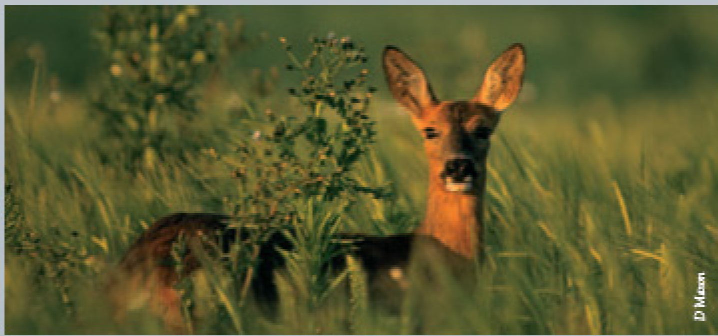
Neither too many nor too few?



The myth of 'social regulation' of roe deer populations has lasted for almost 50 years, say John Linnell and Jean Michel Gaillard. The cumulative research of the last decades is now finally in a position to bury it - but with what shall we replace it?

Roe deer are notoriously difficult beasts to count, much to the frustration of researcher and estate manager alike. Being largely solitary and elusive, the casual observer rarely gets any impression of the number of individuals inhabiting any given forest, beyond the frequency of glimpses of vanishing back-quarters. This refusal to stand up and be counted has led to much debate about the size of roe deer populations and the factors influencing them.

Early observers believed that roe deer appeared to spread out relatively evenly throughout the landscape, avoiding the clumps of locally high density often seen in other species, especially fallow deer for example. By the 1970's and 1980's this simple observation had been turned into a scientific 'fact'- the idea of social regulation. The idea was simple enough: as density increased, more young individuals would be driven out of the population to prevent it becoming too dense. Thus a roe deer population should always live in 'harmony' with its food supply due to social pressure preventing increase. Superficially an appealing idea, with a certain appealing logic. The only problem is that it's wrong. However, like many superficially appealing ideas, the social regulation of roe deer became an established fact, which has been hard to dislodge from the public's mind. How did it come to this?

Within the scientific world the issue really started in 1977 with a publication by the Polish researcher Boguslaw Bobek in the prestigious scientific journal Nature. The paper presents some data about the relationship between roe deer density and food availability which is

unproblematic. However, the paper states the mechanism as being "The sizes of unexploited populations of roe deer are regulated by spring migration" (i.e. dispersal) without any supporting data. It is stated as just a simple fact of roe deer biology. This accessible publication led to the idea spreading widely. As his source Bobek quoted the famous Danish researcher Helmut Strandgaard whose monograph from 1972 is one of the classics of roe deer biology which has inspired several generations of researchers. Strandgaard presented lots of really good data which still stands today, but some of his interpretations were influenced by the norms of his times. Relevant to the issue of social regulation is his observation that many young animals were leaving the study population and getting shot outside. He felt that the magnitude of this emigration was severely limiting the population's growth rate. As an explanation Strangaard offered the following: "the reason for this emigration lies in the fact that the population can only reach a certain density." Again social regulation was stated as a background fact rather than as a result of his study. For support Strandgaard cited a previous researcher at the same study site, Johs Andersen, who had in turn written an influential classic monograph in 1953. This monograph also states that: "Under all circumstances a certain amount of emigration from crowded areas is to be expected because there is a limit to the number of deer a district can support." Again, social regulation is expected as a natural property of populations. Andersen refers to a Danish hunting magazine from 1943 for support, but from here the trail goes cold. In parallel to these continental studies, two British researchers, H G Cummings and P S Bramley, were studying territorial behaviour of roe deer and speculating about how it might relate to social regulation.

The result was a body of ground-breaking roe research conducted in the 1950s, 1960's and early 1970's which produced much useful data, but which was erroneously interpreted based on the dominant ideas of the times. These ideas revolved around the group selection ideas of Wynne-Edwards which, simply put, proposed the group, or the population, as the unit on which natural selection operated. In this view, individuals would make decisions for the benefit of the population rather than for themselves. Hence, it was expected that young animals would disperse to prevent the population increasing too much. Current ideas of the evolution of social systems focus almost exclusively on the individual being the unit for natural selection. Therefore, the whole premise for the social regulation hypothesis falls away. The myth could also have been avoided if researchers at that time had had the same access to scientific databases that we have today. There is actually an article (in a very obscure Russian language journal from Lithuania) from 1973 that demonstrates that increasing density had negative effects on several reproductive parameters in a Lithuanian roe population studied from 1963-1970, a finding that automatically undermines social regulation. The one good thing about this longstanding myth is that it has motivated a wide range of studies in many countries to try and determine which factors actually influence the size of roe deer populations.

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When researchers discuss population dynamics we separate between two processes. Firstly, we discuss 'limiting' factors. These are not factors that set an upper limit on population size, rather they are all the factors that have a negative influence on the rate at which populations grow. Secondly, we discuss 'regulating' factors. These are a subset of limiting factors that respond in a density-dependent way, i.e. as population density increases, the magnitude of their impact increases, thus slowing population growth. Quantifying the magnitude of limiting factors and determining if they are density-dependent or not requires a great deal of research effort. Fortunately, roe deer have been widely studied throughout Europe and have often been the subject of long term studies. Of greatest significance have been the studies in Chedington woods, Dorset (1961-1989 conducted by Robin Gill and colleagues), Chize Reserve, France (1979-ongoing), Trois Fontaines Reserve, France (1975-ongoing, both directed by Jean Michel Gaillard and the Office National de la Chasse), and Bogesund, Sweden (1988-ongong conducted by Petter Kjellander and Olof Liberg), to name just the longer studies. In addition come the shorter studies from Norway (Storfosna Island and southeastern Norway conducted by Reidar Andersen and John Linnell) and from central Italy (conducted by

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Stefano Focardi). The combination of all these studies has given us a dramatically improved, but constantly expanding, understanding of the factors that influence roe deer populations.

A wide range of factors affect the reproduction and survival of roe deer. Roe die from a wide range of causes, including human harvest, vehicle collisions, accidents (a surprising number die from drowning or falling), starvation (often due to snow and severe winters), and predation. All these have the potential to act as limiting factors. What is often surprising in roe deer studies is the great rarity of death from disease or parasites. In the cases where it is found it is often brought on by starvation or otherwise poor condition. In addition to these mortality factors we have also seen that reproduction can be affected by a wide range of environmental factors such as weather. Various studies have shown that weather in both winter (snow) and spring (affecting food conditions in late pregnancy and just after birth) can influence the birth and survival of offspring. However, listing all these limiting factors only tells us a small part of the story. The real question of interest is how many of them are influenced by population density and can thus function as regulatory factors?

The long term studies that have been conducted to date have demonstrated ample examples of density-dependence on reproduction. A general pattern is that these are most pronounced in the early stages of the life cycle, i.e. on litter size during pregnancy or at birth, on the survival of fawns during their first year and also on the body weights that fawns achieve during the first year of life. Therefore, researchers have demonstrated a wide range of density-dependent factors that have the potential to regulate (i.e. stabilise) roe deer populations.

However (there is always a "however"), what we have seen is that the magnitude of these density-dependent responses is often too small to prevent often dramatic changes in population size. During a period of population growth, for example following a relaxation of harvest pressure, animals born and raised during good years (of low population density) will manage to maintain very high reproductive rates despite an increasing competition for food. This will imply that the population can grow rapidly, and that growth will not slow until extreme densities are reached. Likewise, individuals born during periods of high food competition (periods of high density) may never actually catch up, even if environmental conditions improve, for example following a reduction in density. The existence of these time lags in response and the persistent effects of conditions following birth (called cohort effects) implies that roe deer populations left to themselves will probably demonstrate fluctuations in size, potentially overshooting 'carrying capacity' (a controversial topic in biology) before density dependence effects kick-in significantly. The picture becomes

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even more complicated when we consider that weather and climatic conditions can greatly modify the effects of density. For example a heavy winter will have greater effects at high density than low density. A final level of complication is added by the frequent finding of fine scale differences in the population dynamics of populations over distances of just a few kilometres, or even between females occupying different home ranges.

And what about dispersal? In a previous article I described how roe deer display high rates of juvenile dispersal – which does act as a limiting factor on a local scale – but our available data indicate that it acts in an anti-regulatory manner, with clear declines in dispersal frequency as density increases.

In summary we now have a good understanding of the many factors that influence roe deer population dynamics, but it is not so easy to accurately predict the fate of a specific population over time because of the great complexity of the issues and the fact that the relative importance of different factors will vary between populations. In other words, we still have a long way to go to integrate our new knowledge into practical management. However we have at least come to a stage where we can begin this task with a solid platform of knowledge.

A final cautionary note, which may not be so relevant for British readers but is of increasing importance for managers on the continent, is that virtually all these detailed and long term studies from which our understanding of roe deer dynamics comes have been conducted in the absence of large predators such as wolves and lynx. As we see an expansion of these large predators across Europe, we will be forced to ask ourselves many new questions about how they influence roe deer dynamics. A roe deer researcher's work is never done. (Luckily!).

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