World Rabbit Congress
2016
Qingdao, China

PROCEEDINGS OF THE 11th WORLD RABBIT CONGRESS

Qingdao (China) - June 15-18, 2016
ISSN 2308-1910

Session
Breeding and Genetics

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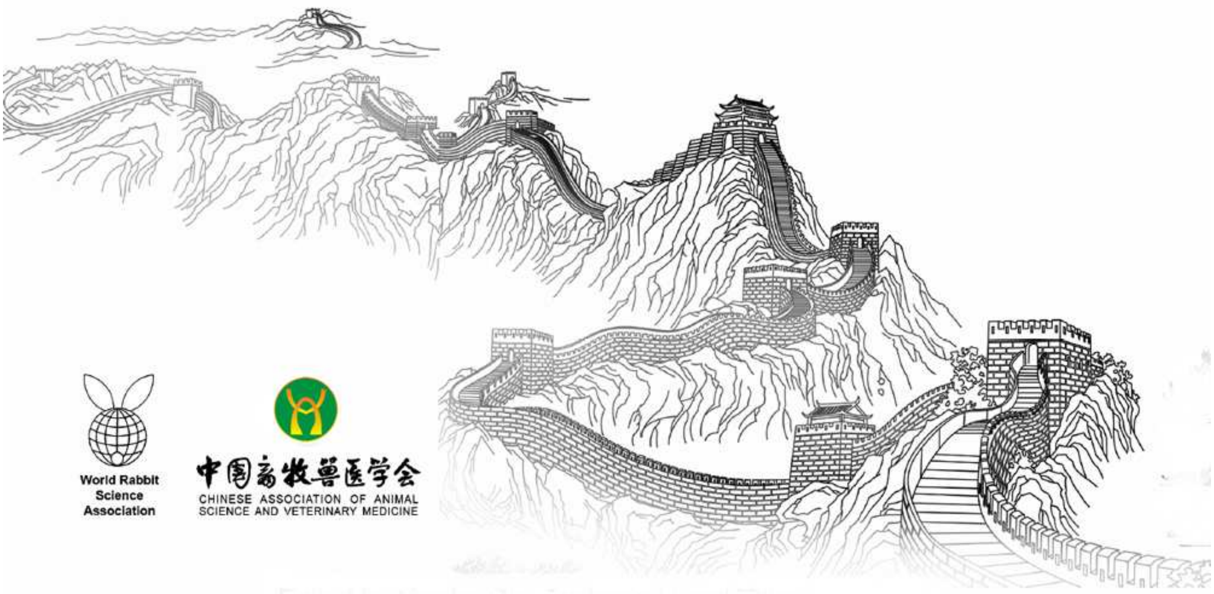
Full text of the communication

How to cite this paper :
Savietto D., Ródenas L., Martínez-Paredes E., Pascual J.J., 2016 - Adjusting the age pyramid to promote a more sustainable and healthful rabbit production system. *Proceedings 11th World Rabbit Congress - June 15-18, 2016 - Qingdao - China, 123-126.*



World Rabbit Science Association

中国畜牧兽医学会
CHINESE ASSOCIATION OF ANIMAL SCIENCE AND VETERINARY MEDICINE

ADJUSTING THE AGE PYRAMID TO PROMOTE A MORE SUSTAINABLE AND HEALTHFUL RABBIT PRODUCTION SYSTEM

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ABSTRACT

On average, a commercial rabbit female currently has no more than six litters her entire life, leading to a young age-structure. Because the investment in maintenance that prolongs lifespan trades-off with early reproductive effort, a more sustainable and healthful rabbit-production system would increase the proportion of females with more than six litters. The arguments for this suggestion are based in parts of life-history theory that have been experimentally confirmed in other organisms. Here we explore the effect on the age-structure of arbitrarily lowering the overall culling rate of a typical commercial population by 25 points of percentage (from 191 to 138 females culled). When we assumed a lower culling rate, we found that the age-structure of this commercial population would change to a more balanced proportion of mature (*i.e.* females having six or more litters) and young females. The new-age structure would improve adaptation to local conditions, favor health and robustness, and lengthen potential lifespan.

Key words: Rabbit, Age-structure, Lifespan, Health, Life-history theory.

INTRODUCTION

This paper focuses on the beneficial effects of changing the age-structure of a rabbit population to promote better health and reproductive performance. The concepts used here are derived from life-history theory. Life-history theory is the part of evolutionary biology that aims to understand the variability in the strategies that different species and individuals adopt to achieve reproductive success (Stearns, 1992). The questions shared by evolutionary biologists and by animal scientists interested in efficient animal production are these: 1) How fast should an animal develop? 2) At which age and size should it mature and start reproducing? 3) How many and how large should its offspring be? 4) How many times should it reproduce? and 5) How long should it live?

Animal breeders have long selected rabbits to grow faster (Estany *et al.*, 1992; Rochambeau *et al.*, 1996; Gómez *et al.*, 1999) and to have more viable offspring (Estany *et al.*, 1989; García and Baselga, 2002; Garreau *et al.*, 2008), but little attention has been paid to lifespan and the physiological mechanisms that prolong it, including disease resistance. In fact, although a new rabbit line was recently founded from females having exceptionally long productive lives (Sánchez *et al.*, 2008), longevity is still considered a trait of little economic interest (Cartuche *et al.*, 2014), because the costs of rearing a female are diluted by the number of offspring she produces, which take precedence over lifespan.

The dilution argument is reasonable. But it is also reasonable to think that for each additional litter the dilution factor increases. Thus long reproductive lives can be economically beneficial – a scenario not considered by Cartuche *et al.* (2014), who assumed a fixed monthly-culling rate of 10 per cent, which is a value very close to that observed in commercial farms (Rosell and de la Fuente, 2009). The consequence of assuming a fixed culling rate is a limited reproductive life, which in such farms is limited to no more than six litters.

Constant replacement rates can be justified. Animals die for no apparent reason, farmers cull infertile, less productive, and sick animals (Rosell and de la Fuente, 2009), and others are simply replaced by the 'new genetic' that are made available. If natural mortality, infertility and sickness are a stochastic process, then constant replacement rates are only possible if some females with no apparent biological problems are replaced. The consequences of this practice are the risks of replacing a proven female by another that may or may not be more profitable and the evolutionary risk implicit in a young age-structure, which is the evolution of less investment in maintenance and more investment in reproduction. In fact, economic studies, like Cartuche *et al.* (2014), often ignore the negative effect of increasing the reproductive effort or daily weight gain on the immune system (Ferrian *et al.*, 2012; García-Quirós *et al.*, 2014), depleting the global health of the farm.

Here we present a theoretical analysis based on an actual commercial rabbit population to support the argument that a lower culling rate leading to a longer reproductive life would be both economically beneficial and would lead to the evolution of more disease-resistant rabbits.

MATERIAL AND METHODS

Data come from a commercial rabbit population in Spain whose management was described by Savietto *et al.* (2012). In that study a total of 673 females were followed, of which 461 were mated at least once (197 females died and 15 females were culled before reaching mating age). Culling reasons were infertility (three consecutive matings with no pregnancy), low reproductive performance (less than 7 offspring weaned on 3 consecutive births), and disease. No females were culled due to age. Here we explore the effect on the age-structure of this commercial rabbit population of lowering culling rate by 25 points of percentage (from 191 to 138 females culled). The culling rate reduction can be visualized in Figure 1 A (labeled as ‘Reduction’). We assumed that the natural mortality rate did not change.

RESULTS AND DISCUSSION

Practices influencing the age-structure

Populations experiencing artificial selection are normally managed in closed populations with discrete generations of nine months. This means no introduction of new individuals, no mating between individuals of different generation, and the elimination of all individuals in one generation at a fixed time when the next generation begins. The reproductive rhythm of these populations is also controlled. Females are first mated when 18 weeks old and then follow a planned reproductive rhythm of 42 days (*i.e.* they are re-mated 11 days after birth), weaning their litters 28 days after birth. This timing – the most common – limits the population age-structure to females with six litters or less, and favors individuals with an exceptional reproductive effort early in life (Savietto *et al.*, 2015).

Although commercial populations are not managed in discrete generations of nine months, similar replacement rates are observed. In a study of commercial farms, Rosell and de la Fuente (2009) reported high elimination rates in the first 2 litters (above 15%), stable values between litters 3 and 11(~13%), and a final increase at litter 12 (above 15%). This produces a young age-structure, where the average number of litters per female is also six.

High culling rates on later reproductive cycles may reflect the perception that the rabbits are becoming less productive as they age. While some farmers perceive a 14-litter female as “old,” others are not concerned about age before litter 20. Rabbit females can have extremely long and productive lives (more than 25 litters, Sánchez *et al.* 2008; one female having 50 litters, Rosell pers. comm.). But, if farmers are not concerned about age, why is the frequency of mature females not higher? This may result from technology transfer from selection to commercial farms. If a farmer uses culling practices similar to those in selection populations, more mature females will be eliminated than necessary. This results in the observed negative correlation between culling and female age (-0.74, $P<0.001$; Rosell and de la Fuente, 2009).

A typical Spanish commercial rabbit population is represented in Figure 1A and 1B. This population is characterized by an overall culling rate of 41.4% and high mortalities between litters 7, 8, 9 and 10, which shape its age-structure. If rabbit females can sustain longer reproductive careers (Sánchez *et al.*, 2008), then more mature populations can be maintained if culling is not high as in selection populations. When we assumed a lower culling rate, we found that the age-structure of this commercial population would change to a more balanced proportion of ’mature’ and young females (Figure 1C: barred to solid bars).

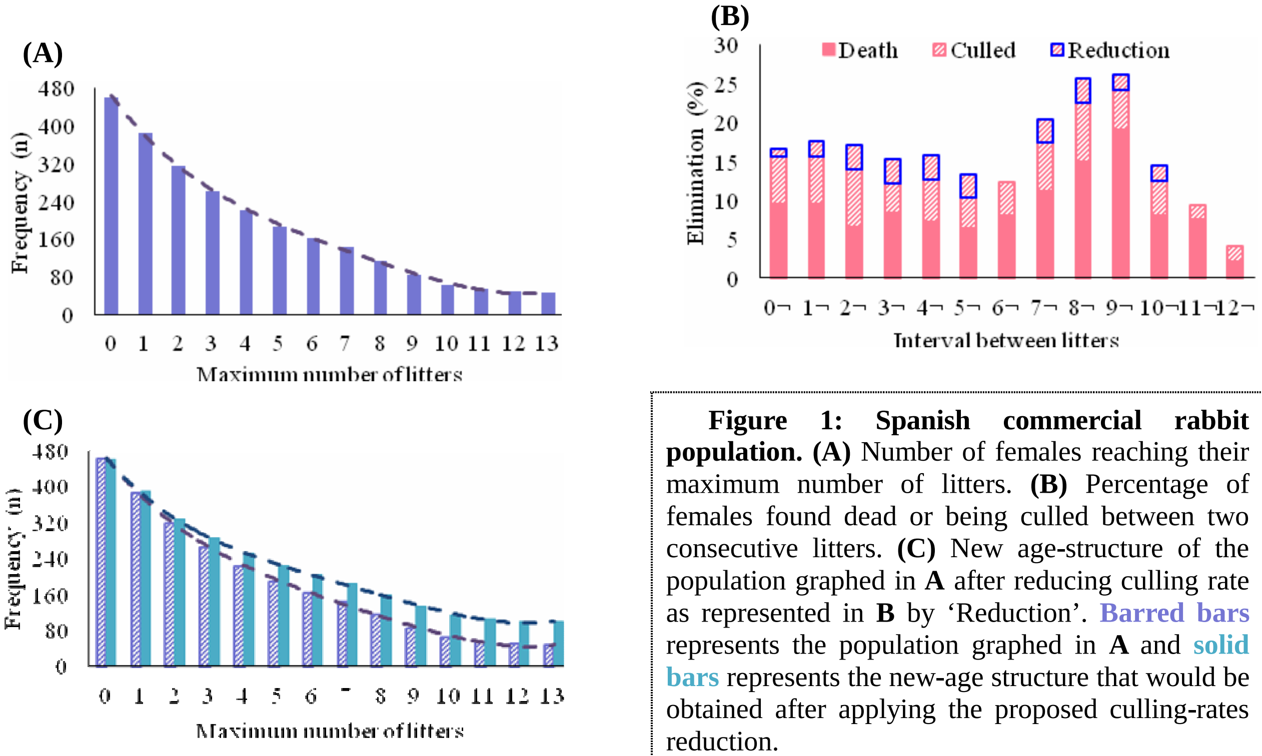

Figure 1: Spanish commercial rabbit population. (A) Number of females reaching their maximum number of litters. **(B)** Percentage of females found dead or being culled between two consecutive litters. **(C)** New age-structure of the population graphed in **A** after reducing culling rate as represented in **B** by ‘Reduction’. **Barred bars** represents the population graphed in **A** and **solid bars** represents the new-age structure that would be obtained after applying the proposed culling-rates reduction.

Life-history theory and the benefits of a mature population

Because farms greatly vary in their practices and rearing conditions (Rosell, 2003), genotype × environment interactions are expected. Animals adapted to selection conditions may not perform well in the different environment of a particular farm. In extreme cases, replacing a mature female that has survived on a local farm is risky because an individual from the selection population that is only potentially good replaces one known to be well adapted. The farm we describe is an excellent example of how a bad environment (bad insulated building, cases of mange and rabbit hemorrhagic disease) can increase the risks of replacing proven females (197 replacing females died before their first mating: at ~160 days old).

The benefits of a more mature population are linked to the evolutionary responses caused by trade-offs between reproduction and survival. Trade-offs between reproduction and survival, which are a cornerstone of life history theory (Williams, 1966; Stearns, 1992), are well documented (Clutton-Brock *et al.*, 1983; Stearns and Partridge, 2001; Wang *et al.*, 2013). Optimal life histories are obtained by balancing the costs and benefits of increasing or decreasing the reproductive effort at a given age (Roff, 2002).

When a population is constrained by high adult mortality to have a short reproductive life – as happens for rabbit populations in selection facilities – the resulting high reproductive effort early in life should be trade-off with lifespan. Although this trade-off has not yet been documented in rabbit populations experiencing artificial selection (Sánchez *et al.*, 2006), it is likely that selection solely for reproduction reduces the capacity of rabbit females to sustain reproductive effort in the face of environmental constraints (Savietto *et al.*, 2013). The innate immune responses of both rabbit females (Ferrian *et al.*, 2012) and their offspring (García-Quirós *et al.*, 2014) seem to be negatively affected by selection for reproduction. Like reproduction, immunity has a cost that depends on the environment where the population evolved (Lochmiller and Deerenberg, 2000). For this reason, selection solely for reproduction under strongly controlled conditions that include intense use of antibiotics and disinfectants may reduce the benefits of maintaining a functional immune system. The high incidence of infectious diseases at rabbit farms may thus be a consequence of trading production for immunity.

CONCLUSIONS

A small reduction in culling rates would significantly change the age-structure of a commercial rabbit population in ways that would improve adaptation to local conditions, favor health and robustness, and lengthen potential lifespan.

ACKNOWLEDGEMENTS

We express our gratitude to Professor Stephen C. Stearns (Yale University) and to Dr. Laurence Fortun-Lamothe (INRA UMR 1388 GenPhySE) for their valuable comments in the initial versions of this paper.

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