Z. Säugetierkunde **65** (2000) 257–270

http://www.urbanfischer.de/journals/saeugetier

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Comparison of reproductive biological parameters in male wolves and domestic dogs

By E. Haase

Institut für Haustierkunde, Christian-Albrechts-Universität, Kiel, Germany

Receipt of Ms. 07. 03. 2000
Acceptance of Ms. 12. 07. 2000

Abstract

Effects of domestication on the reproductive biology in the species *Canis lupus* were studied by comparing some reproductive biological parameters in male wolves and domestic dogs living under similar conditions.

1. Seasonal changes in the concentrations of the two androgens testosterone (T) and 5α-dihydrotestosterone (DHT) in the peripheral plasma and in the relative testicular weights (testes/carcass weight) were observed in the wolves with maximal values during the winter, their natural mating season. In the domestic dogs such seasonal changes were not seen, androgen concentrations and relative testicular weights were high during all seasons.

2. An allometric comparison of testicular and epididymal weights revealed no differences among the various breeds of domestic dogs studied here. The weights of the testes and epididymides increased almost isometrically with body weight. Compared to the corresponding values in wolves during the mating season the weights of the testes and epididymides had increased by about 40% in domestic dogs.

3. Plasma T- and DHT-concentrations in 4 standard poodles, 2 toy poodles, and 3 wolves rose steeply in their 28th, 32nd, and 34th week of life, respectively. Thus, poodles and wolves living under similar conditions in captivity reach physiological sexual maturity at nearly the same age.

According to these findings domestication had no or little effect on the onset of puberty in the species *Canis lupus*. The seasonality of reproduction as it was observed in wolves, has vanished in the domestic dog and is replaced by the capability to reproduce during any season. The testes, sites of sperm production, and the epididymides, sites of sperm storage, have been enlarged by about 40% during domestication

Key words: *Canis lupus*, domestication, seasonal reproduction, puberty, testicular size

Introduction

Among the numerous effects of domestication the changes concerning the reproductive biology seem to be very striking and have been repeatedly described (Darwin 1875; Keller 1905; Haase and Donham 1980; Price 1984; Herre and Röhrs 1990; Setchell 1992; Benecke 1994). According to Keller (1905, p. 46) the unrestrained function of the reproductive system is a most important precondition for the development of domestic animals.

However, a closer inspection of the literature reveals that many examples for an enhanced reproduction in domestic animals compared to their wild ancestors do not withstand a critical examination since the different performances were achieved under differ-

0044-3468/00/65/05 – 257 $ 15.00/0

ent environmental conditions (see HAASE and DONHAM 1980; HERRE and RÖHRS 1990). Characters that, on the one hand, can effectively influence reproductive performances and, on the other hand, seem to be susceptible to alterations during domestication are the age of puberty and the duration of the reproductive season. Both these characters are amenable to proximate environmental factors (BRONSON and RISSMAN 1986; CATLING et al. 1992), thus emphasizing the necessity to perform comparisons under identical conditions.

The canids kept in the zoological garden at the Institut für Haustierkunde in Kiel live(d) under similiar conditions. Some observations on reproductive biological parameters in male domestic dogs and wolves will be reported in this communication.

Material and methods

The data from 38 wolves (mainly *C. l. lupus* and *C. l. pallipes*) and 90 domestic dogs (36 New Guinea dingoes, 12 hairless dogs, 20 standard poodles, 10 toy poodles, 12 specimens from various breeds, size range: long-haired dachshund to rottweiler) were used for gravimetrical studies. These animals were at least 10 months old. Except for the 12 specimens from various breeds the canids had lived for long periods of times or all their lives in the zoological garden at the Institut für Haustierkunde under the climatic conditions of Kiel (54° N), Germany. They were kept in large outdoor enclosures provided with indoor shelters including heating appliances. After sacrifice they were dissected according to a standard protocol introduced by HERRE 50 years ago. The following data were used for this investigation: 1. gross body weight, taken immediately after death. 2. net body weight = carcass weight, which is obtained by subtracting the weights of the fur (including subcutaneous fat) and the viscera of the thoracic and abdominal cavities from gross body weight. 3. testes weight (left and right combined). 4. weight of the epididymides (left and right combined).

For the estimation of seasonal changes in testicular weight it seemed reasonable to compensate for an expected influence of body weight on gonadal size. For this purpose "relative testes weight" was calculated by dividing testes weight by net body weight. The latter was preferred to gross body weight since KRUSKA (1996) in studies on the effects of domestication on brain size in mammals found it to be a more reliable measure for body size.

Allometric comparisons of testicular and epididymal sizes between the different canid groups were performed using net body weight and – for the reason of comparability with data from the literature – also gross body weight as the independent variable. Logarithmically transformed the allometric power function describes a linear function

$$\log y = b \cdot \log x + \log a$$

where y is organ weight, x is body weight (gross or net), b represents the slope of the regression line and log a the intercept of this line with y-axis at x = 0 and thus the position of the line. Slopes and positions of the regression lines between the canid groups were tested for differences using an analysis of covariance (ANCOVA) and subsequent multiple comparisons (SOKAL and ROHLF 1995). Additionally, all domestic dogs were pooled in one group and tested against the wolves. For reasons of comparability, "relative testes size" as introduced by KENAGY and TROMBULAK (1986) (1.0 representing the average relative testes size in 133 mammalian species), was calculated for domestic dogs and wolves. Due to high age, striking lateral asymmetries, or seasonal involution 13 of the 90 domestic dog specimens and 31 of the 38 wolves were excluded from the data sets for allometric comparisons.

3 wolves (*C. l. lupus*) born around May 15, 4 standard poodles born June 30, and 2 toy poodles from October 26 were used for studies on the onset of puberty. The wolves were hand reared and after weaning kept together with the standard poodles and their female littermates in a mixed group. The toy poodles with their sister and other female canids lived in a separate enclosure. At 3–4 week intervals blood samples were drawn from a brachial vein beginning on June 21 (wolves), November 2 (standard poodles), and December 15 (toy poodles) in their 6th, 18th, and 8th week of age, respectively. The heparinized blood samples were centrifuged and the plasma was stored in a deep freezer until assayed for androgens by radioimmunoassays (RIA) The assay procedure essentially followed the method of WINGFIELD and FARNER (1975) with slight modifications introduced by SCHEDEMANN (1991). Briefly, steroids were extracted from the plasma using Extrelut (Merck) columns and elution

with dichloromethane. Steroids were seperated via Celite column chromatography using 10% and 20% ethylacetate in isooctane for elution of a 5α-dihydrotestosterone (DHT) and testosterone (T) fractions, respectively. Thus, the 2 androgens could be assayed separately using the same antibody (code #EN-5100/4-11/2, kindly provided by Prof E. Nieschlag, Münster, Germany). All samples were assayed in duplicate.

Results

Seasonality

In figure 1 relative testes weights of all wolves were plotted against the days of dissection, day 1 corresponding to May 1. A clear annual cycle is evident: from May through October testes were regressed. In November relative testes weights increased and maxima were attained in December and January. Unfortunately, there were no data for February, but in March a decline was observed which continued in April reaching the level typical for the summer months. If the relative testes weights of the domestic dogs were plotted in the same way (not shown) there were no indications for seasonal changes. This statement held for all domestic dogs considered collectively as well as for the single subgroups.

Seasonality and its loss in relative testes weights of wolves and domestic dogs, respectively, kept under similiar conditions were also obvious from the diagram (Fig. 2). The columns representing the average relative testes weight for 3-month-periods showed a seasonal pattern for the wolves with maximal values during the winter. Average relative testes weight of wolves during this period was significantly above those during the other periods. For the domestic dogs the columns were of similar height throughout the year, the relatively short one for the 4th quarter representing 4 specimens only.

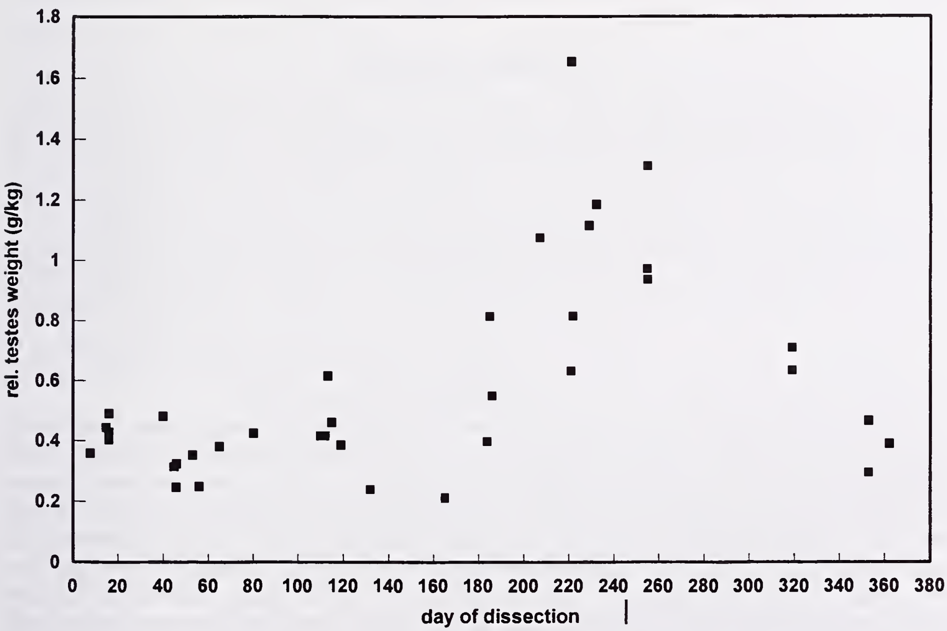

Fig. 1. Relative testes weights (testes weight/net body weight) in wolves plotted against day of dissection, day 1 corresponding to May 1rst (whelping season). Vertical bar underneath abscissa indicates new year. Maximal values were reached during the mating season.

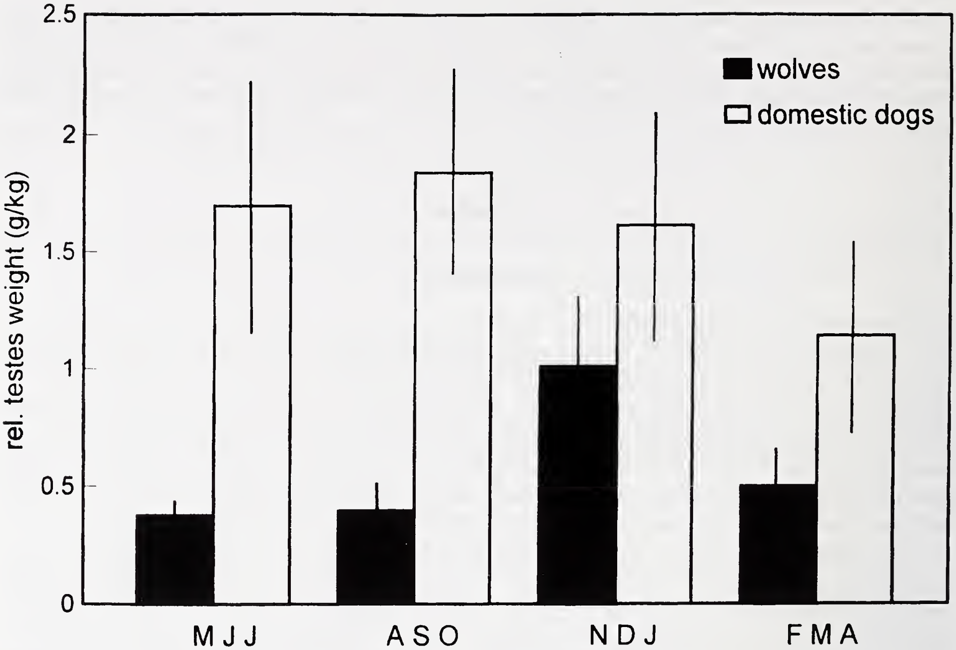

Fig. 2. Relative testes weights (testes weight/net body weight) in wolves (black) and domestic dogs (open). Columns represent mean relative testes weights for 3-months periods. Vertical lines indicate standard deviations.

Allometric comparison

In the sexually mature canids studied here there was a highly significant correlation between testicular weight and net body weight. The slope of the regression line within all canids was $b = 0.94$ and using ANCOVA no significant differences in the slopes of the regression lines could be detected between the different groups. There were, however, significant differences in the positions of the regression lines. Pairwise examinations showed these differences to concern the wolves compared to standard poodles, toy poodles, and New Guinea dingoes, respectively, but never pairwise compared domestic dogs. If the pooled domestic dogs ($b = 0.92$) were compared to the wolves ($b = 1.06$), again, there was no difference between these slopes but a highly significant difference in the position of the regression lines (Fig. 3). Based on the same net body weight testes in domestic dogs were 42.3% heavier than testes in wolves during the mating season.

If the calculations were performed on the basis of gross body weights the results were rather similar. Again, the two variables were correlated with high significance and ANCOVA showed no significant differences in the slopes of the regression lines between the different canid groups (all canids $b = 0.98$; pooled domestic dogs $b = 0.94$; wolves $b = 1.18$). Differences in the position were significant between New Guinea dingoes and wolves and a tendency ($p < 0.1$) for heavier testes was observed in toy poodles compared to wolves. In the pooled domestic dogs the testes were 35.5% larger than in equally sized (gross body weight) wolves during the mating season and this difference was highly significant. In the allometric relation testes weight/gross body weight it was possible to calculate the "relative testes size" in the sense of KENAGY and TROMBULAK (1986). It was 0.46 in the wolves and 0.54 in the pooled domestic dogs.

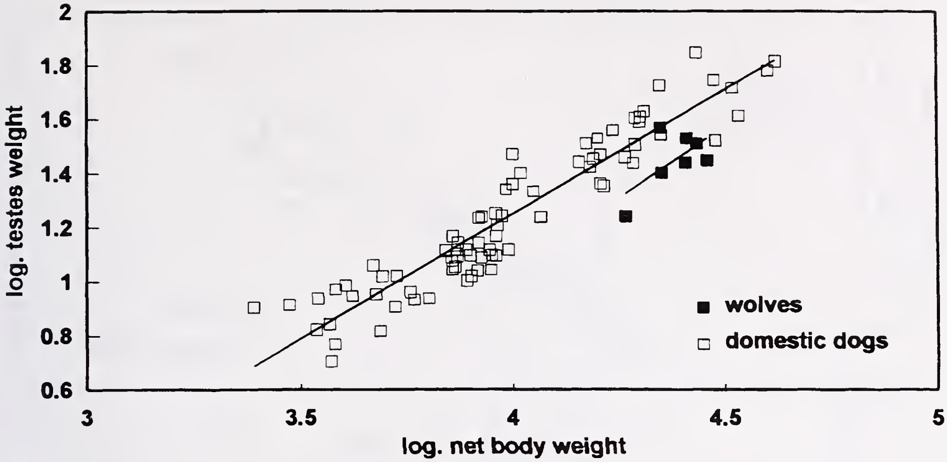

Fig. 3. Allometric comparison of testes weights in wolves during the mating season (black squares) and in domestic dogs (breeds pooled, open squares) in relation to net body weights. Values were logarithmically transformed. The regression lines for wolves and domestic dogs had similar slopes, but differed significantly in their positions resulting in an allometric weight increase of the testes in domestic dogs by 42.3%.

Considering the allometric weights of the epididymides in relation to carcass weights revealed no differences in the slopes but significant differences in the positions of the regression lines between the various canid groups. Pairwise comparisons showed the group "various breeds" to possess heavier epididymides than the wolves and the New Guinea dingoes, respectively, and, there was also a tendency ($p < 0.1$) in wolves for smaller epididymides than in standard poodles. For the pooled domestic dogs and the wolves the slopes of the regression lines relating epididymal weights to net body weights were almost identical (pooled domestic dogs $b = 0.88$; wolves $b = 0.94$). The line for the domestic dogs was situated well above the one for the wolves ($p < 0.01$) (Fig. 4). On the basis of the same net body weight epididymides of domestic dogs were 42.7% heavier than those of wolves during the mating season.

If epididymal weights were related to gross body weights the results strongly resembled those described above. Again, the pooled domestic dogs ($b = 0.90$) had heavier epididymides than wolves ($b = 1.14$) during the mating season and this allometric increase amounted to 36.1%.

Puberty

In the 4 standard poodles born in June a marked increase in plasma testosterone levels was observed in the 28th week of life (early January). Thereafter, apart form transient depressions average testosterone concentrations remained high (>3 ng/ml) in these dogs (Fig. 5). Similarly, a steep increase of plasma DHT concentrations from 0.058, 0.084, and 0.280 ng/ml in the 18th, 22nd, and 25th week, respectively, to 0.985 ng/ml in the 28th week was seen in the standard poodles with moderate variations around this latter value until the end of the observation period.

In the 2 toy poodles born in October plasma testosterone and DHT levels were low at all sampling dates during the first 28 weeks of life. In the 32nd week (end of May) a severalfold increase was noted in the plasma concentrations of the two androgens (Fig. 6). Apart from some fluctuations high levels persisted until the end of the sampling period.

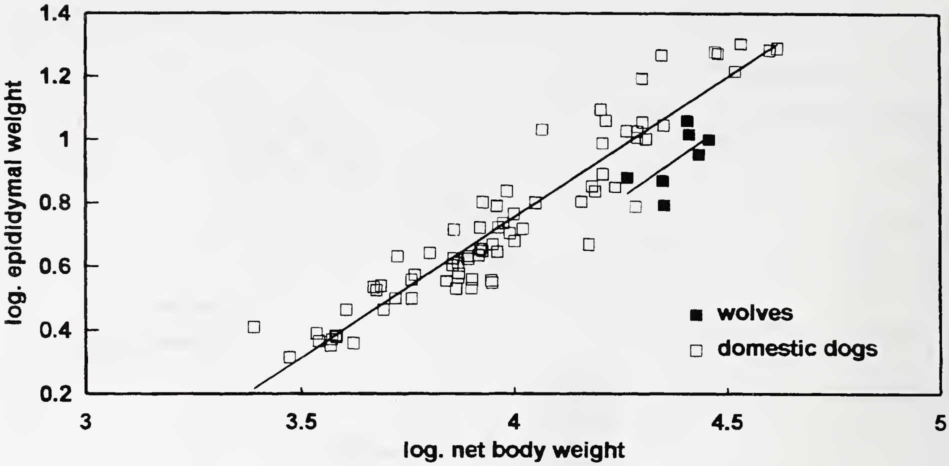

Fig. 4. Allometric comparison of epididymal weights in wolves during the mating season (black squares) and in domestic dogs (breeds pooled, open squares) in relation to net body weights. Values were logarithmically transformed. The regression lines for wolves and domestic dogs had similar slopes, but differed significantly in their position resulting in an allometric weight increase of the epididymides in domestic dogs by 42.7%.

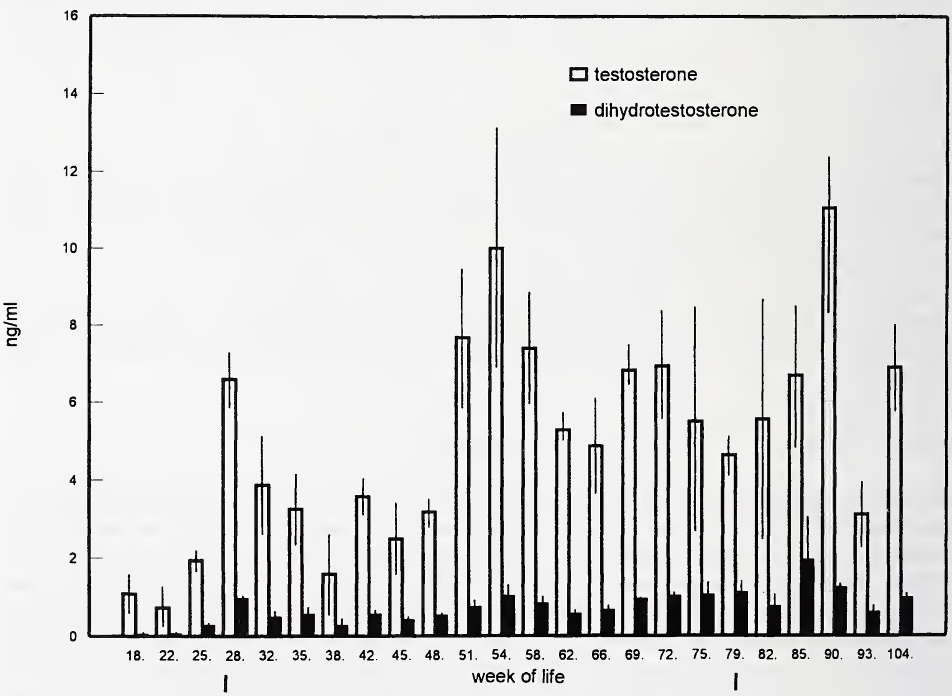

Fig. 5. Concentrations (mean ± SD) of testosterone and 5α-dihydrotestosterone in the plasma of 4 standard poodles (born at the end of June) at different ages. Vertical bars underneath abscissa indicate begin of new calendar years.

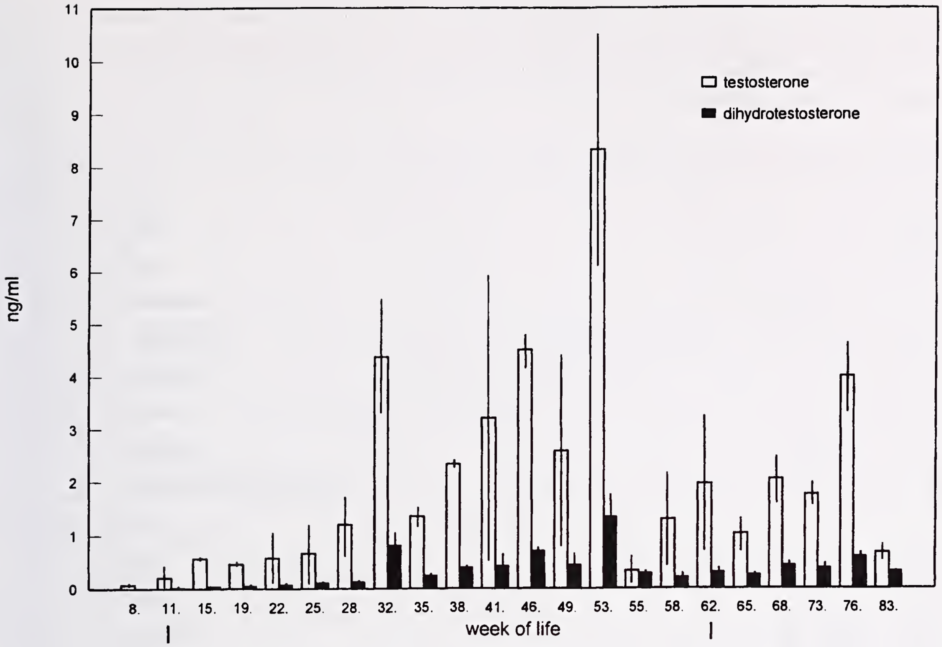

Fig. 6. Concentrations (mean ± SD) of testosterone and 5α-dihydrotestosterone in the plasma of 2 toy poodles (born at the begin of October) at different ages. Vertical bars underneath abscissa indicate begin of new calendar years.

From the 6th through the 31st week of life plasma testosterone and DHT concentrations in 3 wolves born in May remained at low levels. In January (34th week) there was a marked rise in the peripheral androgen levels to about 2 ng/ml (T), and 0.2 ng/ml (DHT) and a further increase took place in February and March. In the following months androgen concentrations fell and reached a new low from May through July. Later in the summer there was a gradual increase which continued during the fall. A second peak was reached during the winter, 12 months after the first one. Subsequently, androgen levels declined steeply in the spring. Thus, in the wolves androgen levels showed a clear seasonal pattern with maximal values during the winter, the natural mating season of the species, and lows during the spring and summer. Interestingly, the first peak commenced at the early age of 34 weeks (Fig. 7).

Discussion

Seasonality

It is widely accepted that seasonal reproduction has evolved as an adaptation to seasonal changes in the environment (Baker 1938; Aschoff 1955; Bronson 1985). In their natural environment wolves like other wild canids reproduce seasonally (Rausch 1967; Ginsberg and McDonald 1990; Asa and Valdespino 1998). Depending on the latitude and climatic factors wolves rut between December and April and parturition takes place between March and June (Mech 1970; Heptner and Naumov 1974; Bibikow 1988; Peters 1993). As judged from observations on sexual behaviour and parturition (Mech 1970; Lentfer

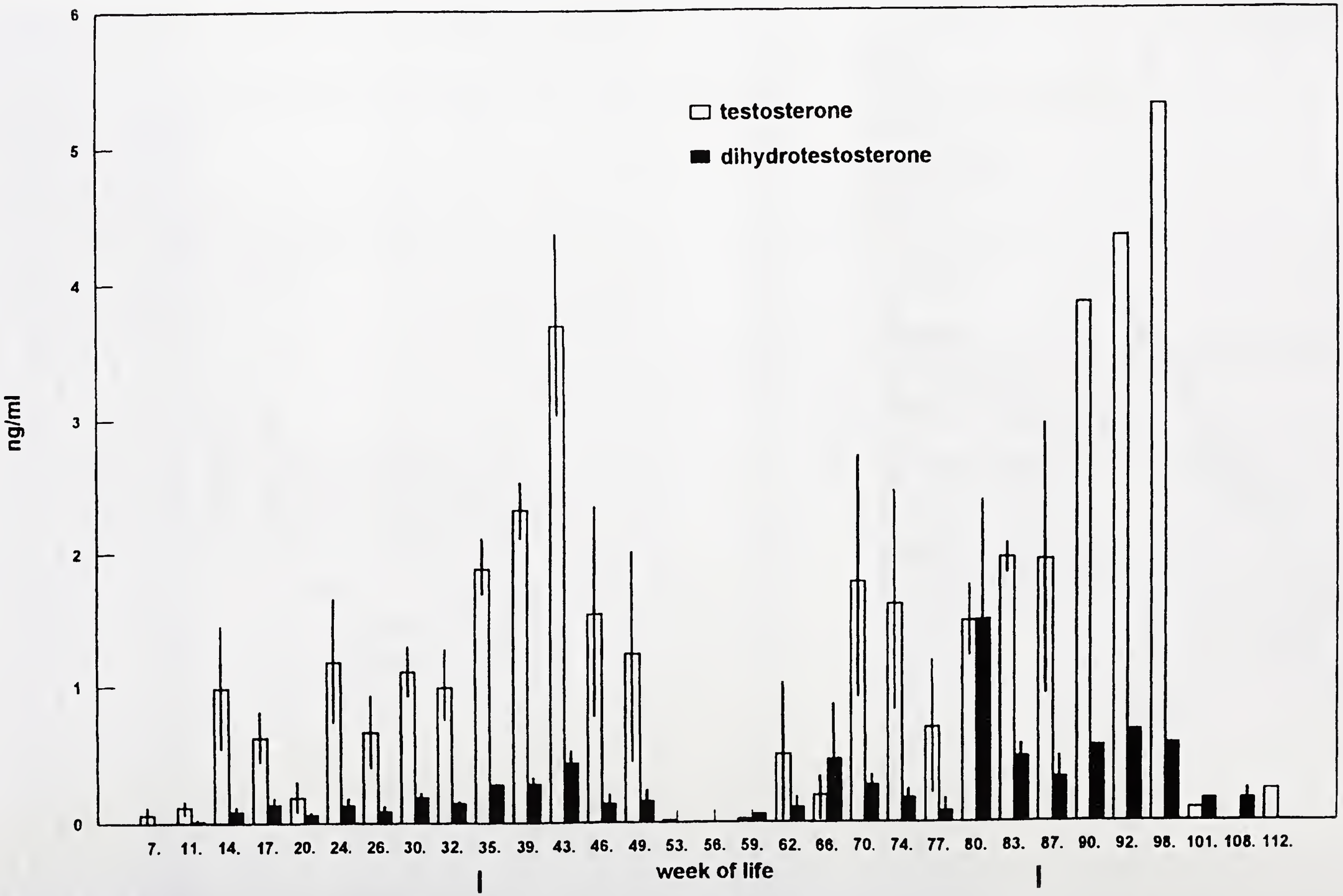

Fig. 7. Concentrations (mean ± SD) of testosterone and 5α-dihydrotestosterone in the plasma of 3 wolves (born at the middle of May) at different ages. Vertical bars underneath abscissa indicate begin of new calendar years.

and SANDERS 1973; SEAL et al. 1979; ASA et al. 1990) this seasonality of reproduction seems to persist in captivity, and this was also repeatedly observed in the zoological garden at the Institut für Haustierkunde (unpubl.). But like in wild dogs in Australia (JONES and STEVENS 1988) a single breeding season each year may not preclude fertility throughout the year in the male.

The findings of this investigation on relative testes weights and on peripheral androgen levels clearly favor the persistence of seasonal fertility of male wolves in captivity. A seasonal pattern of serum testosterone levels after LHRH stimulation and of a testicular size index with maximal values during the winter was reported by ASA et al. (1986, 1990) for captive wolves. For male red foxes captivity seems to have no effect on the seasonality of genital activity (JOFFRE 1976).

NOVIKOV (1962) stated that in wolves "the weight of the testicles increases fivefold before the rutting season" but unfortunately he provided no data or sources. In the present investigation the lowest and highest testicular weights were 5.6 g (June) and 37.0 g (December), respectively, and from these extremes a 6.6 fold increase could be calculated. However, a more reliable estimation may be gained from relative testes weights. In 7 specimens from the breeding season (which were also used for allometric comparisons) relative testes weight averaged 1.2 g/kg, whereas outside the breeding season it amounted to 0.4 g/kg, thus resulting in a threefold augmentation.

Generally, in domestic dogs, there seems to be no seasonal breeding cycle. According to ENGLE (1946) the estrus cycle of pure bred dogs of 4 breeds appears rather uniformly throughout the year. The length of estrus intervals in breeding bitches in Britain varied between 16 and 56 weeks with a median of 29 and 32 weeks in non-pregnant and pregnant bitches, respectively (CHRISTIE and BELL 1971). In this situation, where the occurrence of the next estrus appears unpredictible, a male would improve his chances to reproduce if he was fertile throughout the year. Relative testes weights and plasma androgen levels in the domestic dogs remained rather high during all seasons indicating a loss of reproductive seasonality during domestication in this species. This result basically agrees with earlier findings in the mallard (*Anas platyrhynchos*) where domestication was shown to flatten the seasonal oscillations of testicular size and plasma concentrations of reproductive hormones (HAASE and DONHAM 1980).

For some domestic dog strains seasonal reproduction has been described: In basenji estrus is under photoperiodic control (FULLER 1956, males not mentioned). In free-ranging dogs in Katwa, West Bengal, pups (64 litters) were born exclusively during the winter (Oct.–March) (PAL et al. 1998, no data on males). In dingoes most females have an annual estrus cycle, whereas males can breed continuously in all habitats except hot and arid regions where they have an annual testis cycle (CORBETT 1995). This testis cycle was more pronounced during drought than in flush periods (CATLING et al. 1992) and if Central Australian dingoes were housed in Canbarra they did not have a testicular cycle. Here, they exhibited breeding season including elevated testosterone levels, but this was entirely governed by the female (CATLING 1979). These findings underline the importance of environmental factors for the expression of reproductive parameters and emphasize the necessity to perform comparisons under identical conditions. There were no signs for seasonal testicular weight changes in the New Guinea dingoes studied here, but it should be mentioned that the overwhelming majority of specimens was sacrificed from July to December.

The timing of reproduction in silver foxes (FORSBERG et al. 1989) and basenji dogs (FULLER 1956) is under photoperiodic control and the same very likely applies to wolves. An intraspecific heterogeneity in the response to photoperiodic cues was observed in rodent species and a genetic basis for this variability was documented by selection experiments (BRONSON 1985). In this context, the weakening or even loss of reproductive seasonality during domestication may be understood as a consequence of the changed environmental conditions and of the resulting alterations in selection pressure which a species experiences during domestication. When food and shelter are provided by man offsprings which are born outside the original breeding season have a chance to survive and to pass their genes to following generations.

Allometric comparison

The allometric calculations uncovered a highly significant linear correlation between logarithmically transformed testes weights and net body weights. The slope for the regression line was close to 1.0 and this means that in this species testes increase in size in an almost isometric proportion to the increase in net body weight. Thus, "relative testes weight" as it was used in the preceding chapter on seasonality is a rather fair compensation for the influence of body size on testicular size.

Allometrically related to net body weight the testes of domestic dogs irrespective of the breeds studied here were 42.3% heavier than those of wolves during the mating season. In mallards, too, domestication has increased testicular weights (Haase and Donham 1980). According to Kenagy and Trombulak (1986) an increased copulatory frequency should promote selection for larger testes and this should occur with decreasing number of days in which a given number of matings must be accomplished. With other factors being equal Kenagy and Trombulak (1986) predicted that males of a species with a shorter mating season should have larger testes than males with a longer mating season. Obviously, in *Canis lupus* and *Anas platyrhynchos* domestication has lengthened the duration of the reproductive season and at the same time increased testes size. Clearly "other factors" in the sense of Kenagy and Trombulak (1986) were influenced by domestication, too, and of outstanding importance seems to be the mating system. In wolves as in many other wild canid species the mating system is monogamy (Kleiman 1977; Asa and Valdespino 1998). Although preferential mating has been well documented for bitches (Beach and Le Boeuf 1967), a tendency to promiscuity is evident for domestic dogs. The "extreme is the almost totally promiscuous behavior of the Venezuelan Mucuchies dogs; males were observed to line up and breed a female sequentially, with little aggression between them" (Coppinger and Coppinger 1998). Also, in feral dogs in central Italy, Boitani et al. (1995) "found no evidence that exclusive mating occurred within the group's breeding pairs, nor that the males in each pair were the fathers of the female's offspring". Monogamy in wolves includes paternal care (Asa and Valdespino 1998). If under the conditions of domestication man is involved in the care for the pups the reproductive success of a male dog is no longer linked to its paternal care as it was in the wolf. This should facilitate a tendency to promiscuity. Further, in directed dog breeding the mates of a pair are chosen by the breeder. Preferential monogamous mating behavior and refusal to accept the mate chosen by man would often result in reproductive failure, whereas promiscuous behavior would be advantageous under these conditions.

Kenagy and Trombulak (1986) related testes weight to gross body weight in 133 mammal species and calculated a "relative testes size". In the average of all 133 species "relative testes size" was 1.0 and it varied from 0.11 in *Notomys alexis* to 24.65 in *Phocoena phocoena*. If species were grouped according to their mating system mean "relative testes size" was 0.54 and 1.68 for 23 species with a single-male (including monogamous) mating system and 31 species with a multi-male (including promiscuous) mating system, respectively. The authors concluded that a functional relationship exists in many mammals between relative size of the testes and mating system. The value for the wolf reported here (0.46) fits well into this scale. The value for the pooled domestic dogs (0.54) indicates that the increase in relative testicular size during domestication of this species was rather modest compared to the evolutionary changes mentioned above.

The evolution of large testes was, among others, attributed to high sperm production (see KENAGY and TROMBULAK 1986) and, therefore, a dog probably produces more sperm than an equally sized wolf. The findings concerning the epididymides showed an allometric weight increase in the pooled dogs of 42.7% and 36.1% related to net and gross body weight, respectively, compared to wolves during the mating season. These values are practically identical with those for the testes. Thus, domestication affected the weights of the sperm production site and of the sperm storage site to the same extent.

Puberty

DARWIN (1875) was among the first to state that domestic animals sometimes breed at an earlier age than their wild ancestors. Many authors (MECH 1970; HEPTNER and NAUMOV 1974; LENTFER and SANDERS 1973; BIBIKOW 1988; PETERS 1993; ASA and VALDESPINO 1998) agree that puberty in wolves usually begins at the age of 22 months. According to HEPTNER and NAUMOV (1974) males do not participate in reproduction before their third or fourth year. In the domestic dog, sexual maturity is reached at a much earlier age (6–18 months, BEAVER 1977; 6–9 months, FOX 1978).

A spectacular decline in the age of human puberty has occurred in Europe and the United States during the last 100 years and is still going on in the developing countries (SHORT 1976). These findings point to the role of environmental factors in the timing of puberty and, therefore, comparative studies concerning the onset of sexual maturation should reasonably be performed under identical conditions.

The standards developed by TANNER (1962) as signs of sexual maturation in the human depend on physical characters which are essentially controlled by sexual hormones. The production of testosterone rises sharply at the time of puberty (SETCHELL 1978). Therefore, in the present study, steep elevations in the peripheral plasma androgen concentrations were used to determine the onset of puberty. According to this criterium, puberty started in the 28th and 32nd week of life in standard poodles and toy poodles, respectively. This means that sexual maturity in poodles begins in the age of 7–8 months, irrespective of the date of birth (June and October) or season. These findings fit well into the data on domestic dogs mentioned above. The slight difference between the two breeds must not be overestimated, especially, since blood sampling was performed in 4 week intervals, only. Nevertheless, it is interesting in this context that skeletal maturation as judged from epiphyseal synostosis was completed later in toy and miniature poodles than in standard poodles (WIECHERING 1981).

In the young wolves a steep increase in peripheral androgen levels and, thus, the onset of puberty was observed in the 34th week of life. This unexpected early start of sexual maturation in wolves in captivity markedly contrasts with statements in the literature concerning wolves and seems to fit well with the findings in domestic dogs. The slight difference in the occurrence of increased androgen levels of 2 and 6 weeks to toy poodles and standard poodles, respectively, may be due to differences in the dependence on seasonal cues in the neuroendocrine control of reproduction between wolves and dogs. The external seasonal "zeitgeber" for the timing of gonadal recrudescence and puberty in wolves is probably the photoperiod. In a primitive dog breed, the basenji, seasonal heat was experimentally shown to depend on the photoperiod (FULLER 1956). In another canid species, the silver fox, FORSBERG et al. (1989) could shift the seasonal spermatogenetic activity by photoperiodic manipulations. Thus, one may speculate that through appropriate photoperiodic stimulation the onset of puberty in wolves could be advanced by a few weeks leaving no temporal difference to domestic dogs.

In the literature, too, there are some notes concerning the onset of puberty in wolves during their first year. In 2 of 246 pups less than a year old from Alaska RAUSCH (1967) found Graafian follicles larger than 3 mm. One of 3 captive first-year females studied by

SEAL et al. (1979) came into heat and produced a litter, whereas the 2 others only showed elevated LH levels during January not accompanied by significant increases in ovarian activity. A report on vaginal bleeding, estrus, and breeding in several 9 and 10 month-old captive female wolves is given by MEDJO and MECH (1976). These authors also reported a 10 month-old captive male who sired a litter. Moreover, in the zoological garden at the Institut für Haustierkunde there were at least 2 pregnancies in first-year wolves during the last 40 years (unpubl. observ.). The two 10 month-old wolves included in chapter "Seasonality" of this study (see Fig. 1 day 319) contained numerous sperm in their epididymides (unpubl.). Thus, sexual maturation seems to be not uncommon in captive first-year wolves.

The early onset of sexual maturation in captive wolves clearly indicates that the genetic potential for an early puberty is inherent in this species. MEDJO and MECH (1976) suggested that nutritional and social factors (the animals were removed at an early age from their parents) were important factors for the early breeding in their wolves. The role of a nutritional, especially energetic regulation of puberty was discussed by SHORT (1976) and BRONSON and RISSMAN (1986). As to the social environment, the 3 young wolves studied here were hand reared and, therefore, inhibiting stimuli from their parents or other members of their family were precluded. Finally, it should be mentioned that the 3 young males did not show overt sexual behaviour during their first winter when, according to physiological criteria, they became sexually mature, whereas the standard poodles, although they were 6 weeks younger and lived in the same enclosure, did show activity (FEDDERSEN-PETERSEN, pers. comm.). In this mixed group the poodles clearly dominated and the lack of sexual behaviour in the wolves may have been due to suppression. Suppression of sexual behaviour in postpubertal males by social factors was recently shown in common marmosets (BAKER et al. 1999). Alternatively, one may suggest that a temporal dissociation between the physical and the mental events of puberty occurs in wolves. Under adequate nutrition physical puberty is reached in the first year. The behavioural development may need another year or more and may be importantly influenced by the social environment. Only under exceptional conditions (as in the case descibed by MEDJO and MECH 1976) sexual behaviour may develop in the first year and then result in reproductive activities in first-year males. The frequent use of sexual behaviour and actual reproduction as criteria would explain why in most sources 22 months was named for the onset of puberty. The essential effects of domestication on sexual maturation in *Canis lupus* would, then, seem to concern mainly the behavioural and less the physiological changes.

Acknowledgements

I thank Dr. DORIT FEDDERSEN-PETERSEN, Dr. EDGAR PAULKE, and Dr. CHRISTINE SCHLEIFENBAUM for collecting the blood samples from poodles and wolves, HEIDRUN LIESSEGANG, RENATE LÜCHT, and HEINRICH LUTTMANN for technical assistance, and Prof. Dr. EBERHARD NIESCHLAG, Münster, for the generous gift of testosterone antiserum.

This study is gratefully dedicated to late Prof Dr. Dr. h.c. WOLF HERRE, founder and for 30 years Head of the Institut für Haustierkunde.

Zusammenfassung

Vergleich einiger reproduktionsbiologischer Parameter bei Wolfs- und Haushundrüden.

In dieser Studie sollten Auswirkungen der Domestikation auf die Reproduktionsbiologie der Art *Canis lupus* durch den Vergleich einiger reproduktionsbiologischer Parameter von Haushund- und Wolfsrüden, die unter gleichen Bedingungen lebten, untersucht werden.

1. Bei Wölfen änderten sich die Konzentrationen der Androgene Testosteron (T) und 5α-Dihydrotestosteron (DHT) im peripheren Plasma und das relative Hodengewicht (Hodengewicht/Netto-Körpergewicht) in Abhängigkeit von der Jahreszeit. Maximalwerte dieser Parameter wurden im Winter, der Ranzzeit der Wölfe, gefunden. Bei Haushunden waren derartige saisonale Schwankungen nicht zu erkennen, die gemessenen Größen zeigten zu allen Jahreszeiten hohe Werte.

2. Ein allometrischer Vergleich der Hoden- und Nebenhodengewichte ließ keine Unterschiede zwischen den untersuchten Haushundrassen erkennen. Die Hoden- und Nebenhodengewichte stehen in fast isometrischer Abhängigkeit vom Körpergewicht. Bezogen auf die Werte von Wölfen während der Ranzzeit sind die Hoden und Nebenhoden der Haushunde um etwa 40% schwerer.

3. Messungen der T- und DHT-Konzentrationen im Plasma von 4 Großpudeln, 2 Zwergpudeln und 3 Wölfen während des ersten Lebensjahres zeigten deutliche Anstiege der beiden Androgene in der 28., 32. bzw. 34. Lebenswoche der jeweiligen Gruppe. Unter den gewählten Haltungsbedingungen wurden Pudel und Wölfe in annähernd gleichem Alter physiologisch geschlechtsreif.

Nach diesen Befunden hat sich die Domestikation in der Art *Canis lupus* auf den Beginn der physiologischen Geschlechtsreife nicht oder wenig ausgewirkt. Die Saisonalität der Fortpflanzung beim Wolf ist in der Domestikation der Fähigkeit zur Reproduktion in allen Jahreszeiten gewichen. Der Hoden als Bildungsstätte und der Nebenhoden als Speicher der Spermien sind bei der domestizierten Form um etwa 40% vergrößert.

References

Asa, C. S.; Valdespino, C. (1998): Canid reproductive biology: an integration of proximate mechanisms and ultimate causes. Am. Zool. **38**, 251–259.

Asa, C. S.; Mech, L. D.; Seal, U. S.; Plotka, E. D. (1990): The influence of social and endocrine factors on urine-marking by captive wolves (*Canis lupus*). Horm. Behav. **24**, 497–509.

Asa, C. S.; Seal, U. S.; Plotka, E. D.; Letellier, M. A.; Mech, L. D. (1986): Effect of anosmia on reproduction in male and female wolves (*Canis lupus*). Behav. Neural Biol. **46**, 272–284.

Aschoff, J. (1955): Jahresperiodik der Fortpflanzung bei Warmblütern. Studium gen. **8**, 742–776.

Baker, J. R. (1938): The evolution of breeding seasons. In: Evolution: Essays on Aspects of Evolutionary Biology. Ed. by G. R. Beer. Oxford: Clarendon Press. Pp. 161–177.

Baker, J. V.; Abbott, D. H.; Saltzman, W. (1999): Social determinants of reproductive failure in male common marmosets housed with their natal family. Anim. Behav. **58**, 501–513.

Beach, F. A.; Leboeuf, B. J. (1967): Coital behaviour in dogs. I. Preferential mating in the bitch. Anim. Behav. **15**, 546–558.

Beaver, B. V. (1977): Mating behavior in the dog. Vet. Clinics North Am. **7**, 723–728.

Benecke, N. (1994): Der Mensch und seine Haustiere. Die Geschichte einer jahrtausendealten Beziehung. Stuttgart: Theiss.

Bibikow, D. I. (1988): Der Wolf. Die Neue Brehm-Bücherei 587. Wittenberg Lutherstadt: Ziemsen.

Boitani, L.; Francisci, F.; Ciucci, P.; Andreoli, G. (1995): Population biology and ecology of feral dogs in central Italy. In: The Domestic Dog – its Evolution, Behaviour and Interaction with People. Ed. by J. Serpell. Cambridge: Univ. Press. Pp. 217–244.

Bronson, F. H. (1985): Mammalian reproduction: an ecological perspective. Biol. Reprod. **32**, 1–26

Bronson, F. H.; Rissman, E. F. (1986) The biology of puberty. Biol. Rev. **61**, 157–195.

Catling, P. C. (1979): Seasonal variation in plasma testosterone and the testis in captive male dingoes, *Canis familiaris dingo*. Aust. J. Zool. **27**, 939–944.

Catling, P. C.; Corbett, L. K.; Newsome, A. E. (1992): Reproduction in captive and wild dingoes (*Canis familiaris dingo*) in temperate and arid environments of Australia. Wildl. Res. **19**, 195–209.

Christie, D. W.; Bell, E. T. (1971): Some observations on the seasonal incidence and frequency of oestrus in breeding bitches in Britain. J. small Anim. Pract. **12**, 159–167.

Coppinger, R.; Coppinger, L. (1998): Differences in the behavior of dog breeds. In: Genetics and the Behavior of Domestic Animals. Ed. by T. Grandin. London: Academic Press. Pp. 167–202.

Corbett, L. K. (1995): The Dingo in Australia and Asia. Ithaca, London: Comstock/Cornell.

Darwin, C. (1875): The Variation of Animals and Plants under Domestication. 2nd. ed. London: John Murray.

Engle, E. T. (1946): No seasonal breeding cycle in dogs. J. Mammalogy **27**, 79–81.

Forsberg, M.; Fougner, J. A.; Hofmo, P. O.; Madej, M.; Einarsson, E. J. (1989): Photoperiodic regulation of reproduction in the male silver fox (*Vulpes vulpes*). J. Reprod. Fertil. **87**, 115–123.

Fox, M. W. (1978): The Dog. Its Domestication and Behavior. New York, London: Garland STPM Press.

Fuller, J. L. (1956): Photoperiodic control of estrus in the Basenji. J. Hered. **47**, 179–180.

Ginsberg, J. R.; Mcdonald, D. W. (1990): Foxes, wolves, jackals, and dogs: an action plan for the conservation of canids. Gland: International Union for Conservation of Nature and Natural Resources.

Haase, E.; Donham, R. S. (1980): Hormones and domestication. In: Avian Endocrinology. Ed. by A. Epple and M. H. Stetson. New York, London, Toronto, Sydney, San Francisco: Academic Press. Pp. 549–565.

Heptner, V. G.; Naumov, N. P. (Eds.) (1974): Die Säugetiere der Sowjetunion. Bd. 2: Seekühe und Raubtiere. Jena: VEB Gustav Fischer.

Herre, W.; Röhrs, M. (1990): Haustiere – zoologisch gesehen. 2nd. ed. Stuttgart, New York: Gustav Fischer.

Joffre, M. (1976): Puberté et cycle génital saisonnier du renard male (*Vulpes vulpes*). Ann. Biol. anim. Bioch. Biophys. **16**, 503–520.

Jones, E.; Stevens, P. L. (1988): Reproduction in wild canids, *Canis familiaris*, from the eastern highlands of Victoria. Aust. Wildl. Res. **15**, 385–394.

Keller, C. (1905): Naturgeschichte der Haustiere. Berlin: Paul Parey.

Kenagy, G. J.; Trombulak, S. C. (1986): Size and function of mammalian testes in relation to body size. J. Mammalogy **67**, 1–22.

Kleiman, D. G. (1977): Monogamy in mammals. Quart. Rev. Biol. **52**, 39–69.

Kruska, D. (1996): The effect of domestication on brain size and composition in the mink (*Mustela vison*). J. Zool. (London) **239**, 645–661.

Lentfer, J. W.; Sanders, D. K. (1973): Notes on the captive wolf (*Canis lupus*) colony, Barrow, Alaska. Can. J. Zool. **51**, 623–627.

Mech, L. D. (1970): The Wolf. Garden City, New York: The Natural History Press.

Medjo, D. C.; Mech, L. D. (1976): Reproductive activity in nine- and ten-month-old wolves. J. Mammalogy **57**, 406–408.

Novikov, G. A. (1962): Carnivorous Mammals of the Fauna of the USSR. Jerusalem: Program for Scientific Transl.

Pal, S. K.; Ghosh, B.; Roy, S. (1998): Dispersal behaviour of free-ranging dogs (*Canis familiaris*) in relation to age, sex, season and dispersal distance. Appl. Anim. Behav. Sci. **61**, 123–132.

Peters, G. (1993): *Canis lupus* Linnaeus, 1758 – Wolf In: Handbuch der Säugetiere Europas. Ed. by M. Stubbe und F. Krapp. Wiesbaden: Aula Vol. **5/I**, 47–106.

Price, E. O. (1984): Behavioral aspects of animal domestication. Quart. Rev. Biol. **59**, 1–32.

Rausch, R. A. (1967): Some aspects of the population ecology of wolves, Alaska. Am. Zool. **7**, 253–265.

Schmedemann, R. (1991): Zur Wirkung von Testosteron und Testosteron-Metabolismushemmern auf das Verhalten kastrierter Stockerpel (*Anas platyrhynchos* L.). Diss. Thesis, University Kiel.

Seal, U. S.; Plotka, E. D.; Packard, J. M.; Mech, L. D. (1979): Endocrine correlates of reproduction in the wolf. I. Serum progesterone, estradiol and LH during the estrous cycle. Biol. Reprod. **21**, 1057–1066.

Setchell, B. P. (1978): The mammalian testis. London: Elek.

Setchell, B. P. (1992): Domestication and reproduction. Anim. Reprod. Sci. **28**, 195–202.

Short, R. V. (1976): Definition of the problem. The evolution of human reproduction. Proc. Roy. Soc. Lond. B **195**, 3–24.

Sokal, R. R.; Rohlf, F. J. (1995): Biometry. 3rd ed. New York: W. H. Freeman and Company.

Tanner, J. M. (1962): Growth at Adolescence. Springfield/I1.: Charles C. Thomas.

Wiechering, G. (1981): Untersuchungen über den Epiphysenfugenschluß bei Wölfen und Haushunden. Schr. Arch.-Zool. Arbeitsgr. Schleswig-Kiel **5**, 1–68.

Wingfield, J. C.; Farner, D. S. (1975): The determination of five steroids in avian plasma by RIA and competitive protein-binding. Steroids **26**, 311–327.

Author's address: Prof. Dr. Eberhard Haase, Institut für Haustierkunde, Universität Kiel, Olshausenstr. 40, D-24118 Kiel, Germany (e-mail: ehaase@ifh.uni-kiel.de)