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Reproductive patterns in the domestic dog—A retrospective study of the Drever breed

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Abstract

The aim of this study was to examine the differences, between seasons of the year, in the distribution of matings and whelpings, litter size, pup deaths, and sex ratio in domestic dogs. Furthermore, we wanted to examine the effects of age and parity of the bitch at the time of whelping on litter size, as well as the effect of litter size on gestational length. A final aim was to investigate the fertility and frequency of whelping problems in a private kennel of Drever dogs. Data from the Swedish Kennel Club (SKK) registry for the Drever breed during 1995–2006, comprising a total of 2717 litters, were analyzed together with more detailed data from a private, professional kennel of Drevers, with a total of 285 matings and 224 whelpings, during the same time period. The most matings took place during winter, and the fewest during summer; consequently, most whelpings occurred during the winter and spring seasons. Of the 285 mated bitches, 78.6% whelped, 6.25% experienced dystocia, and 5.36% underwent Cesarean section. The pup death rate was 7.6%. The largest litters were born during spring. Litter size was negatively correlated with duration of pregnancy ($r = -0.18$). Each pup more than average caused a shortening of the gestation by 0.25 days, and each pup less a corresponding lengthening. Bitches giving birth to their first litter after 4 years of age produced a smaller litter than younger bitches. Litter size decreased after 5 years in all bitches. The number of born pups at the private kennel increased from the first to the third parity, then decreased. The number of registered pups increased from the first to the second parity in the SKK data and from the second to the third parity in the data from the private kennel, then decreased. Mating a bitch only once resulted in a smaller litter size. None of the studied factors had any effect on the sex ratio of the pups. There were significant differences between males in whelping rate among the mated bitches, but no difference in mean litter size, which indicates a female problem rather than a male one. Available data suggest that the domestic dog is still under considerable seasonal influence, although modified by ambient and management factors.

Keywords: Seasonality; Age; Parity; Fertility; Gestational length; Dystocia

1. Introduction

Despite a long history of cohabitation between humans and dogs (*Canis familiaris*), there are still many aspects of canine reproduction that are not well understood. Domestication of the dog from its ancestor, the wolf, is thought to have occurred at least 14,000 years ago [35], although recent research using molecular genetic tools indicates that it may have started as early as around 40,000 years ago. Changes that have occurred over time have been profound, from the diversity of body size and shape (from that of the

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wolf to the 1.5 kg Chihuahua and the 100 kg or more giant breeds of dogs) and of behavior, food intake, etc., to the reproductive pattern [31]. The wolf is a seasonal breeder, the female having only one estrous period per year, from January to March, during which the male also produces spermatozoa. By contrast, domestication has led the domestic dog to undergo cycles twice or sometimes even three times per year, while the males are fertile throughout the year [28]. The reproductive pattern of the canids is different from that of other mammalian species and a better understanding of these differences would be of value to enable us to determine such factors as the regulation of onset of estrus, and the factors that influence the recognition of pregnancy, the duration of gestation, the timing of parturition in the bitch, and the litter size. The dog is also used as a model for research in humans and other species. A better understanding of the differences in reproductive function would, therefore, also be of importance in comparative studies.

Domestic dogs are traditionally considered to be nonseasonal breeders. A major difference between the dog and the noncanid mammalian species is that in dogs, each estrous period is followed by a long interestrous interval (diestrus and anestrus, or sexual quiescence), and their reproductive pattern is, therefore, described as monocyclic [14]. Although a number of studies have been published on the effects of factors such as breed, age, parity, and litter size on the length of the interestrous period and duration of gestation in the bitch, e.g. refs. [5,8,10,26] and on effects of season of the year on the reproductive pattern, e.g. refs. [5–7,20,24,28,30,32], results have been contradictory.

Due to the peculiar reproductive pattern of the dog, and the great individual variation, especially in cyclicity among bitches, but also in reproductive function among males, research aiming to study factors that influence the reproductive functions in this species needs to encompass a large number of individuals, and in order to avoid bias from variations in climate between years it should also preferably cover a period of several calendar years. Breed differences in fertility have also been described [18,19]. The present study, however, focuses on reproduction in one breed over several years.

Information from kennel club registries is usually only available for matings that were successful, resulting in the birth of a litter of pups. Litters are usually registered at 4–8 weeks of age. Only rarely are a breeder's more detailed kennel records available for research purposes. In addition, dog breeding in Scandinavia is usually a hobby, and few breeders have more than a few animals at any one time. For this study, however, we had access to the kennel records for a 12-year period of a private, professional breeder of Drevers, a Swedish hunting dog. We also obtained all the data recorded at the Swedish Kennel Club (SKK) for this breed over the same time period. The Drever has the same pattern of producing more litters during the winter and spring than during the other seasons as previously shown to be the case for the vast majority of the dog breeds in Sweden [37], the exceptions being some of the breeds that are well known to be seasonal breeders (autumn breeders), in particular the Basenji [13], and to a certain degree also some of the primitive Spitz breeds such as the Chow Chow [32,37].

The aims of this study were to define differences between seasons of the year regarding the distribution of matings and whelpings, frequency of dystocia and Cesarean section, litter size, pup deaths, and sex ratio of pups. Also, we wanted to study the effects of age and parity of the bitch at the time of whelping on litter size, as well as the effect of litter size on the length of gestation, and differences in fertility among the males of the Drever breed.

2. Materials and methods

2.1. Animals

The Drever is a short-legged scent hound, with an ideal height at withers of 35 cm for the male and 33 cm for the bitch, and with a body weight of between 10 and 15 kg. This retrospective study is based on the records of the data for all litters of the Drever breed that were registered at the SKK during 1995–2006 (SKK data) (http://www.skk.se). In addition, more detailed information about all matings and whelpings, including the incidence of dystocia, at one private, professional kennel of Drevers (private kennel data) during the same 12-year period was also analyzed. All the acquired data from the private kennel was verified in the SKK database.

Feeding and housing varied for the dogs in the SKK data, many living as family dogs, but were uniform at the private, professional kennel. These dogs were kenneled in separate pens, 1.5 m × 1.5 m to 1.5 m × 3 m, with free access to individual runs of 1.8 m × 11 m, and with 1–2 h daily exercise in a 70 m × 70 m run. They were fed Priima dog food (Priima Hundfoder, Örby, Sweden) twice daily, and had access to water ad libitum. Daylength in Sweden varies over the year, and from north to south, the extreme being the midnight sun in summer and total darkness during winter north of the polar circle. In the middle parts of

Sweden the shortest days are 6 h in winter, and the longest 18 h in summer, but then there is no real night, just dusk. The dogs in this study were kept under the same lighting conditions as their owners. During the winter season this means that most of them were exposed to artificial light from around 6 a.m. until 10 p.m.

The SKK data set contained information on the registered names and SKK registration numbers of each male and female dog, the dates of their birth, the dates of birth of each litter, and the number of registered male and female pups. It did not, however, provide any information about the estrous cycles during which the bitches were not mated, or were mated but did not produce a litter of pups, or the actual dates of the matings, any problems during parturition, or the number of born and dead or euthanized pups, as this information is not routinely registered in the SKK database. Therefore, neither the whelping rates nor gestational length, cases of dystocia, Cesarean sections, or actual litter sizes at the time of birth could be calculated for these litters.

The private kennel data set consisted of the registered names and SKK registration numbers of each male and female dog, the dates of their birth, the date of mating(s) (one or more), the date of whelping(s), cases of dystocia and of Cesarean section, the number of pups born in each litter, the number of dead or euthanized pups, and the number and sex ratio of pups registered with the SKK. Only those sets of data for which all the information was available were included in this study. No information was, however, available for the estrous cycles during which the bitches were not mated.

The data from the private kennel is included in the SKK data set, which represents the total data for the Drever breed in Sweden, except in the part of this study that deals with a comparison of the data from the private kennel and the mean from all other breeders of Drevers that had registered litters with the SKK during the time period 1995–2006.

2.2. Statistical analyses

The data was analyzed using SAS (SAS, Inc., Cary, NC, USA). The General Linear Model (GLM) procedure was used to analyze and test the significance of different effects in the models, and Chi-squared test was used for comparing differences between seasons in number of matings and whelpings. The results are given as overall means ± standard deviation (S.D.) or least squares means (LSM). $p < 0.05$ was set as the level of significance. The basic statistical models included year and season of whelping, and parity number or age of the bitch at the time of whelping.

2.2.1. Differences between years and seasons of the year

The effect of the year and season during the period 1995–2006 on the number of whelpings and on the number of registered pups was analyzed in both data sets, and for the private kennel the number of matings, the duration of pregnancy, litter size at the time of birth, and number of dead pups were also analyzed.

The months were grouped into four seasons: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November).

In both sets of data, the sex ratio of all registered pups at the time of registration was also analyzed.

2.2.2. Effect of the age of the bitch

The effects of the age of the bitch on litter size and number of registered pups were analyzed in both sets of data. The effect of age of the bitch at the time of the first whelping was calculated separately in both data sets. These data were then also included in the calculations of the effects of the age of the bitch on the number of registered pups in all the whelpings.

For the statistical calculations, the age of the bitch at the time of having its first litter was categorized into the following groups: bitches up to 2 years of age, bitches from 2 to 3 years of age, and so forth.

When the data for all the whelpings were analyzed, the age of the bitch was categorized in the same way. In the model for all litters, parity was not included due to confounding with age.

2.2.3. Effect of the parity of the bitch

The effect of parity on the number of registered pups was studied in the SKK data. In the data from the private kennel, the effect of parity on the duration of pregnancy, litter size, pup death rate, and number of registered pups was studied. The whelpings were grouped into parities 1–5. The parity 5 group also included the few whelpings in higher parities.

2.2.4. Effect of number of days between the first and the last mating in each estrous cycle

In order to study the effects of the number of days between the first and the last mating in each estrous cycle on whelping rate, duration of pregnancy, and litter size in the private kennel, the data was categorized into six groups, as follows:

- 0—only one mating.
- 1—one day between the first and the last mating.
- 2—two days between the first and the last mating.
- 3—three days between the first and the last mating.
- 4—four days between the first and the last mating.
- 5—five or more days between the first and the last mating.

In this analysis, year, season, age or parity at whelping, and number of days between the first and the last mating were included in the model. The effect of one versus several matings was also analyzed (group 0 compared with groups 1–5 together).

2.2.5. Gestational length

At the private kennel, to calculate the duration of pregnancy, the date of the mating, or of the last mating when bitches were mated several times during the estrous period, was used as day 1, and the registered date of birth was used as the last day of pregnancy. In this analysis, year, season, parity, and litter size at birth were included as covariates in the model.

2.2.6. Comparison between the private kennel and the Swedish Kennel Club data

All the data that were provided in both data sets were compared to find similarities and differences between the private kennel data as a model (sample) of the SKK data. Differences in the effect of year and season, as well as the effects of age and parity of the bitch at the time of whelping, on the number of registered pups were studied. The differences in the frequencies of whelpings during different seasons were also studied.

For the comparisons of the results in the private, professional kennel data with those of all other Drever breeders in the SKK data set, the data from the studied kennel was excluded from the SKK data. The effect of year, season, and parity on the number of registered pups was analyzed.

2.2.7. Effect of the male dog

Only the male dogs that had performed 10 matings or more at the private kennel during the 12-year period were used to study male effects on whelping rate and litter size. The model when analyzing litter size included year and season of whelping, parity, and the male dog.

3. Results

3.1. Animals

The descriptive data for the SKK and the private kennel are given in Table 1. Most of the bitches had two estrous periods per year.

3.1.1. Differences between years and seasons of the year

The number of registered pups differed between years in the SKK data ($p < 0.001$). This difference was not observed at the private kennel. There were significant differences in the distribution of matings between seasons (at the private kennel) ($p < 0.001$), with the most matings taking place during the winter and the fewest during summer (Fig. 1). Consequently, there were also significant differences between seasons in the distribution of whelpings. These differences were more pronounced in the SKK data ($p < 0.001$) than at

Table 1
Descriptive data from the Swedish Kennel Club (SKK) and the private kennel for the Swedish Drever breed during 1995–2006

SKK data		Private kennel
Number of female dogs	1665	113
Number of male dogs	668	31
Number of matings	Not available	285
Number of whelpings	2717	224
Whelpings per year (range)	226.4 (159–310)	18.7 (13–26)
Whelping rate (%)	Not available	78.60
Dystocia (%)	Not available	6.25
Caesarean section (%)	Not available	5.36
Number of first whelpings	1416	71
Total number of pups born	Not available	1525
Number of pups per litter (range)	Not available	6.81 ± 2.11 (1–12)
Number of dead pups per litter (range)	Not available	0.90 ± 1.23 (0–7)
Number of registered pups per litter (range)	5.00 ± 2.31 (1–12)	5.91 ± 2.11 (1–10)
Duration of pregnancy (days) (range)	Not available	61.48 ± 2.24 (56–72)
Male pups at the time of registration (%)	50.5	49.6

Data are given as means ± standard deviation (S.D.) (range).

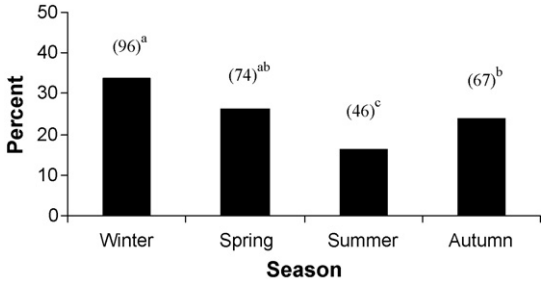

Fig. 1. The distribution of matings by season at the private kennel. The number of matings is given in parentheses. Different superscript letters denote significant differences.

the private kennel ($p = 0.015$) (Fig. 2). Whelping rates in the private kennel were 75.0% for the matings done in the winter season, 79.7% in spring, 78.3% in summer and 82.1% in autumn. The differences were not significant. However, there were significant differences in litter size and number of registered pups between seasons in the private kennel (Fig. 3), with the largest litters being born during the spring and, consequently, more pups registered from those litters. By contrast, no such difference was observed for the number of registered pups in the SKK data. No differences were found in duration of pregnancy between seasons at the private kennel.

The sex ratio among registered pups in both sets of data was similar, the percentage of male pups being 50.5% in the SKK data and 49.6% in the data from the private kennel (Table 1). No significant effect of year, season, or age or parity of the bitch at the time of whelping was found on the sex ratio at the time of registration.

The frequencies of dystocia (6.25%), Cesarean section(5.36%) and pup deaths (7.6%) in the private kennel were too few to study differences in the basic statistical model.

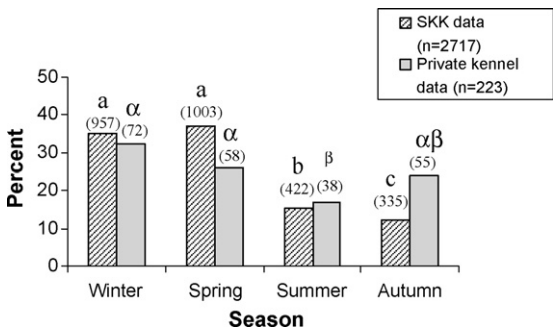

Fig. 2. The distribution of whelpings by season in the Swedish Kennel Club (SKK) data set and at the private kennel. The number of whelpings is given in parenthesis. Different letters (SKK data latin; Private kennel greek) denote significant differences.

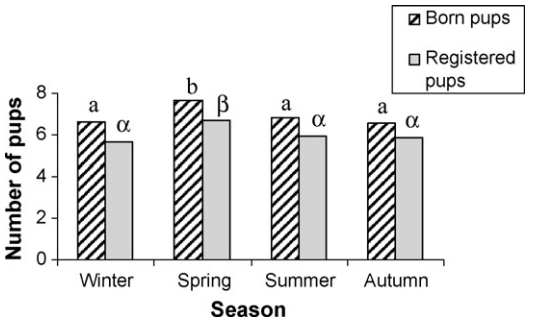

Fig. 3. Number of born and of registered pups per litter (least square means, LSM) by season at the private kennel. Different letters (born pups latin; registered pups greek) denote significant differences.

3.1.2. Effect of the age of the bitch

The numbers of first whelpings and the total number of whelpings in both data sets, grouped by the age of the bitch at the time of whelping, are given in Tables 2a and 2b. Significant effects of the age of the bitch at the time of both the first whelping and all whelpings on the number of registered pups were found in the SKK data. A significantly lower number of registered pups was observed among bitches that were 4 years of age or older when they whelped for the first time. The mean number of registered pups per first born litter for bitches up to 4 years of age was 5.19, compared with 4.70 registered pups per litter for bitches that were >4 years old (Table 2a). Among all the whelpings, a significant decrease in number of registered pups per litter was observed after 5 years of age in the SKK data (Table 2b). The mean number of registered pups per litter in 4–5-year-old bitches was 5.18 and this decreased to 4.24 pups per litter in bitches that were >7 years old. No such differences were observed at the private kennel (Tables 2a and 2b).

3.1.3. Effect of the parity of the bitch

Numbers of whelpings and litter size and the number of registered pups, grouped by parity, are given in Table 3. Parity was found to have a significant effect on the number of registered pups in both sets of data, and at the private kennel also on the litter size at birth. Litter size at the time of birth, and the number of registered pups increased slightly from the first to the third parity at the private kennel ($p = 0.004$), and the number of registered pups increased with the second parity in the SKK data ($p < 0.001$), and then decreased (Table 3).

3.1.4. Effect of number of days between the first and the last mating in each estrous cycle

At the private kennel, a variety of mating schedules was practiced, from only one mating to multiple matings with different numbers of days between the first and the

Table 2a
Number of whelpings and registered pups from the first whelping, grouped by the age of the bitch at the time of whelping in the Swedish Kennel Club (SKK) database and in the database of the private kennel, and in the private kennel data also including the litter size (least square means, LSM)

Age of the bitch at the time of giving birth to the first litter (years)	SKK data		Private kennel data		
	Number of whelpings	Number of registered pups	Number of whelpings	Number of born pups	Number of registered pups
≤2	161	5.11[a]	28	6.24	5.18
>2–3	311	5.18[a]	28	6.30	5.25
>3–4	354	5.19[a]	14	5.44	4.30
>4–5	294	4.70[b]	0	–	–
>5–6	181	4.00[c]	0	–	–
>6 to >7	115	3.62[c]	0	–	–

Different superscript letters (a–c) denote significant differences

last mating (Table 4). No effect was found of the number of days between the first and the last mating on the litter size or on the number of registered pups. Mating only once, however, resulted in a 0.52 pups smaller mean litter size at birth and 0.68 fewer registered pups compared with all the other mating schedules analyzed together ($p < 0.05$). The duration of pregnancy was significantly affected when the time from the first to the last mating was 5 days or more (Table 4).

3.1.5. Gestational length

At the private kennel, the litter size at birth was found to have a significant negative correlation with the duration of pregnancy ($p < 0.001$) ($r = -0.18$). With the number of born pups included in the model as a regression, each extra pup above the mean number caused a shortening of the gestation period by 0.25 days, and each pup less increased it by 0.25 days. The duration of pregnancy was also found to be significantly affected by the number of days between the first and the last mating in each estrous cycle ($p < 0.001$). Neither year, nor season, age, or parity of the bitch was found to influence the duration of gestation.

3.1.6. Comparison between the private kennel and the Swedish Kennel Club data

A comparison between the SKK and the private kennel data demonstrated some differences. In the SKK data, an effect of the age of the bitch at the time of whelping on the number of registered pups could be seen ($p < 0.001$), while no such effect was observed in the private kennel data. In the SKK data, the mean number of registered pups per litter was independent of season, but at the private kennel, a difference between seasons in the mean number of born and registered pups per litter was found. Parity had a significant effect on number of registered pups in both data sets, but was more pronounced in the SKK data. Although there were significant differences in the frequency of whelpings between seasons also at the private kennel ($p = 0.015$), this difference was less pronounced than in the SKK data ($p < 0.001$).

Table 2b
Number of whelpings and number of registered pups for all the whelpings, grouped by the age of the bitch at the time of whelping in the Swedish Kennel Club (SKK) database and in the database of the private kennel, and in the private kennel data also including the litter size

Age of the bitch at the time of giving birth, for all litters (years)	SKK data		Private kennel data		
	Number of whelpings	Number of registered pups	Number of whelpings	Number of born pups	Number of registered pups
≤2	167	5.09[a]	29	6.04	5.04
>2–3	381	5.38[a]	43	6.74	6.08
>3–4	519	5.38[a]	48	6.86	5.69
>4–5	527	5.18[b]	33	6.93	6.16
>5–6	463	4.86[c]	35	7.38	6.61
>6–7	323	4.48[c]	31	6.82	6.03
>7 to >8	337	4.24[d]		Included in 7	

Data are given as least square means (LSM). Different superscript letters (a–d) denote significant differences. The number of bitches in the private kennel that were more than 8 years old at the time of whelping were few, and therefore included in the age group >6–7 years.

Table 3
Number of whelpings, litter size, and number of registered pups, grouped by parity of the bitch, in the Swedish Kennel Club (SKK) database and in the private kennel

Parity number	SKK data		Private kennel		
	Number of whelpings	Number of registered pups	Number of whelpings	Number of born pups	Number of registered pups
1	1416	4.82[a]	71	6.09[a]	5.22[a]
2	669	5.34[b]	61	7.16[b]	6.19[a]
3	326	5.20[b]	37	7.31[b]	6.41[b]
4	189	5.05[ab]	32	7.02[b]	6.26[a]
≥5	117	4.80[ab]	20	7.02[ab]	6.06[a]

Data are given as least square means (LSM). Different superscript letters (a and b) denote significant differences.

Comparing the results in the private kennel with the results of all the other breeders that had registered litters of Drevers in the SKK database (excluding the results from the private kennel), a significant difference was found in the mean number of registered pups per litter ($p < 0.001$), with a larger mean litter size at the private kennel (5.87 pups compared with 4.93 pups for all the other breeders). The number of registered pups increased at the second parity in both data sets.

3.1.7. Effect of the male dog

Whelping rates among the mated bitches and litter sizes for the 10 male dogs at the private kennel that performed more than 10 matings during the 12-year study period are given in Table 5. There were significant differences in resulting whelping rates between the males ($p = 0.003$). Three of the males (Nos. 1, 3, and 6) had a lower than normal whelping rate [9,11,24], but no difference in mean litter size compared with the other seven dogs (Table 5).

4. Discussion

The present study provides data concerning the reproductive pattern of the Swedish dog breed the Drever, which is known not to be strictly seasonal like the Basenji [13], or an autumn breeder like some of the primitive Spitz breeds [32,37].

The difference between the studied years in number of registered pups mirrors the changes in popularity of this breed over time, which was reflected in the SKK data, but is not evident from the data of the professional kennel. The reason for this discrepancy is most likely that the private, professional breeder has a constant demand for all the pups he produces, while smaller and newer hobby breeders will suffer when there is a decrease in popularity for a breed. This is probably also the reason for the somewhat less pronounced variation in frequency of whelpings by season at the private kennel.

It was not possible to obtain information about all the estrous cycles, only those during which the bitches in the private kennel were mated, successfully or unsuccessfully, and only about the successful matings in the SKK data base. In the present study the frequencies of matings and whelpings varied significantly between seasons. In both data sets, more litters were produced in winter and spring. This may to a degree be due to that the breeders chose to mate more bitches in winter and spring because of a higher demand for pups that are born early in the year and can be raised and housetrained during the summer, and begin the

Table 4
Number of whelpings, grouped by number of days between the first and the last mating, number of born and of registered pups per litter, and duration of pregnancy at the private kennel

Number of days between the first and the last mating	Number of whelpings	Number of born pups	Number of registered pups	Duration of pregnancy (days)
0	36	6.33[a]	5.31[a]	61.0[a]
1	19	24[b]	6.81[b]	60.6[a]
2	77	6.90[b]	6.09[b]	61.2[a]
3	39	7.00[b]	6.03[b]	61.5[a]
4	28	6.81[b]	5.84[b]	61.9[a]
≥5	22	6.50[b]	5.5[b]0	63.1[b]

Data are presented as least square means (LSM). Different superscript letters (a and b) denote significant differences.

Table 5
Number of matings and whelpings, and resulting whelping rates among the mated bitches (%) and litter sizes for the 10 male dogs at the private kennel with more than 10 matings during 1995–2006

Male dog number	Number of matings	Number of successful matings	Whelping rate (%)	Litter size
1	10	5	50.0[b]	7.40
2	10	9	90.0[a]	7.25
3	11	7	63.6[b]	6.35
4	12	12	100.0[a]	6.63
5	13	13	100.0[a]	6.75
6	17	8	47.1[b]	7.70
7	25	21	84.0[a]	6.40
8	35	28	82.4[a]	7.31
9	36	30	83.3[a]	6.12
10	39	32	82.1[a]	6.09

Data are presented as least square means (LSM). Different superscript letters (a and b) denote significant differences.

training to hunt during the autumn and winter. However, although most bitches, also those in the present study, cycle twice a year, there are several studies [7,20,28,32] demonstrating that more bitches are actually coming into estrus during the winter and spring than during autumn, and especially compared with summer. This observed seasonal pattern is in accordance with that of the dog's ancestor, the wolf, with a reproductive period from January through March in this part of the world, and is probably a vestige of the more strict seasonality of the species.

Previous studies of the effects of season on the cycle and reproductive pattern of the bitch [5–7,20,24,28,30,32] show conflicting results. Bouchard et al. [5], studying 67 colony bitches during 210 estrous cycles over 4 years, found that the overall probability that an estrus would occur at any month of the year was the same for each month. Also, Sokolowski et al. [30], studying 57 bitches in seven breeds, found no influence of season on estrous frequencies by month of the year. In Kenya, south of the equator, a higher frequency of bitches was in estrus during October and a lower frequency in April. However, the authors of that study could not confirm seasonality and only suggested that the peak and nadir of estrous events were in those two months, depending on locality and on the month in which some bitches attained puberty, which is connected with other factors, such as nutrition, breed, and/or poor estrous observations [24]. By contrast, Christie and Bell [7], studying 1561 cycles in 449 privately owned bitches of 40 breeds of dogs in the UK, found a significantly higher estrous frequency in the period from February to May, compared with June to September ($p < 0.001$) and October to January ($p < 0.01$). Similarly, Tedor and Reif [32], studying 87,880 litter registrations in the USA, observed a distinct, repetitive seasonal distribution of births, with a primary peak in the spring and early summer, like in the present study. Most births in their study occurred in May, and the authors ascribed this pattern to human intervention as well as to genetic factors and environmental conditions. This conclusion is in line with the findings of Linde-Forsberg and Wallén [20]. Compiling data from 319 interestrous intervals in 36 Beagles, 36 German Shepherd dogs, and 20 Labrador Retrievers in Sweden, these authors found that there was an influence of season in the Beagles which were kept as a colony and housed outdoors without heating or supplementary light. The authors noted a peak of cycles in the Beagles in May, but no obvious seasonal influence in the other two breeds that were kept as family dogs. It has been commonly observed that bitches housed together tend to synchronize their estrous periods, which may contribute to a seasonal accumulation of bitches in estrus. Another factor that was found to influence the estrous frequency was whether the bitches had given birth to and nursed a litter of pups in the preceding cycle, something that prolongs the interestrous interval by 4–8 weeks [5,7,20,24]. In Thailand, the conditions of the rainy season, during September, have been reported to have a positive effect on conception and lead to the highest whelping rate [6].

Litter size, too, has been said to be influenced by climate factors such as temperature and humidity [6], which is in agreement with the results of the present study, proving significant differences between seasons in litter size and number of registered pups, with the lowest numbers in summer. No differences in litter size were found between the months of the year in German Shepherd bitches in Africa over a 15-year period [24,25], while in the present study such differences were found during the 12-year period at the private kennel, but not in the SKK data. These differences most likely reflect a more directed and professional breeding effort by the private kennel, compared with average breeders.

In Mexico, an increase in the incidence of bitches in estrus was seen in December [28]. Also, it was observed that temperature and humidity can markedly increase fetal losses during summer [27], which is in agreement with our findings. The study concluded that stray dogs in Yucatan are not true seasonal breeders, but their reproductive pattern is modified by environmental factors, such as temperature, humidity, and, probably, photoperiod. Others have suggested that high temperature and substantial rainfall in the tropical zone may reduce serum testosterone concentrations in dogs, which can influence fertility in male dogs under such conditions [22]. The study, however, comprised a relatively small number of dogs, which made it difficult to detect significant seasonal differences. Hossein et al. [12] flushed Fallopian tubes to collect in vivo-matured canine oocytes for assisted reproductive technology (ART) by laparotomy from 124 bitches, and found a seasonal influence on number of corpora lutea, being highest in the spring (March–May), with no difference between the other three seasons. The authors also retrieved significantly more oocytes per bitch during the spring compared with winter (December–February). Supporting these findings are those of the present study and also the observation that more artificial inseminations (AIs) are being performed during winter and spring than during summer [17]. In one study, AIs that were done during summer resulted in a lower conception rate [17]. In the present study, the largest litter size and number of registered pups were also observed in the optimal season for taking care of a litter, i.e. spring, at the private kennel. Such variation was not found in the SKK data, probably due to being disguised by the variety in husbandry and breeding management between the different smaller kennels.

Consequently, data suggest that the domestic dog is still under considerable seasonal influence, with a tendency to cycle during what would be the most favorable time of the year in the wild, providing the best climate and the best supply of food for raising a litter. Daylight, climate, environment, and management factors such as housing, exercise, feeding and mating procedures are modulating this tendency of seasonality.

The present study also found effects of age and parity of the bitch at the time of whelping, on litter size. At the private kennel, the data for first litters could not be analyzed statistically because there was too little variation in the bitch's age at whelping the first litter, i.e. most bitches were mated the first time at around the same age, but in the SKK data, a large variation was found (and the 1416 first litters could be compared with all 2717 whelpings). Previous studies have found an association between the reproductive ability and age of the bitch, and the length of the anestrous period, which increased in the older bitches. Also, a decrease in the conception rate and litter size has been reported with increasing age [1,2,24,25,34], the latter being in accordance with our findings. Effects of parity on number of registered pups per litter were found in both sets of data, with slight differences between them. The main reason for these differences could be a tendency to breed the bitches at an earlier age, and more often during their most fertile period of life, at the private, professional kennel, compared with most other kennels in Sweden. One study suggests that parity can have an effect on litter size, but not before the fifth whelping, and that reproductive efficiency declines in German Shepherd bitches after 6 years of age [25]. This is the first study to report on differences in litter size, depending on the age and parity of the bitch at the time of whelping before the fifth parity.

The number of days between the first and the last mating per cycle in the present study had no influence on litter size. Mating only once, however, resulted in a smaller litter size, compared with all other mating schedules. This is in accordance with the findings of Linde-Forsberg and Forsberg [19] that the pregnancy rate was significantly higher in bitches inseminated twice with fresh semen than in those inseminated once, and Thomassen et al. [33], that two inseminations yielded a higher mean litter size (6.0 ± 0.2) than one (5.1 ± 0.2). In a previous publication [29], effects of day of mating and gestational length on reproductive efficiency were examined. Surprisingly, it was found that mating 7 days after the luteinizing hormone (LH) peak resulted in a significantly longer gestation period compared with matings performed earlier, i.e. 3 or 5 days after the LH peak. However, few animals were used in each treatment group, and the authors did not consider the possible effect of the variation in litter size between groups on gestational length. The litters from matings on day 7 were the smallest, which may have resulted in a longer gestation.

This is a retrospective study and the bitches had not been tested for LH or progesterone levels before mating. Gestation length was therefore calculated from the last day of mating, to reduce much of the variation (Table 4). Litter size was found to influence the duration of pregnancy, by each single pup more, or less, than the average litter size, with a significantly shorter gestation period in the larger litters and significantly longer in the smaller litters. This finding is in agreement with, but more precise than, previous studies showing that a litter size of four or fewer than four pups prolongs gestation by 1 day compared with larger litters [10], and that

duration of pregnancy was longer for bitches pregnant with one or two pups compared with larger litters [33]. In one study of 152 bitches of 39 breeds [38], bitches were divided into three groups by litter size (small, average, and large) within breed. Results showed that the group with small litter size for the breed had a significantly ($p < 0.001$) longer gestation period than the groups of bitches whelping a litter of average or large size. Okkens et al. [26], studying 113 bitches of six breeds, also found a negative correlation between litter size and gestational length ($r = -0.73$; $p = 0.03$) for litters comprising $\leq$13 pups, but suggested that the breed was the major determinant of the duration of pregnancy. In our study in the Drever breed, we could in fact demonstrate a within-breed difference in duration of pregnancy being 0.25 days shorter per extra pup above average, and a corresponding 0.25 days longer pregnancy for each pup less. In contrast to the above findings and to our findings in the Drever breed, however, several previous studies on a variety of other breeds of dogs found no influence of litter size on gestational length [15,16]. The different results may be due to the considerably higher number of observations in our study, but there may possibly also be differences between breeds. A previous study of the influence of parity on the duration of gestation found that only bitches with nine pregnancies were more likely to have a longer gestation [10]. The study included only five bitches with this parity, and the authors suggested that the small sample size made this estimate unreliable. In the present study with a large number of observations, no effect of parity on gestational length was found.

The percentage of male pups of 50.5% (SKK data) and 49.6% (private kennel) in the present study is in agreement with the average ratio of 50.6% male pups previously reported by Tedor and Reif [32], although these authors observed considerable differences between breeds. We found no effects of year, season, or age or parity of the bitch at the time of whelping on the sex ratio of the pups, which also is in accordance with the findings of Tedor and Reif [32].

A comparison between the larger SKK data for the Drever breed and the data of the private kennel showed many similarities, and proved that the private kennel data can serve as a model (sample) of all Drever data in the country for the parameters that were not available in the SKK registry, i.e. matings that did not result in a litter of pups, the date(s) of the matings, litter size at birth, and, possibly, dystocia. However, there were some differences between the data sets, notably a more consistent way of breeding from the bitches in the professional kennel, in the age when bitches are mated for the first time, in the interval at which they are bred during their most fertile years, in selecting for the best producers, and, probably, in having a better surveillance of the heat periods and matings. In addition, the breeder at the private kennel uses a fresh, frozen food originally developed for farmed mink and modified for dogs, and claims that when he introduced this many years ago, the litter size increased by one pup on average also in the other breeds of this kennel. A comparison of the SKK data and the private kennel data for the Jämthund breed during the same 12-year period showed that the mean litter size for this breed in the SKK database (3040 litters) was 6.32 registered pups, compared with 7.25 pups (64 litters) in the private, professional kennel. The findings in these two breeds are therefore consistent, and the larger mean litter sizes in the private, professional kennel may be the result of better kennel management, and selection of breeding stock.

The mean duration of pregnancy, of 61.48 ± 2.24 days, calculated from the last day of mating, shows that the bitches in the private kennel in general were mated on the optimal days during estrus, 2 days after ovulation [8,14,15,21]. The longer pregnancy resulting from mating the bitches over 5 or more days shows that these matings started too early during the estrous period. The resulting whelping rate of 78.6% is close to the expected normal range of 80–95% [9,11,24]. The incidence of dystocia (6.25%) and of Cesarean sections (5.36%) in the present study are at the estimated average level for dogs in general [36], and within the 5–10% found in two previous studies in the Drever breed (K. Andersson, personal communication). They are low compared with the 16% reported in the Swedish insurance company, AGRIA's, database on ~200,000 bitches of different breeds [3]. The pup death rate in the private kennel was 7.6%, which is low compared with previous reports of 11.6–11.9% among Swedish breeders [18,19] and 10–30% reported by Mosier [23]. The pup death rate was also too low to detect any effects of year, season, or parity of the bitch.

Three male dogs achieved a lower than normal whelping rate [9,11,24] among the mated bitches. Although no semen samples were examined from these males, the fact that they had no difference in mean litter size compared with the other seven males with normal fertility makes it probable that the low fertility of these males may have been due either to a variation in their semen quality over time or, more likely, to female factors, for instance, low fertility of the bitch or management factors, such as mating on the wrong day of the cycle. Beuing et al. [4], analyzing large data sets

from 14 breeds in Germany (for some breeds data from up to 25 years), found that the genetic male effect on the conception rate was negligible and the permanent, nongenetic effect low, and that the influence of the male partner on litter size was near zero in nearly all breeds. This is in accordance with the present study, although we used a comparatively small sample size.

In conclusion, the results of our study support those earlier publications that claim a certain remaining seasonal pattern of reproduction in the domestic dog. Furthermore, they suggest that this pattern is modified by a number of environmental and management factors that are not yet well understood. The superior results in the private kennel may be due to good management, with a more consistent way of selecting, feeding and breeding the dogs. Age and parity of the bitch affects litter size, and litter size influences gestational length. If kennel clubs would register more details about the breedings, much valuable information could be obtained concerning canine reproductive physiology and pathology in the future.

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