In: Phillips R.L. & Jonkel C., Edits. Proceedings of the 1975 Predator symposium. Bulletin of Montana Forest Conservation Experimental Station. *Missoula: University of Montana*.
- MECH L.D. 1986. Wolf population in the Central Superior National Forest, 1967-1985. *U.S.D.A., North Central Forest Experimental Station Research Paper NC-270: 1-6*.
- MECH L.D. & NELSON M.E. 1989. Polygyny in a wild wolf pack. *Journal of Mammalogy* 70: 675-676.
- MECH L.D. & NELSON M.E. 1990. Non-family wolf, *Canis lupus*, pack. *The Canadian Field Naturalist* 104: 482-483.
- MESSIER F. 1985. Social organization, spatial distribution and population density of wolves in relation to moose density. *Canadian Journal of Zoology* 63: 239-245.
- MURIE A. 1944. The wolves of Mount McKinley. *U.S. National Park Service Fauna Series* 5: 1-238.
- NELSON M.E. & MECH L.D. 1981. Deer social organization and wolf predation in Northeastern Minnesota. *Wildlife Monograph* 77: 1-53.
- NESBITT W.H. 1975. Ecology of a feral dog pack on a wildlife refuge, pp. 391-395. In: Fox M.W., Edit. The wild canids. *New York: Van Nostrand Reinhold*.
- OLSON J.C. 1974. Movements of deer as influenced by dogs. *Indiana Department of Natural Resources, Job Progress Report Project W-26-R-5: 1-36*.

- PACKARD J.M. & MECH L.D. 1980. Population regulation in wolves, pp. 135-158. In: Klein A.G. & Cohen M., Edits. Biosocial mechanisms of population regulation. *New Haven: Yale University Press*.
- PACKARD J.M., MECH L.D. & SEAL U.S. 1983. Social influences on reproduction in wolves, pp. 66-77. In: Carbyn L.N., Edit. Wolves in Canada and Alaska. Their status biology and management. *Canadian Wildlife Service Report Series No. 45*.
- PACKARD J.M., SEAL U.S., MECH L.D. & PLOTKA E.D. 1985. Causes of reproductive failure in two family groups of wolves (*Canis lupus*). *Zeitschrift für Tierpsychologie* 68: 24-40.
- PERRY M.C. & GILES R.H. 1971. Free running dogs. *Virginia Wildlife* 32: 17-19.
- PETERS L. & MECH L.D. 1975. Scent-marking in wolves. *American Scientist* 63: 628-637.
- PETERSON R.O. 1977. Wolf ecology and prey relationship on Isle Royale. *National Park Service Scientific Monographs Series* 11: 1-210.
- PETERSON R.O., WOOLINGTON J.D. & BAILEY T.N. 1984. Wolves of the Kenay peninsula, Alaska. *Wildlife Monograph* 88: 1-52.
- PRICE E.O. 1984. Behavioural aspects of animal domestication. *The Quarterly Review of Biology* 59: 1-32.
- PROGULSKE D.R. & BASKETT T.S. 1958. Mobility of Missouri deer and their harassment by dogs. *Journal of Wildlife Management* 22: 184-192.
- RABB G.B., WOOLPY J.H. & GINSBURG B.E. 1967. Social relationships in a group of captive wolves. *American Zoologist* 7: 253-265.
- RAUSCH R.A. 1967. Some aspects of the population ecology of wolves, Alaska. *American Zoologist* 7: 253-265.
- ROTHMAN R.J. & MECH L.D. 1979. Scent-marking in lone wolves and newly formed pairs. *Animal Behaviour* 27: 750-760.
- SANTAMARIA A., PASSANNANTI S. & DI FRANZA D. 1990. Censimento dei cani randagi in un quartiere di Napoli. *Acta Medica Veterinaria* 36: 201-213.
- SCOTT M.D. & CAUSEY K. 1973. Ecology of feral dogs in Alabama. *Journal of Wildlife Management* 37: 253-265.
- SCOTT J.P. & FULLER J.L. 1965. Genetics and the social behaviour of the dog. *Chicago: University of Chicago Press*.
- SEAL U.S. & MECH L.D. 1983. Blood indicators of seasonal metabolic patterns in captive adult gray wolves. *Journal of Wildlife Management* 47: 704-715.
- SEAL U.S., MECH L.D. & VAN BALLEMBERGHE V. 1975. Blood analyses of wolf pup and their ecological and metabolic interpretation. *Journal of Mammalogy* 56: 64-75.
- SEAL U.S., PLOTKA E.D., MECH L.D. & PACKARD J.M. 1987. Seasonal metabolic and reproductive cycles in wolves, pp. 109-125. In: Frank H., Edit. Man and wolf. *The Netherlands: Junk Publisher*.
- SWEENEY J.R., MARCHINTON R.L. & SWEENEY J.M. 1971. Responses of radiomonitored white-tailed deer chased by hunting dogs. *Journal Wildlife Management* 35: 707-716.
- URIOS V., VILA C. & CASTROVIEJO J. 1993. Foraging strategies of the Iberian wolf (*Canis lupus signatus*). *Symposium Internacional sobre el Lobo (Leon, 19-23 October, 1993, Spain)* (abstract).
- VAN BALLEMBERGHE V. 1983. Two litters raised in one year by a wolf pack. *Journal of Mammalogy* 64: 171-173.
- VAN BALLEMBERGHE V., ERICKSON A.W. & BYMAN D. 1975. Ecology of the timber wolf in North-eastern Minnesota. *Wildlife Monograph* 43: 1-43.
- VAN BALLEMBERGHE V. & MECH L.D. 1975. Weights, growth, and survival of timber wolf pups in Minnesota. *Journal of Mammalogy* 56: 44-63.
- VILA C., URIOS V. & CASTROVIEJO J. 1993. The iberian wolf: a persecuted species. *Symposium Internacional sobre el Lobo, (Leon, 19-23 October, 1993, Spain)* (abstract).
- VON SCHANTZ T. 1984. Carnivore social behaviour: does it need patches? *Nature* 307: 389.
- WORLD HEALTH ORGANIZATION 1988. Report of WHO consultation on dog ecology studies related to rabies control. *WHO/Rab. Res./88.25*.
- ZEUNER F.E. 1963. A history of domesticated animals. *London: Hutchinson & Co. Publishers*.
- ZIMEN E. 1976. On the regulation of pack size in wolves. *Zeitschrift für Tierpsychologie* 40: 300-341.

- ZIMEN E. 1982. A wolf pack sociogram, pp. 282-382. In: Harrington F.H. & Paquet P.C., Edits. *Wolves of the world. Perspectives of behavior, ecology and conservation. New Jersey: Noyes.*
- ZIMEN E. & BOITANI L. 1975. Number and distribution of wolves in Italy. *Zeitschrift für Säugetierkunde* 40: 102-112.