A Review of Competition between Rabbits (*Oryctolagus cuniculus*) and Hares (*Lepus europaeus*)

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Introduction

The concept of competition "is of no practical use for field biologists . . . But for theoretical ecology the concept is vital. On the assumption that competition occurs in nature, both between species and between individuals of the same species, it has been possible to make simple models of the natural world which have led to our most perceptive understandings of how species are separated, and kept distinct; and of how the populations of many animals and plants are restricted in nature" (Colinvaux 1973). In this review, I use the wide definition of competition to include both interference (or contest) and exploitation (or scramble) competition, because the distinction is usually obvious from the context.

If competition is very strong, the geographical ranges of the competing species may meet at a sharp boundary. Thus, four species of pocket gophers (*Geomys*, *Cratogeomys*, and *Thomomys* spp.) meet without overlap in Colorado, appearing to behave as a single species competing for space (Miller 1964, quoted by Krebs 1978). A good indicator of competition is the ability of either of two species to occupy the range of the other if it is absent, as found in the chipmunks *Eutamias dorsalis* and *Eutamias umbrinus*; although the former is dominant, the latter can out-compete it where trees are close enough to allow rapid escape (Hall 1946; Brown 1971; quoted by Krebs 1978).

Hares (genus *Lepus*) are widely distributed in grassland, steppe and desert over most continents. They are of relatively recent origin, and the approximately 30–32 species currently recognised (Flux and Angermann 1990; Chapman and Flux 2008; this book) are normally allopatric. The few cases of sympatry that have been studied, e.g. in Ireland, Finland, Russia, and Sweden, where *Lepus timidus* (Mountain hare) is endemic but *Lepus europaeus* (European hare) was introduced in the 19th and early 20th centuries, appear to be transitional, with the European hare driving the Mountain hare from the plains (Barrett-Hamilton 1912; Lind 1963; Gaiduk 1982; Thulin 2003), although Millais (1906) disagrees: "With this view I do not agree at all, for the two species are in no sense antagonistic to each other…" and "do not occupy

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the same ground as a rule, simply because their habits and food are different." (This apparent conflict seems based on misunderstanding, because Barrett-Hamilton also says: "It is certain that, although the blue hare as a species retreats before its larger relative, there is no active antagonism between the individuals of either".) Hewson (1990) observed a European hare among Mountain hares which appeared to treat it as conspecific. In Kenya *Lepus capensis* (Cape hare) and *Lepus crawshayi* feed side by side in parts of the Great Rift Valley where regular scrub fires alter the habitat to favour *capensis*, but regrowth favours *crawshayi* (Flux and Flux 1983); in Colorado *Lepus californicus* (Black-tailed jackrabbit) and *Lepus townsendii* (White-tailed jackrabbit) co-exist, using scrub and fields (Flinders and Hansen 1973); and in Mexico *L. californicus* and *Lepus callotis* (White-sided jackrabbit) co-exist on semi-desert and grassland, respectively, (Desmond 2004). Moreover, replacement of one species by another has often been recorded following climatic or anthropomorphic changes to the environment (e.g. *Lepus americanus* (Snowshoe hare) *by L. townsendii* in Wisconsin (Leopold 1947), *L. townsendii* by *L. californicus* in Kansas (Brown 1947) and *Lepus arcticus* (Artic hare) by *L. americanus* in Canada (Fitzgerald and Keith 1990, who write: "It is highly unlikely that interference competition with snowshoe hares is responsible for the current restriction of arctic hares to barrows and tundra.").

The geographic ranges of hares, however, frequently encompass those of rabbits of several genera; indeed this seems the rule except for isolated island forms like *Pentalagus* and *Nesolagus*. For example, *L. americanus* and *Sylvilagus floridanus* (Eastern cottontail), *L. californicus* and *Sylvilagus nuttallii* (Mountain cottontail), *L. townsendii* and *Brachylagus idahoensis* (Pigmy rabbit), *L. capensis* and *Pronolagus rupestri*s (Smith's red rock hare), *L. ruficaudatus* and *Caprolagus hispidus*, *L. crawshayi* and *Poelagus marjorita* (Bunyoro rabbit) (see Chapman and Flux 1990). This review examines the relationship between the European hare, *L. europaeus,* and the European rabbit, *Oryctolagus cuniculus*, the best-studied pair.

Geographic Distribution

Before human intervention *L. europaeus* was restricted to central Europe, and *O. cuniculus* to the Iberian Peninsula, where it was sympatric with *Lepus granatensis* (Liberian hare) (Flux 1994). Hence overlap between *L. europaeus* and *O. cuniculus* is relatively recent, but now widespread (because both species were important game animals) over much of Europe, South America, Australia, and New Zealand (Chapman and Flux 1990). In all areas except Australia hares occupy far more of the country than rabbits do; why hares cannot live where rabbits can in Australia remains a puzzle, but is unlikely to be due to competition because hares were liberated first and failed to spread even in the absence of rabbits (Jarman 1986).

At a regional scale it is possible to show allopatry associated with the preferred habitat of each species, and this is emphasised by most field guides: (rabbit) sandy soil, light clay, coniferous woods; (hare) cultivated land, deciduous woods (van den Brink 1967), (rabbit) dry heaths, short pasture, agricultural land close to cover, edges of pine woods; (hare) cereal fields, pasture, woods and shelterbelts (Corbet and Harris 1991), (rabbit) sunny aspect, light soil, and adequate cover; (hare) sand dunes, cropland, pasture, clearings in scrub or forest (King 1990).

On the local scale, also, there is a very old and widespread opinion among shooters and country folk that hares and rabbits avoid each other: "The hare is essentially a fastidious animal. Like sheep, it refuses to graze on grass lands which rabbits have defiled" (Macpherson 1896). "Field naturalists are unanimous that the animals are naturally antipathetic, and will not even thrive well on the same ground. This may be because rabbits, when in numbers, bully, chase and worry hares to death, or, perhaps, because the rabbits eat or taint the food of the more delicately feeding hares, or because the former infect the latter with epidemics to which they are themselves immune"(Barrett-Hamilton 1912). Similar views are found throughout Europe (Fraguglione 1960); in Australia after rabbits arrived Creed (1917) recorded: "and now a hare is never seen except in large areas of fenced country"; in New Zealand: "hares are not seen where rabbits are found in any numbers and vice versa" (Cox 1976) and in Chile, South America, they "do not occur in the same areas because the hares drive the rabbits away" (Housse 1953). In Argentina there are reports of "a similar process with the "tapeti" (*Sylvilagus brasiliensis*) which was replaced by the hare in only six years" (Grigera and Rapoport 1983).

Yet in all these places hares and rabbits can be found grazing side by side, and several studies of their diet show major overlap (e.g. Homolka 1987; Chapuis 1990): indeed, more overlap than the diets of some allopatric species of *Lepus* where their ranges meet (Flux 1970; Stewart 1971).

Myxomatosis

The removal of rabbits by myxomatosis in Britain and much of Europe in the 1950s provided a natural experiment, and there were early reports of increases in hare numbers in England (Moore 1956; Rothschild and Marsh 1956) and France (Rothschild 1958) as would be expected if rabbits and hares were in competition. However, more detailed analysis of a French shooting estate (Birkan and Pepin 1983) showed this increase was short-lived, and the hare and rabbit populations were responding to different climatic factors. In Britain, similarly, field observation, and an analysis of extensive game bag records, led Barnes and Tapper (1986) to suggest that the increase in grass cover may have allowed higher leveret survival; and the decline in hare numbers since the 1960s "appears to be quite unrelated to the recovery of the rabbit

population" but "how hares benefit from the absence of rabbits is not properly understood" (Boag and Tapper 1992). In Hungary, Katona et al. (2004) found no increase in hares when disease eliminated a dense rabbit population from their study area in 1994–95 and concluded that the competitive effect of rabbit on sympatric hares had been low or expressed in some unstudied factors. In Australia, according to Frith (1970) "There seems little doubt that since the reduction of rabbit populations (by myxomatosis in 1950) the numbers of hares have increased in some places and this trend seems to be continuing". New Zealand introductions of myxomatosis failed, but following the illegal introduction of RHD in 1997, the number of hares shot has increased (G. Norbury pers. comm.). None of these correlations, however, give any indication of the mechanism involved.

Behavioural Observations

Antagonism between rabbits and hares has often been reported, both in captivity and in the wild. Gayot (1868) bred hares successfully in cages, and found rabbits mutilated hares. This was also reported by Thierry (1907) and Kunstler (1908). In Britain, in the wild, a rabbit was watched attacking a hare until it screamed (Booth 1883, quoted by Barrett-Hamilton 1912). Rabbits "are sufficiently bold to drive the hares before them. This can easily be verified by observation in the early hours of the day, in any place where both species happen to be numerous" (Macpherson 1896). Millais (1906) states that "Rabbits have the greatest objection to Hares, and will give them no peace until they have driven them away from the neighbourhood of their burrows."

More recent scientific observations, however, appear to indicate that overt antagonism is very rare. On the Isle of Wight, England, hares and rabbits fed together peacefully, leading Moore (1956) to ask: "How many of us have seen hares and rabbits fighting? I never have done, and would be interested to know if anyone else has." In a classic study in the Netherlands, Broekhuizen (1975) analysed 1,241 meetings between rabbits and hares: only in 1% was there an attack, "sometimes by the hare, mostly by the rabbit"; and because there were many rabbit vs. rabbit attacks, he suggested that some rabbit vs. hare attacks may be mistakes. He concluded "that hares are not driven out by aggressive behaviour of rabbits, that hares do not avoid land used by rabbits and that they do not avoid rabbits in general." In southern England, Barnes and Tapper (1986) counted by spotlight on nine arable farms in spring and autumn of 2 years. They found rabbits and hares were positively associated on cultivated land in spring, and on stubbles in autumn, with no evidence that hares avoid rabbits: "Nor have we seen any evidence of competition; in general rabbits feed along the edges of fields while hares are more likely to be

in the middle of the same fields", although there was some evidence of a reduction in hare numbers where rabbit density was very high.

In New Zealand, when rabbit populations were severely reduced by poisoning in the 1950s, farmers and professional rabbit-control personnel noted a widespread increase in hares, and I was appointed to study the problem in 1960. An area of 3 ha in Travers Valley, Nelson Lakes National Park had a resident population of about 25 rabbits that declined to zero in 2 years. It was also the main feeding ground for about ten hares, and their interactions were recorded for a week once a month for 2 years. Most rabbits and hares ignored each other and often fed within 1 m of each other. The totals of the chases seen in 2,314 observed encounters were: hare vs. hare, 142; rabbit vs. rabbit, 155; and hare vs. rabbit, 55, of which 45 were of rabbits chasing hares (Flux 1981).

Since 1972 I have recorded all hares and rabbits seen from our house overlooking a 3-ha area of uniform sheep pasture, later used for horse grazing. Both rabbits and hares were present at extremely low densities, and months could elapse without any being seen. Over 32 years of observation, the number of rabbits has increased as they have over most of New Zealand since the rabbit control organisation was disbanded in 1981 (Flux 1997). Grouped in 8-year totals, the proportion of rabbits to hares was 1/67 (1.5%), 21/67 (31%), 10/22 (45%) and 59/98 (60%). Group sizes for the two species were similar, averaging 1.32 (1–5) for rabbits and 1.36 (1–5) for hares. In contrast, the corresponding figures for the high density populations in Travers Valley were 3.39 (1–17) and 1.91 (1–8). At Belmont, the totals of chases seen in 265 observations were: hare vs. hare 47, and rabbit vs. rabbit 17; hares and rabbits were seen together 16 times, but without any interaction at all.

Shared Diseases

The idea that rabbits carry diseases to which hares are more susceptible has a long history reviewed by Barrett-Hamilton (1912). Broekhuizen (1975) investigated this in the Netherlands and concluded that *Graphidium strigosum* was an original parasite of rabbits that could harm hares entering areas where rabbits were abundant, but more information was needed to verify a causal relationship. In Britain, Barnes and Tapper (1986) considered the infection rates too low to be involved. The concept of competition via host-parasite relationships is well discussed by Barbehenn (1969), who suggested that *Sylvilagus* could be introduced to spread myxomatosis to *Oryctolagus*, but "The Australians would have lined the shores with shotguns to keep out another rabbit." The experiment has now been carried out in Europe with successful introductions of *S. floridanus* since 1966. Only in Piedmont, Italy, did it spread rapidly, apparently because it faced little competition there (Spagnesi and De Marinis 2002).

Competition on Islands

Van Laar (1981) reviewed the history of mammal introductions on the Wadden Sea islands, the Netherlands, and considered that hare competition excluded rabbits on Pellworm, and rabbits excluded hares from Vlieland until the construction of polders made the area more suitable for hares.

Rabbits have been liberated on more than 800 islands worldwide (Flux and Fullagar 1992) and data are available on the fate of the populations on 607 of these islands, analysed by Flux (1993). The rabbits died out, presumably because of adverse environmental conditions, on 11.2% of these, and this mortality was not related to the island size. Myxomatosis removed rabbits from 10.1% of 119 islands, more efficiently from smaller islands, and not from any of over 1,000 ha. Cats removed rabbits from 11.3% of 80 islands, including 7% of the islands in the 1,000–10,000 ha category. Hares, however, were far more efficient at removing rabbits, clearing 26.7% of 105 islands, including 5% of those in the 100,000+ ha category. These figures appear to indicate that the force of competition is relatively twice as strong as predation by cats; or by myxomatosis, which can kill 99% of a susceptible rabbit population.

Discussion

European hares and European rabbits became sympatric relatively recently, and they occupy agricultural or pastoral habitats which are also of recent origin. Hence one explanation of the rather unusual interspecific aggression historically reported as displayed by rabbits to hares is that they were in the process of establishing or re-defining their ecological niches.

The high level of interspecific aggression recorded by early writers was not supported by careful observers like Moore (1956) and Broekhuizen (1975). This discrepancy could be explained by the far lower densities of rabbit populations following myxomatosis. European hare populations are also lower throughout Europe than they were 100 years ago (Niethammer and Krapp 2003), so the chances of observing aggression is much reduced; indeed the reason for it may no longer exist.

Their diets when studied in the same locations are remarkably similar (Homolka 1987; Chapuis 1990), and Wolfe et al. (1996) suggest that the species can co-exist by avoiding competition in spatial use, as proposed by Hulbert et al. (1996) for mountain hares and rabbits. I find this unconvincing, because both species will occupy most of the habitat of the other in its absence. However, as the two species operate at a different scale, their overlap or avoidance may depend on the interaction between the structure of the vegetation (patch size) relative to their very different home range sizes (V. Altbäcker in lit. 2005).

On islands, individual species of vertebrates reach higher densities than on the adjacent mainland, and this holds for hares (e.g. Angerbjorn 1981). There are also more species on large islands than on smaller ones. These relationships would affect the outcome of liberations of rabbits and hares on islands, but there appear to be no behavioural studies of interactions or aggression. Because either species may take over the island depending on the balance of favourable factors (van Laar 1981), it seems unlikely that a disease is involved to which one species is more susceptible, as suggested by Barrett-Hamilton (1912), and Broekhuizen (1975).

Other genera of rabbits and *Lepus* species seem to co-exist without aggression, and there is no popular belief that jackrabbits and *Sylvilagus*, for example, are antagonistic. Orr (1940) often "observed jack rabbits feeding within a few feet of both brush rabbits and cottontails. No animosity was ever apparent between these species at such times". European rabbits, perhaps because they are feral domesticated stock, reach population densities with a biomass about ten times higher than any other lagomorphs (Flux 2001). This certainly explains why they can degrade the vegetation and make it unsuitable for hares (Fraguglione 1960), but not how hares are able to remove rabbits from islands so efficiently, unless rabbit populations overeat the food supply and are basically unstable (Wynne-Edwards 1962).

The mechanism involved in maintaining allopatry in different species of *Lepus* is unknown, but must be remarkably strong to result in such clear and relatively fixed boundaries. An individual European hare, for example, is easily capable of traversing the entire range of *Lepus castroviejoi* (Broom hare) in a few hours, yet apparently never does. But aggression seems not to be involved. It is likely that the same or a very similar mechanism is used in interspecific competition between European hares and European rabbits: in both cases, the species in contact seldom show aggression and, if they do, the level of interaction is of the order expected for intraspecific conflicts. The resolution of this problem could be the key to population regulation in lagomorphs.

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