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## **Long-term implications of feed energy source in different genetic types of reproductive rabbit females : III. Fitness and productivity**

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Additional Information

1 **Long-term implications of feed energy source in different genetic types of**  
2 **reproductive rabbit females. III. Fitness and productivity**

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15

16 Short title : Diet x genetic in does: Fitness and productivity

17 **Abstract**

18 The specialization process associated with genetic selection could be associated with  
19 functional disorders, affecting the reproductive success of females ('fitness'). We  
20 hypothesized that by modulating energy acquisition and allocation of females we could  
21 balance productivity and reproductive success. To test this hypothesis, we used 203  
22 rabbit females belonging to three genetic types: H (n=66) maternal line specialised in  
23 prolificacy, LP (n=67) generalist maternal line, R (n=70) paternal line specialised in  
24 growth rate. We fed each genetic type with two diets specifically designed to promote  
25 milk yield (AF) or body reserves recovery (CS). We controlled females between their  
26 first and fifth reproductive cycles, recording traits related with productivity and fitness  
27 of females. H females fed CS had on average  $11.2 \pm 0.43$  kits with an individual weight  
28 of  $54 \pm 1.2$  g at birth and  $525 \pm 11$  g at weaning. Their conception rate when multiparous  
29 was 44% and their survival rate at the end of the experiment 30%. When they were  
30 fed AF, the individual weight of kits was 3.8 g heavier ( $P < 0.05$ ) at birth and 38 g heavier  
31 at weaning ( $P < 0.05$ ), the conception rate when multiparous increased 23 percentage  
32 points ( $P < 0.05$ ) and the survival rate at the end of the experiment 25 percentage points  
33 ( $P < 0.05$ ). LP females fed CS had on average  $10.8 \pm 0.43$  kits with an individual weight  
34 of  $52 \pm 1.2$  g at birth and  $578 \pm 11$  g at weaning. Their conception rate when multiparous  
35 was 79% and their survival rate at the end of the experiment 75%. When they were  
36 fed AF, it only increased individual weight of kits at weaning (+39 g;  $P < 0.05$ ). R females  
37 fed CS had on average  $8.4 \pm 0.43$  kits with an individual weight of  $60 \pm 1.2$  g at birth and  
38  $568 \pm 11$  g at weaning. Their conception rate when multiparous was 60% and their  
39 survival rate at the end of the experiment 37%. When they were fed AF, they presented  
40 1.4 kits less at birth ( $P < 0.05$ ) but heavier at birth (+4.9 g;  $P < 0.05$ ) and at weaning (+37  
41 g;  $P < 0.05$ ). Therefore, we observed that genetic types prioritised different fitness

42 components and that diets could affected them. In this sense, seems that more  
43 specialised genetic types, were more sensitive to diets than the more generalist type.

44 **Keywords:** Functionality, productivity, priority, trade-off, long term.

45 **Implications**

46 In a context in which sustainable strategies are demanded, obtaining productive but  
47 also balanced and functional animals is crucial. In this sense, understanding the way  
48 animals acquire and allocate resources is becoming highly relevant, as well as finding  
49 out how to modulate it. In the first work of this series we found that by modifying the  
50 energy source of the diet we could alter partition of energy between milk and body  
51 reserves of different genetic types. In this work, we have evaluated how these changes  
52 impact on productivity, functionality and fitness of each genetic type. This information  
53 could be used to develop specific nutritional strategies for each genetic type in order  
54 to maximise their productivity while maintaining their functionality.

55

## 56 **Introduction**

57 To better estimate the response per generation to artificial selection, animals within  
58 selection programmes are usually raised in highly stable environments. However,  
59 focusing on one environment could underestimate the factors that occur over the whole  
60 range of environments (Lewontin, 1974), triggering a situation where specialised  
61 animals could be favoured (Kolmodin *et al.*, 2003). The net result would be a  
62 specialisation process that could alter the way selected animals acquire and allocate  
63 resources (Saviotto *et al.*, 2015). In fact, current genetic types are the consequence of  
64 their whole genetic background (e.g. criteria used to select animals for the generation  
65 0 of the line and criteria used during the selection process; Ragab and Baselga, 2011;  
66 Mínguez *et al.*, 2015). Moreover, selection exclusively for productive criteria could be  
67 accompanied by undesirable negative side effects in behavioural, physiological or  
68 immunological traits (Rauw *et al.*, 1998). Consequently, strategies addressed to obtain  
69 productive but also balanced and functional animals under commercial conditions  
70 could be a more sustainable strategy in the long term. These strategies could be  
71 related to genetic selection, but also to specific-nutrition for each genetic type  
72 according to their genetic background.

73 This is the last of three consecutive scientific papers that aim to evaluate the effect of  
74 energy source of the diet on different genetic types. The main hypothesis of the series  
75 is that varying the main energy source of the diet we could alter the way each genetic  
76 type acquires and allocates resources over time, impacting in the immunological status  
77 of females or their fitness and productivity. In the first paper, we investigated the way  
78 three genetic types differing greatly in their genetic background acquire and allocate  
79 resources when fed with diets specially designed to influence either the milk production  
80 or body reserves (Arnau-Bonachera *et al.*, 2017). In the second paper, we investigated

81 parameters related to the immune system of these genetic types across time and how  
82 previous diets affected them (Penadés et al., 2017). In this work, we aimed to evaluate:  
83 (i) The effects of energy source of the diet and genetic type on productive, functional  
84 and fitness traits. (ii) The impact of feed energy source on these traits for each genetic  
85 type over time according to its genetic background.

## 86 **Material and methods**

87 The experimental procedure was approved by the Animal Welfare Ethics Committee  
88 of the Universitat Politècnica de València (UPV) and carried out following Spanish  
89 Royal Decree 53/2013 on the protection of animals used for scientific purposes and  
90 the recommendations of the European Group on Rabbit Nutrition (Fernández-  
91 Carmona *et al.*, 2005).

### 92 *Animals*

93 A total of 203 female rabbits were used from their first artificial insemination (AI; 19  
94 weeks old) until their sixth parturition (from December 2011 to April 2013). Rabbit  
95 females belonged to three genetic types developed at the Institute for Animal Science  
96 and Technology of the Universitat Politècnica de València (UPV), differing greatly on  
97 their breeding goals. Line H (n=66), founded by hyper-prolific criteria at birth and  
98 selected by litter size at weaning; line LP (n=67), founded by functional hyper-longevity  
99 characterised by a high robustness; line R (n=70), selected for average daily gain  
100 during the growing period. For a further description of the lines, see (Arnau-Bonachera  
101 *et al.*, 2017).

### 102 *Diets*

103 Two experimental diets were formulated and pelleted, according to the  
104 recommendations of De Blas and Mateos (2010) for reproductive rabbit does,  
105 enhancing major differences in energy source. CS diet was prepared promoting cereal  
106 starch [237 g of starch and 21 g of ether extract (EE) per kg DM], whereas in the AF  
107 diet part of the starch was replaced by animal fat (105 g of starch and 86 g of EE per  
108 kg DM). Nevertheless, both diets were design to be isoenergetic and isoproteic [on av.  
109 11.3 MJ of digestible energy (DE) and 126 g of digestible protein per kg DM]. For a  
110 further description of the diets, see (Arnau-Bonachera *et al.*, 2017).

### 111 *Experimental procedure*

112 Animals were housed under conventional environmental conditions (average daily  
113 temperatures varying from 13.3 to 26.1 °C), with an alternating cycle of 16 h of light  
114 and 8 h of darkness. At 19 weeks of age, all the female rabbits were inseminated (with  
115 pooled semen from their respective lines), and housed in individual cages (700 x 500  
116 x 320 mm). Although not all the females began the experiment at the same time (231  
117 days between the first and the last female), most of them did so during the first three  
118 months, when the lowest temperatures of the experiment were recorded (for details,  
119 see Arnau-Bonachera *et al.*, 2017). The entry of animals from each of the three genetic  
120 types was distributed over time similarly. Despite unintended, this procedure implied  
121 that it was not possible to separate properly the effect of first reproductive cycle from  
122 the effect of low temperature. At day 28 of gestation we provided cages with a nest for  
123 litters. After the first parturition, the animals from the three genetic types were randomly  
124 assigned to one of the reproductive diets. Until this point, all the animals had received  
125 the same commercial diet for reproductive rabbit does. Both experimental diets were  
126 provided *ad libitum* and the animals from each group (within genetic type and  
127 reproduction diet) were homogeneously distributed across the experimental farm.

128 Litters were standardised to 8-9 kits at first parturition and 9-11 onwards. This  
129 procedure was performed to equalise the energetic effort during lactation among  
130 females, in order to compare each genetic type under similar lactational effort. This  
131 procedure also allows us to decrease the data coefficient of variation which increases  
132 the statistical accuracy of the estimates (Fernández-Carmona *et al.*, 2005). Females  
133 were inseminated at 11 days postpartum (dpp) and litters were weaned at 30 dpp.  
134 Status at palpation at eleven days after insemination was recorded to evaluate whether  
135 the female had conceived or not. Non-pregnant females were re-inseminated ten days  
136 after palpation, up to a maximum of three times.

### 137 *Traits*

138 Individual adult life weight (AW; 110 records from 110 females) was considered for  
139 females reaching the sixth parturition as the average weight at effective insemination  
140 of fourth, fifth and sixth reproductive cycles. Maturity of females at effective  
141 insemination was calculated for females reaching the sixth parturition as the weight at  
142 that insemination divided by their AW (617 records from 110 females). Interval between  
143 parturitions was determined as the days between two consecutive parturitions (854  
144 records from 203 females). Conception rate was the percentage of females getting  
145 pregnant at first attempt (854 records from 203 females). Productivity of females (203  
146 records from 203 females) was calculated as the cumulated number of weaned  
147 offspring divided by the time (expressed in years) the female stayed in the experiment  
148 (from first parturition to death or the end of the experiment at sixth parturition). Survival  
149 rate of females was evaluated as the percentage of females at parturition of each  
150 reproductive cycle compared to the initial number of females (203 records from 203  
151 females). Litter size traits were total born, born alive, stillborn (851 records from 203  
152 females), standardised at birth and weaned (660 records from 203 females). Individual

153 weight of the offspring was calculated as the litter weight divided by the litter size for  
154 total born (851 records from 203 females), born alive (792 records from 203 females),  
155 stillborn (383 records from 203 females), standardised at birth (707 records from 203  
156 females) and weaned (657 records from 203 females). Maturity of the offspring was  
157 calculated as the individual weight of the offspring divided by adult weight of their  
158 mother for total born (616 records from 110 females), born alive (581 records from 110  
159 females), stillborn (269 records from 110 females), standardised at birth (503 records  
160 from 110 females) and weaned (479 records from 110 females). Survival rate of the  
161 offspring was recorded for each kit at parturition (8 395 kits) and during lactation (6  
162 769 kits). The cumulated number of offspring per female was evaluated for born alive  
163 and weaned (203 records from 203 females).

#### 164 *Statistical analysis*

165 For the statistical analysis we considered as main effects: Genetic type ( $GT_g$ ; 3 levels;  
166 H, LP, R), energy source of the diet ( $ES_d$ ; 2 levels: AF, CS) and reproductive cycle  
167 ( $RC_r$ ; 5 levels; 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, 4<sup>th</sup>, 5<sup>th</sup>). Depending on the evaluated trait, we used one of  
168 the six models listed below. In these models we included some or all of the main effects  
169 described above and their interactions as fixed effects. In these models 'y' (with the  
170 corresponding subscript) represents one record of a given trait and 'e' (with the  
171 corresponding subscript) the random residual term.

172 Adult live weight, productivity of females, cumulated offspring born alive and cumulated  
173 offspring weaned were analysed using a linear model ([1]; Proc GLM of SAS).

174 [1]  $y_{gd} = GT_g | ES_d + e_{gd}$  (generalized linear models)

175 Interval between parturitions, litter size traits, individual weight and maturity of the  
176 offspring traits were analysed using a linear mixed model ([2]; Proc Mixed of SAS). The

177 error ( $e_{gdri}$ ) and permanent effect of the female ( $p_i$ ) were included as random effects,  
178 considering that the residuals could be decreasingly correlated among reproductive  
179 cycles (assuming that the higher the lag between parturitions, the lower the correlation  
180 between residuals; Littell *et al.*, 1998).

181 [2]  $y_{gdri} = GT_g | ES_d | RC_r + p_i + e_{gdri}$  (linear mixed models)

182 Maturity of females at effective insemination was also analysed using a linear mixed  
183 model [3], but considering that variance could change across reproductive cycles, and  
184 residuals were correlated assuming that the higher the lag was between parturitions,  
185 the lower would be the correlation between residuals (Proc Mixed of SAS).

186 [3]  $y_{gdr} = GT_g | ES_d | RC_r + e_{gdr}$  (linear mixed models)

187 Cumulated survival rate of the females was evaluated using a generalized linear mixed  
188 model [4], with a binomial probability distribution for the response and a logit  
189 transformation  $[\ln(\mu/(1-\mu))]$  as the link function (Proc Glimmix of SAS).

190 [4]  $y_{gdr} = GT_g | ES_d | RC_r + e_{gdr}$  (generalized linear mixed models)

191 Conception rate of females, was evaluated using a generalized linear mixed model [5],  
192 with a binomial probability distribution for the response and a logit transformation  
193  $[\ln(\mu/(1-\mu))]$  as the link function (Proc Glimmix of SAS). The error ( $e_{gdri}$ ) and permanent  
194 effect of the female ( $p_i$ ) were included as random effects.

195 [5]  $y_{gdri} = GT_g | ES_d | RC_r + p_i + e_{gdri}$  (generalized linear mixed models)

196 Survival rate of the offspring at parturition and during lactation were evaluated using a  
197 generalized linear mixed model [6], with a binomial probability distribution for the  
198 response and a logit transformation  $[\ln(\mu/(1-\mu))]$  as the link function (Proc Glimmix of

199 SAS). The error ( $e_{gdri}$ ), the permanent effect of the female ( $p_i$ ), and the effect of the  
200 litter in which the kit was raised ( $c_l$ ), were included as random effects.

201 [6]  $y_{gdri} = GT_g | ES_d | RC_r + p_i + c_l + e_{gdri}$  (generalized linear mixed models)

## 202 **Results**

203 *P-Values* for all the effects tested in the models are presented in Tables S1 and S2 of  
204 the supplementary material. Here we present means of the main effects and the most  
205 relevant interactions. Traits related to females according to the genetic type (H, LP, R)  
206 or diet (AF, CS) are presented in Table 1. R females surviving until sixth parturition  
207 presented an adult weight 37.6% heavier than H and LP females ( $P<0.05$ ). Conception  
208 rate at first attempt was not different between LP and R females, but it was 15  
209 percentage units lower in H females ( $P<0.05$ ). Interval between parturitions was 6 days  
210 shorter for LP females compared to H and R females ( $P<0.05$ ). Productivity and  
211 survival rate up to sixth parturition were higher for LP females (on av. +12 weaned per  
212 year and +37 percentage units of survival rate compared to H and R females;  $P<0.05$ ).  
213 Regarding the energy source of the diet, no significant differences were observed for  
214 these traits. However, some interactions of genetic type with the reproductive cycle  
215 and the diet are presented below.

216 Figure 1 shows the evolution of females' maturity (as proportion of weight compared  
217 to the AW at the effective insemination) depending on the genetic type. At first  
218 insemination, each genetic type presented a different proportion of its adult weight;  
219 Considering females ending the experiment, LP females presented at first  
220 insemination the highest proportion of their AW (+2.9 and +9.1 percentage units  
221 compared to H and R females;  $P<0.05$ ), whereas H females presented a higher  
222 proportion compared to R females (+6.2 percentage units;  $P<0.05$ ). Moreover, LP

223 females reached the 95% of adult weight at second reproductive cycle, whereas H and  
224 R females did at third. Figure 2 shows the evolution of cumulated survival rate of  
225 females at parturition throughout the reproductive cycles depending on the genetic  
226 type. At second parturition, LP animals presented a significantly higher survival rate  
227 compared to H and R animals (94 vs. 77 and 77%, respectively;  $P<0.05$ ), and this  
228 difference was maintained or even increased from this point on (72 vs. 42 and 29% at  
229 sixth parturition, respectively;  $P<0.05$ ).

230 Conception rate at first attempt varied depending on genetic type, energy source and  
231 reproductive cycle (Figure 3). When nulliparous, no evidence for any difference among  
232 groups was found, but different patterns were observed from this point on. Conception  
233 rate of R females decreased over reproductive cycles (27 percentage points lower in  
234 multiparous compared to nulliparous,  $P<0.05$ ) independently of the diet. Decrease in  
235 conception rate with time was less evident for LP females, except for primiparous fed  
236 with CS (-24 percentage points compared to nulliparous,  $P<0.05$ ). Conception rate of  
237 H females was approximately halved from nulliparous to primiparous (on av. from 85%  
238 to 43%, respectively;  $P<0.05$ ). Later, this poor conception rate only increased in H  
239 females fed with AF (+27 percentage points when multiparous compared to  
240 primiparous,  $P<0.05$ ).

241 Traits related with the offspring according to the genetic type or diet are presented in  
242 Table 2. For litter size traits and compared to R females, females from maternal lines  
243 (H and LP) presented higher numbers of live born (on av. 3.8 offspring more;  $P<0.05$ )  
244 and lower numbers of stillborn (on av. 0.8 offspring less;  $P<0.05$ ). Moreover, for the  
245 same standardised litter size at birth (on av. 9.7 offspring), litters from the maternal  
246 lines also presented higher numbers of weaned kits (on av. 0.55 offspring more;  
247  $P<0.05$ ). Survival rate of the offspring was higher for the maternal lines than for R

248 animals (on av. +16 percentage points at birth and +8 percentage points during  
249 suckling;  $P<0.05$ ). At the end of the experiment, H females had 17 more offspring born  
250 alive than R females ( $P<0.05$ ). Nevertheless, LP females presented the highest  
251 number of cumulated live born (+12 and +29 to H and R females, respectively;  $P<0.05$ )  
252 and weaned (on av. +9;  $P<0.05$ ). For traits related to the individual weight of the  
253 offspring, R females had heavier offspring throughout the cycle than H females. In  
254 contrast, LP females had the lightest offspring at birth ( $P<0.05$ ), but they were as heavy  
255 as R at weaning. For individual maturity, R offspring always presented the lowest  
256 maturity rates throughout lactation ( $P<0.05$ ). Compared to LP, H offspring presented a  
257 higher maturity rates at birth, but lower at weaning ( $P<0.05$ ). Regarding the effect of  
258 diet, litters from females fed with CS had 0.9 total born more than those fed with AF  
259 ( $P<0.05$ ). For the individual weight, the offspring of females fed with AF were always  
260 heavier than those of females fed with CS (8% heavier;  $P<0.05$ ).

261 Despite no effect of energy source was observed for survival rate of the offspring  
262 during lactation, an interaction for this trait was observed between energy source,  
263 genetic type and reproductive cycle (Figure 4). In the first lactation, offspring survival  
264 rate in maternal lines with AF was quite poor (on av. 45%) and much lower than those  
265 with CS (20 percentage units lower;  $P<0.05$ ). On the contrary, survival of R offspring  
266 with AF was 25 percentage units higher to those with CS ( $P<0.05$ ). From the second  
267 lactation on, survival of offspring with AF was higher or similar to those with CS,  
268 independently of genetic type. In general, offspring survival rate increased from the  
269 first and the second lactation, but decreased progressively from this point on in R  
270 offspring.

271 Finally, Figure 5 summarises the live history traits for each genetic type according to  
272 the dietary energy source received. LP females were the least affected by diet, only

273 differing in the higher maturity at weaning of their offspring when fed with AF ( $P<0.05$ ).  
274 The survival rate of H females fed with AF until 6<sup>th</sup> parturition was 24 percentage units  
275 higher than those fed with AF ( $P<0.05$ ). In addition, the offspring of H females fed with  
276 AF always presented higher maturity than those fed with CS ( $P<0.05$ ). R females fed  
277 with CS had higher litter size, but were less mature, at parturition ( $P<0.05$ ).

## 278 **Discussion**

### 279 *Energy source*

280 In the present study, we observed that our animal fat enriched diet (AF) resulted in  
281 heavier and more mature offspring at weaning. It was the consequence of the higher  
282 milk yield of females fed with that diet (see first paper of the series; Arnau-Bonachera  
283 *et al.*, 2017), which increased the amount of milk available for each kit. Diet AF also  
284 affected the number and size of offspring at birth differently to our cereal-starch diet  
285 (CS). While females fed on diet CS had more total born with lighter weight, females  
286 fed diet AF delivered fewer but heavier total born. Although the effect of energy source  
287 on litter size at birth has not been properly elucidated (Pascual *et al.*, 2003), Fortun-  
288 Lamothe *et al.* (1999) observed that when lactation and pregnancy overlap, rabbit  
289 females are unable to increase their energy intake to cover both functions and a  
290 competition between the gravid uterus and the mammary gland is then established. In  
291 this scenario, energy source would also have shifted energy partitioning at this point;  
292 when females were fed with a diet rich in an energy source that is primarily used by  
293 the mammary gland (diet AF), less energy would have been available for the initial  
294 gestation process (e.g. higher energy deficit; Fortun-Lamothe and Prunier, 1999).  
295 Fewer offspring of bigger sizes were produced (Vicente *et al.*, 1995). Therefore, it  
296 seems that energy source of the diet also could alter the way concurrent lactating-

297 gestating animals allocate resources when homeorhetic process are involved,  
298 affecting fitness traits.

### 299 *Genetic type*

300 Selection for post-weaning average daily gain is accompanied by an increasing of AW  
301 (Blasco *et al.*, 2003). Consequently, females from paternal lines are heavier than  
302 females from the maternal lines (Pascual *et al.*, 2015). Apart from a greater body  
303 weight, R females were also characterised in the present study by few offspring of  
304 higher weight (Vicente *et al.*, 1995), higher gestational losses (Vicente *et al.*, 2012).  
305 Baselga (2002a) reported 7.7 offspring born, 57 days between parturitions, 4300 g of  
306 live weight at first AI and 600 g of the offspring at weaning as mean values for this line.  
307 These results are in agreement with those shown in the present study. However, that  
308 work reported a lower proportion of stillbirths (11 vs 28%) and lower litter size at  
309 weaning (6.1 vs 7.2) compared to the present study. This discrepancy in the results  
310 could be related to the standardisation of litters at birth we performed. We equalize  
311 litters to compare genetic types under similar lactational effort. However, when litters  
312 were standardised to 9.7 offspring, we forced R females to nurse many offspring of  
313 large size with non-adapted energy intake and milk output (Arnau-Bonachera *et al.*,  
314 2017). In other words, we set the reproductive effort to be much greater than that  
315 initially set by R females' genetic potential. All these facts highlight the difficulty of  
316 comparing such different genetic types, especially if we consider that the  
317 consequences of an increased reproductive effort also depend on genetic type  
318 (Theilgaard *et al.*, 2009). Consequently, this increased reproductive effort could be  
319 related with the low survival rate of the offspring observed for this line during lactation.  
320 Moreover, it could have altered energy balance while females were concurrently  
321 pregnant and lactating (Fortun-Lamothe *et al.*, 1999), increasing the risk of death of

322 unborn offspring and accelerating senescence of females (decreasing conception rate  
323 of females and survival rate of the offspring during lactation with age). Females  
324 reached the first insemination with a lower maturity (interpreted as proportion of their  
325 AW; Figure 3). Both facts, increased reproductive effort and lower maturity at first  
326 insemination, could be related to the low survival rate of R females (Rosell and de la  
327 Fuente, 2009).

328 In contrast, maternal lines were characterised by lower AW with larger litters but lighter  
329 offspring at birth, although it varied between genetic types. LP offspring were lighter  
330 than H offspring at birth but heavier at weaning, due to the higher milk yield of LP  
331 females (Arnau-Bonachera *et al.*, 2017; Savietto *et al.*, 2015). Moreover, LP females  
332 were characterised by a high survival rate at the end of the experiment, which  
333 coincides with the results reported by Sánchez *et al.* (2008) and EL Nagar (2015). On  
334 the other hand, Baselga (2002b) reported for the H line, 10.5 offspring born, 46 days  
335 between parturitions, 3279 g at first insemination, 7.9% of stillbirths and 530 g of the  
336 offspring at weaning as mean values. Except for the large interval between parturitions  
337 we observed, which varied with reproductive cycle and diet (Figure 3), all results are  
338 in agreement with those shown in the present study. Therefore, we have shown that  
339 different genetic types had different features for fertility, number and size of the  
340 offspring and survival of females, suggesting that they prioritise different components  
341 of fitness.

#### 342 *Genetic type x energy source*

343 We observed that different genetic types prioritised different components of fitness,  
344 which has been proposed as being shaped by their genetic background (conditions  
345 and criteria at foundation and during selection; Savietto *et al.*, 2015). These priorities

346 may arise because the environment limits the amount of resources an animal can  
347 acquire, which means they subsequently have to split them among fitness components  
348 (Beilharz and Nitter, 1998). As energy source can alter the way animals allocate  
349 energy, it could affect fitness components differently depending on the genetic type.

350 *Paternal line.* When R females were fed with a diet promoting milk yield (AF), it initially  
351 improved survival rate of the offspring during lactation (Figure 4) and their individual  
352 weight at weaning (Figure 5). In the first work of this series, we reported that R females  
353 increased their lactational effort as lactation progress more than maternal lines (Arnau-  
354 Bonachera *et al.*, 2017). We could not elucidate whether it was the consequence of  
355 selection for growth rate or the consequence of the standardization process we  
356 performed. Anyway, it seems that in that situation, the competition between mammary  
357 gland and gravid uterus would be higher for R females fed with AF than for maternal  
358 lines fed with the same diet, producing fewer but heavier offspring (Figure 5).  
359 Moreover, as the reproductive effort was set even further than they naturally would  
360 have done when they were fed with AF, it increased the negative effects of the  
361 excessive reproductive effort with age (e.g. higher decrease of survival rate of the  
362 offspring during lactation between second and fifth RC; Figure 4).

363 *Maternal lines.* The low survival rate of the offspring during suckling (less than 50%) of  
364 primiparous females from the maternal lines fed with AF was directly related to the low  
365 milk yield of these females during this period (Arnau-Bonachera *et al.*, 2017).  
366 Considering the low temperature existing in the farm during that period, we could not  
367 elucidate properly whether these results were the consequence of the reproductive  
368 cycle, temperature or an interaction between them (see Arnau-Bonachera *et al.*, 2017).  
369 Anyway, the lower milk yield of females from the maternal lines fed AF under these  
370 conditions could be a strategy which improves fitness. For example, in poor or

371 uncertain environments, animals that continue investing in the current litter are  
372 seriously penalised if doing so reduces their chances of survival. On the contrary, those  
373 animals reducing the investment in the current litter would live longer to explore more  
374 reproductive events, while waiting for better conditions (Hrdy, 1979; Stearns, 1992). It  
375 seems that this strategy could have been an attempt by the maternal lines to cope with  
376 that challenging situation (low temperatures with incomplete development): females  
377 fed with AF did not live less than those fed with CS and they offset the lower survival  
378 rate during the first reproductive cycle with a higher rate in subsequent cycles.

379 Criteria at foundation and for selection of H females were focused on prolificacy. In a  
380 selection context where large litters in a short interval are demanded by farmers and  
381 breeders, females have little time to recover fat between weaning and the next  
382 parturition. In this context, it seems that H females tend to store body reserves  
383 whenever possible to cope with future reproduction (Arnau-Bonachera *et al.*, 2017)  
384 and to prevent risk arisen from poor body condition (Theilgaard *et al.*, 2006; Sánchez  
385 *et al.*, 2012). However, when fed with a diet promoting the restoration of body reserves  
386 (CS) they could become overfat, increasing the risk of not getting pregnant (Figure 3)  
387 or death (Figure 5). Moreover, this situation could be especially risky if we consider  
388 that H females presented some symptoms of aging of their immune system at second  
389 parturition, which increased with age (Penadés *et al.*, 2017). Therefore, despite the  
390 results from the first reproductive cycle, fitness traits of H females were globally more  
391 favoured when fed with AF compared to CS (Figure 3), not affecting mean productivity  
392 at sixth parturition.

393 LP females have been selected for litter size at weaning over 7 generations. However,  
394 due to the criteria used at the foundation of the line, there are two important goals for  
395 these animals, productivity and survival in commercial farms. Commercial farms are

396 characterised by a great variability in their environmental control, size, management  
397 or reproductive rhythm (Rosell and de la Fuente, 2009), leading to highly variable  
398 environments between and within farms. It has been proposed (Philippi and Seger,  
399 1989; Olofsson *et al.*, 2009) that in highly variable and unpredictable environments,  
400 strategies addressed to reduce risks could be better strategies than adaptive ones  
401 (generalist instead of specialist). For example, amongst other reasons, mammals  
402 accumulate reserves to cope with the uncertainty of food in the future. However, the  
403 probability of a female of not finding food in a farm is close to zero, so the accumulation  
404 of excess body reserves for their later utilisation may not offset the risk of being too fat  
405 or too thin in the long term (Theilgaard *et al.*, 2006). In other words, the uncertainty is  
406 not based on food availability.

407 By using a particular pattern for acquisition and allocation of resources (Arnau-  
408 Bonachera *et al.*, 2017), LP animals could have adopted this generalist safety as a  
409 way to be productive and cope with the uncertainty of farms conditions (Saviotto *et al.*,  
410 2015). We reported that LP females had a great acquisition capacity, but they were  
411 able to adapt their energy intake and allocation of resources to changing requirements.  
412 This way, they could safeguard body condition and reach critical points of their life  
413 trajectory in good metabolic or immunological status (Arnau-Bonachera *et al.*, 2017;  
414 Penadés *et al.*, 2017). For example, at second parturition, females are still growing  
415 and their acquisition capacity is not fully developed, but they are under highly  
416 productive conditions. Consequently, this point has been described as the moment  
417 with the highest risk for females to be removed from farms (Rosell and de la Fuente,  
418 2009). However, at this point, LP females presented high values of blood glucose, low  
419 levels of NEFA and BOHB (Arnau-Bonachera *et al.*, 2017) and higher counts of  
420 lymphocytes T and B (Penadés *et al.*, 2017), which suggest a better metabolic and

421 immunologic status at this point. Therefore, the main consequence of this low risk  
422 strategy would be the highest survival rate at second parturition of LP females (Figure  
423 2). Moreover, this higher survival remained until the end of the experiment  
424 independently of the diet (Figure 5). The higher proportion of weight compared to AW  
425 (used as indicator of degree of maturity) and the lower incidence of diet or reproductive  
426 cycle on fertility would also have reduced the risk of death or culling under farm  
427 conditions (Rosell and de la Fuente, 2009). So, from all the possible strategies allowing  
428 animals to be productive, LP animals seem to use the one minimising risks, which  
429 enabled them to survive and become highly productive in the long term with little  
430 influence of energy source of the diet.

#### 431 **Conclusions**

432 Genetic types differing greatly in their genetic background seem to prioritise different  
433 fitness components. Females from the paternal line (R females) were characterised by  
434 greater adult weight and few but heavier offspring, although it seems they could be  
435 more immature at weaning. When R females were fed a diet with animal fat as main  
436 energy source, they invested more in the current litter, whereas when fed a diet with  
437 cereal starch as main energy source, it seems that they invested more in recovering  
438 for future reproduction. On the contrary, females from the maternal lines were smaller  
439 and had numerous but lighter offspring, but each genetic type used different strategies.  
440 The strategy used by H females makes them more sensitive to the energy source of  
441 the diet, increasing the risk of failing to ensure future reproduction when fed with cereal  
442 starch (low conception rate in multiparous females or higher mortality of females).  
443 However, the strategy used by LP females seems to be more generalist, allowing them  
444 to ensure high performance of the current litter without neglecting future reproduction  
445 and with less sensitivity to the energy source than for the other genetic types.

446 Therefore, energy source of the diet, which affected to energy acquisition and  
447 allocation, also affected the fitness components. Moreover, the response to energy  
448 source varied with genetic types. It seems that more specialised genetic types, which  
449 base reproduction on body reserves, were more sensitive to energy source than the  
450 more generalist and robust type, which base reproduction on energy intake.

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**Table 1** Effect of genetic type and energy source on rabbit female traits

|  | n   |     | Genetic type <sup>1</sup> |                   |                   |                  |         | Energy source |               |                  |         |
|--|-----|-----|---------------------------|-------------------|-------------------|------------------|---------|---------------|---------------|------------------|---------|
|  |     |     | H                         | LP                | R                 | SEM <sup>2</sup> | P-Value | Animal Fat    | Cereal Starch | SEM <sup>2</sup> | P-Value |
| Weight at first AI (kg)                                  | 203 | 203 | 3.62 <sup>a</sup>         | 3.65 <sup>a</sup> | 4.61 <sup>b</sup> | 0.040            | <0.001  | 3.97          | 3.94          | 0.033            | 0.545   |
| Adult live weight <sup>3</sup> (AW; kg)                  | 110 | 110 | 4.10 <sup>a</sup>         | 4.19 <sup>a</sup> | 5.71 <sup>b</sup> | 0.077            | <0.001  | 4.69          | 4.64          | 0.070            | 0.287   |
| Conception rate (pregnant at 1 <sup>st</sup> attempt; %) | 203 | 854 | 63 <sup>a</sup>           | 79 <sup>b</sup>   | 78 <sup>b</sup>   | -                | 0.004   | 74            | 73            | -                | 0.867   |
| Interval between parturitions (days)                     | 203 | 854 | 56 <sup>b</sup>           | 49 <sup>a</sup>   | 55 <sup>b</sup>   | 1.3              | <0.001  | 52            | 55            | 1.1              | 0.098   |
| Productivity (weaned per year)                           | 203 | 203 | 33 <sup>a</sup>           | 43 <sup>b</sup>   | 29 <sup>a</sup>   | 1.9              | <0.001  | 35            | 35            | 1.5              | 0.132   |
| Survival rate up to 6 <sup>th</sup> parturition (%)      | 203 | 203 | 42 <sup>a</sup>           | 72 <sup>b</sup>   | 28 <sup>a</sup>   | -                | <0.001  | 47            | 48            | -                | 0.038   |

n: Number of animals. Records: Number of observations per trait. <sup>1</sup>Line H: maternal line characterised by prolificacy. Line LP: maternal line characterised by functional longevity. Line R: Paternal line characterised by daily gain during the growing period. <sup>2</sup>SEM: Pooled standard error of the means for traits analysed with linear mixed models. <sup>3</sup>AW calculated as the average weight at fourth, fifth and sixth insemination for females reaching sixth parturition. <sup>a,b</sup> Means in a row within an effect not sharing superscript differ significantly ( $P<0.05$ ).

**Table 2** Effect of genetic type and energy source on offspring traits of rabbit females

|   | n     | Records | Genetic type <sup>1</sup> |                   |                   |                  |         | Energy source     |                   |                  |         |
|---|-------|---------|---------------------------|-------------------|-------------------|------------------|---------|-------------------|-------------------|------------------|---------|
|   |       |         | H                         | LP                | R                 | SEM <sup>2</sup> | P-Value | Animal Fat        | Cereal Starch     | SEM <sup>2</sup> | P-Value |
| <b>Litter size</b>                                      |       |         |                           |                   |                   |                  |         |                   |                   |                  |         |
| Total born  | 203   | 851     | 10.8 <sup>b</sup>         | 10.6 <sup>b</sup> | 7.7 <sup>a</sup>  | 0.32             | <0.001  | 9.2 <sup>a</sup>  | 10.1 <sup>b</sup> | 0.26             | 0.016   |
| Born alive  | 203   | 851     | 9.3 <sup>b</sup>          | 9.5 <sup>b</sup>  | 5.6 <sup>a</sup>  | 0.35             | <0.001  | 7.8               | 8.5               | 0.29             | 0.061   |
| Stillborn   | 203   | 851     | 1.4 <sup>a</sup>          | 1.0 <sup>a</sup>  | 2.0 <sup>b</sup>  | 0.18             | <0.001  | 1.4               | 1.6               | 0.15             | 0.554   |
| Standardised  | 203   | 678     | 9.7                       | 9.7               | 9.6               | 0.03             | 0.240   | 9.7               | 9.7               | 0.03             | 0.947   |
| Weaned  | 203   | 660     | 7.7 <sup>b</sup>          | 7.8 <sup>b</sup>  | 7.2 <sup>a</sup>  | 0.15             | 0.013   | 7.6               | 7.5               | 0.12             | 0.577   |
| <b>Survival rate (%)</b>                                |       |         |                           |                   |                   |                  |         |                   |                   |                  |         |
| At parturition  | 8 395 | 8 395   | 87 <sup>b</sup>           | 89 <sup>b</sup>   | 72 <sup>a</sup>   | -                | <0.001  | 84                | 84                | -                | 0.919   |
| During suckling   | 6 769 | 6 769   | 73 <sup>b</sup>           | 77 <sup>b</sup>   | 67 <sup>a</sup>   | -                | <0.001  | 74                | 72                | -                | 0.393   |
| <b>Cumulated number at 5<sup>th</sup> weaning</b>       |       |         |                           |                   |                   |                  |         |                   |                   |                  |         |
| Born alive  | 203   | 203     | 37 <sup>b</sup>           | 49 <sup>c</sup>   | 20 <sup>a</sup>   | 1.7              | <0.001  | 34                | 36                | 2.1              | 0.478   |
| Weaned  | 203   | 203     | 23 <sup>a</sup>           | 30 <sup>b</sup>   | 19 <sup>a</sup>   | 1.7              | <0.001  | 24                | 25                | 1.4              | 0.753   |
| <b>Individual weight (g)</b>                            |       |         |                           |                   |                   |                  |         |                   |                   |                  |         |
| Total born  | 203   | 851     | 55.9 <sup>b</sup>         | 52.8 <sup>a</sup> | 62.3 <sup>c</sup> | 0.95             | <0.001  | 58.6 <sup>b</sup> | 55.4 <sup>a</sup> | 0.78             | 0.004   |
| Born alive  | 203   | 792     | 56.6 <sup>b</sup>         | 53.7 <sup>a</sup> | 65.5 <sup>c</sup> | 0.94             | <0.001  | 60.6 <sup>b</sup> | 56.6 <sup>a</sup> | 0.76             | <0.001  |
| Stillborn   | 203   | 383     | 39.7 <sup>a</sup>         | 41.1 <sup>a</sup> | 49.0 <sup>b</sup> | 2.5              | 0.017   | 46.6 <sup>b</sup> | 39.9 <sup>a</sup> | 2.0              | 0.022   |
| Standardised  | 203   | 707     | 54.2 <sup>b</sup>         | 51.8 <sup>a</sup> | 59.6 <sup>c</sup> | 0.63             | <0.001  | 55.9 <sup>b</sup> | 54.5 <sup>a</sup> | 0.52             | 0.049   |
| Weaned  | 203   | 657     | 542 <sup>a</sup>          | 600 <sup>b</sup>  | 586 <sup>b</sup>  | 8.2              | <0.001  | 596 <sup>b</sup>  | 556 <sup>a</sup>  | 6.5              | <0.001  |
| <b>Individual maturity<sup>3</sup> (% of female AW)</b> |       |         |                           |                   |                   |                  |         |                   |                   |                  |         |
| Total born  | 110   | 616     | 1.44 <sup>c</sup>         | 1.34 <sup>b</sup> | 1.01 <sup>a</sup> | 0.022            | <0.001  | 1.26              | 1.27              | 0.018            | 0.827   |
| Born alive  | 110   | 581     | 1.47 <sup>c</sup>         | 1.36 <sup>b</sup> | 1.04 <sup>a</sup> | 0.019            | <0.001  | 1.29              | 1.29              | 0.015            | 0.879   |
| Stillborn   | 110   | 269     | 0.97                      | 1.06              | 0.84              | 0.078            | 0.124   | 1.05 <sup>b</sup> | 0.87 <sup>a</sup> | 0.061            | 0.042   |
| Standardised  | 110   | 503     | 1.38 <sup>c</sup>         | 1.29 <sup>b</sup> | 1.06 <sup>a</sup> | 0.021            | <0.001  | 1.25              | 1.24              | 0.017            | 0.819   |
| Weaned  | 110   | 479     | 13.8 <sup>b</sup>         | 15.0 <sup>c</sup> | 10.6 <sup>a</sup> | 0.26             | <0.001  | 13.6 <sup>b</sup> | 12.8 <sup>a</sup> | 0.21             | 0.009   |

n: Number of animals. Records: Number of observations per trait. <sup>1</sup>Line H: maternal line characterised by prolificacy. Line LP: maternal line characterised by functional longevity. Line R: Paternal line characterised by high daily gain during the growing period. <sup>2</sup>SEM: Pooled standard error of the means for traits analysed with linear mixed models. <sup>3</sup>Estimated exclusively with litters from females reaching the sixth parturition. <sup>a,b,c</sup> Means in a row within an effect not sharing superscript differ significantly ( $P<0.05$ ).

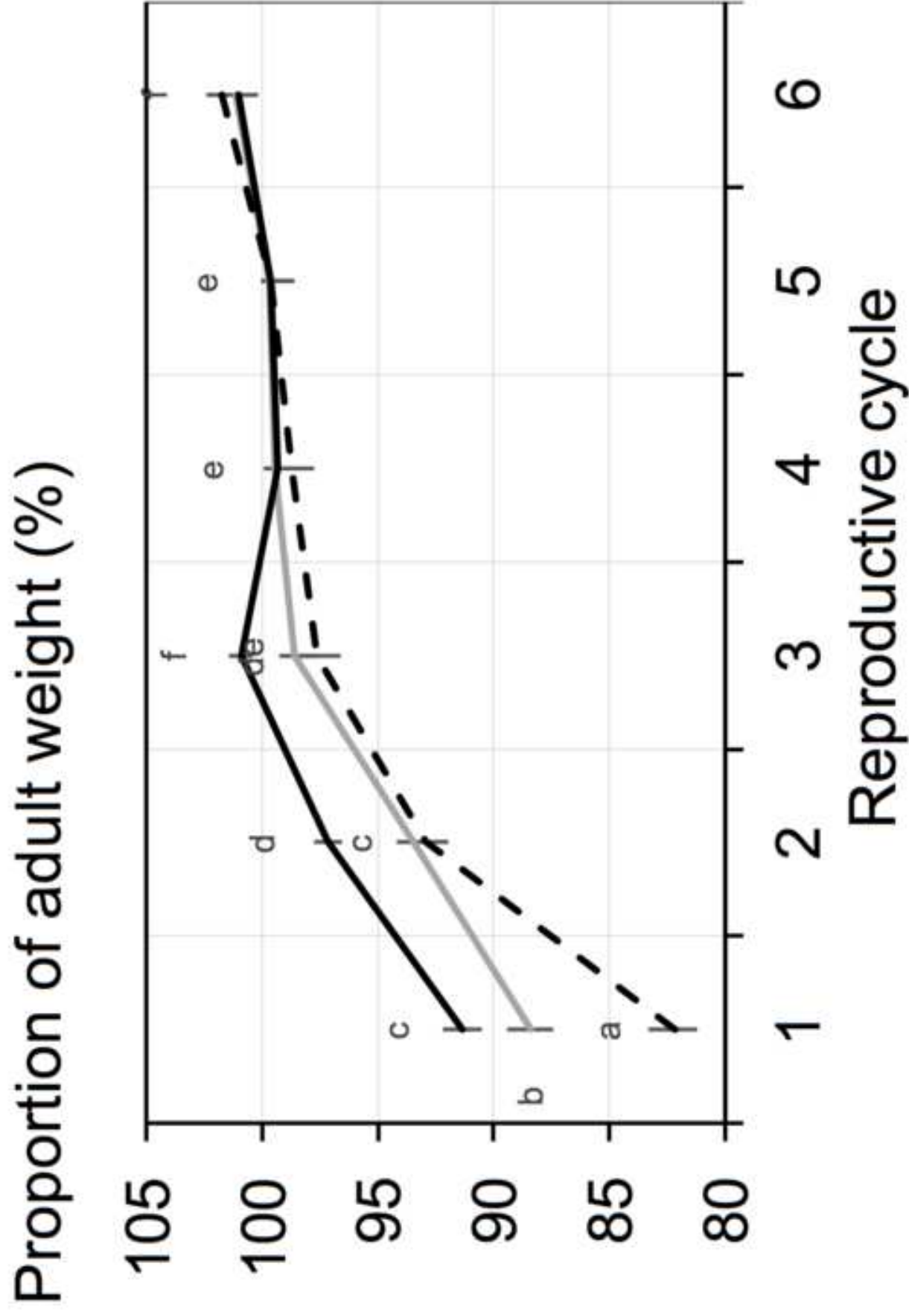
541 **Figure 1** For rabbit females reaching the 5<sup>th</sup> reproductive cycle: Percentage of adult  
542 weight (AW) at insemination for the subsequent RC depending on the genetic type [H  
543 in dark grey, LP in black, R in black dashed line]. AW calculated as the average  
544 weight at fourth, fifth and sixth insemination for females reaching sixth parturition.  
545 <sup>a,b,c,d,e,f</sup> Means not sharing letter differs significantly ( $P<0.05$ ).

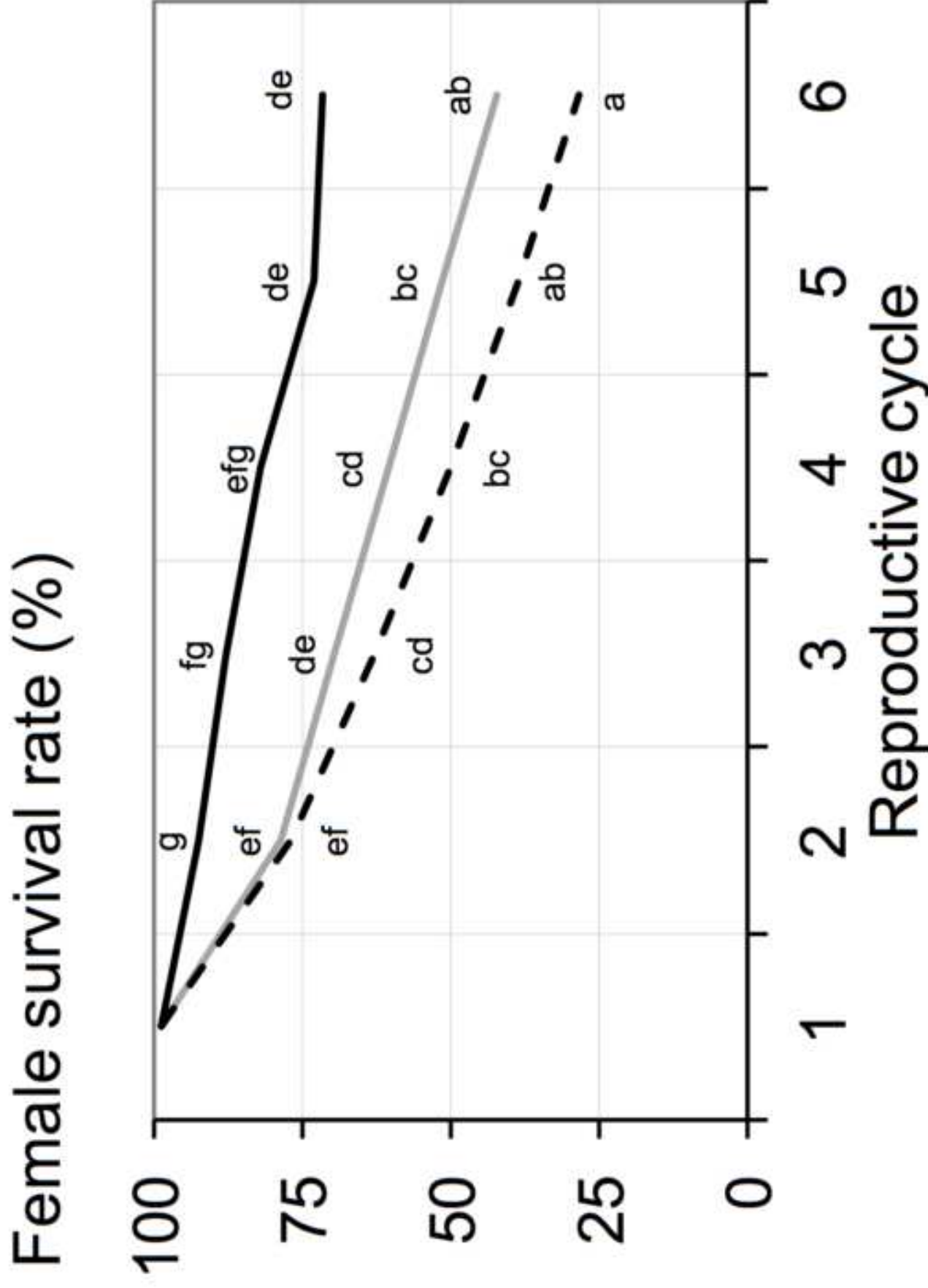
546 **Figure 2** Cumulated survival rate of rabbit females (%) at parturition in each  
547 reproductive cycle depending on genetic type [H in dark grey, LP in black, R in black  
548 dashed line]. <sup>a,b,c,d,e,f,g</sup> Means not sharing letter differs significantly ( $P<0.05$ ).

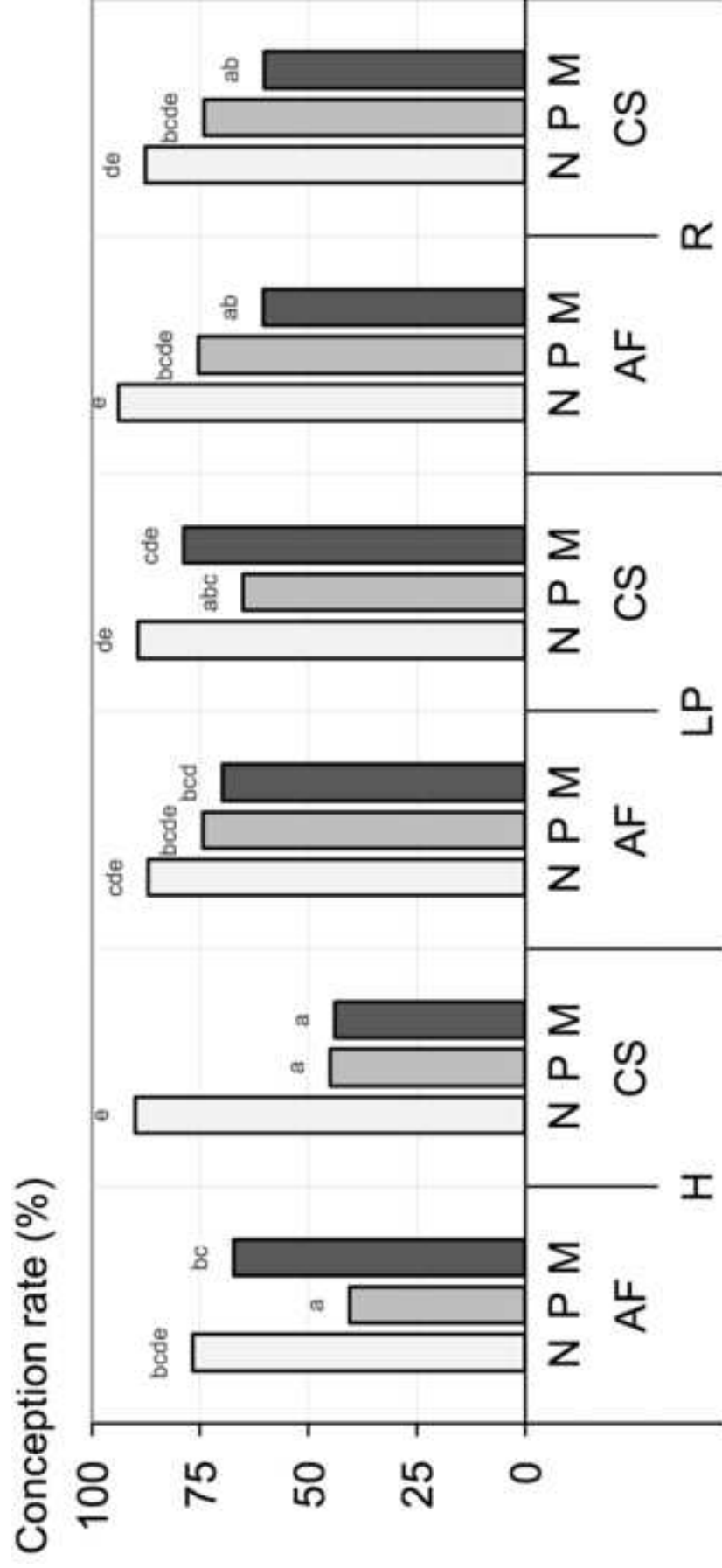
549 **Figure 3** Conception rate (Pregnant at first attempt; %) of rabbit females for  
550 nulliparous (N, light grey) primiparous (P, medium grey) and multiparous (M, dark  
551 grey) depending on genetic type (H,LP,R) and energy source of the diet (AF, CS).  
552 <sup>a,b,c,d,e</sup> Means not sharing lower case letter differ significantly ( $P<0.05$ ).

553 **Figure 4** Offspring survival rate of rabbit females during lactation in each reproductive  
554 cycle (RC) according to the energy source of the diet [AF (○);CS (●)]. Panel A: Line H,  
555 Panel B: Line LP, Panel C: Line R. <sup>a,b,c,d,e,f</sup> Means not sharing letter differ significantly  
556 ( $P<0.05$ ).

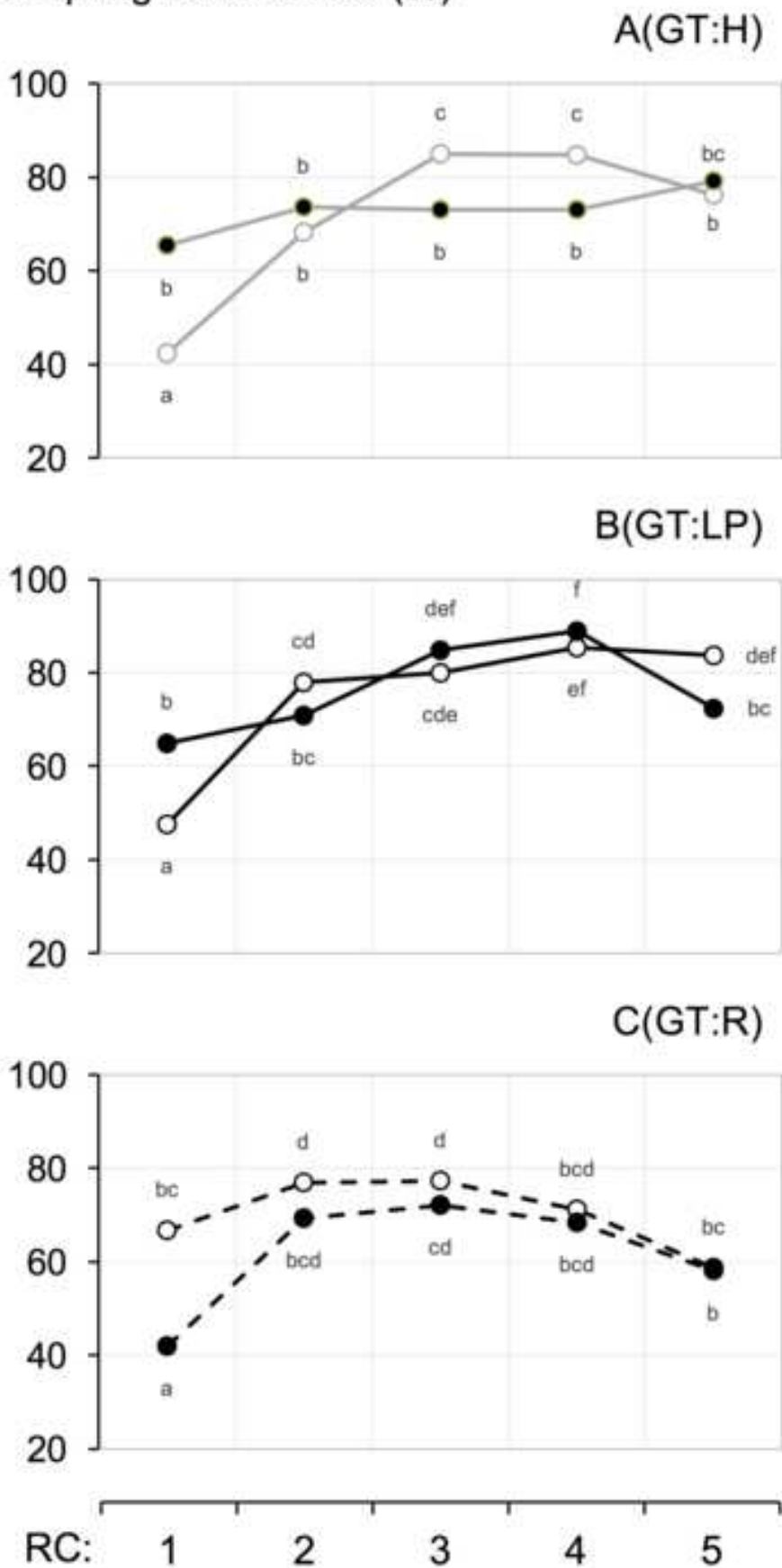
557 **Figure 5** Live history traits of rabbit females for each genetic type (H, LP, R) depending  
558 on the energy source of the diet (AF: dashed line and white background, CS: solid line  
559 and grey background). Total litter size (TLS), Individual offspring weight at parturition  
560 (OWP) and individual offspring weight at weaning (OWW) expressed in standard  
561 deviation ( $\sigma$ ) compared to the global mean ( $\mu$ ). Offspring survival rate at parturition  
562 (OSRP), offspring survival rate at weaning (OSRW), doe conception rate (DCR) and  
563 doe survival rate (DSR) expressed as rate (%) compared to the mean ( $\mu$ ). \* Means for  
564 diets within a genetic type of the corresponding trait differ significantly ( $P<0.05$ ).

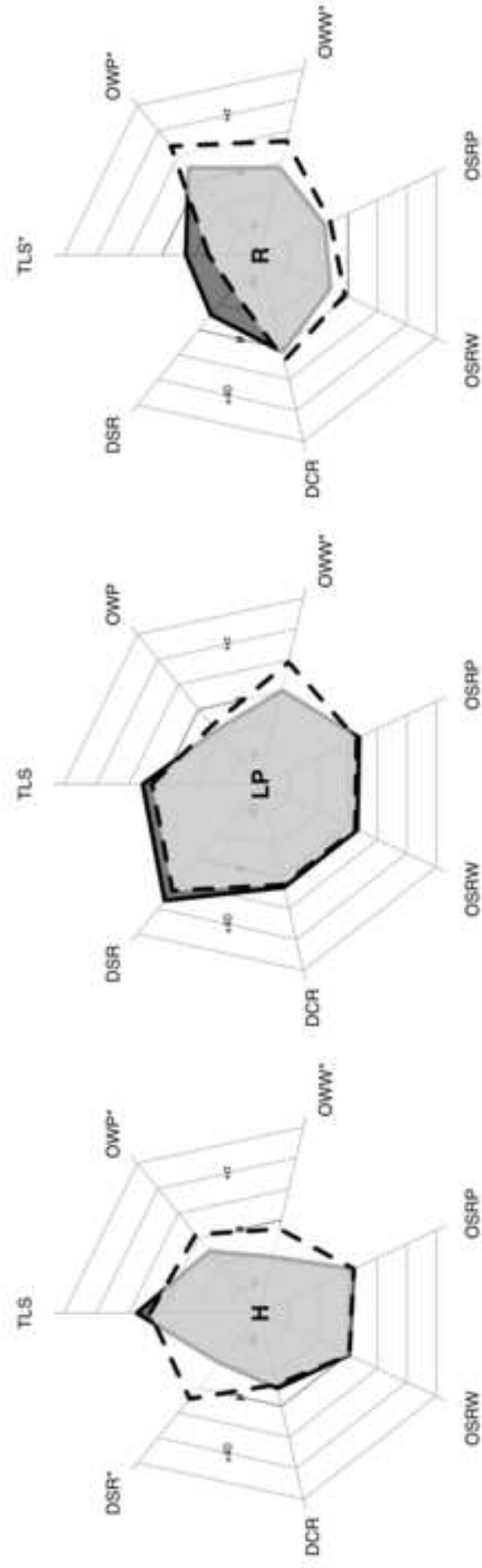






Offspring survival rate (%)





### Long-term implications of feed energy source in different genetic types of reproductive rabbit females. III. Fitness and productivity

A. Arnau-Bonachera, D. Savietto and J.J. Pascual.

**Table S1** *P-Values for all the effects considered in the models used to analyse female traits*

|                                | Genetic type (GT) | Energy source (ES) | Reproductive cycle (RC) | GTxES  | GTxRC  | ESxRC  | GTxESxRC |
|--------------------------------|-------------------|--------------------|-------------------------|--------|--------|--------|----------|
| Weight at first AI             | <.0001            | 0.5449             | -                       | 0.8787 | -      | -      | -        |
| Adult live weight <sup>1</sup> | <.0001            | 0.2869             | -                       | 0.9433 | -      | -      | -        |
| Conception rate <sup>2</sup>   | 0.0039            | 0.8660             | <.0001                  | 0.7524 | 0.1031 | 0.8135 | 0.0414   |
| IBP <sup>3</sup>               | 0.0002            | 0.0979             | 0.1336                  | 0.2467 | 0.1524 | 0.8822 | 0.0535   |
| Productivity <sup>4</sup>      | <.0001            | 0.7504             | -                       | 0.1320 | -      | -      | -        |
| Survival rate <sup>5</sup>     | <.0001            | 0.8608             | -                       | 0.0375 | -      | -      | -        |

<sup>1</sup>AW calculated as the average weight at fourth, fifth and sixth insemination for females reaching sixth parturition.

<sup>2</sup> Pregnant at first attempt. <sup>3</sup> IBP: Interval between parturitions. <sup>4</sup> Weaned per year. <sup>5</sup> Percentage of females reaching up to 6<sup>th</sup> parturition. – Effect not included in the model.

**Table S2** *P-Values for all the effects considered in the models used to analyse litter traits*

|   | <b>Genetic<br/>type<br/>(GT)</b> | <b>Energy<br/>source<br/>(ES)</b> | <b>Reproductive<br/>cycle<br/>(RC)</b> | <b>GTxES</b> | <b>GTxRC</b> | <b>ESxRC</b> | <b>GTxESxRC</b> |
|---|----------------------------------|-----------------------------------|--|--------------|--------------|--------------|-----------------|
| Litter size                                 |                                  |                                   |  |              |              |              |                 |
| Total born                                  | <.0001                           | 0.0162                            | <.0001                                 | 0.6519       | 0.5778       | 0.0691       | 0.6050          |
| Born alive                                  | <.0001                           | 0.0606                            | 0.0009                                 | 0.9902       | 0.1661       | 0.4707       | 0.3034          |
| Stillborn                                   | 0.0008                           | 0.5536                            | 0.0772                                 | 0.2230       | 0.5903       | 0.3155       | 0.7402          |
| Standardized                                | 0.0239                           | 0.9472                            | <.0001                                 | 0.8936       | 0.0404       | 0.8776       | 0.9568          |
| Weaned                                      | 0.0133                           | 0.5766                            | <.0001                                 | 0.0481       | 0.0197       | 0.2386       | 0.0259          |
| Survival rate                               |                                  |                                   |  |              |              |              |                 |
| At parturition                              | <.0001                           | 0.9197                            | 0.0023                                 | 0.7657       | 0.0002       | 0.0073       | 0.0006          |
| During suckling                             | 0.0024                           | 0.3933                            | <.0001                                 | 0.3320       | <.0001       | 0.0591       | <.0001          |
| Cumulated number at 5 <sup>th</sup> weaning |                                  |                                   |  |              |              |              |                 |
| Born alive                                  | <.0001                           | 0.4776                            | -                                      | 0.4618       | -            | -            | -               |
| Weaned                                      | <.0001                           | 0.7530                            | -                                      | 0.1776       | -            | -            | -               |
| Individual weight                           |                                  |                                   |  |              |              |              |                 |
| Total born                                  | <.0001                           | 0.0036                            | 0.1606                                 | 0.3171       | 0.0299       | 0.0751       | 0.1454          |
| Born alive                                  | <.0001                           | 0.0003                            | 0.0340                                 | 0.2036       | 0.0768       | 0.0340       | 0.3419          |
| Stillborn                                   | 0.0166                           | 0.0215                            | 0.9558                                 | 0.0408       | 0.0612       | 0.0150       | 0.1976          |
| Standardized                                | <.0001                           | 0.0525                            | <.0001                                 | 0.5289       | 0.3522       | 0.3737       | 0.1475          |
| Weaned                                      | <.0001                           | <.0001                            | 0.0255                                 | 0.9973       | 0.4515       | 0.8540       | 0.8752          |
| Individual maturity <sup>1</sup>            |                                  |                                   |  |              |              |              |                 |
| Total born                                  | <.0001                           | 0.8272                            | <.0001                                 | 0.6799       | 0.0059       | 0.3656       | 0.0376          |
| Born alive                                  | <.0001                           | 0.8797                            | 0.1950                                 | 0.9027       | <.0001       | 0.8139       | 0.3034          |
| Stillborn                                   | 0.1244                           | 0.0423                            | 0.5185                                 | 0.0380       | 0.0359       | 0.1105       | 0.2711          |
| Standardized                                | <.0001                           | 0.8195                            | <.0001                                 | 0.9548       | 0.4348       | 0.6065       | 0.0097          |
| Weaned                                      | <.0001                           | 0.0094                            | 0.2041                                 | 0.9565       | 0.7034       | 0.5802       | 0.6903          |

<sup>3</sup> Estimated exclusively with litters from females reaching the sixth parturition as the ratio