Rabbit haemorrhagic disease: theoretical implications for the ecology and management strategies of European wild rabbit

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Abstract

Modelling approaches to disease-host population dynamics can be used to improve the conservation strategies applied and to emphasize the lacks of knowledge. In this article I analysed the case of European wild rabbit (*Oryctolagus cuniculus*) and the Rabbit Haemorrhagic Disease (RHD), a pathogen-host system with deep implications for conservation and hunting activity. I evaluated the possible outcomes of habitat management, control of mortality factors, immunization campaigns against RHD and translocations on rabbit population growth under the theoretical insights obtained in a previous RHD epidemiology modelling approach. Under the model assumptions, habitat improvement was the only way, alone or in combination with other management strategies, to increase rabbit density in populations at equilibrium with the disease in a habitat. The application of any other management strategies without habitat improvement could yield only temporal positive or negative population growth rates depending on the subsequent RHD dynamic. The promotion of rabbit populations that had not yet reached the equilibrium with RHD seemed to be more complex due to possible interactions of disease with other factors like predation. Future research devoted to evaluate which management strategy, or combination of them, could yield the quickest population improvement should be carried out. The misuse of translocations arose as an added obstacle to rabbit enhancement because of underlying mechanisms, such as apparent disease-mediated competition, that could yield harmful effects on native populations. The main conclusions were that, to this date, there was still a considerable lack of knowledge about actual implications of RHD on rabbit biology and that most of current rabbit management programs should be revised to optimize the use of available resources in the attainment of an effective rabbit density increase.

Introduction

The development of theoretical models describing the biology of infectious agents have made possible to incorporate the epidemiology of diseases within wildlife programs to review conservation strategies applied and to emphasize the lacks that should be researched in the future (e.g. Anderson et al. 1981, Barlow & Kean 1998, Kaden 1999). In this article, I explore the case of the European wild rabbit and the Rabbit Haemorrhagic Disease (RHD) in Spain, where rabbit is a primary small game species (Angulo & Villafuerte 2003) but, also, constitutes the diet of more than 30 predator species (Delibes & Hiraldo 1981), including the highly endangered predator species Iberian imperal eagle *Aquila adalberti* and the Iberian lynx *Lynx pardinus* (Palomares 2001, Ferrer & Negro 2004). Therefore, this pathogen-host system has deep implications for conservation and hunting management.

Rabbit hemorrhagic disease is an infectious viral disease, mainly transmitted by direct contact. The main epidemiological feature of this disease is that lethality of RHD-virus among rabbits older than 8 weeks usually reaches values of about 90%, but it is lower in younger rabbits (see review of Cooke & Fenner 2002). In Europe, the initial spreading of RHD in wild rabbit populations took place from the end of 80's to start of 90's (Cooke 2002). RHD impact showed a clear north-south gradient, with the greatest recorded declines in rabbit abundance in Iberian Peninsula (Villafuerte et al. 1995), whereas in Great Britain and other areas of northern Europe, RHD had a less severe impact because of the occurrence in these areas of a putative, preexisting, protective, non-pathogenic RHD-like virus (Rodak et al. 1991, Trout et al. 1997, White et al. 2001, 2002). This virus, however, has not been isolated from wild populations and there is no evidence of its presence in southern European rabbit populations (Cooke & Fenner 2002, Marchandeau et al. 2005).

From the initial impact of disease in Spain, many populations have continued decreasing or have been extinct. Consequently, considerable efforts have been made in the recent pass and will be made in the future to enhance wild rabbit populations for conservation and hunting goals. Management strategies implemented to date include habitat management, predator control, hunting effort limitation and translocations (Moreno & Villafuerte 1995, Angulo 2003, Calvete & Estrada 2004), but the success of these strategies, however, has been generally negligible. In some areas, however, there has been a clear tendency for wild populations to naturally recover in presence of RHD (Calvete et al. 2006), but the factors that enable the coexistence of high population densities of rabbits with RHD-virus are still unknown.

Recently, a modeling approach showed that the impact of RHD could be highly dependent on rabbit population dynamics and that the presence of a unique, highly pathogenic RHD virus could be compatible with the existence of high-density populations at equilibrium with the disease (Calvete 2006a). In basis on the outcomes of this modeling approach, I derive potential implications of RHD on rabbit biology, evaluate the probable outcomes of the strategies commonly used in current rabbit management programs in Spain, and delineate potential management strategies to be explored. The main goal of the present work is to provide to researchers and, especially to wildlife managers and conservation agencies from a theoretical background that would allow a better design and interpretation of their applied management tasks for rabbit promotion and the subsequent validation/rejection of the wild rabbit-RHD system proposed by the model.

Theoretical insights about RHD and rabbit population abundance

In absence of RHD, we define carrying capacity (K) as the maximum density of reproductive individuals in a habitat, and it is conditioned as much for intrinsic habitat features that condition rabbit productivity and survival as for extrinsic mortality factors different to RHD (Figure 1). For simplicity, I assumed a linear relationship between rabbit density before RHD arrival and K (continuous line), rabbit density being low at values around K_0, and medium or high at values around K_1 or K_2 respectively.

RHD had a differential short-term initial impact on naïve populations. In Australasia works showed that higher initial impact of RHD was associated with higher rabbit population densities (Henzell et al. 2002, Parkes et al. 2002, Story et al. 2004), since high densities of susceptible rabbits favored the initial transmission of virus. In Iberian Peninsula a similar pattern has been described, suggesting that short-term initial impact of disease was higher in populations located in more suitable habitats, but the disease needed several years more to yield the highest RHD-impact in populations located in medium-low suitability habitats (Cooke 2002, Calvete et al. 2006). Lacking more precise studies about the short-term initial impact of RHD, I assumed its relationship with K as it is shown in Figure 1 by dotted line. RHD affected populations at rabbit density higher than a threshold density value (D_{th}) necessary to effective virus transmission and posterior virus persistence. The short-term initial RHD impact was higher in more dense populations (around K_2 values) and lower in populations around K_1 values.

From this situation originated from the initial impact of RHD, we assumed that rabbit populations tended towards reaching their long-term equilibrium state with the disease (dashed line) following model predictions (Calvete 2006a). In agreement with outcomes of this model, in the range from K_0 to K_1 there are not marked variations in rabbit density but RHD exhibits the highest increase of the impact on populations in relation to K values, so that the highest long-term RHD impact is reached in populations at medium-low pre-RHD density levels (around K_1 values). In contrast, disease impact is lower around K_0 due to the reduced transmission rates of the virus and in high-density populations located around K_2 values, due to a higher viral transmission rates and therefore lower mean age of rabbit infection. When the mean age of infection lessens, a greater proportion of rabbits is infected at ages at which

RHD virus lethality is reduced by age resilience or the presence of maternal antibodies, resulting in a lower mortality from RHD at population level (Calvete 2006a).

Actually, dashed line is an oversimplified way for representing the long-term impact of RHD, as, following model outcomes; it should be a cloud of points with higher dispersion in relation to vertical axis at K values around K_1. This dispersion being determined to a greater extent by rabbit population productivity and less by mortality due to other factors different to RHD.

If we assumed that the transition of populations from the short-term initial RHD impact situation (dotted line) to the long-term equilibrium state with disease (dashed line) was highly dependent both on population dynamic and the life-history of each population (Calvete et al. 2006), different population dynamics or concurrence of factors limiting populations growth such as hunting pressure, stochastic climatic events, or predator impact could be easily argued to explain the current observed highly variable pattern of rabbit abundance and population trends (Virgós et al. 2003, Calvete et al. 2004a, Fernández 2005). This pattern comprising populations with increasing or decreasing trends, and many sites with current low abundance or no rabbit populations appearing to be as suitable as habitat for rabbits as other sites in which are abundant.

RHD and predation impact

Predation is one of the main mortality factors affecting wild rabbit populations. Fox (*Vulpes vulpes*) is the main predator of wild rabbit, and several predator-prey studies have demonstrated that rabbit populations can be regulated by foxes (Newsome et al. 1989, Pech et al. 1992). Regulation of rabbit populations can take place when rabbit densities have dramatically declined as a consequence of other major factors such as environmental perturbations or diseases. Foxes are generalist predators, and the drop of rabbit populations can be supplied by other secondary preys or food resources (eg carrion or garbage) so that fox density is affected to a smaller extent. In this situation, rabbit populations can be maintained at low densities by foxes unlike environmental perturbation has ceased. This is the theoretical predator-prey interaction so-called “predator-pit”. Pech et al. (1995) defined one theoretical predation model that could be used to describe this interaction between fox predation response and rabbit population. The graphical description of this model it is shown in Fig. 2.

Following Pech et al. (1995) the interaction of a predator population and that of a prey species is described by a total-response function. The total-response is the product of the numerical response and the functional response. A Holling Type III functional response is assumed, so that the total response is density dependent at low prey densities and inversely density dependent at high prey densities. Two predator total-response levels (dotted lines) corresponding to two levels of predator density are shown. The percentage of recruitment of prey as a function of prey density is represented as a continuous line. It is assumed that percentage of prey recruitment is constant until eventually habitat resources become limiting. When this happens recruitment declines and the prey population stabilizes at the density K, that is the habitat carrying capacity.

The relative positions of the recruitment curve and the total-response determine the theoretical equilibrium density of the prey. Thus, at level 1 fox total-response, corresponding to a low fox density, rabbits are not regulated, and only one stable state is reached at high rabbit densities at *a*. At level 2 fox total-response there are two stable states at *b* y *d* separated by an unstable state at *c*. The low rabbit density state, *d*, is regulated by foxes whereas the high density state, *b*, occurs when the rabbit escapes fox regulation. The range of densities between D_c (corresponding to *c*) and D_d (corresponding to *d)* is the “predator pit”. If rabbit density is greater than D_c but less than D_d, it will be driven by predation towards *c*, whereas that if rabbit density is greater than D_d, for example, after a temporary reduction in fox density, then it should increase up to D_b.

Now, I have extended the predation model incorporating the theoretical impact of RHD to rabbit population dynamics (dashed lines). Given that the actual relative position of the rabbit recruitment curve in presence of RHD and the fox total-response curve is unknown, I have considered two scenarios represented. Firstly I have considered a rabbit population located in a habitat with high carrying capacity (Figure 2A), i.e. similar to a habitat with carrying capacity around K_2 in Figure 1. In this scenario, after a dramatic rabbit population reduction due to initial impact of RHD alone or in combination with other negative factors, rabbit recruitment will increase to reach the new maximum carrying capacity of the habitat in presence of RHD. Following the outcomes of the RHD model (Calvete 2006a), however, during this transitional process, it is hoped that once rabbit density be higher than a density threshold value (D_{th}) necessary to RHD-virus effective transmission, RHD-mortality will increase, lowering rabbit recruitment rate, and then RHD-mortality will decrease in correspondence to increase in rabbit density and the subsequent decrease of the mean age of infection of rabbits. Thus, for rabbit populations that were not regulated by foxes under level 1 total-response in absence of RHD, a predator-pit possibility arises in presence of the disease. On the contrary, of two possible stable states under level 2 fox total-response in absence of RHD, only the stable state in which rabbits are regulated by foxes remains in presence of the disease, but also at lower densities than in absence of RHD. Between both levels of predation there is a gradient of possible interactions where rabbit populations, in presence of RHD, are more prone to be regulated by foxes than in absence of disease due to the lowering of the range of density population between *b* y *c* states and increasing the range between *c* y *d*, i.e. rabbit populations increase their probabilities that harmful effects of other factors (eg adverse environmental perturbations, hunting or other diseases) derive in a stable state at low rabbit density regulated by predation.

In the another scenario (Figure 2B) it is assumed that rabbit populations is located in a habitat with carrying capacity K similar to K1 of Fig. 1. In this case, in presence of RHD, level 1 fox total-response yields only one stable state at lower rabbit density than in absence of the disease, whereas for the level 2 fox total-response, only the regulated low rabbit density state *d* remains. The actual form of rabbit recruitment curve in presence of RHD, however, probably will be highly dependent of rabbit population dynamics, therefore, a gradient of outcomes of fox-rabbit interaction should be hoped in the field.

Despite predation and RHD models are still theoretical approaches, they show how RHD and predation impacts combined could reduce rabbit populations at lower densities than each one working alone, in agreement with the empirical evidences found by Reddiex et al. (2002).

Habitat management

Habitat management is the most widely applied strategy for improving rabbit populations in Spain (Angulo 2003). Despite the traditional importance of habitat management, there is a lack of research, exhaustive works about effects of habitat management on rabbit populations after the arrival of RHD (e.g. Moreno & Villafuerte 1995, Angulo et al. 2004, Cabezas 2005, Muñoz 2005). The greatest part of efforts devoted to improve rabbit populations by habitat management have been carried out by sportive hunting associations or within conservation programs aimed to conserve endangered predators populations, so that, there is no information about most outcomes of management, or if any, it is mainly in hard accessible or poorly detailed “gray literature” (Angulo 2003). In general, however, the effects of habitat management on rabbit populations seem to have been poor, and the objectives of getting a notable rabbit improvement have not been reached.

The most frequent applied strategies have been scrub management to create natural pastures, construction of artificial refuges and creation of artificial pastures (Angulo 2003). However, due to the generally limited funding and logistic resources, habitat management strategies have been hardly maintained throughout time at local scale (Angulo et al. 2004), and for example, many times artificial pastures are sowed only once at the start of management programs.

Habitat management, not only is aimed to increase carrying capacity of the habitat but also rabbit productivity, so that, habitat management would be the best way to enhance rabbit populations in presence of RHD (Calvete 2006a). However, following Figure 1, the improvement of habitat could not always yield positive growth in populations. For example, we would consider a rabbit population at equilibrium with RHD located in a habitat with carrying capacity around K_0. In an attempt to enhance rabbit population we would perform a habitat management program that only increased habitat carrying capacity until values around K_1. It is obvious that the results would be fairly disappointing as no positive change in rabbit density would take place, although epidemiology of RHD would have changed dramatically.

This scenario would arise under poorly funded management programs in which long-term habitat improvement was low or under not well designed programs, in which habitat improvement was high but only during a short time. In this case, if habitat management was depending on the temporary availability of funding, then, rabbit population would be subjected to recurrent perturbations from its equilibrium with RHD by increasing the impact of the disease. This way, a well designed habitat management program should comprise the necessary funding to the long-term maintenance of habitat improvement, independently of the short-term results obtained in rabbit abundance, to increase habitat carrying capacity to some value around K_2, something that is not frequent in management programs carried out by local governments or sportive hunting associations.

The main way to increase rabbit productivity is managing habitat to increase the quantity and the quality of available food during breeding seasons (Richardson & Wood 1982, Villafuerte et al. 1997). After the spread of RHD, the highest rabbit densities are usually located in agricultural landscapes mainly devoted to yearly farming Gramineas (Chapuis & Gaudin 1995, Virgós et al. 2003, Calvete et al. 2004*a*, Calvete et al. 2006). In addition, studies on food habits of rabbits have showed that they preferentially feed on yearly cultivated Gramineas during the breeding season (Homolka 1988, Muñoz 2005). Given that rabbit management programs primarily consist of scrub management to create natural pasture areas or creation of crops that are cultivated only once (Angulo 2003, Angulo et al. 2004), the former signs suggest that the latter management practices probably are insufficient for reaching a population density at which RHD impact decreases. These matters should be assessed by future research.

Control of mortality factors and harvesting of populations

Since outcomes of the RHD model (Calvete 2006a) suggested that, at equilibrium with RHD, managing mortality factors has little effects on RHD epidemiology in comparison with habitat management, control of mortality factors could be useful in some populations under the equilibrium state with the disease or in situations in which a previous improvement of habitat had been performed.

Predator control, mainly performed by fox removal, and reduction of hunting efforts are the most frequent management strategies implemented by hunters to reduce rabbit mortality (Angulo 2003). After habitat improvement, a temporal predator control would help to a quicker increase of rabbit populations. The same adequacy of predator removal could arise in rabbit populations under the equilibrium state with the disease, where predation control could help rabbits escaping from predator regulation.

Effective hunting reduction should have similar implications in rabbit recovery that predation control. Moreover, outcomes of the RHD-model suggested that the decrease in rabbit density caused by excessive hunting pressure or over-harvesting, leading to the translocation of rabbits to areas of low population density, may increase the impact of RHD. Thus, a sustainable harvesting is essential to rabbit maintenance. Several theoretical approaches have been carried out to estimate the impact of harvesting on rabbit populations in Iberian Peninsula in absence of RHD (Angulo & Villafuerte 2003, Calvete at al. 2005a). The discrepancies in results of both works are, however, a clear evidence that, to date, we are still far of designing sustainable harvesting plans, and that more future research, including RHD impact, is necessary.

Vaccination against RHD

The use of vaccination as a disease prevention method in wild rabbits has increased greatly in the past several years in Spain (Angulo 2003). The success of vaccination campaigns has also been negligible, although their effectiveness has been tested in very limited short-term field experiments, and only at the individual level (Calvete et al. 2004*b*, Calvete et al. 2004*c*, Cabezas et al. 2006).

The only theoretical approach available to date for evaluating the effectiveness of vaccination campaigns against RHD at the population level showed that vaccination campaigns in populations at equilibrium with the disease could yield positive or negative population growth rates, depending on rabbit population dynamics and subsequent RHD dynamics (Calvete 2006b). Negative growth rates were observed in simulated populations located in habitats with carrying capacity around or under K_1 (Figure 1). Since low density populations are the main targets of vaccination campaigns, this model suggested that current immunisation programs might have harmful effects on many managed rabbit populations.

Other different, but not explored, scenarios would arise if vaccination campaigns were carried out in populations that had not yet reached equilibrium with the disease. In this situation, vaccination, alone or in combination with other management tools, may facilitate a quicker recovery of populations, until they reach equilibrium with the disease. It is important therefore to evaluate the outcomes of vaccination campaigns performed under these scenarios.

Translocations

Rabbit translocations carried out in Spain can be all classified as either re-introductions or population supplementations (IUCN 1996, Angulo 2003). Rabbit translocations are frequently performed for hunting purposes, with thousands of wild or captive-born individuals being translocated every year. However, given the relative low success to improve rabbit populations for preserving endangered predator species, rabbit translocations have dramatically increased also in last years within conservation programs as a way to, not only to recuperate rabbit populations, but also to provide temporary preys to predators. For example, at least 18,000 wild rabbits have been translocated into Doñana National Park in southern Spain during the last 15 years to favor lynxes and imperial eagles (Angulo et al. 2004).

After the arrival of RHD, many efforts have been devoted to identify the processes that condition rabbit translocations. It has been shown that short-term mortality is a critical issue in translocation success (Calvete et al. 1997, Letty et al. 2003, Calvete & Estrada 2004) and several release protocols have been assayed to enhance short-term rabbit survival (Letty et al. 2000, Letty et al. 2002, Calvete et al. 2005*b*). However, the few surveys carried out to evaluate the medium- long-term success of rabbit translocations have showed that it is generally low and that some of main mechanisms underlying this management strategy remain unknown (Moreno et al. 2004, Angulo et al. 2004, Cabezas 2005, Muñoz 2005).

Coming back to Figure 1, if native rabbit populations at equilibrium with RHD are reinforced with translocated rabbits it is hoped that the effects of these supplementations be similar to that of vaccination campaigns. Taking into account that most of translocated rabbits are temporally immunized against RHD by vaccination before their release, successive translocation trials in populations in which supplementation yielded negative growth rate due to the increase of RHD-mortality would derive in a process of apparent competition mediated by disease, in which translocated rabbits (probably worst adapted to the new environment) predominate on native rabbits, deteriorating population long-term fitness.

For native populations that have not reached yet the equilibrium with the disease, supplementation, in a similar way that other management strategies, might be an effective tool to recover populations more quickly, especially in low density populations regulated by predators. However, in theses cases, apparent competition mediated by disease would yield dramatic results.

Another interesting point would arise when the supplementation was carried out in an area where RHD-virus was absent because rabbits had been extinct or native population was at density lower than the threshold density level necessary to RHD-virus persistence. In these cases when the new population increased in density the accidental introduction of the virus would cause a RHD outbreak that would dramatically lessen population density again. To prevent this and increase probabilities that new rabbit population growths in presence of the disease it was necessary that rabbits and RHD-virus be translocated simultaneously. Given that there are reservoirs and chronically RHD infected rabbits that may eliminate virus for long time (Shien et al. 2000, Forrester et al. 2003), the join translocation of rabbits and virus could be performed by translocating a relatively high number of rabbits from populations that already had reached the equilibrium with the RHD at high population density, and where a high proportion of rabbits had been already infected by the virus. Conversely, the translocation of captivity-born rabbits without previous contact with the virus or translocation of rabbits from populations where virus transmission was reduced be the worst option to get this goal.

One exciting option would be the controlled release of RHD virus during translocation and during the growth process of the new population, until the population and the virus reached equilibrium. This management practice could be applied independent of the origin of the translocated rabbits and may reduce the uncertainty of success of translocations and their dependence on initial RHD dynamics.

Conclusion

The theoretical scenario delineated by RHD model suggested that for populations at equilibrium with the disease the long-term increase of habitat carrying capacity by means of habitat improvement was the only way so that the most negatively affected populations can reach stable densities similar to pre-RHD ones. The application of any other management strategy without habitat improvement could yield only temporal positive or negative population growth rates depending on the subsequent RHD dynamic. On the other hand, in populations at density lower than that at equilibrium with the disease, their promotion so that they could reach the disease-equilibrium state in the same habitat seemed to be more complex due to possible interactions of disease with other factors like predation.

Currently, many efforts are being carried out to promote rabbit populations with hunting and conservation goals in Spain, but results are negligible. Under the assumptions of the theoretical approach to rabbit-RHD system dynamics, I have shown that the effects of applied management strategies seem to be unclear and that the current rabbit management programs would be more an expensive “lottery” than well designed management strategies in attainment of clear objectives. To date, there is still a considerable lack of knowledge about actual implications of RHD on rabbit biology, and future research devoted to this issue and to evaluate which strategy or combination of them would yield the best results to get population improvement should be carried out, including the validation/rejection of the RHD modeling approach considered in this article and the assumptions upon it is based.

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Figure legends

Figure 1. Theoretical relationship between rabbit density and carrying capacity K of the habitat before the arrival of RHD. Continuous line: rabbit density before the arrival of RHD. Dotted line: rabbit density after the short-term impact of RHD. Dashed line: rabbit density at long-term equilibrium with RHD following the model of Calvete (2006*a*). D_{th}: Threshold rabbit density for effective RHD-virus transmission.

Figure 2. Fox-rabbit dynamics and the impact of RHD. The graph shows the interaction between fox predation total-response (dotted lines) and rabbit population recruitment (continuous lines) in a habitat of carrying capacity K, in which rabbits are the main prey of foxes, but foxes can subsist on other secondary food sources when rabbits are scarce (Pech et al. 1995). Two levels of predation (low, level 1; high, level 2) are represented. In the absence of RHD and at predation level 1, rabbits are not regulated by foxes and a single stable state at high densities exists at *a*. At predation level 2, there are two stable states, at high (*b*) and low (*d*) rabbit densities, separated by an unstable state at *c*. Rabbits are regulated by foxes at *d*. The range of densities between D_c (corresponding to *c*) and D_d (corresponding to *d)* is the "predator pit". If rabbit density is greater than D_c but less than D_d, it will be driven by predation towards *c*, whereas if rabbit density is greater than D_d (e.g. after a temporary reduction in fox density), then it should increase to D_b. In the presence of RHD, rabbit recruitment curves are modulated (dashed lines) for a rabbit population located in habitats of high (A) and low (B) carrying capacity. (A) At predation level 1, the possibility of a predator pit situation arises whereas at predation level 2 there is a single stable state at low rabbit density. (B) At predation level 1, there is only one stable state at lower rabbit density in the

presence than in the absence of disease, whereas, at level 2, only the regulated low rabbit density state *d* remains. D_{th}: Threshold rabbit density for effective RHD-virus transmission.

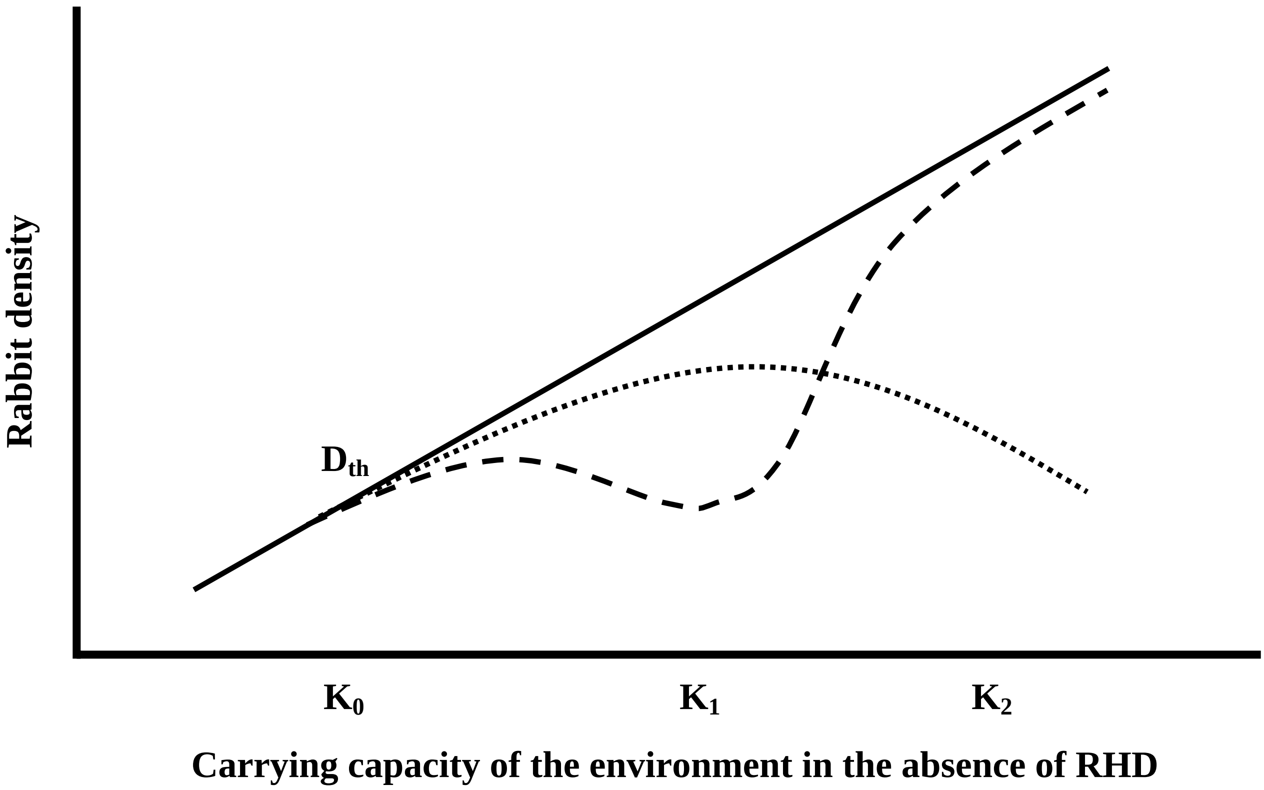
Rabbit density
D_{th}
K0
K1
K2
Carrying capacity of the environment in the absence of RHD

FIGURE 1

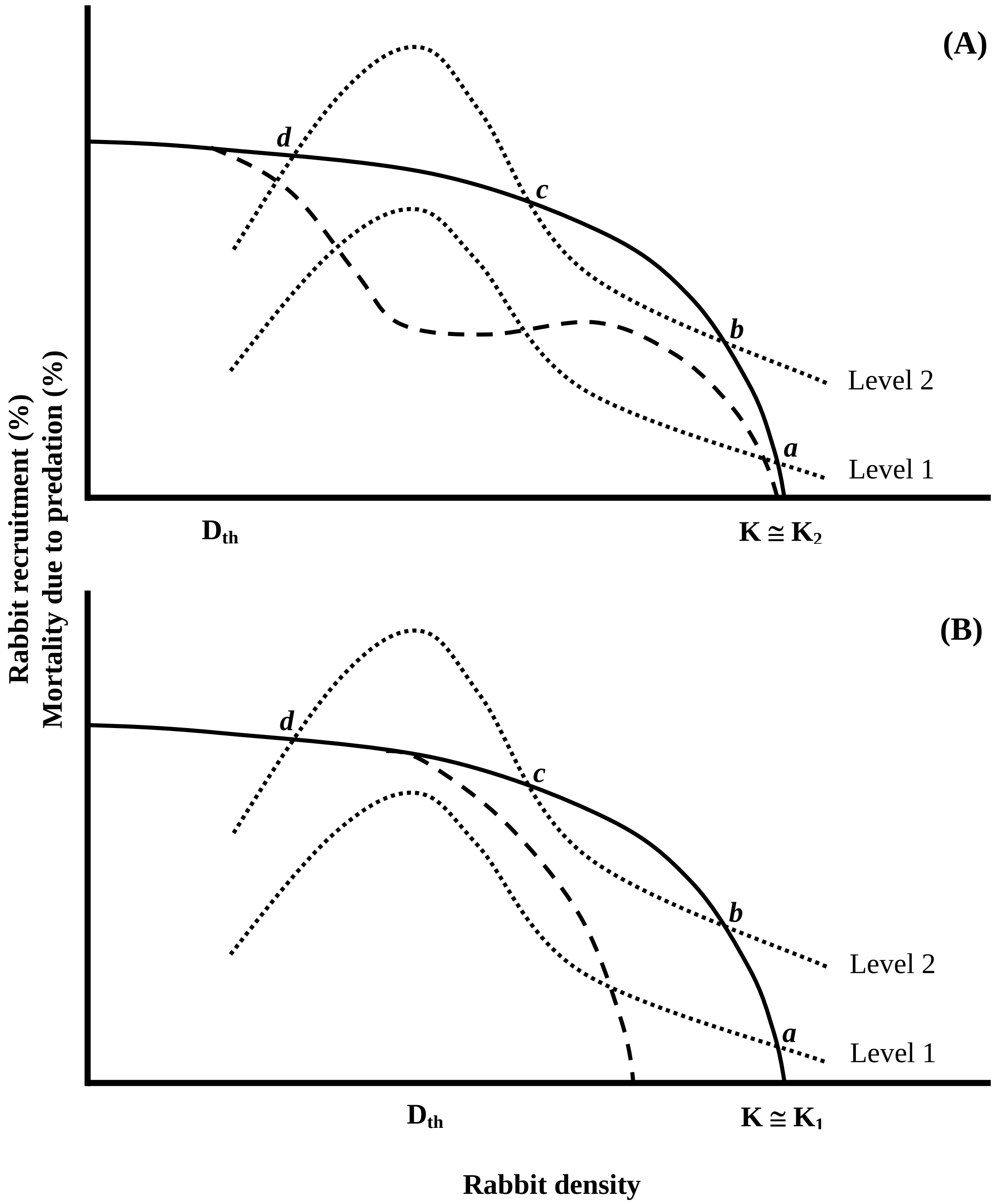
(A)
d
c
b
a
Level 2
Level 1
Dth
K ≅ K2
(B)
d
c
b
a
Level 2
Level 1
Dth
K ≅ K1
Rabbit recruitment (%)
Mortality due to predation (%)
Rabbit density

FIGURE 2