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Llibertat Tusell, Ingrid David, Loys L. Bodin, Andres Legarra, O. Rafel, et al.. Using the product threshold model for estimating separately the effect of temperature on male and female fertility. *Journal of Animal Science*, 2011, 89 (12), pp.3983-3995. 10.2527/jas.2011-3924 . hal-02643845

HAL Id: hal-02643845

<https://hal.inrae.fr/hal-02643845>

Submitted on 28 May 2020

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JOURNAL OF ANIMAL SCIENCE

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J ANIM SCI 2011, 89:3983-3995.

doi: 10.2527/jas.2011-3924 originally published online July 15, 2011

The online version of this article, along with updated information and services, is located on the World Wide Web at:

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Using the product threshold model for estimating separately the effect of temperature on male and female fertility¹

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ABSTRACT: Animals under environmental thermal stress conditions have reduced fertility due to impairment of some mechanisms involved in their reproductive performance that are different in males and females. As a consequence, the most sensitive periods of time and the magnitude of effect of temperature on fertility can differ between sexes. The objective of this study was to estimate separately the effect of temperature in different periods around the insemination time on male and on female fertility by using the product threshold model. This model assumes that an observed reproduction outcome is the result of the product of 2 unobserved variables corresponding to the unobserved fertilities of the 2 individuals involved in the mating. A total of 7,625 AI records from rabbits belonging to a line selected for growth rate and indoor daily temperature records were used. The average maximum daily temperature and the proportion of days in which the maximum temperature was greater than 25°C were used as temperature descriptors. These descriptors were calculated for several periods around the day of AI. In the case of males, 4 periods of time covered different stages of the spermatogenesis, the transit through the epididymus of the sperm, and the day of AI. For

females, 5 periods of time covered the phases of pre-ovulatory follicular maturation including day of AI and ovulation, fertilization and peri-implantational stage of the embryos, embryonic and early fetal periods of gestation, and finally, late gestation until birth. The effect of the different temperature descriptors was estimated in the corresponding male and female liabilities in a set of threshold product models. The temperature of the day of AI seems to be the most relevant temperature descriptor affecting male fertility because greater temperature records on the day of AI caused a decrease in male fertility (−6% in male fertility rate with respect to thermoneutrality). Departures from the thermal zone in temperature descriptors covering several periods before AI until early gestation had a negative effect on female fertility, with the pre- and peri-implantational period of the embryos being especially sensitive (from −5 to −6% in female fertility rate with respect to thermoneutrality). The latest period of gestation was unaffected by the temperature. Overall, magnitude and persistency of the temperatures reached in the conditions of this study do not seem to be great enough to have a large effect on male and female rabbit fertility.

Key words: fertility, heat stress, product threshold model, rabbit, temperature

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J. Anim. Sci. 2011. 89:3983–3995
doi:10.2527/jas.2011-3924

INTRODUCTION

Animals exposed to climatic thermal stress have problems in the maintenance of their regular productive and reproductive performances. Males and females are affected in a different way by thermal stress (see review by Marai et al., 2002); rabbit does exposed to heat stress reach puberty later and have reduced conception and embryonic developmental rates, whereas in the case of bucks, testosterone concentration, spermatogenesis, libido, and some seminal traits are also factors affected by heat stress. Success of AI involves different male and female physiological events that could be spe-

¹This research was supported by the Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA, Madrid, Spain) project RTA2005-00088-CO2. Part of it was carried out during a visit of the first author to INRA (Castanet-Tolosan, France), Toulouse. Llibertat Tusell Palomero received a fellowship from the INIA. The authors are grateful to the staff of Unitat de Cunicultura, Institut de Recerca i Tecnologia Agroalimentàries (Caldes de Montbui, Barcelona, Spain) for their valuable cooperation.

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Received January 31, 2011.

Accepted June 29, 2011.

cifically affected by temperature conditions. Therefore, the most sensitive period around insemination time and the effect of the intensity or the duration of the exposure to this environmental factor or both could also be sex dependent. The knowledge of the existence of these sexual differences concerning sensitivity to environmental temperature could lead to implement different strategies of farm and breeding management and even of selection if the goal is to obtain animals tolerant to thermal stress.

The product threshold model (David et al., 2009) is an interesting model to separately establish the effect of temperature conditions on male and female fertility. This model assumes that an observed reproduction outcome is the result of the product of 2 unobserved variables corresponding to the fertility of the 2 individuals involved in the mating. This approach, compared with the classical analysis using the additive threshold model, has the advantage to provide specific estimates of the effects affecting each one of the members involved in the process. The objective of the present study was to determine the effect of temperature conditions at different periods around insemination time on male and on female rabbit fertility and to find the temperature descriptor that gives a better description of the effect of temperature on these traits.

MATERIALS AND METHODS

The research protocol was approved by the animal care and use committee of the Institut de Recerca i Tecnologia Agroalimentàries.

Fertility Data

Animals used in this study came from the Caldes line (Gómez et al., 2002), which is selected for growth rate during the fattening period. This line is bred and reared on an experimental farm belonging to the Institut de Recerca i Tecnologia Agroalimentàries in Caldes de Montbui (Barcelona, Spain). After weaning at 32 d of age, animals are housed in cages of 8 individuals with a photoperiod of 16 h light/d. They are fed ad libitum with a commercial diet (15.5% CP, 2.3% fat, 17.2% fiber) until 60 d of age. After this period, selected replacement males are located in another building of the farm, whereas replacement females remain in the same building. After 60 d of age, males and females are individually housed and fed restricted to 180 g/d of a commercial diet (16% CP, 4.3% fat, 17% fiber). Fresh water is always available.

Young males start the training to ejaculate extraction with an artificial vagina at 4.5 mo of age. One ejaculate per male is collected weekly during the next 2 wk. At 5 mo of age, males started their reproductive life and 2 ejaculates per male are collected weekly, with an interval of 30 min between collections. To prepare the AI doses, gel plugs are removed and, by visual detection, only the ejaculates with presence of urine or calcium carbonate deposits are discarded. Ejaculates are

diluted 1:4 (vol/vol) in a commercial extender (Galap, IMV Technologies, Saint Ouen sur Iton, France), and the AI doses of 0.5 mL are applied within 1 h after collection.

Females follow a semi-intensive reproductive rhythm: first AI at approximately 4.5 mo of age, with subsequent 42-d reproductive cycles. At 48 h before AI, all females are treated with 15 IU of eCG (subcutaneously; Foligon, Intervet International B.V., Booxmeer, Holland). Ovulation is induced immediately after AI with 0.02 mg of Gonadorelin (intramuscularly; Fertagyl, Intervet Internacional B.V. Booxmeer, Holland). Does are placed in maternal cages and fed ad libitum 2 wk before parturition.

Diagnosis of pregnancy is made by abdominal palpation 14 d after AI, but the fertility score is assigned at birth: 1 if the female gave birth and 0 otherwise. A total of 7,625 fertility records after AI were obtained from June 2006 to October 2009.

Temperature Records

Daily temperature was automatically recorded every 30 min in a data logger (Tinytag, Gemini Data Loggers, Chichester, UK) in the male and female buildings during the same period of collection of fertility data. Both buildings have isolated roof, walls, and cooling ventilation systems to avoid animal exposure to extreme temperatures. However, because the buildings were not totally isolated, the indoor temperature records partially reflected the seasonality of the outdoor temperature. Table 1 shows summary statistics of the AI data and the daily maximum temperature records of the male and female buildings.

Three types of temperature descriptors were used: 1) the maximum temperature on the day of AI (**T_{max}**, °C), 2) the average of maximum daily temperatures during a time period (**avgT_{max}**, °C), and 3) over the same period, the proportion of days with maximum temperature greater than 25°C (**DI**, percentage). This last type of descriptor encompasses the duration and intensity of the hot conditions.

To accommodate the possible nonlinear effect of these variables on AI success, the continuous values of the T_{max} and avgT_{max} descriptors were classified into to 5 categories: ≤18°C, 19 to 22°C, 23 to 24°C, 25 to 26°C, and ≥27°C. The DI descriptors were classified into to 5 categories as well: 0 to 20%, >20 to 40%, >40 to 60%, >60 to 80%, and >80 to 100%.

The temperature descriptors were calculated for several periods covering the main physiological events that lead from gamete maturation in both sexes to gestation and birth after AI. Figure 1 shows these different events and the corresponding temperature descriptors.

Temperature Descriptors Used for Male (β_♂)

The temperature descriptors used for the male covered the whole spermatogenesis period, which lasts ap-

Table 1. Distribution of AI data and maximum temperature on the day of AI

Fertility data	Value	
Number of records	7,625	
Number of females	2,960	
Number of males	331	
Mean (SD) number of records per female	2.58 (2.13)	
Mean (SD) number of records per male	23.03 (15.99)	
Observed fertility, %	71	
	Female building	Male building
Maximum temperature records, °C		
Mean (SD)	23.11 (3.52)	22.63 (3.56)
Minimum, maximum	10.4, 39.9	10.4, 39.9

proximately 38 to 41 d in the adult buck (Alvariño, 2000). Subsequently, 4 temperature descriptors from the day of AI to 40 d backward according to the main phases established in rabbits by Swierstra and Foote (1965) were used (see Figure 1):

1) The $\text{avgTmax}_{40_20_♂}$ and $\text{DI}_{40_20_♂}$ were calculated in the period from d 40 to 21 before AI, which encompasses the initial stages of spermatogenesis with proliferation and maintenance of spermatogonia by mitotic divisions

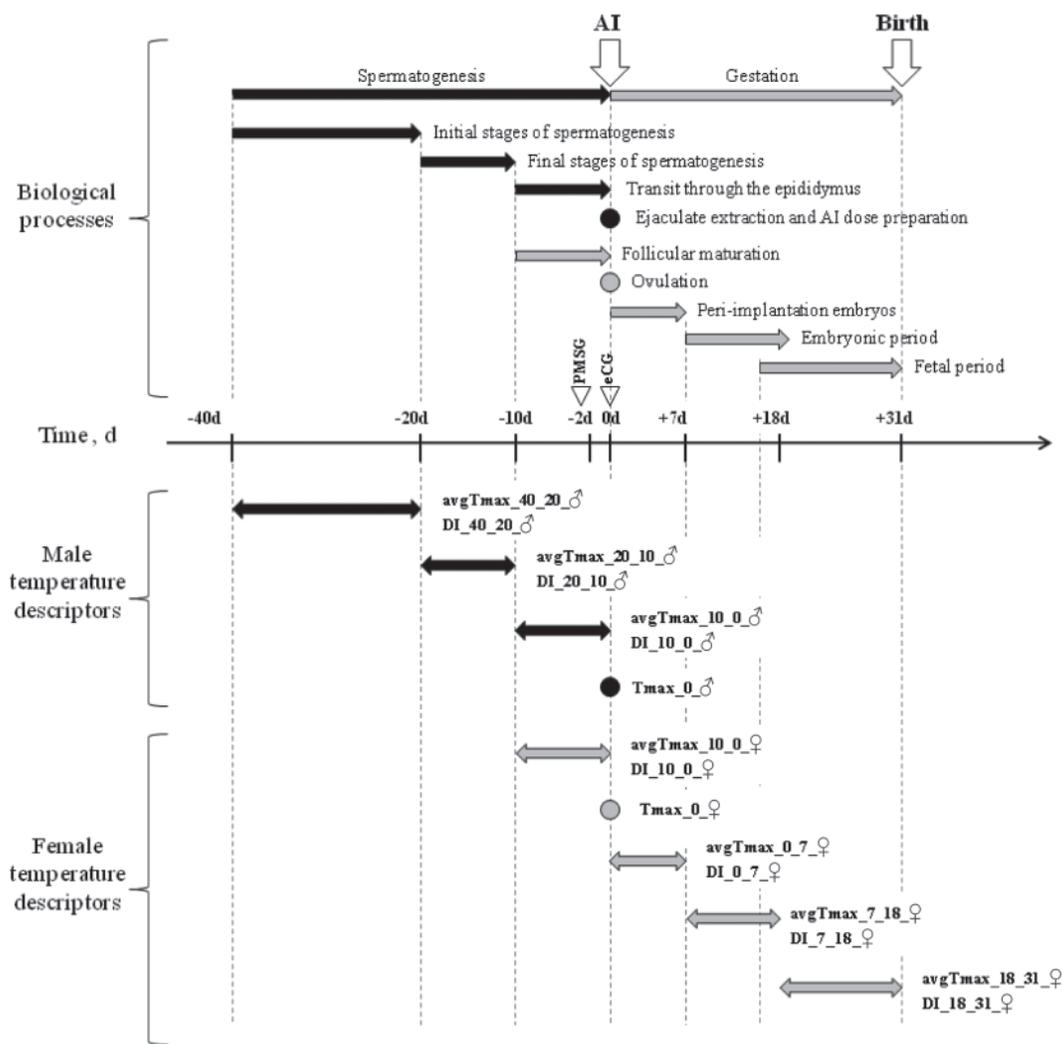


Figure 1. Correspondences between the biological processes involved in fertilization (above the chronological line) and the different temperature descriptors used in the analyses for male and female fertility (below the chronological line). Black and gray arrows refer to processes and temperature descriptors used for male and female, respectively. The term $\text{avgTmax}_{i_j_k}$ is used to denote the average of maximum temperatures during a period that lasts from day i to day j for the male or female (k). The term $\text{DI}_{i_j_k}$ is used to denote the temperature descriptor of proportion of days of the period from the i th to the j th day in which the maximum temperature was greater than 25°C for the male or female. The term Tmax_{0_k} denotes the male and female maximum temperature on the day of AI for the male or female.

and the subsequent meiosis until the formation of spermatids occurs.

- 2) The $\text{avgTmaxT}_{20_10_♂}$ and $\text{DI}_{20_10_♂}$ were calculated in the period ranging from d 20 to 11 before day of AI, which covers from spermatid stage until the end of spermatogenesis.
- 3) The $\text{avgTmax}_{10_0_♂}$ and $\text{DI}_{10_0_♂}$ were calculated in the period from d 10 until the day previous to AI and covers the maturation processes occurring during the transit and the storage of the sperm through the epididymus.
- 4) The $\text{Tmax}_{0_♂}$ is the maximum temperature in the day of AI, which encompasses the AI dose preparation, insemination, and changes related to the fertilization process.

Temperature Descriptors Used for Female ($\beta_{\text{♀}}$)

The following temperature descriptors were used for the female (see Figure 1):

- 1) The $\text{avgTmax}_{10_0_♀}$ and $\text{DI}_{10_0_♀}$ were calculated in the period from d 10 before AI until the day previous to AI. That approximately covers the period of lifespan of the mature follicles (Hill and White, 1933), which can be present in the ovarian surface until the period previous to ovulation. Under commercial conditions of AI, does are superovulated by hormonal treatment 48 h before AI (Alvariño, 1993), which improves receptivity and increases and synchronizes follicle growth as well as ovulation rate (Maertens et al., 1995).
- 2) The $\text{Tmax}_{0_♀}$ is the maximum temperature on the day of AI. That encompasses the ovulation event, the migration of the ova to the fertilization site, and the fertilization process (Harper, 1963). The gestation length in the female rabbit lasts 30 to 32 d (Prud'hon, 1970).
- 3) The $\text{avgTmax}_{0_7_♀}$ and $\text{DI}_{0_7_♀}$ were calculated in the period from the day after AI until d 7 after AI to cover the period of peri-implantation embryonic development (International Committee on Veterinary Embryological Nomenclature, 1994; Lee and De Mayo, 2004).
- 4) The $\text{avgTmax}_{7_18_♀}$ and $\text{DI}_{7_18_♀}$ were calculated in the period from d 8 to 18 after AI, which covers the embryo and early fetal gestation (International Committee on Veterinary Embryological Nomenclature, 1994).
- 5) The $\text{avgTmax}_{18_31_♀}$ and $\text{DI}_{18_31_♀}$ were calculated in the period from d 19 to 31 after AI covering late gestation until birth.

Model and Statistical Analysis

The product threshold model assumes that conception after AI (the observed phenotype) occurs when

both male and female are fertile. Thus, the probability of AI success is the product of the probability of 2 binary unobserved phenotypes corresponding to the male and female fertilities (David et al., 2009). These hidden phenotypes can be modeled using 2 unobserved, underlying continuous variables (liabilities), each one having a fixed threshold that divides its continuous scale into 2 response categories: success and failure (Wright, 1934). In matrix notation, the product threshold model used in this study can be expressed as follows:

$$\Pr(\mathbf{y} = 1 \mid \beta_m, \beta_f, \beta_{ps}, \mathbf{p}_m, \mathbf{p}_{md}, \mathbf{p}_f) = \Phi(\mathbf{X}_m \beta_m + \mathbf{Z}_{1,m} \mathbf{p}_m + \mathbf{Z}_{2,m} \mathbf{p}_{md}) \times \Phi(\mathbf{X}_{1,f} \beta_f + \mathbf{X}_{2,f} \beta_{ps} + \mathbf{Z}_f \mathbf{p}_f),$$

where \mathbf{y} is the vector of the observed AI results (1: success to conception, 0 otherwise); Φ is the standard cumulative distribution function of a standard normal distribution; β_m and β_f are the vectors of temperature descriptor effects described previously for male and female, respectively; β_{ps} is the vector of the effect of the physiological status of the female (3 levels: nulliparous, multiparous in lactation, and multiparous not in lactation at AI); \mathbf{p}_m is the vector of male effects; \mathbf{p}_{md} accounts for the interaction between male and day of AI; and \mathbf{p}_f is the vector of female effects. Random effects \mathbf{p}_m , \mathbf{p}_{md} , and \mathbf{p}_f were considered uncorrelated. Terms \mathbf{X}_m , $\mathbf{X}_{1,f}$, $\mathbf{X}_{2,f}$, $\mathbf{Z}_{1,m}$, $\mathbf{Z}_{2,m}$, and \mathbf{Z}_f are incidence matrices relating data with the systematic and random effects included in the model.

In our study, we have considered different models that only differed by the systematic effects β_m and β_f . Due to the large colinearity between temperature descriptors within sex, all these models included only 1 temperature descriptor for each hidden phenotype. Most of the possible combinations between male and female temperature descriptors were previously analyzed in several models (data not shown), and because they provided similar estimates for the effect of the male temperature descriptor, irrespective of the temperature descriptor used for the female, and vice versa, only the results of 11 different models are presented (Table 2).

The season effect was not considered in the analysis because it is greatly confounded with the environmental temperature. The age of the male was also not included because of the nonrelevant effect found in preliminary analyses. The age of the female is partially encompassed with the physiological status of the female, included in the female side of the model.

A Bayesian framework was adopted for inference. The assigned prior distributions for the parameters of the models were

$$p(\beta) \sim k; p(\mathbf{p}_i \mid \sigma_i^2) \sim N(\mathbf{0}, \mathbf{I} \otimes \sigma_i^2)$$

for $i = m, f, md$. The term k is a constant, σ_i^2 is the variance for male, female, and the interaction between

Table 2. Different product threshold models including several temperature descriptors in the male and the female liabilities of fertility (β_{σ} and β_{φ} , respectively)¹

Model	β_{σ}	β_{φ}
1	avgTmax_40_20_♂	avgTmax_0_7_♀
2	DI_40_20_♂	DI_0_7_♀
3	avgTmax_20_10_♂	avgTmax_0_7_♀
4	DI_20_10_♂	DI_0_7_♀
5	avgTmax_10_0_♂	avgTmax_10_0_♀
6	DI_10_0_♂	DI_10_0_♀
7	Tmax_0_♂	Tmax_0_♀
8	avgTmax_40_20_♂	avgTmax_7_18_♀
9	DI_40_20_♂	DI_7_18_♀
10	avgTmax_20_10_♂	avgTmax_18_31_♀
11	DI_20_10_♂	DI_18_31_♀

¹The term avgTmax_*i*_*j*_*k* denotes the average of maximum temperatures during a period that lasts from day *i* to day *j* for the male or female (*k*). The term DI_*i*_*j*_*k* denotes the temperature descriptor of the proportion of days of the period from the *i* to the *j* day in which the maximum temperature was greater than 25°C for the male or female (*k*). The term Tmax_0_*k* denotes the male and female maximum temperature of the day of AI for the male or female (*k*).

male and day of AI random effects, respectively. Flat bounded priors were used for variances. Thresholds and residual variances were fixed to 0 and 1, respectively. For details, see David et al. (2009). The marginal posterior distributions of the parameters of interest were derived from the joint posterior density of all the unknown parameters. The Gibbs sampler algorithm was used to estimate the marginal posterior distributions of the systematic effects and the variance components. Single chains of 200,000 iterations were run for all the analyses. The first 20,000 iterations of each chain were discarded, and samples of the parameters of interest were saved every 100 rounds. The number of discarded samples was, in all cases, much larger than the required burn-in determined by using Raftery and Lewis (1992) and Geweke (1992) procedures. The sampling variance of the chains was obtained by computing Monte Carlo SE (Geyer, 1992). Summary statistics from the marginal posterior distributions were calculated directly from the samples saved.

Male and female unobserved phenotypic variances were obtained as the sum of all corresponding variance components of each sex. Ratios of variance were obtained dividing each variance component by the corresponding unobserved phenotypic variance.

Criteria Used to Test the Relevance of the Effect of Temperature Descriptors on Male and Female Fertilities

Rabbit comfort temperature is considered to be around 21°C (Marai et al., 2002). Consequently, the second level of Tmax and avgTmax descriptors would correspond to zone of thermal neutrality (ranging from 19 to 23°C) at which other levels were compared. For the DI descriptors, in absence of references in the literature concerning the effect of a persistently high tem-

perature over a period on the fertility, we chose arbitrarily the second level as the reference (20 to 40% of days in the period with maximum temperature greater than 25°C). Estimates of the other levels of the temperature descriptors were obtained as contrasts to those second levels, which were set to 0. Probability of a positive/negative value of the contrast was considered. The highest posterior density intervals at 95% (HPD_{95%}) of the contrasts were also computed.

RESULTS AND DISCUSSION

Table 3 shows correlations among the different temperature descriptors used in this study. As expected, the largest correlations were encountered among those temperature descriptors that were measured in the same period of time and also among those ones that were measured closer in time. Moreover, it is important to note that the temperature descriptors for the male were moderate to highly correlated with those for the female. This means that in an additive model, it would not be possible to include both factors to analyze the effects of the temperature on global fertility because there would be a colinearity effect on these estimates.

Figure 2 shows the monthly percentage of AI success and the average maximum temperature per month in the male and female buildings recorded during the experimental period of this study. A regular decrease of the AI success was observed from February to July when the temperature increased. The greatest observed AI success was reached during the coldest period of the year, and the least observed success occurred during the summertime. The detrimental effects of heat stress on conception rate have been described by several authors, especially in countries with hot climate conditions (Marai et al., 2006; Yassein et al., 2008). In rabbits, the number of functional sweat glands is scarce and their fur does not allow for a great amount of perspiration. The increase of respiration rate, changes in body position, and heat dissipation via ear lobes appear to be the main mechanisms to mitigate heat in this species (Harkness, 1988). When those mechanisms are not efficient enough to dissipate the amount of heat above the zone of thermal neutrality, deterioration of growth, less resistance to diseases, and impairment in reproductive performance appear with the subsequent economic losses for breeders (reviewed by Marai et al., 2002).

The posterior means of the probabilities of success (David et al., 2009) were approximately 0.87 for male and approximately 0.83 for female fertility in all models. Equal Monte Carlo SE were obtained for both estimates in all the models (0.002). With a similar data set of the same line of rabbits and using the same product threshold model, David et al. (2011) found very close values for the probabilities of fertility success.

Estimates of the posterior mean of total variance of each underlying variable, ratios of variance attributable to male, and the interaction between male and day of

Table 3. Correlations among the different temperature descriptors used to estimate the effect of thermal stress in male and female fertility

Item	avgTmax_40_20_♂	DL_40_20_♂	avgTmax_20_10_♂	DL_20_10_♂	avgTmax_10_0_♂	DL_10_0_♂	Tmax_0_♂	avgTmax_10_0_♀	DL_10_0_♀	Tmax_0_♀	avgTmax_7_18_♂	DL_7_18_♂	avgTmax_18_31_♀	DL_18_31_♀
avgTmax_40_20_♂	1.00													
DL_40_20_♂	0.91	1.00												
avgTmax_20_10_♂	0.76	1.00	1.00											
DL_20_10_♂	0.81	0.77	0.77	1.00										
avgTmax_10_0_♂	0.76	0.77	0.90	1.00	1.00									
DL_10_0_♂	0.81	0.77	0.73	0.89	0.69	1.00								
Tmax_0_♂	0.91	0.77	0.73	0.89	0.69	1.00	1.00							
avgTmax_10_0_♀	0.76	0.77	0.90	1.00	1.00	1.00	0.45	1.00						
DL_10_0_♀	0.81	0.77	0.73	0.89	0.69	1.00	0.45	1.00	0.60	0.38				
Tmax_0_♀	0.91	0.77	0.73	0.89	0.69	1.00	0.45	1.00	0.60	0.38	0.56			
avgTmax_7_18_♂	0.76	0.77	0.90	1.00	1.00	1.00	0.45	1.00	0.60	0.38	0.56	0.52		
DL_7_18_♂	0.81	0.77	0.73	0.89	0.69	1.00	0.45	1.00	0.60	0.38	0.56	0.52	0.52	0.36
avgTmax_18_31_♀	0.76	0.77	0.90	1.00	1.00	1.00	0.45	1.00	0.60	0.38	0.56	0.52	0.52	0.36
DL_18_31_♀	0.81	0.77	0.73	0.89	0.69	1.00	0.45	1.00	0.60	0.38	0.56	0.52	0.52	0.36
Tmax_0_♀	0.91	0.77	0.73	0.89	0.69	1.00	0.45	1.00	0.60	0.38	0.56	0.52	0.52	0.36
avgTmax_7_18_♀	0.76	0.77	0.90	1.00	1.00	1.00	0.45	1.00	0.60	0.38	0.56	0.52	0.52	0.36
DL_7_18_♀	0.81	0.77	0.73	0.89	0.69	1.00	0.45	1.00	0.60	0.38	0.56	0.52	0.52	0.36
avgTmax_18_31_♂	0.76	0.77	0.90	1.00	1.00	1.00	0.45	1.00	0.60	0.38	0.56	0.52	0.52	0.36
DL_18_31_♂	0.81	0.77	0.73	0.89	0.69	1.00	0.45	1.00	0.60	0.38	0.56	0.52	0.52	0.36
Tmax_0_♂	0.91	0.77	0.73	0.89	0.69	1.00	0.45	1.00	0.60	0.38	0.56	0.52	0.52	0.36
avgTmax_7_18_♀	0.76	0.77	0.90	1.00	1.00	1.00	0.45	1.00	0.60	0.38	0.56	0.52	0.52	0.36
DL_7_18_♀	0.81	0.77	0.73	0.89	0.69	1.00	0.45	1.00	0.60	0.38	0.56	0.52	0.52	0.36
avgTmax_18_31_♂	0.76	0.77	0.90	1.00	1.00	1.00	0.45	1.00	0.60	0.38	0.56	0.52	0.52	0.36
DL_18_31_♂	0.81	0.77	0.73	0.89	0.69	1.00	0.45	1.00	0.60	0.38	0.56	0.52	0.52	0.36

[†]The term avgTmax_{i,j,k} denotes the average of maximum temperatures during a period that lasts from day *i* to day *j* for the male or female (*k*). The term DL_{i,j,k} is used to denote the male or female temperature descriptor of proportion of days of the period from the *i* to the *j* day in which the maximum temperature was above 25°C. The term Tmax_{0,k} denotes the male and female maximum temperature of the day of AI.

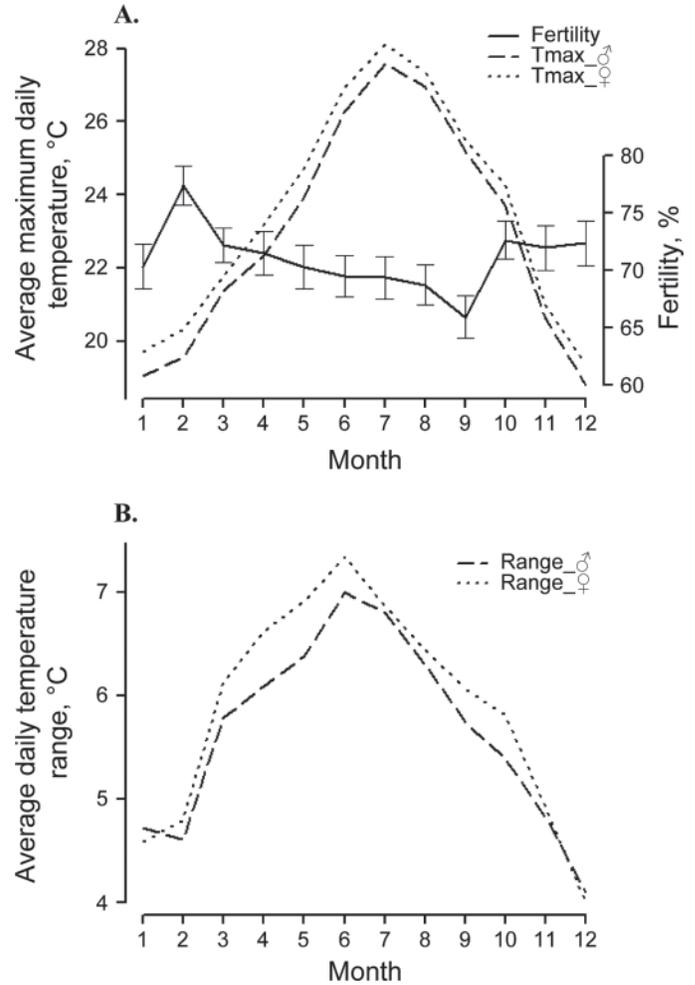


Figure 2. Panel A: average maximum daily temperature recorded per month in the male and female building (Tmax_♂ and Tmax_♀, respectively) and average percentage of fertility success per month (SE in bars). Panel B: average daily temperature range recorded per month in the male and female building (Range_♂ and Range_♀, respectively).

AI in the male liability as well as the ratio of variance due to the female effect in the female liability were similar among the models. Surprisingly, in model 4 (Table 2) the posterior SD of the estimates of these figures were larger than the corresponding ones obtained in the other models.

Figures 3 and 4 as well as Figures 5 and 6 show estimates (posterior means) and their corresponding confidence intervals (HPD_{95%}) of the effect of the temperature descriptors in male and female unobserved fertility on a 0 to 1 scale, respectively. The effect of some temperature descriptors were estimated in more than one model (obtaining the same estimates). For simplicity, only the estimates obtained in models 1 to 7 and models 1, 3 to 11 for the male and female temperature descriptors, respectively, are presented (Table 2).

Effect of Temperature Descriptors on Male Fertility

High maximum daily temperatures on the day of AI represented a loss of 6% in male fertility rate with re-

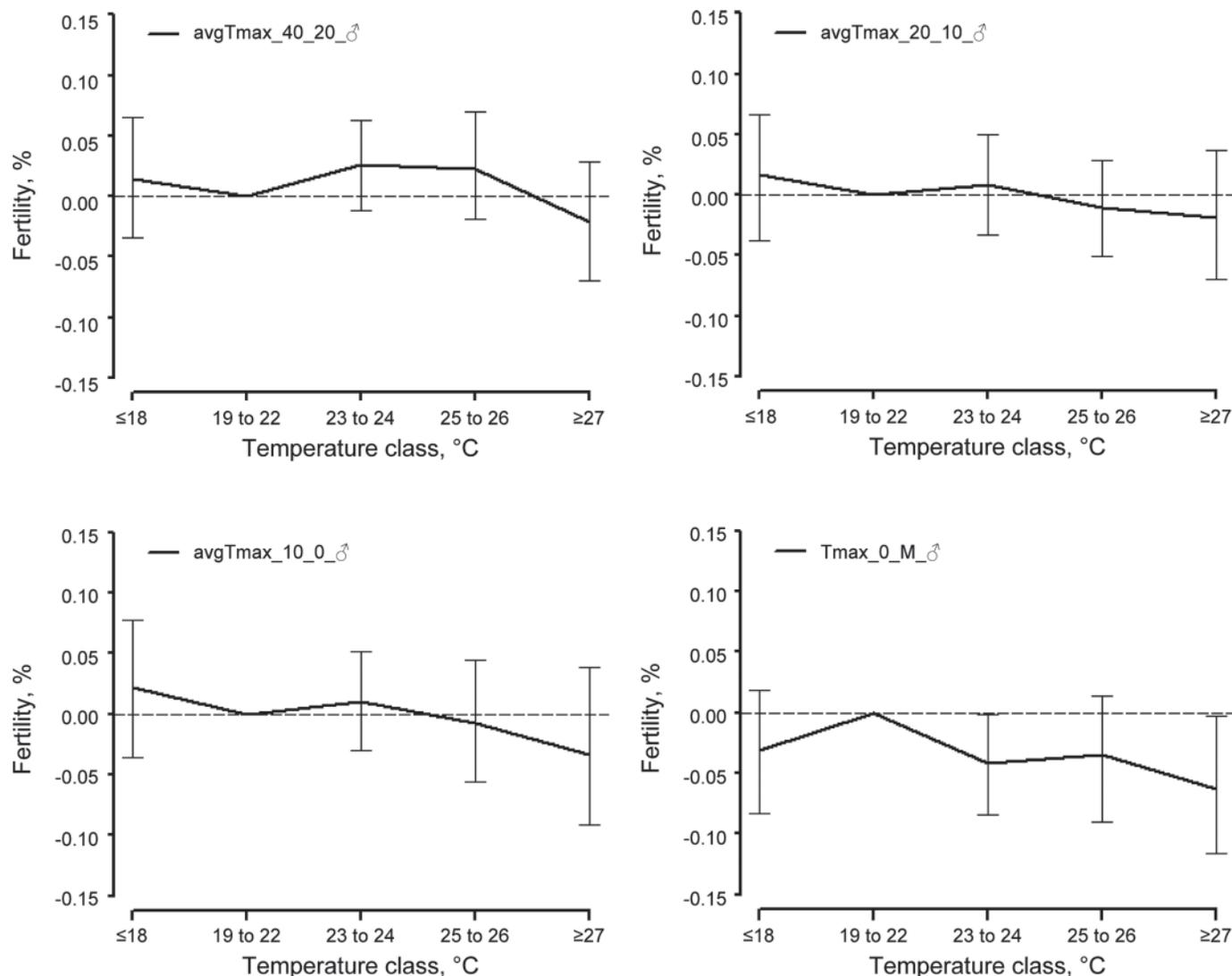


Figure 3. Posterior mean and highest posterior density interval at 95% of the effects on male fertility rate of the average maximum daily temperatures in the periods from 40 to 21 d before AI, from 20 to 11 d before AI, and from 10 to 1 d before AI (avgTmax_40_20_♂, avgTmax_20_10_♂, and avgTmax_10_0_♂, respectively) and effect on male fertility rate of the maximum temperature the day of AI (Tmax_0_♂). Estimates of each figure were obtained in models 1, 3, 5, and 7, respectively.

spect to thermoneutrality (Tmax_0_♂, Figure 3). This result indicates the susceptibility of the sperm to a high temperature during all the handling processes from the preparation of the AI doses until the time of insemination. Because doses of 1 male in a specific day have been exposed to the same environmental temperature, it is possible that the random effect resulting from the interaction between male and day of AI could be removing part of the effect of Tmax_0_♂. However, we preferred to include this random effect in the models because it takes into account all possible environmental factors that could have had an effect on all the AI doses prepared from one male in a specific day of AI, whereas the effect of temperature on the day of AI is common to all the doses of all the males that have been prepared on a specific day. Other results obtained in another rabbit fertility study by Tusell et al. (2010) indicated that the male random effect with the greatest

variance was the interaction between male and day of AI. In a similar way, this effect partly encompassed the high sensitivity of the semen to the effect of environmental factors during the processes of dose preparation and application. However, a proportion of the variation obtained for this effect in the 2 models cannot be properly compared. The additive threshold model considers the existence of a unique linear variable underlying the categorical trait and the proportion of variance of a certain male or female effect is referred to phenotypic variation of this common underlying variable. However, under the product threshold model, it is assumed that 2 underlying variables exist: the liability of male fertility (nonobservable male phenotype) and the liability of female fertility (nonobservable female phenotype). In that case, the proportion of variance of a certain effect is referred to the phenotypic variation of the corresponding male or female liability. In this work, none of

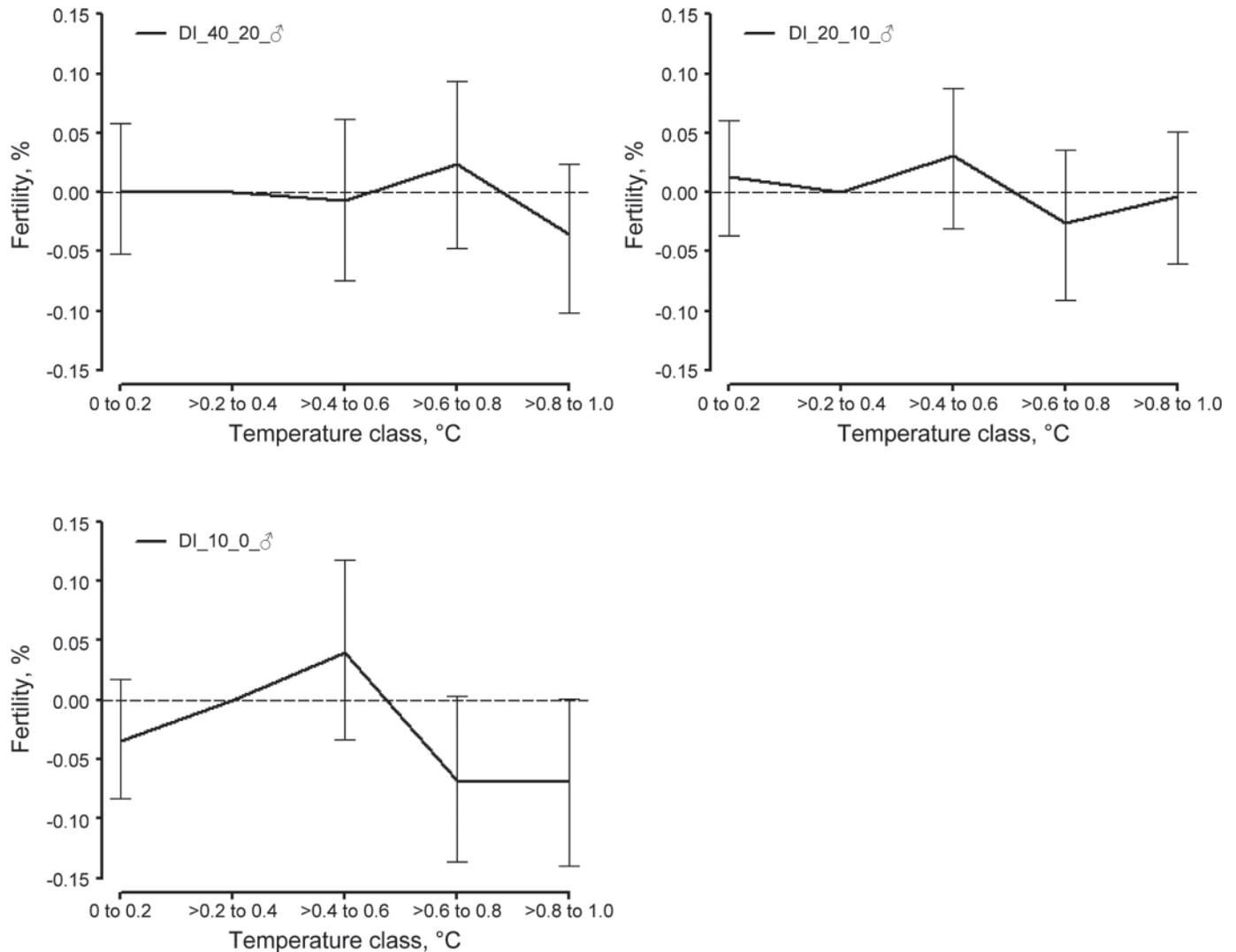


Figure 4. Posterior mean and highest posterior density interval at 95% of the effects on male fertility rate of the percentage of days with maximum temperature greater than 25°C in the periods from 40 to 21 d before AI, from 20 to 11 d before AI, and from 10 to 1 d before AI (DI_40_20_♂, DI_20_10_♂, and DI_10_0_♂, respectively). Estimates of each figure were obtained in models 2, 4, and 6, respectively.

the temperature descriptors covering spermatogenesis had a clear influence on male fertility (period from 40 to 10 d before AI, Figures 3 and 4).

Low and high values of maximum temperatures covering the epididymis transit stage also did not affect male fertility (avgTmax_10_0_♂; Figure 3). However, large percentages of days with maximum temperature greater than 25°C during the epididymal transit of the sperm (DI_10_0_♂, Figure 4) produced a relevant decrease in male fertility (−7% in the contrasts with the 2 greatest levels, with a probability of a negative value of 97%). Some seminal quality traits related to male fertility (Gadea, 2005; Lavara et al., 2005; Garcia-Tomás et al., 2006) such as sperm concentration, sperm abnormalities, and acrosome integrity were analyzed by Roca et al. (2005). These authors found a negative effect of the temperature-humidity index (THI) on semen quality and suggested that spermatogenesis but not epididymal transit was affected, according to the time elapsed between the THI stress and the occurrence of impaired

semen quality, under commercial conditions. However, their results should be taken with caution because season, light treatment, and THI were included as different effects in the same model, leading presumably to confounded effects. On the other hand, Finzi et al. (1995) compared the characteristics of the spermatozoa from ejaculates obtained in consecutive weeks in males moved from thermoneutrality to heat stress conditions in a climatic chamber. They concluded that the stage of spermatid formation in the seminiferous tubules was the critical period in the formation of sperm abnormalities. The effect of this kind of seminal trait on fertility could not be observed if the sperm dosage is high (Saa-cke et al., 2000), which occurs in our study. This could lead to not observing a detrimental effect on male fertility under heat stress conditions in the period from 40 to 10 d before AI. However, it has been demonstrated that, in the presence of thermal stress in both the testis and the epididymis, motile and morphologically normal sperm could be obtained, but with defective chromatin

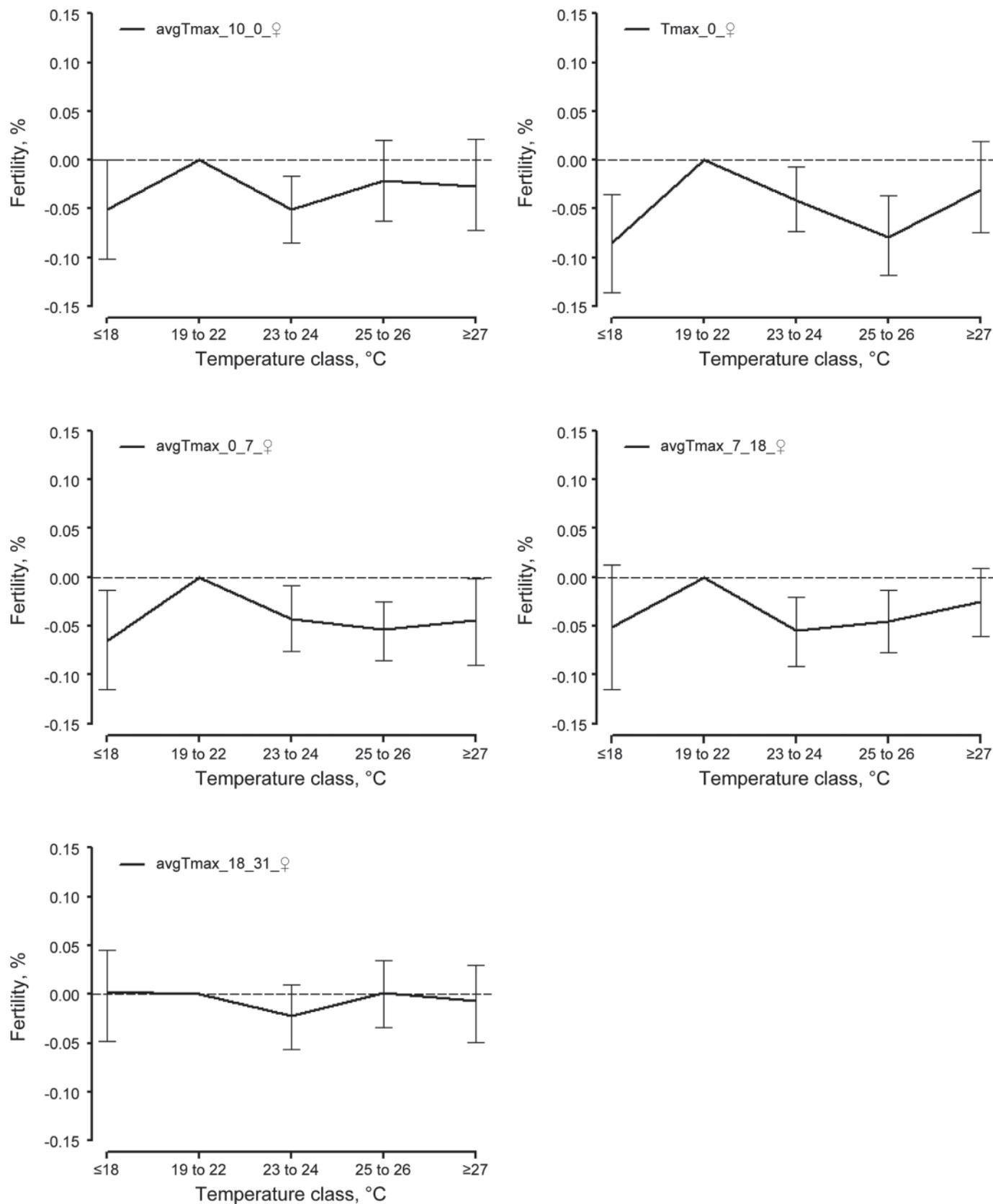


Figure 5. Posterior mean and greatest posterior density interval at 95% of the effects on female fertility rate of the average maximum daily temperatures in the periods from 10 to 1 d before AI, from 1 to 7 d after AI, from 8 to 18 d after AI, and from 19 to 31 d after AI (avgTmax_10_0_♀, avgTmax_0_7_♀, avgTmax_7_18_♀, and avgTmax_18_31_♀, respectively) and effect on female fertility rate of the maximum temperature the day of AI (Tmax_0_♀). Estimates of each figure were obtained in the models 5, 7, 1, 8, and 10, respectively.

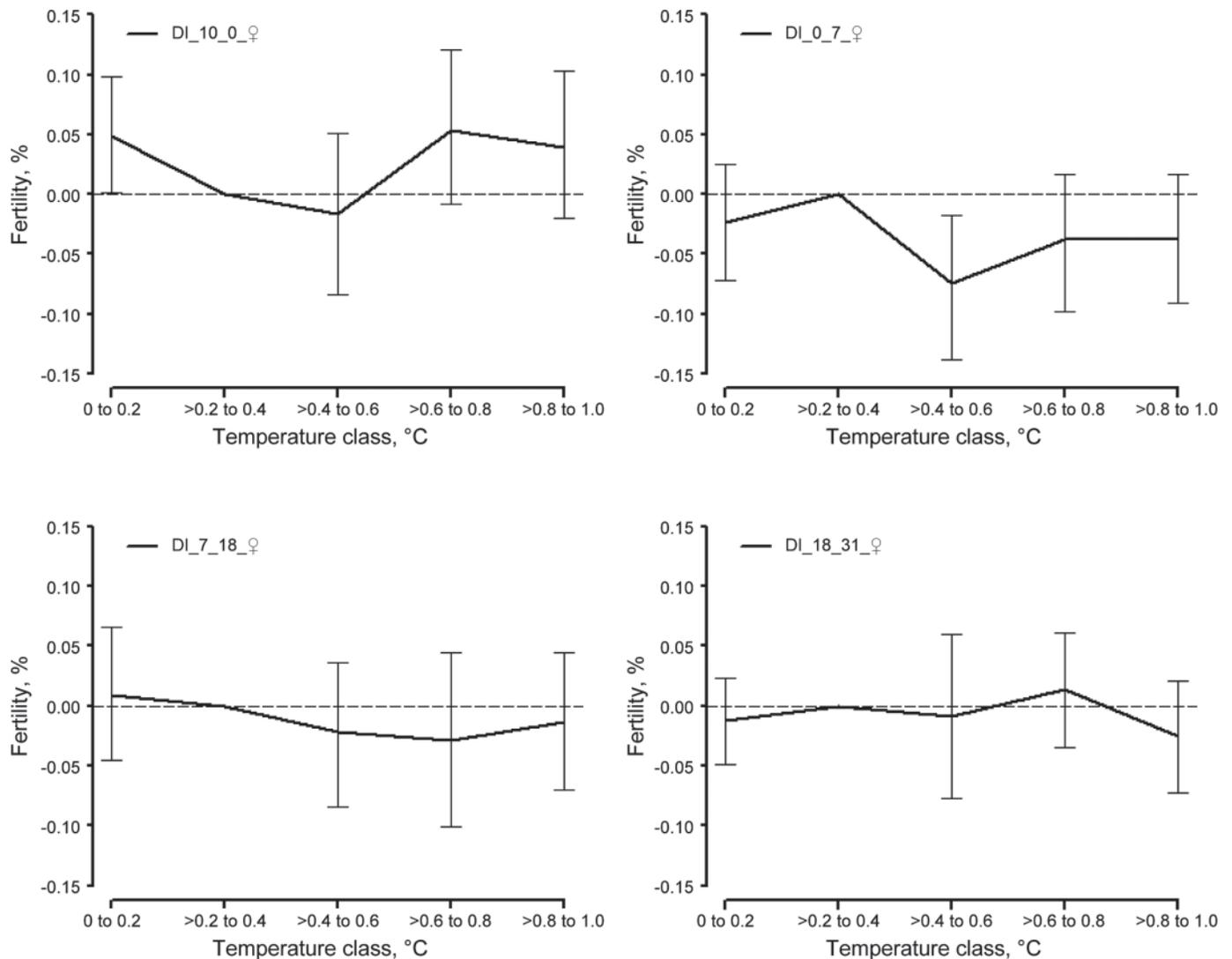


Figure 6. Posterior mean and greatest posterior density interval at 95% of the effects on female fertility rate of the percentage of days with maximum temperature greater than 25°C in the periods from 10 to 1 d before AI, from 1 to 7 d after AI, from 8 to 18 d after AI, and from 19 to 31 d after AI (DI_10_0_♀, DI_0_7_♀, DI_7_18_♀, and DI_18_31_♀, respectively). Estimates of each figure were obtained in the models 6, 2, 9, and 11, respectively.

(in mice; Banks et al., 2005). In turn, altered sperm DNA has a negative effect on fertility, especially during embryonic development (Saacke et al., 2000; D'Occhio et al., 2007), which could explain the negative effect of a persistently high temperature during the epididymal transit of the sperm observed in our work, if it can be demonstrated that DNA structure is more sensitive to heat stress in this stage. This kind of deficiency of the spermatozoa cannot be compensated for by increasing the sperm concentration of the AI dose.

Previous results obtained in the same line showed that cold to moderate THI indices seemed to negatively affect some quantitative and qualitative semen traits (Garcia-Tomás et al., 2008). This result is not confirmed after analyzing fertility results of the same line in our study because no relevant detrimental effects were obtained in the contrasts with the lowest levels of the temperature descriptors. To our knowledge, there

is no other information in the literature concerning the effect of cold to moderate temperatures on male reproductive performance. However, it is known that endothermic mammals can better tolerate low body temperatures than high body temperatures (Hansen, 2009).

Effect of Temperature Descriptors on Female Fertility

Although some of the temperature contrasts had a HPD_{95%} that did include 0, the general tendency among the female descriptors Tmax_♀ and avgTmax (except for the avgTmax_18_31_♀; Figure 5) was that departures from the thermal comfort zone had a negative effect on female fertility. Heat stress produces impairment in several physiological processes involved in female reproductive performance that lead to a decrease in conception rate (Marai et al., 2002). To our knowl-

edge, there is no information in the literature concerning the effect of low temperatures on female fertility that could confirm our results.

Cheng et al. (1999) observed that does exposed to high temperature before mating had a greater embryonic degeneration than those maintained in thermoneutral conditions. A reduction in the development of mature follicles and in the number of developing oocytes has been observed in rabbits during summer heat stress (Yassein et al., 2008). It has also been reported in cattle and goats that heat stress affects follicular dynamics and ovulation rate (Doney et al., 1973; Roth, 2008). Although a tendency is observed in our results, we cannot confirm the detrimental effect of high temperatures during the follicular maturation period and preimplantation phase of embryos on fertility, but low temperatures during the period from 10 d to AI had a negative effect on female fertility (avgTmax_10_0_♀; Figure 5). Although estimates were imprecise, a small proportion of hot days during the 10 d before AI, as well as a large proportion of hot days during the same period, seemed to favorably affect female fertility (DI_10_0_♀; Figure 6). This surprising result needs to be confirmed and could be in part related to temperature gradients that exist in the ovarian tissues of mature animals, which are generated at least in part as a consequence of endothermic reactions within Graafian follicles (Hunter et al., 2000).

Low and high temperatures during the day of AI negatively affect female fertility. Ovulation in does occurs approximately 10 h after the injection of LH at AI (Harper, 1963). Thus, it seems that processes related to the female such as ovulation and migration of the oocytes to the ampulla of the oviduct and fertilization could be affected by the environmental temperature of the farm on the day of AI. In addition, females could be less fertile because a hyperthermic reproductive tract can also affect the fertilizing ability of the sperm and the posterior embryo survival (Howarth et al., 1965; Hansen et al., 2001). In rabbit AI, the sperm is deposited deep in the vagina and close to the cervix. Then sperm have to migrate through the cervix and the uterus, then reach the isthmus of the oviduct, and remain trapped and held in a sperm reservoir until ovulation (Harper, 1973a; Overstreet and Cooper, 1978). Once the oocytes reach the ampulla of the oviduct, hyperactivation (Ho and Suarez, 2001) and capacitation (Dziuk, 1965) of spermatozoa allow the release of sperm from the reservoir and the migration to the oocytes. Capacitated sperm is thermotactically sensitive to the gradient of temperature that exists at ovulation time between the isthmus sperm reservoir and the fertilization site. The existence of this gradient enables the migration of the sperm to the oocytes (David et al., 1972; Bahat and Eisenbach, 2006). This temperature-dependent process could be affected by thermal stress if excess heat is not correctly dissipated in the female, reducing the ability of the sperm to reach the oocytes.

It is important to note that most of the studies dealing with the impact of high ambient temperatures on preovulatory follicle maturation, fertilization, and embryo development were carried out in climatic chambers or in vitro under extreme conditions of high and constant temperature. However, in commercial farm conditions such as the ones used in this study, there is a wide range of daily temperature, especially in summer (Figure 2). Even in the hot season, the thermoneutrality zone is reached during the night when rabbit activity is at a maximum and animals eat (Prud'hon, 1975), which could enhance the heat tolerance of animals.

Departures from thermoneutrality during the pre- and peri-implantation embryonic development caused a decrease in female fertility (avgTmax_0_7_♀; Figure 5). A similar pattern was observed for DI_0_7_♀ (Figure 6), but the majority of the contrasts included the 0 in their HPD_{95%}. Several authors described that this period of gestation was very sensitive to thermal stress, leading to a decrease in the latter embryo development and survival (Putney et al., 1988; Ealy et al., 1993; Hansen et al., 2001). However, early embryos respond differently to thermal stress depending on their age and developmental status arriving to acquire thermotolerance in more advanced stages of development (Ealy et al., 1993; Hansen, 2009). A threshold of thermotolerance exists in rabbit preimplantation embryos exposed to high temperatures in vitro (Makarevich et al., 2007).

It seems that high and low temperatures during the embryo and early fetal gestation periods also compromise female fertility because the probability of a negative value for the contrasts between the lowest and highest levels with the reference level was 94 and 92%, respectively (avgTmax_7_18_♀; Figure 5). However, female fertility seems to be unaffected by the proportion of days with high temperature in the same period (DI_7_18_♀; Figure 6). Embryo survival in utero under heat stress conditions has been more attributable to changes in maternal physiology than to changes in the embryo itself (Hansen, 2009).

As long as the gestation advances, embryos become more resistant to the maternal exposure to heat stress (Ealy et al., 1993; Hansen et al., 2001). Accordingly, a reduction in the effect of the temperature on female fertility seemed to occur as the temperature descriptor is measured later in the gestation period. Therefore, the temperature descriptors covering gestation from 18 d after AI until birth had no influence on female fertility (avgTmax_18_31_♀ and DI_18_31_♀; Figures 5 and 6, respectively).

Finally, it is important to mention that because of the high correlation existing among the temperature descriptors it is difficult to establish which effects of temperature are the most important. Moreover, the season of the year was not included in the model because of the confounding effect with the temperature. Therefore, temperature descriptors encompass not only the temperature effects but also all the possible season

effects associated with it, such as environmental humidity and photoperiod, that could affect the AI results. However, as noted by Flowers (2008), it is likely that the most important effects observed were due mostly to temperature, especially in this study where photoperiod was artificially controlled.

Effect of the Physiological Status of the Female on Female Fertility

Fertility of nulliparous females is about 6% (SD 0.01) less than the multiparous females in all of the models. That agrees with the decreased values obtained for prolificacy traits in the first parities with respect to the second and subsequent parturitions in other rabbit lines (Baselga et al., 1992; Piles et al., 2006). In our study, no effect of lactation was encountered. This disagrees with the negative effect observed after AI of crossbred females from 2 maternal lines (Tusell et al., 2011), as well as results obtained after natural mating of females of the same line as the one used in this work. However, no negative effect of lactation was encountered in females of a maternal line (Piles et al., 2005), which could mean that the effect of lactation on fertility is dependent on line and type of mating.

The product threshold model appears as an interesting model to separately estimate the effect of some environmental factors relating male and female contributions to the fertility output (such as the different temperature descriptors analyzed in this work). However, this model assumes conditional independence between male and female fertility events. This fact does not allow taking into account the estimation of the effect of interactions between male and female factors that exists in the mating process, as described by several authors in the reproduction field (e.g., ovulation-associated alterations leading to changes in the pattern of sperm motility, ova stimulation of the migration of sperm from the reservoir to the fertilization site; Harper, 1973b; Overstreet and Cooper, 1978). Moreover, not only the male and the female but also embryos are a component contributing in any fertility outcome. Further work should be done in this direction to incorporate in the product threshold model the possibility to estimate possible interactions between the 2 fertility events.

In conclusion, the environmental temperature of the day of AI seems to be the most relevant temperature descriptor affecting male fertility because high temperature records in the day of AI caused a decrease in male fertility. This effect could be indicative of the high sperm sensitivity to temperature changes during the processes of preparation and application of the AI doses. However, some sperm physiological processes occurring around the fertilization time could also be affected by temperature. From a practical point of view, it seems to be advisable to handle the sperm to be used for AI in a rapid and careful manner to not compromise its fertilizing ability.

Departures from the thermal zone in temperature descriptors covering several periods before AI until early gestation had a negative effect on female fertility, with the pre- and peri-implantational period of the embryos being especially sensitive. The latest period of gestation seemed to be unaffected by the temperature confirming the results described previously in other studies about the gain of thermotolerance reached in the latest stages of gestation.

The product threshold model allowed determining that male and female fertility are specifically affected by temperature in different periods around the insemination time. However, the magnitude and the persistence of the temperatures reached in the commercial conditions of this study did not seem to have a large effect on male and female rabbit fertility. Nevertheless, it is possible that the effect of temperature in prolific species leads to a reduction of the number of surviving embryos that could not be detected through the analysis of the pregnancy vs. nonpregnancy result of AI. The analysis of prolificacy outcomes would be a different study, and it could not take advantage of the use of the product threshold model.

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