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Agricultural Changes and Population Outbreaks of Grassland Voles

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GUIDING QUESTIONS. —

How do landscape, land use and their evolution determine, on several scales, the population dynamics of agricultural pests?

How does the predator community respond to changes in the abundance of main prey, and what are the risks to secondary prey?

What are the variations in pathogen community patterns in such systems?

How does long-term observation create the conditions for quasi-experiments?

How can this knowledge be used to implement an integrated control plan for grassland vole populations?

How do these processes fit into a regional “system”?

What new constraints are emerging with global warming?

What are the socio-anthropological and epistemological necessities and limitations to conducting and applying such studies?

Socioecosystems,

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1.1. Introduction

Rodent outbreaks have, in historical memory and at more or less regular intervals, massively affected crops and stored goods locally and sometimes even regionally. They have also carried diseases that are transmissible to humans, such as plague, and continue to carry both old and new emerging diseases.

However, they still elude most explanations and no simple remedy has been found to date. Beyond the myths and legends inspired by such proliferations, they have attracted the attention of scholars since the 19th century.

Charles Elton was one of the historical contributors to this research in the early 1920s. In 1942, he described the phenomenon with humor:

Voles multiply. Destruction reigns. There is dismay, followed by outcry, and demands to Authority. Authority remembers its experts or appoints some: they ought to know. The experts advise a Cure. The Cure can be almost anything: golden mice, holy water from Mecca, a Government Commission, a culture of bacteria, poison, prayers denunciatory or tactful, a new god, a trap, a Pied Piper. The Cures have only one thing in common: with a little patience they always work. They have never been known entirely to fail. Likewise, they have never been known to prevent the next outbreak. For the cycle of abundance and scarcity has a rhythm of its own, and the Cures are applied just when the plague of voles is going to abate through its own loss of momentum. (Elton 1942)

The story told in this chapter spans more than 70 years, including some 40 years of research that is still ongoing. It is therefore part of a worldwide research process, still unresolved, which has led to a colossal body of literature in ecology and led some critics to think that the problem was unsolvable and therefore of no interest. We shall see later that this is not the case. Population fluctuations in rodents are still one of the classic problems of animal ecology (Krebs 2013).

The damage that species in this group cause to agrosystems and stored commodities can equal almost the entirety of some crops (Buckle and Smith 2015). This is the case in the Jura Mountains, where outbreaks of the montane water vole, *Arvicola amphibius*, formerly known as *Arvicola terrestris*, a taxonomically complex grassland species (Chevret *et al.* 2020), can reach a density of several thousand individuals per hectare, such that an entire grassland is devastated (Figure 1.1).



Figure 1.1. *Water vole tumuli in the commune of Les Combes in February 2012, during a population peak (photo: Fredon de Bourgogne Franche-Comté). For a color version of this figure, see www.iste.co.uk/giraudoux/socioecosystems.zip*

When, at the end of the 1970s, researchers from the National Institute for Agricultural Research (*Institut national de recherche agronomique*; now INRAE, *Institut national de recherche pour l'agriculture, l'alimentation et l'environnement*) were called in by the Ministry of Agriculture and requested to find a solution to the new recurrence of regional vole population outbreaks in the Jura Mountains, Charles Elton's description was still relevant. They did not find any result in the scientific literature that would allow them to propose a sustainable control solution based on the knowledge of the causes of the outbreaks and their cyclicity. The agronomic crisis could only be addressed by phytosanitary measures at the level of the individual plot of land, in accordance with the simplistic responses of agronomy at the time. It was based on burying bait containing a rodenticide anticoagulant, often too late in the outbreak cycle to be effective in preserving the crop (Delattre and Giraudoux 2005). The implementation of large-scale collective chemical control (several thousand hectares in the Doubs department alone), supposedly curative, only during outbreak phases, continued for 30 years, until the beginning of the 21st century. The environmental consequences of these treatments were evident from the end of the 1980s until the beginning of the 2000s with the mortality of hundreds of carnivores consuming rodents, by secondary poisoning (buzzards, red kites, foxes, etc.) or directly by consuming bait (wild boar, etc.) (Berny *et al.* 1997). A paroxysmal phase in 1998 constituted a tipping point toward changes in practices and prevention, based on the results of research conducted during an earlier

multisectoral regional program from 1992 to 1996, but which had been deliberately neglected by farmers. Naturalist associations and hunting federations have increased the mobilization of public opinion and raised the awareness of the agricultural world to the environmental and socio-economic risks of the “all-chemical” approach, which led to a period of broad consultation between all stakeholders from 2000 to 2006, within the framework of a State-Region plan contract (Delattre and Giraudoux 2009). The research conducted under this multisectoral program and thereafter complemented the main results obtained in the 1990s. They have more strongly integrated economic and socio-anthropological components and have led to the representation of a regional multi-scale system explaining outbreaks, in a context taking into account their multiple causes and consequences, and to a profound revision of control methods, then preventive, now proven effective and sustainable (Giraudoux *et al.* 2017).

The purpose of this chapter is to present this regional system and to discuss the human, structural and epistemological conditions that prevailed in its discovery and implementation, and the various constraints that must be taken into account because of its multifunctionality. We will specify the research obstacles that need to be overcome in order to understand the processes involved and explore the consequences. We will also see how this system is linked to other components of the regional socioecosystem presented in the following chapters.

1.2. The European Common Agricultural Policy and its national implementation, voles and their predators...

1.2.1. *Establishment of practices and landscape*

The Jura Massif is known, among other things, for its cheese specialties with several emblematic protected designations of origin (PDO), such as Comté, Morbier, Mont-d’or and Bleu de Gex. From 67,154 tons in 2018, Comté production, for example, currently generates nearly 8,000 direct jobs. It accounts for 80% of the PDO cheeses in the Jura Massif and a quarter of the French PDO cheeses – but this was not always the case. In the 1950s, in this region of medium-altitude mountains (250–1,718 m), grassland covered between 20% and almost 75% of farmland, regardless of altitude (Figure 1.2). In the 1960s, common European and national agricultural policies encouraged the renovation of farms (consolidation and enlargement of plots, mechanization, etc.) and their specialization throughout France. Farmers above 500 m in the Jura have thus been encouraged to specialize in modernized dairy and cheese production. The shift from traditional mixed farming to exclusive livestock production led them to convert fields formerly ploughed for cereal or potato production into permanent grassland and, as a result, to increase the

proportion of permanent grassland to 75%–100% farmland. This has also led to an increase in forage productivity from 2 to 3 tons of dry matter per hectare per year in the 1950s to 4 to 9 tons today. Milk production itself has increased from less than 2,000 l per cow per year in 1951 to an average of about 7,000 l today (the range is 5,400–8,500 l).

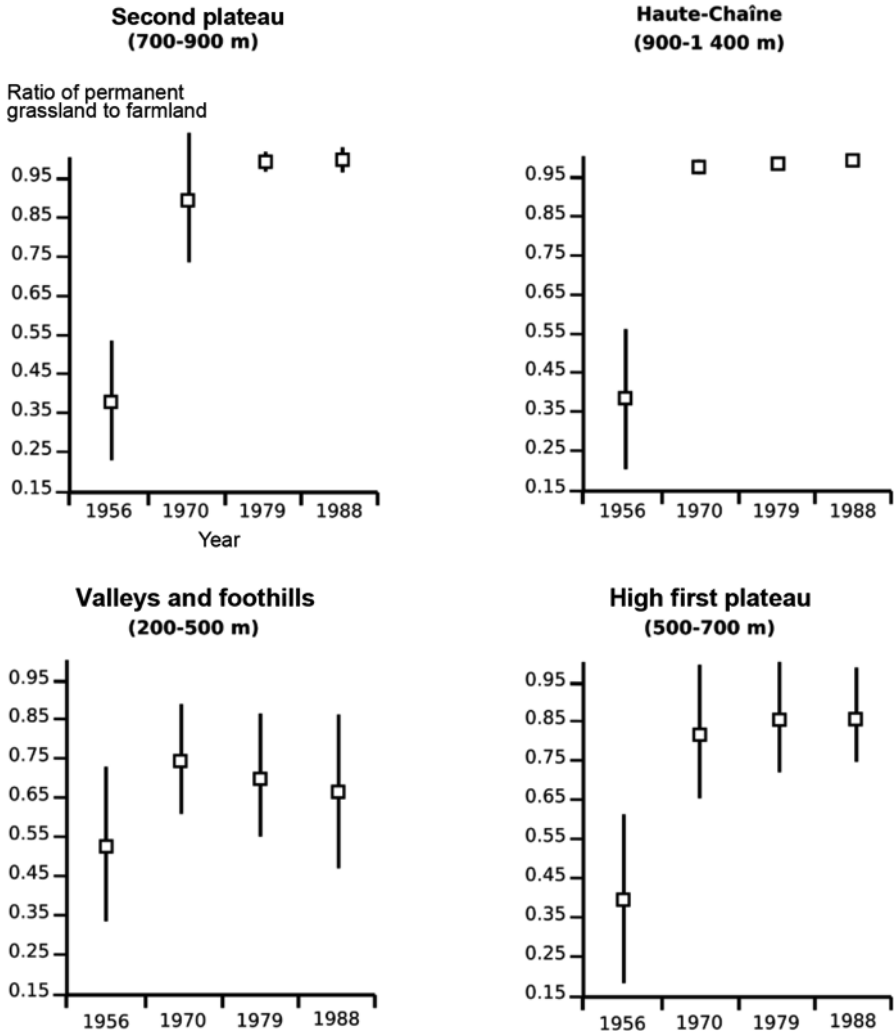


Figure 1.2. Evolution of permanent grassland in the Doubs department, from Giraudoux et al. (1997). The squares represent the average of the communes and the vertical bars the standard deviation

Massive outbreaks of a species of grassland vole, the water vole, *A. amphibius*, with cycles of 5–6 years spreading in the form of a traveling wave over all the mid-altitude grasslands of the Jura Massif, were reported by the Regional Plant Protection Service of the Ministry of Agriculture (*Service régional de protection des végétaux du ministère de l'Agriculture*, SRPV) as early as the 1970s. In the same area, outbreaks of another species of grassland vole, the common vole, *Microtus arvalis*, which was later found to be non-cyclic in the area (Giraudoux *et al.* 2019), were also observed, reaching, like the former species, several thousand individuals per hectare locally. For the past 50 years, the system seems to have stabilized around regular outbreaks of grassland voles, with peaks that can last locally for several years.

1.2.2. Which measurement tools for which observations?

Objective and standardized measurement of the phenomenon to be studied is a prerequisite for any observation, whatever the discipline. In the field of animal populations, there are various methods, but, in the absence of being able to count all individuals directly, those based on sampling, which are widely recognized, derive from two principles: either catch effort (this involves measuring the rate of decrease in capture success as a function of the effort needed for capture) or capture-mark-recapture (this involves measuring the dilution of individuals previously captured and marked or genetically identified in the population). Both methods generally aim to measure absolute abundances. For most species, these methods are logistically very cumbersome. In the case of voles, they require several days to implement for an estimate of only a few thousand square meters. From the late 1970s to the early 1990s, only these methods were calibrated and used, which reduced observation to local areas (a fraction of a farm plot) that were not related to the regional geographic extent of population variations. This put the researchers in the position of a meteorologist trying to understand how thunderstorms are triggered by staying in one place under an umbrella. However, empirical ratings based on the observation of surface activity indicators (earthen mounds, burrows, etc.), carried out by the SRPV in each municipality visited by car, already indicated that high densities of water voles affected very large areas over several tens of square kilometers, and covered all of the department's mid-altitude meadows in a few years (Pascal *et al.* 1985). We therefore decided, at the end of the 1980s, to calibrate these index methods on the standard methods of estimation by catch effort, first of the common vole (Delattre *et al.* 1990; Quéré *et al.* 2000), then of the water vole (Giraudoux *et al.* 1995). Since then, it has been possible to estimate population density variations by walking transects over several tens of kilometers, segmented into 10-step intervals, in which the presence or absence of signs of water vole, common vole or mole activity is

noted. The SRPV communal scoring system was also standardized in the late 1980s (Habert 1988). For a long time, these methods met with reluctance from the editorial staff of international scientific journals on ecology, as they did not correspond to the commonly accepted standards of precision and demographic modeling. It was very difficult to convince the editors that the loss of local precision was acceptable in a system where the amplitude of variations in abundance is great (from zero to several thousand individuals per hectare), and that this loss was compensated for by a geographically broader vision than that offered by the other methods. Once this first obstacle had been removed, research could move from the plot scale to those that included the phenomenon observed at the regional scale.

1.2.3. Landscapes and practices

Examination of the SRPV communal scores confirmed the traveling wave phenomenon in the water vole population (Giraudoux *et al.* 1997; Berthier *et al.* 2014) (Figure 1.3) and the correlation between outbreak risk and landscape composition for the water vole and common vole (Figure 1.4). In addition, threshold effects were detected: for example, at the communal scale, for the common vole, a small increase in permanent grassland beyond the category of 50%–60% of farmland abruptly shifts from a low-risk system to a high-risk system (Figure 1.4(a)). The influence of semi-permanent legume crops (clover, alfalfa, etc.), which can considerably lower this threshold, has also been demonstrated (Delattre *et al.* 1992). In addition, index transects carried out over several hundred kilometers have demonstrated the coincidence between landscape type, as a spatial arrangement of habitats (grasslands, ploughs, hedgerows, forests, etc.), and the amplitude of variation of grassland vole populations, both for the water vole (Giraudoux *et al.* 1997; Duhamel *et al.* 2000; Fichet-Calvet *et al.* 2000; Morilhat *et al.* 2008) and the common vole (Delattre *et al.* 1992, 1996, 1999, 2009) (Figure 1.5). The proximity of wooded structures (hedges, forests) and dwellings, in particular, was generally related to lower average densities and lower density variations of both grassland species.

Finally, at the plot level, water vole population growth was found to be earlier with organic fertilization and in hay meadows. On the other hand, during the high-density phase, lower vole population abundance was observed in environments disturbed by grazing and ploughing (Morilhat *et al.* 2007). Finally, still on this plot scale, we have shown that the existence of networks of galleries dug by the mole (*Talpa europaea*) facilitated colonization by the water vole and accelerated the population growth phase (Delattre *et al.* 2006).

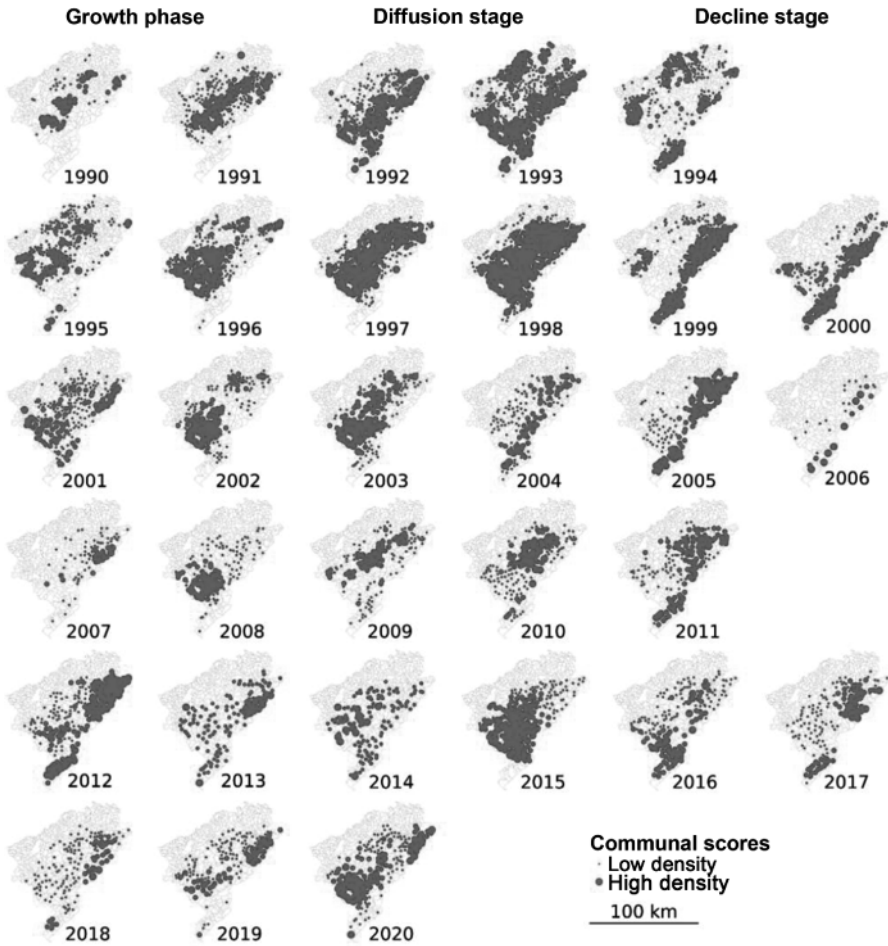


Figure 1.3. Temporal evolution of water vole outbreaks in the Doubs department, during six demographic cycles (source: Fredon/DRAAF Bourgogne Franche-Comté). For a color version of this figure, see www.iste.co.uk/giraudoux/socioecosystems.zip

All of these observations led to a hierarchy of factors correlated with the dynamics of vole populations at the scales where the correlations were observed (Table 1.1). However, the processes leading to these correlations remained hypothetical at this stage.

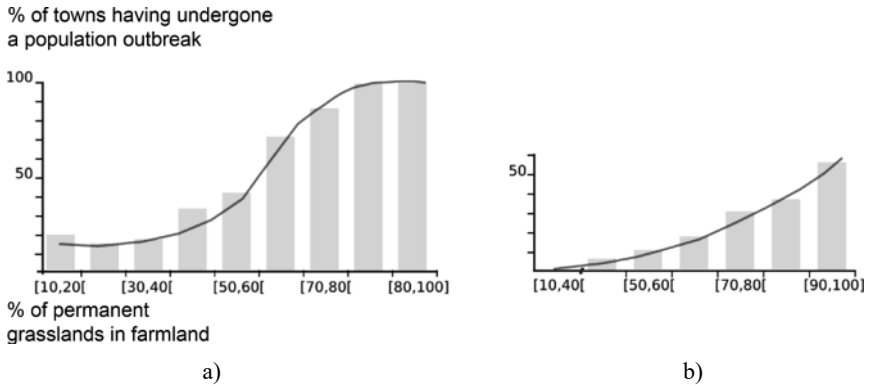


Figure 1.4. Landscape composition and outbreak risk. a) common vole in Côte-d'Or (Delattre et al. 1992). b) Water vole in Doubs (Giraudoux et al. 1997)

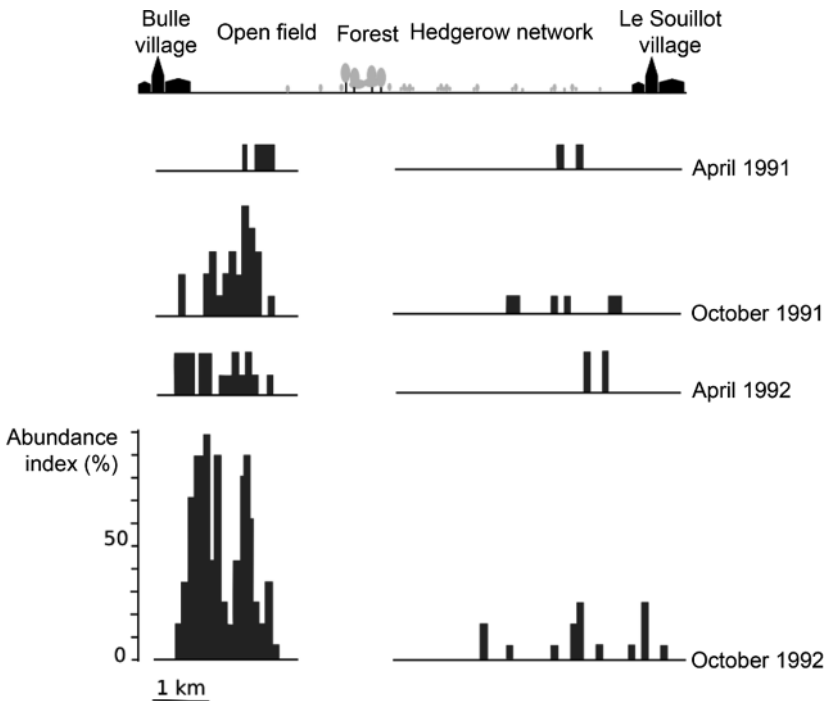


Figure 1.5. Effect of landscape structure on common vole population dynamics. Open field areas occupied by permanent grassland show much greater variation in abundance than areas with hedgerow networks, according to Delattre et al. (1996)

Spatial scale	Main results
Regional (2,500 km ²)	Population dynamics and traveling wave correlated with landscape composition (proportion of permanent grassland).
Landscape (25 km ²)	Magnitude of abundance fluctuations: – diminished by the proximity of hedges, forests and dwellings; – increased by semi-permanent legume crops.
Plot (0.01 km ²)	Population growth: – increased by mole networks; – increased by grass height and fertilization; – decreased by ploughing, trampling by livestock and keeping in short grass (grazing).

Table 1.1. *Hierarchy of factors correlated with variations in montane water vole abundance, from Morilhat et al. (2008)*

1.2.4. Synchronies

From the early 1980s to the mid-1990s, population demographic monitoring of small mammals was carried out in the Septfontaines and Le Souillot area, covering nearly 20,000 hectares. This has shown, in particular, the concomitance of declines and phases of low population density of species as different as those living in wooded environments (hedges, forests) and grasslands (Figure 1.6) (Giraudoux *et al.* 1994). Furthermore, water vole declines were frequently observed synchronously from one plot to another, even in neighboring plots that were more sparsely colonized and where the vegetation was practically intact.

Synchronies were also sought between reproductive parameters, the age structure of common and water vole populations and their population dynamics. For the common vole, demographic parameters (sex, age, reproduction, etc.) were measured over 17 years and correlated with weather conditions (temperature and precipitation). Strong but complex relationships between female reproduction and meteorological variables were then revealed: female spring reproduction was decreased after cold winters. However, the rate of population growth was not correlated with weather conditions (at the time and up to 3 months earlier) or with female reproduction. The population could grow when reproduction was low or decrease when reproduction was at its peak. These results, combined with data on the age structure of the population, indicated that mortality (by predation, disease, stress or a combination of all three) was solely responsible for the observed multi-year population dynamics (Giraudoux *et al.* 2019).

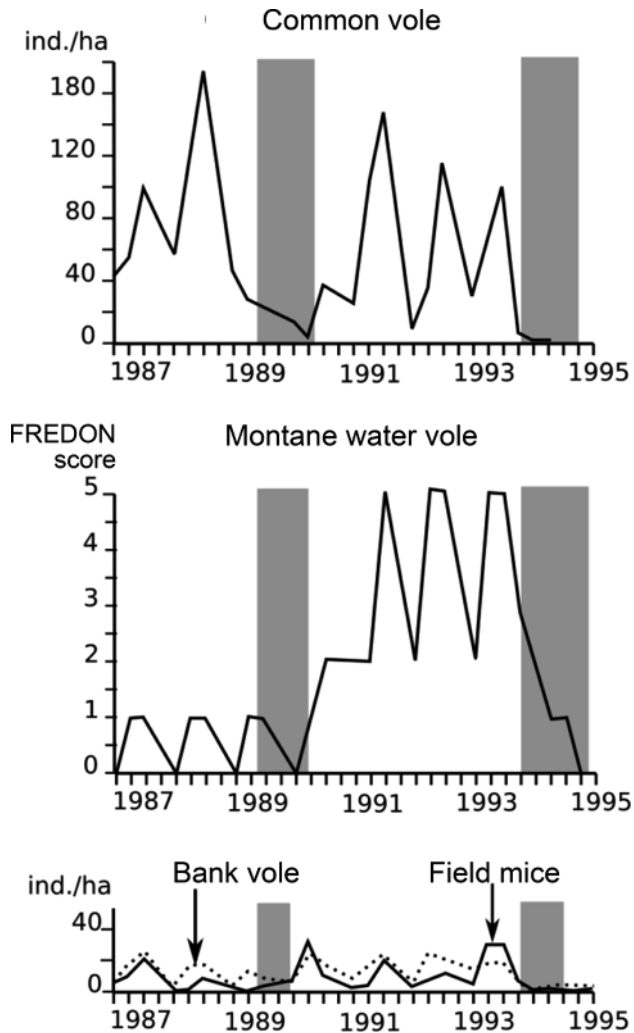


Figure 1.6. Synchrony of decline and low-density phases (rectangles) of small grassland and woodland rodents, after Bernard *et al.* (2010). A Fredon score of 5 corresponds to densities of several hundred individuals per hectare (ind./ha)

We have not been able to collect such a long time series of demographic parameters for the water vole. Studies conducted during two declines have shown contrasting results. In the decline observed in the study by Cerqueira *et al.* (2006), the population was reported to be aging (owing to a lack of recruitment of young) and reproduction of females slowed down. In the decline observed in the Villette

et al. (2020) study, male body condition was poorer during the decline than during the peak of high density, without population aging, and female reproduction was reduced.

Although the approach adopted so far has been purely correlative, that is, it has focused on detecting correlations between variables in the system without being able to prove that they correspond to direct causalities, or to determine the underlying processes, these correlations or lack of correlations have already made it possible to eliminate a certain number of causalities. The existence of “traveling waves” observed among water voles, whose propagation is obviously totally independent of local weather conditions, ruled out the influence of meteorology on population dynamics on a regional scale. The local synchrony of the declines of this species, even in plots still rich in grass, showed that the hypothesis of regulation by the sole effect of the depletion of food resources was insufficient. The fact that the phases of low density were, moreover, synchronous whatever the species and their environment eliminated the action of genetic or other factors internal to each population. The factors responsible for the decline were therefore to be sought in additional non-meteorological causes likely to affect several species at the same time in different environments. The role of predation and diseases, whether combined or not, thus remained one of the most valid explanatory hypotheses.

1.2.5. Predation

It has been suggested that predation is a major driver of fluctuations in rodent populations. Theory predicts that specialist predators, such as weasels or stoats, that feed on a limited number of prey species may destabilize prey populations because they exert a delayed density-dependent mortality, whereas generalist predators, which feed on a wide variety of prey species, cause density-dependent mortality without delay, and thus stabilize prey populations (Andersson and Erlinge 1977). However, experimental tests of this prediction, for example, by predator removal, and comparative field studies provide evidence both supporting and rejecting this hypothesis (Korpimaki *et al.* 2002; Oli 2003; Gilg *et al.* 2006). Measuring the effect of predation on a prey population, when the system includes alternative prey and a large number of predator species capable of different diet or population variations (through breeding, movement or a combination of both), is virtually impossible with the current state of knowledge and techniques. However, it is possible in such systems to measure the functional (diet variation) and numerical (population variation by reproduction or movement) response of some predators to changes in prey abundance, and this has been attempted.

These studies showed that, except during their periods of low density, grassland voles constituted the majority and up to 90% of the prey remains found in the droppings or pellets of carnivores and raptors present in this system. The declines of the grassland voles, which occurred at the same time as the low-density phases of the other rodent species, also systematically showed a broadening of the food spectrum of the predators (Figure 1.7). The multiplicity of alternative prey in the field, however, led to complex responses, with the proportion of one species in the diet depending on both its abundance and the abundance and accessibility of other species (Bernard *et al.* 2010; Raoul *et al.* 2010; Baudrot *et al.* 2016b).

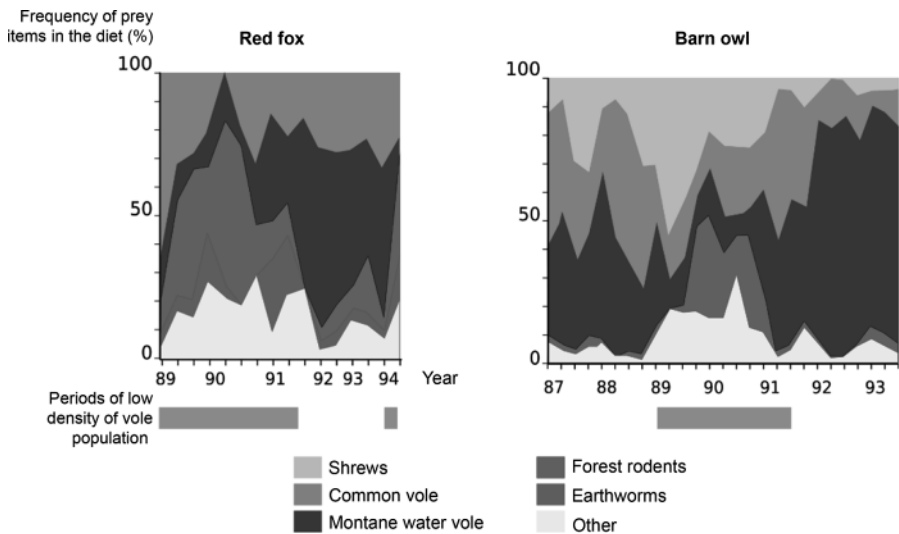


Figure 1.7. Diet variations of foxes and barn owls. Note the diversification of diet during phases of low vole density, according to Quéré *et al.* (original data) for the red fox and Bernard *et al.* (2010) for the barn owl. For a color version of this figure, see www.iste.co.uk/giraudoux/socioecosystems.zip

For 20 years, Fredon de Franche-Comté has been carrying out day and night roadside counts in an experimental vole control zone (*zone expérimentale de lutte anticampagnols*, ZELAC) in the Val des Usiers. However, this technique does not allow monitoring of small mustelid populations, which may play an important role in the regulation of vole populations. Nevertheless, they indicated that in such an ecosystem with large variations in grassland vole populations, although the proportion of each species of predator studied may change over time, the total number of predators present, as well as their total biomass and consumption, followed the outbreak cycles of grassland voles. For example, although the fox

population increased tenfold during the first half of the study, the total number of predators present for a given vole density remained little changed throughout the study, indicating that populations of other predators declined in a compensatory manner. In addition, the higher predator densities observed during the grassland rodent peak were primarily owing to mobile birds of prey (Figure 1.8).

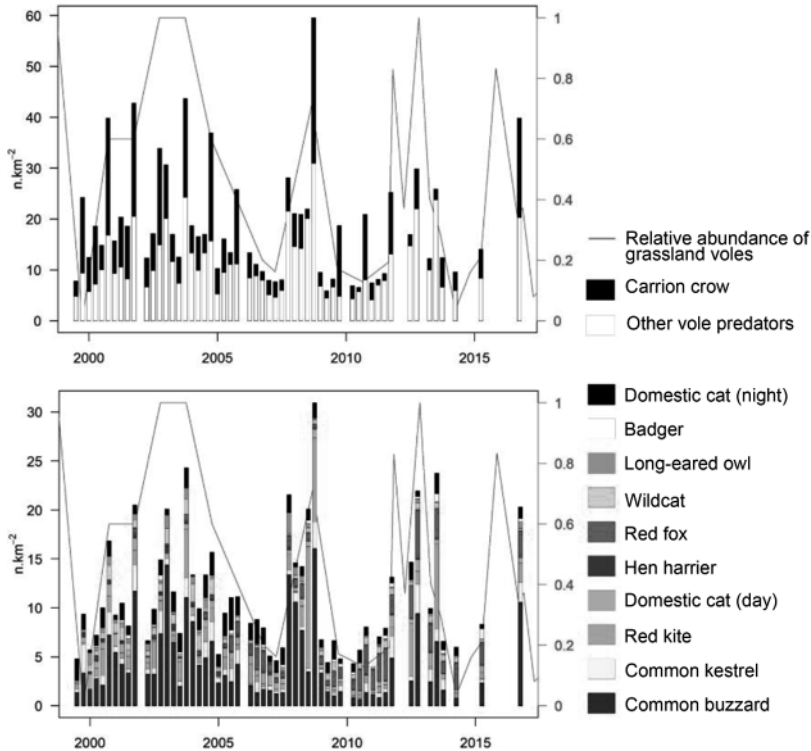


Figure 1.8. Numerical response of vole predators observed by day and night roadside counts in the Val des Usiers, from Giraudoux et al. (2020). The broken line in the background and the y-axis on the right represent variations in the abundance of grassland rodents; the value 1 corresponds to the maximum value observed at the peak of the outbreak. For a color version of this figure, see www.iste.co.uk/giraudoux/socioecosystems.zip

Calculations based on these estimates indicate that the predators observed during the low-density phase of the grassland rodent populations, alone, could slow the increase or even cause the extinction of rodent populations locally. However, the predator densities observed during outbreak peaks are insufficient to explain the decline in rodent populations observed after these peaks: this ecosystem periodically

(permanently, on a large scale) offered an incredible biomass of several tens of kg/ha of easily accessible grassland voles to a large number of predator species, but consumption by the studied predators was multiplied by 7 at its peak, while the biomass of the small mammal population of grasslands was multiplied by thousands (Giraudoux *et al.* 2020). Furthermore, the concomitant increase in fox population with decreases in hare, wild cat and domestic cat suggested that foxes had a negative impact on the other species (Figure 1.9).

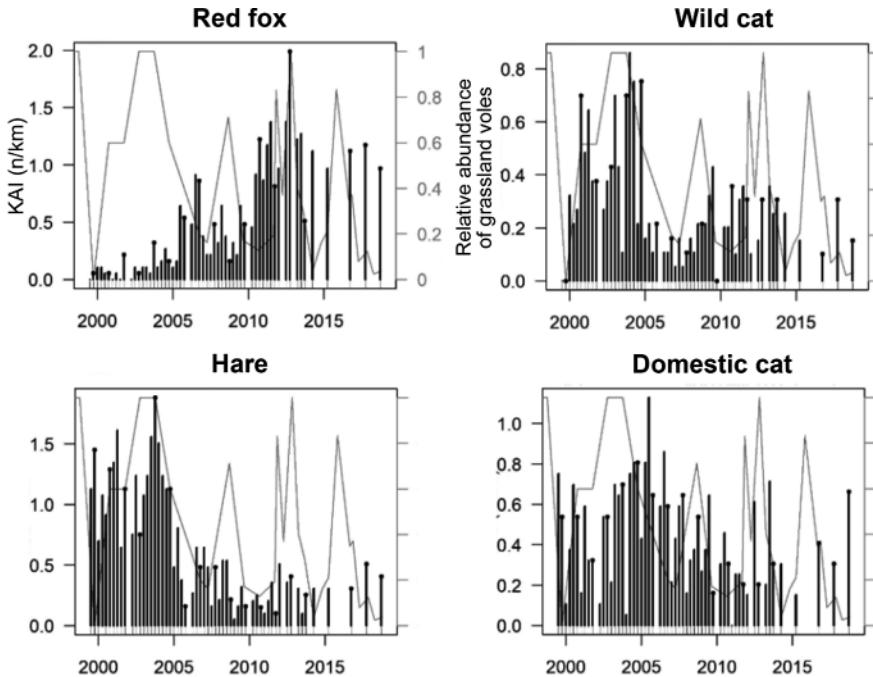


Figure 1.9. Variations in the kilometric abundance index (KAI) of red fox, hare, wild cat and domestic cat, after Giraudoux *et al.* (2020). The broken line in the background and the y-axis on the right represent variations in abundance of grassland rodents and the scale is the same in all figures; the value 1 corresponds to the maximum value observed at peak outbreak

Systems where a prey with high abundance dominates, permanently or periodically, make it possible to establish prey switches or even predation sinks, that is, situations where secondary prey undergoes strong predation that keeps them at low density, owing to the high density of one or more predators or the diversification of their diet during phases of lower density of the main prey. The concomitance between peaks in the abundance of water voles in the Risoux massif

and the production of young capercaillie from 1976 to 1995 has been attributed to this type of process (Leclercq *et al.* 1997).

Finally, the ZELAC predator study indicates that domestic cat populations, concentrated around dwellings, could reach densities of 2.4–9.1 and, exceptionally, up to 18 individuals per km² within a 500 m radius, within which lower vole densities were generally observed (Figure 1.5) (Delattre *et al.* 1996, 1999).

1.2.6. Bacteria and other vole parasites

Predators alone do not appear to be able to trigger peak density declines in grassland voles, and these declines can occur even when food is abundant. Through successive eliminations, diseases caused by pathogens (viruses, bacteria, parasitic protozoa and metazoa), possibly combined with stress, were thus one of the remaining hypotheses to explain the declines. This hypothesis had not been fully tested in the past, as early studies had, for technical reasons, been limited to one or a few candidate infectious agents and proved inconclusive (Krebs 2013). More recent research emphasized the importance of considering pathogen communities as a whole, whose elements may act synergistically, neutrally or antagonistically (Telfer *et al.* 2010, 2011). Massive DNA sequencing techniques, popularized about a decade ago, with a reduction in their cost, make it possible to sequence all of the DNA contained in a sample and, by comparing it to sequences recorded in databases, to infer the taxa present. Nevertheless, the characterization of all the pathogenic organisms present still faces many difficulties: first, the existence of sufficiently informed and validated databases to make identifications possible and reliable; second, the proportion of genetic divergence to be retained in order to separate two species (one prefers to speak of an operational taxonomic unit, or OTU, rather than a species); third, the collection and conservation of samples, especially when it comes to RNA viruses, which are extremely fragile; and fourth, the differentiation between pathogens and commensals, as the functional barrier between the two is permeable. A pathogen that is harmless to a healthy organism can become a formidable pathogen in the case of immunosuppression caused by stress, for example.

Driven by an insistent request from Fredon de Franche-Comté, whose president at the time managed to find the necessary substantial funding over 5 years, outside the usual research funding circuit, we used high-throughput DNA sequencing to characterize bacterial communities during a peak and a decline in water vole populations, from 2014 to 2018. In addition, animal spleens collected by Nathalie Charbonnel's team (INRA) earlier, for other purposes, during another decline from 2003 to 2005, were preserved and frozen (Charbonnel *et al.* 2008), so we could

compare bacterial communities from one decline to another (Villette 2018). The results can be summarized as follows:

- a surprisingly high number of 155 OTUs, representing at least 13 genera in 11 families, were detected, when only a few dozen bacterial species are known to infect the water vole so far;
- the number of OTUs per vole (individual richness) was higher during declines, with vole body condition lower and reproduction reduced;
- the residual OTUs in the low density phase were already present everywhere, from the beginning of the study and throughout the period, and the presence of certain OTUs was correlated with each other;
- the total number of OTUs in the local populations and the total population of voles did not show clear variations during the declines;
- a comparative study of samples that had been collected 10 years earlier, during a phase of decline, shows that the bacterial communities were not entirely the same at that time as those observed during the program.

Without being conclusive about the impact of bacterial communities on the dynamics of water vole populations, these results showed the previously underestimated complexity of bacterial communities and of the interactions between these communities and vole populations. They showed that such studies, in order to account for this complexity, should be conducted at several spatial scales: several times a year, over several years, and at local and long-distance vole dispersal scales (Villette *et al.* 2020).

Studies have also been conducted on other parasitic taxa, some of which are shared between the water vole and the common vole. The water vole hosts a variety of helminths in the region, including the cestodes *Echinococcus multilocularis*, *Taenia taeniaeformis*, *Taenia tenuicollis*, *Taenia crassiceps*, *Anoplocephala dentata*, *Paranoplocephaloides omphalodes*, *Aprostotandrya sp.* and the nematodes *Trichuris arvicurris*, *Capillaria murissilvatici* and *Heligmosomoides laevis*. Several viruses have also been detected, including *Puumala* virus, lymphocytic choriomeningitis virus and bovine pox virus (vaccinia). Research on these parasites focused on the correlation between their prevalence and the phases of the cycle, and its spatial distribution: *Trichuris arvicolae* was most prevalent in increasing and peaking populations and absent from declining populations, while the prevalence of *T. taeniaeformis* was higher in phases of low local small mammal host abundance (<0.1 km²) than during peaks. Vaccinia virus prevalence was higher in late-peak than early-peak populations and seroprevalence was spatially aggregated, with some study sites showing high seroprevalences (>70%), while in others anti-vaccinia

antibodies were completely absent. However, these relationships remain difficult to interpret, as their expression and hypothetical effects depend on the scale of the study and the variability of many other unknown ecological factors that could not be adequately monitored (health status, demographics and distribution of other hosts, other pathogen communities such as viruses and bacteria, etc.) (Charbonnel *et al.* 2009; Villette *et al.* 2020).

The ecology of *E. multilocularis* will be discussed in Chapter 4.

1.3. Controlling outbreaks and their consequences: from correlations to action

The research presented in section 1.2 of this chapter, thanks to data collection mechanisms on several scales of space and time, makes it possible to identify correlations between the variables of the system studied. It can therefore be posited that, being observational, they do not allow formal inference of causal links between these variables. These studies can be described as eco-epidemiological because, like epidemiological studies, they are based on a description of the components of a population system in space and time. Despite their intrinsic epistemological weakness in proving causality, compared to the hypothetico-deductive method chosen as the elective, if not exclusive, method of reductionist approaches (Popper 2006), observational studies are nevertheless powerful allies of the researcher (Ríos-Saldaña *et al.* 2018). They provide crucial data to better identify covariations in these systems and, through a comparative approach, to design tests and properly contextualized modeling at the appropriate locations, times and scales. They are also powerful allies for the manager as they inform decision-making and make adaptive management, necessarily linked to adaptive monitoring, possible (Lindenmayer *et al.* 2011). Adaptive management is a means of validating hypotheses, in line with a Popperian approach. We will demonstrate this here.

1.3.1. Rodenticide treatments as a quasi-experiment

Chemical control using bromadiolone, an anticoagulant, was advocated as early as the late 1970s to control the water vole. This application then became widespread during peak densities, at a time in the cycle when all categories of predators were concentrated in the areas concerned (see section 1.2.5 and Figure 1.8). From the outset, it resulted in massive mortality of vole predators through secondary poisoning, although this was only measured and recognized at a very late stage (Berny *et al.* 1997). The laboratory experiments conducted in the 1980s, which had concluded that the risk of secondary poisoning was low for buzzards and ermine, the

only two wild species tested (Grolleau *et al.* 1989), were undermined by the reality of the field.

The half-life of the molecule in the soil seemed to be consistent with that observed in the laboratory, between 3 and 6 days (Giraudoux *et al.* 2006). However, Régis Défaud, a Fredon technician, observed in the field that water voles used to store poisoned bait (wheat grains) in underground caches of a few hundred cm³.

Based on this observation, Sage *et al.* (2007), by creating artificial caches, showed that voles thus create conditions for the conservation of bromadiolone, multiplying the half-life of the molecule by a factor of 5–10, which can then reach 28–45 days in the spring and autumn, respectively. By reintroducing animals that had never been exposed to bromadiolone into tunnels abandoned after treatment, Sage (2008) also showed that voles recolonizing treated burrows could have access to bait stored by the population eliminated by the treatment and become intoxicated for at least 3 months following the treatment.

These findings, together with the observational studies described in the previous sections, led to a major revision of vole control strategies in the early 2000s, as discussed in section 1.3.2, including a significant reduction in bromadiolone use.

The massive mortality of predators observed in the 1990s made it possible to measure, almost experimentally, the effect of treatments on fox populations and the consequences of an increase in their density on other species living in the same ecosystem. The monitoring was carried out over the long term by the Fredon de Franche-Comté (ZELAC), the *Fédération départementale des chasseurs du Doubs* (472 segments, from 1 to 2 km, distributed throughout the Doubs department) and the researchers. Bromadiolone treatments during the water vole density peaks of the 1980s to 1990s had considerably reduced fox population densities by the early 2000s. The fox population then benefited from the change in control strategy implemented in the 2000s (see section 1.3.2), resulting in a steady increase in the fox population (Figure 1.10). The concomitance of these population changes with those of alternative prey populations, such as hare, wild cat and domestic cat, could be observed at that time, as long-term monitoring schemes were in place (Figure 1.9).

In addition, the negative effect of the considerable decrease in fox populations on the transmission intensity of a cestode parasite, *E. multilocularis* (see Chapter 4), could also be measured during the 1990s (Raoul *et al.* 2003).

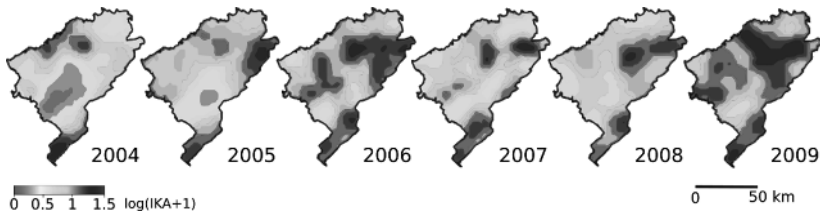


Figure 1.10. Changes in the relative abundance of foxes in Doubs department following the decrease in the quantities of bromadiolone used in vole control operations from Jacquot *et al.* (2013). For a color version of this figure, see www.iste.co.uk/giraudoux/socioecosystems.zip

1.3.2. The toolkit

It took about 20 years to move from a curative, entirely chemical control, often carried out too late during the peak or even shortly before the spontaneous decline of a water vole outbreak, to a preventive control aimed at preventing the densities from exceeding levels unbearable for the farmer. This has led to a change from the administration of a maximum of 40 kg bromadiolone bait per ha in the form of carrots in the 1980s to 20 kg/ha in the late 1990s, and then, by implementing research-based concepts, to an average of no more than 1–2 kg/ha in 2019–2020, compared with the maximum permitted dose of 7.5 kg/ha at that time (Figure 1.11), and to increasingly smaller areas. In practice, this approach has resulted in a local reduction of bromadiolone use by more than 44 times (Giraudoux *et al.* 2020).

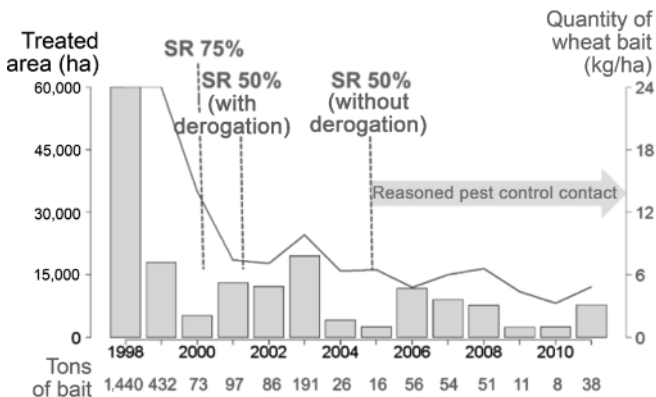


Figure 1.11. Evolution of bromadiolone use in water vole control. RT, regulatory threshold (% of positive intervals in a transect, see section 2.1) from Cœurdassier *et al.* (2014a). Above this threshold, treatment is prohibited. The wheat bait contains 50 mg bromadiolone/kg

It has also significantly reduced the unintended effects of treatments on non-target wildlife (Figure 1.12).

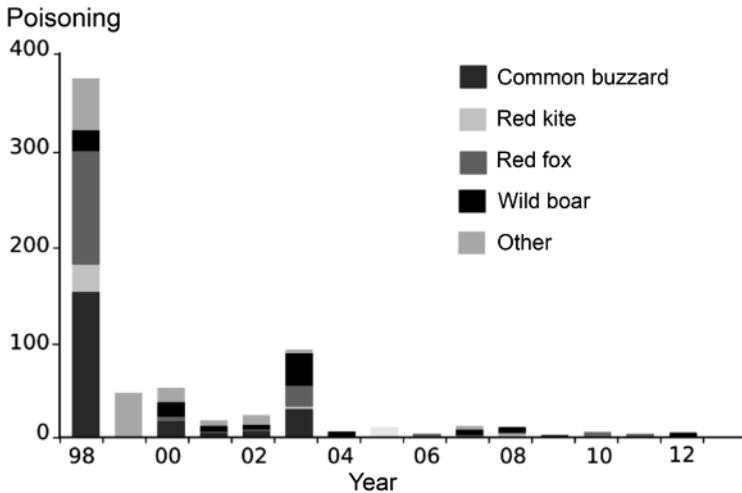


Figure 1.12. Evolution of wildlife mortality with confirmed or suspected death by anticoagulant intoxication in the Doubs department from 1998 to 2013. SAGIR data – ONCFSFNC-FDC network, per Cœurdassier et al. (2014b). For a color version of this figure, see www.iste.co.uk/giraudoux/socioecosystems.zip

The principle of control was based on selecting the correlations identified in the observational studies as possible causes of the observed effects. Since none of the identified variables could, according to the studies, statistically explain the variations in abundance, the multifactoriality of these causes was accepted as a likely hypothesis. Furthermore, the demography of grassland voles is, in the absence of any limitation, exponential (a pair of voles by interlocking generations can produce more than a hundred in a single breeding season). As a result of this reproductive dynamic, late control attempts were failures and it became clear that, to be effective, control had to be early, preventive and carried out on a population that was still numerically weak, in refuge areas considered “sanctuaries” for the population, even though they were still small in size. We will come back to this notion in Chapter 7, in connection with cholera. A toolkit was therefore progressively set up in experimental zones bringing together a few dozen volunteer farmers, first in the Val des Usiers (ZELAC, experimental vole control zone) in 1999, then in the Charquemont area (CLAC, *Comité de lutte anticampagnol de Charquemont*) in 2005, with the technical support of the Fredon de Franche-Comté and researchers. We will come back later on to the human and political conditions

that made this association possible over a sufficiently long period of time to produce results, which is necessarily longer than several vole cycles.

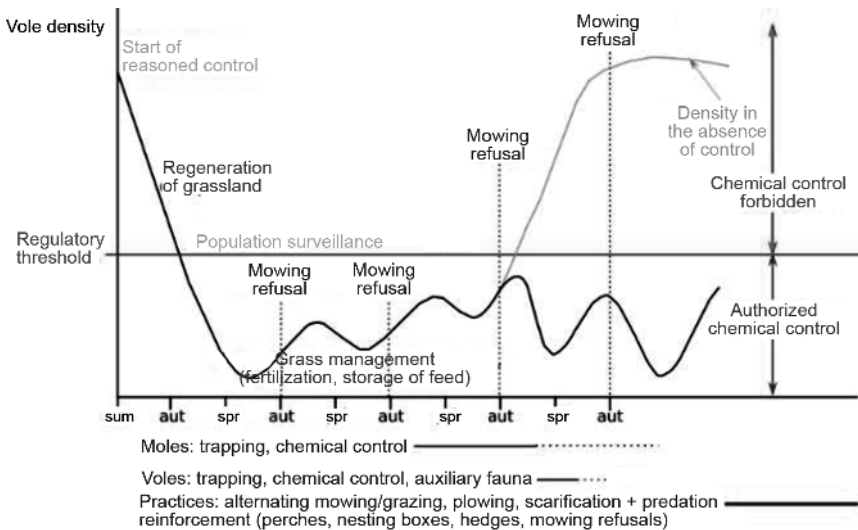


Figure 1.13. *The different proposals in the toolkit over the course of a 5-year control contract, from Couval and Truchetet (2014)*

Based on the research literature, the actions implemented, according to a reasoned chronology (Figure 1.13), were grouped under the triptych “observation, collective engagement, combination of methods” (Couval and Truchetet 2014):

- observation refers to the need for permanent but reinforced surveillance in the low-density phase, in order to identify the first colonies and implement preventive actions before the outbreak. The observation is organized in a regional surveillance network, composed of volunteer farmers and technicians, which feeds a specific plant health bulletin. Distributed to as many people as possible, it allows each farmer to contextualize his or her own surveillance on a more local scale;

- collective commitment is made necessary by the spatial dimension of the outbreak, which can cover areas of several thousand hectares. The speed of colonization of isolated plots of land can therefore defeat attempts at control that are too local, for example, on the scale of a single agricultural plot of a few hectares;

- the combination of methods drawn from a “toolkit” (Table 1.2) includes direct control (trapping and chemical control as soon as the first burrows appear) and indirect control (which acts on the rodents’ habitat and thus on the supposed causes of outbreaks). They can be implemented at different spatial scales (plots, groups of

plots, municipalities) depending on the constraints linked to the farm (size of the plots, fragmentation, working time, size of the herd, agricultural speculation, etc.).

Method of control	Practical applications
Vole trapping	Effective if used at very low density but requires significant human resources.
Chemical control of vole	In the burrow, at low density, using small quantities of bromadiolone* bait, zinc phosphide and, according to a regulatory framework defined by interministerial order of May 14, 2014, hydrogen phosphide generators by certified applicators.
Mole control	Hydrogen phosphide traps or generators by licensed applicators.
Crop and grazing management techniques	Objective: to hinder the installation or re-installation of the water vole, to decrease the proportion of favorable habitats and to increase the visibility of the first colonies: <ul style="list-style-type: none"> – tillage with shallow or deep tools (ploughing). Two scales are possible – on a parcel basis to remove old galleries/burrows or on a rotational basis on a farm scale to reduce the ratio of grassland to farmland; – alternating mowing and grazing to cause the collapse of the underground burrows by the trampling of livestock.
Protection and enhancement of predator action	<ul style="list-style-type: none"> – Establishment of hedge and grove networks; – installation of perches, nesting boxes, re-opening of bell towers and maintenance of shelters favorable to predators (stone walls between plots, called <i>murgers</i> in the Jura Massif, etc.); – regulatory measures for the specific protection of predators.

Table 1.2. Toolkit used in integrated pest management contracts between Fredon and volunteer farmers. *Bromadiolone has been forbidden since May 2021

This set of measures allowed, from then on, the control of vole outbreaks to the farmers who applied them, with lesser unintentional environmental impact (Figure 1.14).

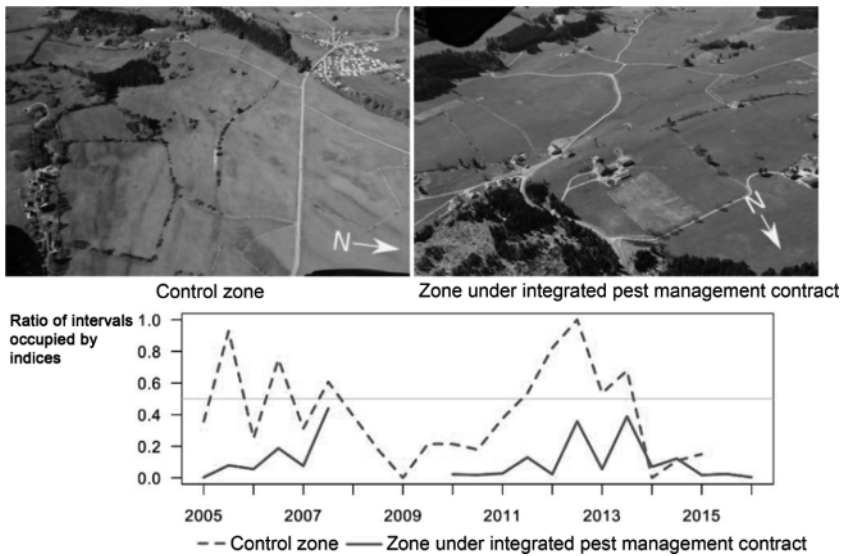


Figure 1.14. Comparison of an area under an integrated pest management contract with a neighboring area in the Charquemont region, Doubs, from Giraudoux et al. (2017). The photos show the difference in vegetation condition in April 2013, at the peak of the outbreak (photos Dominique Mougin), and the graph shows the population dynamics of the water vole. For a color version of this figure, see www.iste.co.uk/giraudoux/socioecosystems.zip

This result proves that, even if not everything is yet understood in the decline processes, the systemic conditions promoting outbreaks are sufficiently described and known to be actionable, in contrast to reductionist studies and single-factor methods. To date, and despite nearly a hundred years of research, none, to our knowledge, has led to the prevention and sustainable control of a pest outbreak cycle and its effects, let alone “with less environmental damage”, but together they have led to a long list of conclusions, all correct, about what does not explain them (Lidicker 1988; Oli 2019) without leading to coherent management recommendations. The effectiveness of the herders’ action constitutes, downstream of the eco-epidemiological approach, a quasi-experiment validating the overall systemic scheme and the spatial and temporal hierarchies that generate it (see Figure 1.16), without validating the details of the processes underlying each of the identified correlations, which is out of technical reach, alas, with the current state of methods. Furthermore, this long-term experimentation and multisectoral collaboration served as the basis for national regulations on the use of rodenticides (Legifrance 2014) and for the development of decision-making support tools.

1.3.3. Anthropology to the rescue of the application

Since the end of the 1970s, farmers' demands have always been expressed through professional organizations and the press, presenting the vole outbreaks in the areas of the Jura Massif producing PDO cheeses as a scourge that threatens the economy of many farms. In fact, without adaptation, it appears that on an intensive farm, 1 year of outbreaks can lead to a loss of gross surplus of up to 10,000 euros per labor unit (Schouwey *et al.* 2014). It is therefore surprising to note that, despite this vivid expression and the objective measurement of the losses due to outbreaks and the gains made by controlling them, among 2,600 family farms in the PDO Comté area (Doubs and Jura), only 126, or less than 5%, subscribed to a control contract (as of June 1, 2020). There is therefore still an unbridgeable gap between, on the one hand, the results of research and their application in experimental areas run by a minority of a few dozen particularly mobilized farmers who are anxious to tackle the problem through a research-action approach (which is ultimately successful) and, on the other hand, a large number of farmers who revolted until the early 2000s ("Get rid of it right away! You have to choose between buzzards and farmers! What is research doing?"), and were then resigned to the losses incurred since.

An anthropological approach, based on long interviews with farmers in Franche-Comté, has allowed us to better understand how the water vole was perceived by the farmers who suffered from its damage (Michelin *et al.* 2014). It combines an assessment of their technical leeway in the management of their livestock and an anthropological analysis of their perception of the vole and control methods. For some farmers, the vole is considered an intruder that must be eradicated. For others, it is a disruption of the ecosystem that must be dealt with. These two opposing conceptions lead them to react differently, preferring certain solutions and rejecting others, even though they are technically effective within the range of possibilities offered by the toolkit (Morlans and Michelin 2014). Michelin *et al.* (2014) infer four classes of farms associated with different profiles of response to outbreaks. Other studies conducted in Auvergne, in comparable ecosystems, reveal three types of perception, according to Yves Michelin and Shantala Morlans, in Couval *et al.* (2013). We are quoting the terms and conclusions of this analysis in full as they seem informative and difficult to reformulate in any other way without misrepresenting them:

On the surface: the vole is perceived through the clods of earth it produces, which do not "look clean" and harm the quality of fodder and milk. The important thing is to make the soil disappear. The fact that a few individuals remain is not a problem if they do not cause any

damage. As a result, during low density periods, these farmers do not consider taking action, although this is when it is most effective.

In depth, it is seen as an animal, with its specific behaviors but also often with a strong symbolism: “There are rats under my meadow that even came and ate my boots when I was in my field the other time.” Some farmers will fight to the last animal, even if it is not necessary.

In dynamics, it is seen as a population, likely to pullulate and invade a production area. The actions carried out then integrate the whole cycle with low density interventions to prevent or at least slow down the start of outbreaks. To do this, the proponents of this approach have developed empirical knowledge of population level diagnosis that helps them to anticipate events.

As a result, whether a farmer fights or not depends of course on the technical or economic impact of the outbreak on the production system, but also on the idea she or he has of it and her or his values: some overestimate the damage while others, preoccupied by other problems, pay little attention to it. The decision to act is based first and foremost on what the farmer observes on her or his plots and on the consequences she or he draws from them regarding the impact on her or his future production. However, not everyone has the same acuity of vision or the same knowledge of possible means of control. Moreover, and above all, they do not attribute the same values (technical, moral, ethical) to the actions to be carried out, in particular to chemical control. Finally, other factors play an important role, such as the image that each farmer intends to give of her or his work and of herself or himself in the eyes of others. This leads some to fight actively to “keep things clean”, because “we are not pigs”, and others to refuse all use of chemical products because “we do not want to be seen as those who sow death in nature”. The structure of the collective is also essential. Depending on whether farmers are used to discussing and working together or whether they are very isolated, it will be more or less easy to take a collective approach.

Finally, other stakeholders such as hunters and naturalists can encourage certain methods (e.g. systematizing trapping in Natura 2000 areas) or move towards confrontation. This indirectly pushes some farmers to stop chemical control, even at low density, following birds of prey or game being poisoned. The farmer therefore always has

reasons to justify her or his decision or refusal to use certain techniques, even if these decisions are not always understood by others. In order to promote the dissemination of integrated pest management methods, it is therefore essential to understand how a vole disrupts the functioning of the production system and to understand how the farmer reacts and on what basis. This is necessary in order to work with the farmer to find the modalities that are best adapted to the constraints of her or his system and way of dealing with the problem (Table 1.3).

Each group represents itself the problem differently	A target = a speech = one solution: it does not work	There is an interconnection of several systems of thought	The solutions are to be co-constructed
<i>Cattle breeders:</i> the water vole is a pest of grasslands	There is no such thing as a universal good practice because it has to be adapted to the local context: – production systems; – of the network of local actors; – ecological processes related to environmental characteristics.	The different ways of thinking of the different actors must be taken into account	– Listen to all parts;
<i>Wrestling technicians:</i> the water vole is invasive and must be regulated		The management of the problem must be collective and not only agricultural	– analyze the constraints of each; – understand the motivations;
<i>Researchers:</i> the water vole is an agricultural problem and prey for predators within an ecosystem that must be managed in its complexity		↓ Change of posture	– facilitate dialog between stakeholders. – Build on knowledge gained through research; – develop an expertise of the phenomenon through observation; – acquire mediation skills.

Table 1.3. *Rethinking advice to better meet needs, from Couval et al. (2013)*

The vole outbreak is primarily a problem of competition for grass resources between farmers and rodents. However, as it is a discreet burrowing species, it is only seen when the populations have already reached such a level that little can be done. When they are not yet visible, it is difficult to motivate farmers to undertake time-consuming

and sometimes costly practices. The “vole” phenomenon is therefore a source of anxiety. Often, it is added to other factors that the farmer does not control: increase in the price of food supplements, drop in the price of milk, drought...

1.3.4. *The status and contribution of models*

“All models are wrong, some are useful.” This popular aphorism invites us to situate the place of modeling in the approach presented in this chapter. Statistical modeling and inference, whether spatial or not, have underpinned the validation of the basic observations of the eco-epidemiological approach from the outset and on a permanent basis. This type of modeling is therefore intrinsically linked to the observational approach in ecology.

Other types of modeling were called upon as needs and collaborations arose, and as convenient tools emerged to implement them. The R¹ development platform, which became popular in the early 2000s, has certainly boosted not only the statistical approaches mentioned above, but also the possibilities of interfacing biologist-statisticians with mathematicians and computer scientists. The first non-statistical models were essentially conceptual, and mathematical-computational tools were only put to good use for process-oriented modeling after eco-epidemiological approaches had sufficiently contextualized the subject in terms of the variables and assumptions about the processes involved, and the hierarchy of spatiotemporal scales of application.

1.3.5. *Conceptual models*

Apart from the dozens that were scribbled on a corner of a table and conference presentations of preliminary versions (Delattre *et al.* 1986, 1988), the first conceptual model that guided the research was proposed internationally in Delattre *et al.* (1992). The aim was to provide a typology of systems linking landscape composition, predation and common vole population dynamics (Figure 1.15). The weasel component of this model could never be validly tested afterward, but the link established between landscape and population dynamics, with all the variants described in the chapter, has still not been invalidated and is still used as a basis for current studies.

¹ <https://www.r-project.org>.

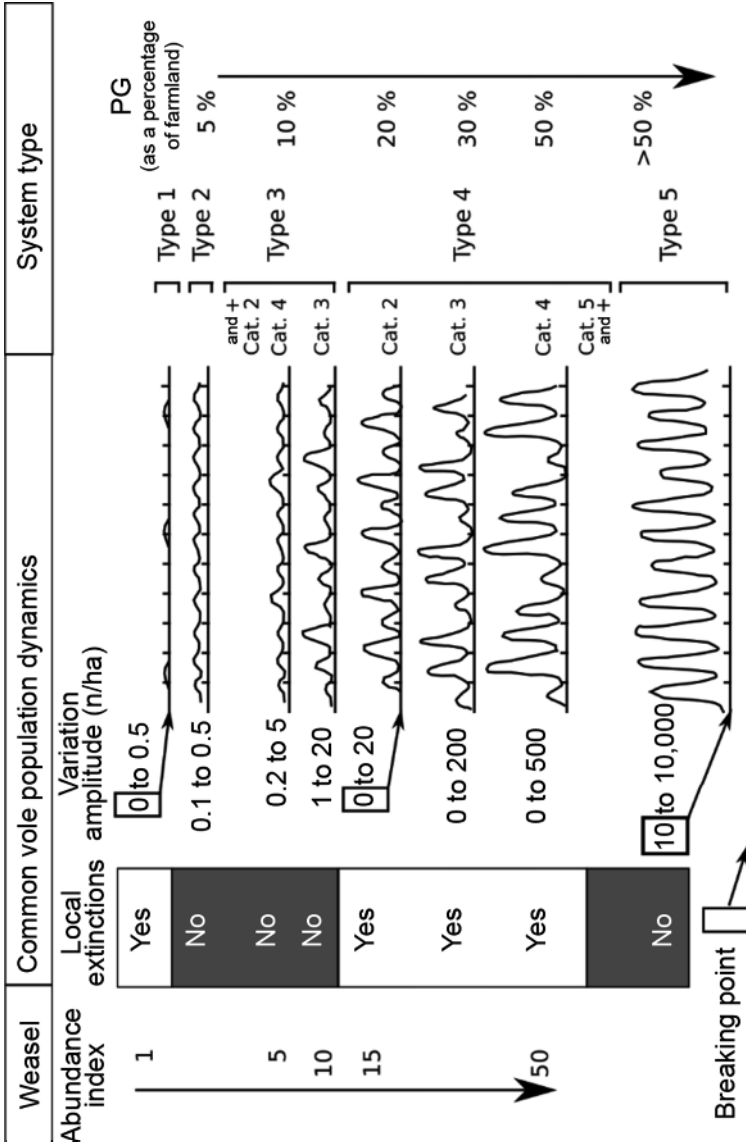


Figure 1.15. Typology of common vole population dynamics according to environmental variables, from Delattre et al. (1992). PG, Permanent grassland

In addition to the hierarchical classification of the system's control variables (Table 1.1), it was not until 2014 that a global synthetic conceptual model of the socioecosystem studied was finalized, focusing on the factors inducing fluctuations in the abundance of water vole populations (Figure 1.16). This allows the conflicts of interest and synergies between the processes and the corresponding agronomic, health and conservation biology domains to be visualized. It also shows the possible linkages with other elements of the system not studied here, but which will be the subject of Chapters 2, 3, 4 and 5.

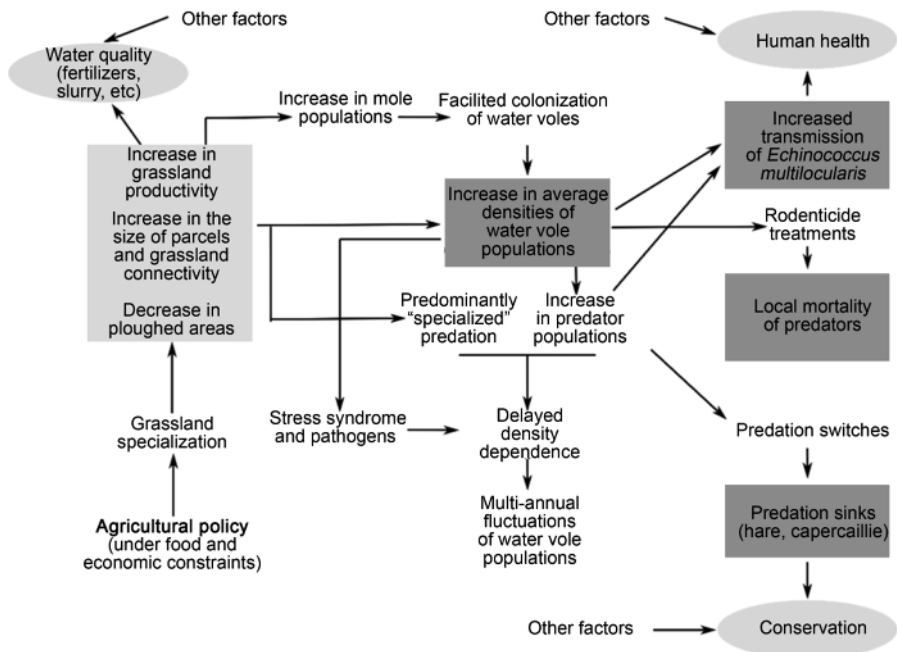


Figure 1.16. Cascade of consequences of grassland specialization on water vole populations, their predators, alternative prey and transmission of *Echinococcus multilocularis*, from Giraudoux (2014). The green box groups the proximal outcomes of grassland agricultural specialization and the red boxes the undesired effects. The blue ovals indicate the distal non-agricultural domains affected in such a system. For a color version of this figure, see www.iste.co.uk/giraudoux/socioecosystems.zip

1.3.6. Quantitative models

Incorporating the spatial heterogeneity of real landscapes into population dynamics remains extremely difficult and is a critical factor at a fundamental level (what is the outcome of interactions of spatial mosaics of interacting communities?),

once the challenge is to advocate management actions. Based on Graphab software (Foltête *et al.* 2012), the first explicitly spatial modeling of water vole outbreaks confirmed that landscape modeling using graph theory can produce parameters consistent with field observations and thus pave the way for simulating the effect of landscape modification on population dynamics (Foltête and Giraudoux 2012). This approach made it possible to compare several strategies for disconnecting grassland networks at the level of the Doubs department and to detect the main theoretical points of weakness in the network (Foltête *et al.* 2016). The external validation of such regional models is still currently hampered by the logistical impossibility of conducting adequate experiments at the required spatial scales and over the required duration.

An explicitly spatial, process-oriented modeling based on the combination of mathematical equations and computer agents was designed to simulate a wave of water vole colonization that had been monitored for 13 years in the Haute-Romanche, an Alpine valley (Marilleau *et al.* 2018), in parallel with and inspired by studies conducted in the Jura Massif. It was made necessary by the fact that equation-based models could not sufficiently consider spatial heterogeneity, and that the number of voles involved, if they had all been modeled as individuals, exceeded the capacity of the clusters of the computing centers. This approach shows that among the 6,059 random simulations of six demographic variables, only 27 combinations of values, which are very different from one another, account for the observed speed of colonization. Compensation effects are therefore possible between the variables, and the same effect (colonization speed) is then observed for different causes. Moreover, the observed colonization speed cannot be reached without a dispersion of at least 1,100 m, concerning between 0.2% and 20% of individuals in the population, thus underlining the theoretical importance of this category of the population in the speed of propagation of outbreaks.

Several non-spatial equation models were explored to account for specific processes. For example, data collected on the diet of barn owls and foxes were used to test a new general multispecies functional response model, disentangling predator preference for prey categories as a simultaneous function of variation in prey frequency and total density, and proposing a new concept of “rank switching” (Baudrot *et al.* 2016b). This approach led to theoretical thinking informed by observational data collected on the parasite *E. multilocularis*, addressing the dynamics of the parasite in a context of multiple intermediate hosts differentiated by their competence, and complex predator foraging behavior (Baudrot *et al.* 2016a).

Finally, based on observational data, a non-spatial equation model was used to explore the theoretical impact of alternating regulation of voles by predation or

chemical treatment in a four-component system: a population of voles, foxes, small mustelids (weasels or stoats) and a chemical treatment likely to poison voles and also, indirectly, predators consuming poisoned voles (Baudrot *et al.* 2020). This model reveals the need to maintain refuges with enough unpoisoned voles to support the mustelids, in order to maintain the predator community, unless we switch to a system where chemical treatments would become permanent owing to the lack of predators.

“[...] some are useful.” A few comments on the usefulness of the non-statistical models presented here are in order. The first is that they can only be designed after observational data have been collected at scales appropriate to justify them – the minimum time periods exceeding those of a pest outbreak cycle, some extending over decades. Early attempts, based on insufficient observation time, sometimes at inadequate spatial scales and with naïve assumptions, which did not take space into account, have all failed to produce useful knowledge in the meantime. Non-statistical modeling therefore accompanies downstream thinking, rather than preceding it, and its main utility is to be able to explore theoretically and elegantly (mathematics has an intrinsic beauty) certain sub-systems in a context framed by long-term observations. One then tests whether or not the small number of assumptions and variables (relative to their number in the real world) in each model is sufficient to explain (in theory) the observations. Although much more favorably received in the major ecological journals than the observational studies that motivate them – we can testify to this – their contribution to knowledge of the system is still marginal at this stage, because of their poor capacity to predict the functioning of the theorized sub-system in the more complex real system with which it interacts. Added to this is the impossibility of testing the predictions when, for example, only logistically and ethically impossible landscape or population manipulations on the appropriate space and time scales allow it. Some of the conclusions may also be disappointingly trivial: for example, concluding that predators in the system must be able to survive in order not to be forced into permanent use of rodenticides does not seem to be a scoop to a practitioner, even if the elegance of the mathematical demonstration provides access to one of the most reputable journals of applied ecology. It should be noted, however, that the inverse resolutions allowed by certain simulations or analytical resolutions, when the population parameters are unknown, make it possible to point out the potential importance of certain variables. This is the case, for example, with regard to the speed of propagation of an outbreak, of the theoretically important role of long-distance dispersers, which only constitute a small fraction of the population. However, this simulation finding refers to the field and to appropriate methods, perhaps genetic, to study rare events in a population. In conclusion, yes, models are locally useful, and we do not hesitate to invest time in them, but much less than their overvaluation in the ecological literature in recent

years has suggested (Ríos-Saldaña *et al.* 2018), to the detriment of descriptive, eco-epidemiological studies, which are the indispensable, but more costly to acquire, basis of knowledge of socioecosystems, which are, alas, generally idiosyncratic in their details.

1.3.7. Toward new questions...

1.3.7.1. Consequences of global warming and the ecological transition

Global changes are of course having an impact on the Jura Massif, starting with the reduction in the duration of snow cover, which determines the duration of tourist operations in ski resorts and is thus an important part of the economy of higher altitude areas. For its part, the grassland production system is increasingly subject to spring and summer heat waves, which considerably modify the phenology of grass production (Figure 1.17).

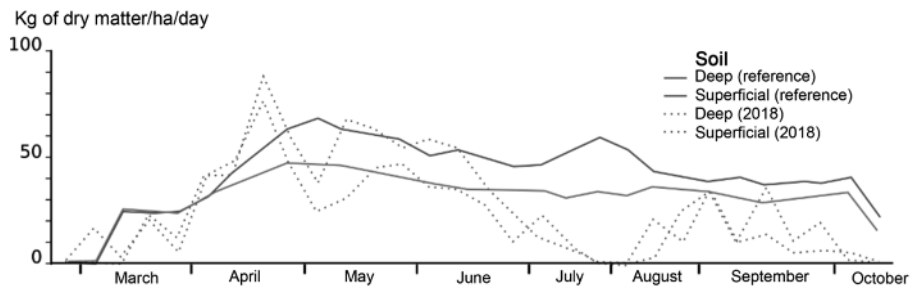


Figure 1.17. Grass growth on the Jura plateaus comparing the standard reference to that observed during the 2018 heat wave, from Jean-Marie Curtil, Interdepartmental Chamber of Agriculture of Doubs, Belfort region. For a color version of this figure, see www.iste.co.uk/giraudoux/socioecosystems.zip

Farmers are currently considering the technical and economic adaptations that will be necessary. At present, earlier grass production at a time when rainfall makes hay difficult to harvest, followed by prolonged summer droughts that block it during the summer months, suggests an overall decrease in forage production, which is all the more noticeable when the production system is intensive. The response of vole populations to such changes in phenology remains an enigma. It may directly affect the length of the breeding season (possibly earlier and later owing to the milder climate, but possibly also slowed or interrupted for further periods owing to reduced summer vegetation growth). The evolution of the economy of the farms can itself integrate more or less ploughing with the evolution of the price of cereals, within the

limits of the specifications of the PDO, which would then result in a variation in the proportion of favorable habitats, which we have seen to have direct consequences on the amplitude and frequency of the peaks of vole abundance. It is therefore the current stability of the socioecosystem that may be affected, to an as yet unappreciated degree, potentially with the same force as it was at the time of the 1960s, which saw massive regional outbreaks of grassland voles at the base of today's complex food webs involving their predators and parasites. This illustrates that regional socioecosystems are not stable in the long term and follow constrained trajectories. Their adaptability to change requires constant monitoring and innovation.

Another category of foreseeable change concerns the ecological transition from productivist agriculture that pays little attention to its environmental externalities (soil preservation, water management, etc.) to conservation agriculture, also known as agroecology. In “large-scale farming” (cereals, oleaginous plants, protein crops and legumes), which takes us away from the Jura Massif and its farmers, simplified cultivation techniques (SCTs), for example, are cultivation methods that avoid ploughing. The advantage is that they maintain vegetation cover throughout the year, and thus limit erosion. However, this is at the cost of increased herbicide use at planting time (which is problematic); they preserve the structure and vertical organization of the soil, its biodiversity, and thus improve carbon storage while reducing input requirements (fertilizer, fuel, etc.). Permanent and very productive vegetation cover is, however, favorable, as we have seen in this chapter, to the development of the common vole (Delattre *et al.* 1992; Delattre and Giraudoux 2005). In “ploughed” systems, which leave an inhospitable, bare and overturned soil throughout the winter, common vole populations are limited to herbaceous margins and semi-permanent legume crops. They only spill over into annual crops at times and seasonally during peak population periods. A new frontier is therefore opening up in action research, namely, that of knowing enough about the ecology of this species, the consequences of future outbreaks in this new socioecosystem, and the margins for modifying production itineraries and their environment, in order to avoid them without deleterious ecological consequences (reduction of biodiversity, use of pesticides, etc.).

1.3.7.2. *Consequences of the environmental drawbacks of a commercial success*

“Why is the Comté being accused of polluting Franche-Comté’s meadows and rivers?” This was the question posed by the media, following a damning scientific report produced in February 2020, “Study of the health status of karst rivers in relation to anthropogenic pressures on their basins” (Badot and Degiorgi 2020). The studies on which this report is based sought to explain the algal blooms in the rivers of the Jura plateaus, which have been observed over the last 20 years. They are accompanied by a rarefaction and, in some cases, an extinction of aquatic species

considered sensitive, such as large plecopterans, the white-clawed crayfish (*Austropotamobius pallipes*), large mayflies and trichopterans, and, as a result, a fivefold decrease in salmonid biomass in less than 20 years. It has become apparent that the main cause of these losses is the increase in nitrate and phosphate concentration, as well as multiple contaminations by phytosanitary products, biocides and active substances from veterinary medicines. In fact, the intensification of agricultural practices over the last few decades is blamed, even if it is inaccurate to attribute it to the Comté alone. Examination of the figures in detail shows that it is in fact an overall increase in cheese production, in which, since the early 1990s, a shift away from Emmental production has been more than compensated for by an increase in the production of Comté, Morbier and Mont-d'Or PDOs (Brischoux *et al.* 2015). This is also the consequence of the switch from a “manure” to a “slurry” effluent treatment system, the latter, owing to its high ammonia fraction, behaving as a mineral fertilizer. We have seen in previous sections that the increase in the dairy performance of the herd (genetics, number of cows, etc.), from the 1960s to the 1970s, led to an increase in grass production and allowed the development of large populations of water voles and common voles. It is therefore very likely that the measures that will be taken to reduce the ecological externalities linked to current cheese production will have consequences on, on the one hand, the technical itineraries of grass production (reduction of manure spreading, attention to biodiversity, limitation of livestock density, etc.) and, on the other hand, the means of controlling grassland vole populations (supervision of soil turning, which is part of the “toolkit” but leads to the rapid mineralization of organic matter and therefore, if no precautions are taken, can contribute to the removal of carbon from the soil and to the eutrophication of rivers, etc.). It is not yet known how vole populations will respond to these changes, the extent of which is currently difficult to predict. However, the necessary ecological transition, which will lead to greater attention being paid to the protection of water, which is itself becoming scarcer as a result of climate change, may once again lead to profound changes in the characteristics of the socioecosystems of the Jura within a few years.

1.4. What methodological lessons can be drawn from this experience?

It has taken about 30 years to describe and understand the factors that determine vole outbreaks in the Jura Massif in PDO grassland areas and to establish the basis for controlling them. Most of this work (research and experimental validation) was completed in 2006, at the end of a State-Region planning contract to which we will return. One may ask whether this period could have been shortened and, if so, what were the obstacles that prevented it. To answer this question, it is necessary to return to the organization of the research and the applications of its results, as described above.

The first incompressible point is the duration of an outbreak cycle. From 5 to 7 years for the water vole, non-cyclic fluctuations for the common vole, but with declines synchronized with that of the water vole and whose outbreaks, even if they can last several years, appear chaotic (Giraudoux *et al.* 2019). Thirty years therefore only offer the opportunity, locally, in longitudinal monitoring, of about five observation replicates. This can be compensated for by a synchronic approach: comparing at a given time locations that are at known stages of a cycle. This approach, which has in fact been implemented, assumes that adequate information is available to make the comparisons. It is therefore necessary that a regional observation network exists that has gathered this information during at least one outbreak cycle, and that the next one (the one during which comparisons are planned) is perfectly identical to the first. This is almost never the case. It is therefore not possible to ensure full comparability of observations (the landscapes and the history of the populations compared are never exactly the same). Moreover, given the logistical burden (trapping, intervention in the environment, etc.) and the limited human and financial resources allocated to this type of study, this reduced comparability cannot be compensated for by the acquisition of large statistical series for each category. Ecology does not benefit from the same volume of funding as that allocated to nuclear physics, astronomy or the conquest of space.

The second point, which is difficult to compress, concerns the sociological evolution of the research network, the formation of which we will return to later. Three periods can be distinguished:

– 1979–1996 (18 years!), a period during which the agricultural demand was, it has to be said, to wait for some kind of magic bullet that would have relieved the farmer of the problem, through a minimum of operations that did not involve major changes in practices. The leitmotif, not always kind to the researchers, was: “What is research doing?” The 1980s was also the period of collection of the first observational data on protocols, which were essential to objectively answer the questions that arose. From 1992 to 1996, a regional contract (Franche-Comté regional council), entitled “Rodents and the management of rural areas”, finally allowed the implementation of action-research protocols bringing together the various parties and the publication of the first results.

– 1997–2000 was a period when the leitmotifs were, with regard to the deleterious effects of chemical treatments on non-target fauna: “You have to choose between the buzzards and the farmers”, “You can’t make an omelette without breaking eggs” and, with regard to the results of research: “The results don’t suit us; one has to find something else”. Consequently, these results were little or not taken into account, and the chemical treatments, too late, in the peak of the outbreak, were extended to even larger areas. The foreseeable crisis generated by these treatments,

with a massacre of hundreds of rodent predators (buzzards, foxes, etc.) and animals consuming poisoned bait (wild boar, etc.) in 1998, made headlines in the national media, mobilized nature protection organizations and, locally, departmental hunters' federations. This situation led to a vigorous response from the Prefect and the regional director of agriculture and forestry at the time, followed by a change in the leadership of the technical agricultural bodies in charge of the issue, resulting in the establishment of a State-Region Planning Contract (CPER) from 2001 to 2006 (i.e. one outbreak cycle) and a steering committee coordinating the funding of research.

– From 2001 onward, therefore, the CPER brought the conflicting parties together on the basis of jointly constructed research projects and the creation of experimental zones (Delattre and Giraudoux 2009). This period of joint work, with the results obtained and their validation in the experimental zones being taken into account, quickly led to a new positioning of the representatives of the agricultural world. Charles Schelle, president of Fredon Franche-Comté, summed it up in May 2015: “We must keep in mind our threefold requirement for our agriculture to be successful: the social aspect, the economic aspect and the environmental issue must be part of our requirements. These requirements are all the more important as the fight against the vole is never-ending. This is why the work done with research is fundamental, because researchers and farmers have a shared destiny.”

It is therefore certain that at least 10 years could have been gained over the 30 years if financial support for research had been less strictly linked to crises, less discontinuous and even less often interrupted at each interval between crises. This perennial precariousness systematically leads to opportunistic dispersion and thematic acrobatics, and thus to an absurd waste of energy in order to adapt conjuncturally to the objectives of short-term calls for tenders available on other issues (according to the thematic trends of the moment), almost irrespective of the content, while trying to keep the guiding line as best as possible over the long term (Figure 1.18). It is impossible to find funding for this alone: “To answer the questions asked, data have been collected for years and it is necessary to continue to do so for years to come.”

It is possible, however, that long periods of time and crises are essential for ideas to percolate, for actors to question their practices with stasis and acceleration, and for consensus to finally be established and lead to action. “Social” time, the time necessary for the evolution of each party's positions, is perhaps not one of the compressible variables. One of the major difficulties in this type of action research is to understand and accept that the time of the vole (and its predators), the researcher and the cattle breeder are not the same (Figure 1.19).

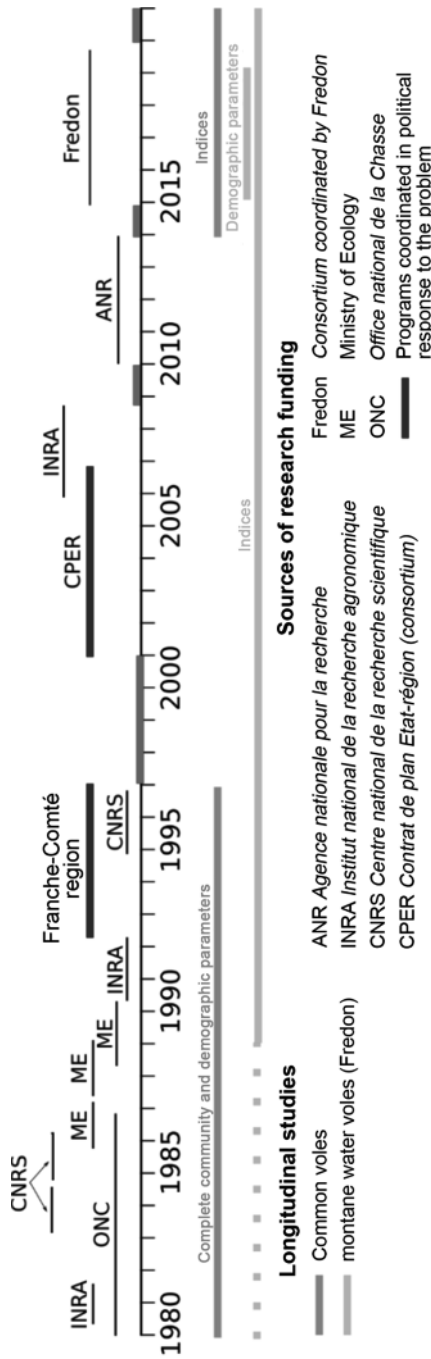


Figure 1.18. Discontinuity, dispersion and short-term sources of research funding, despite the fact that research was conducted over the long term. The red segments mark the periods without any funding. For a color version of this figure, see www.iste.co.uk/giraudoux/socioecosystems.zip

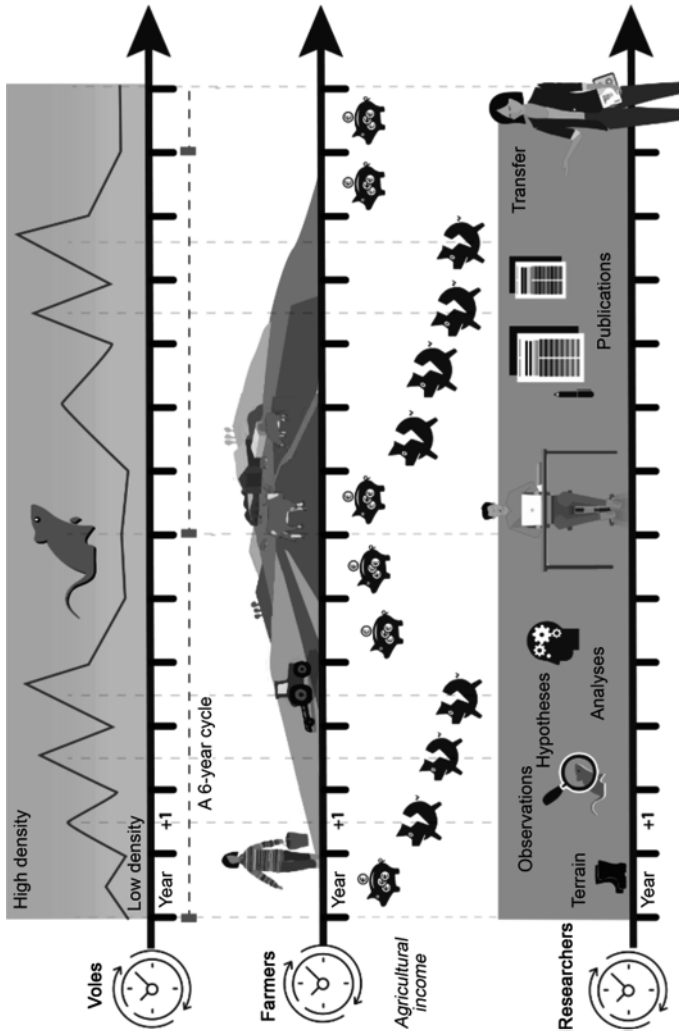


Figure 1.19. The time of the voles, the farmer and the researcher (infographics by Estelle Franc).
 For a color version of this figure, see www.iste.co.uk/giraudoux/socioecosystems.zip

Was this research multidisciplinary? There is no doubt that it was, but to varying degrees. It is customary to distinguish between “major” and “minor” multidisciplinary. The “major” multidisciplinary refers to that which brings together disciplines that are far remote from one another, such as the humanities and the so-called “hard” sciences. The “minor” multidisciplinary was almost permanent, bringing together ecologists, health scientists, geographers, modelers (mathematicians, computer scientists) and tools ranging, to use a cliché, from satellites (space imagery) to microsattelites (molecular genetics). The “major” was also present with the socio-anthropological studies presented in section 1.3.3, but it must be admitted that, like the others, this was an opportunistic addition “in the course of research” to answer the emerging question of the origin of the difficulty of transferring results to cattle breeders. The incorporation of socio-anthropological and economic questions, from the outset, would probably have helped to better anticipate this difficulty, as well as to better understand the functioning of the socioecosystem, as we shall see in Chapter 2. Honesty compels us to add, however, that despite the institutional exhortations to multidisciplinary, no structure in the field in question has the means to mobilize a sufficient budget to carry out all the studies that would be required in the long term. Figure 1.18 clearly shows that over the nearly 40 years of the timeline, there have been only two institutionally coordinated multidisciplinary and multisectoral actions with a specific budget, both in response to crises, and covering a total of only 10 years. Neither incorporated a socio-anthropological or economic component as such. However, beyond what has been already presented in this chapter, the value of integral socio-anthropological studies is also discussed in Chapter 2 and Chapter 4.

The research was also, and equally critically, multisectoral, involving professions interested in the results, but not necessarily tasked with conducting research (Figure 1.20). It was during the periods when research and implementation were coordinated by a specific multisectoral consortium (1992–1996, then 2001–2006) that the most important results were achieved, results that cannot, however, be obtained without the long-term continuity of pre- and post-program observations.

These *ad hoc* umbrella consortia are indeed essential to coordinating the mobilization of the necessary funds, both for research and for application, and thus reflect the overall integration of all elements of the system (Figure 1.16). Without this, the researcher is faced with an exhausting and sterile game of ping-pong between potential funders, with the environment administration passing on to agriculture the burden of dealing with what it sees as an agricultural problem, and agriculture passing on to the environment what it sees as a species protection problem, or to health what it sees as a public health problem, and the public health sector offloading what it considers to be primarily an agricultural problem, all of

them considering that they do not have to finance research because there is a Ministry of Research responsible for it – a Ministry of Research that is of the view that it is not its vocation to finance the operation of environmental observatories, because it does not have the financial means to do so anyway. However, a consortium must not become a bureaucracy and must itself be supportive and adaptive. Multisectoriality is also imposed by the fact that research labs almost never have the human and material resources to maintain long-term observation systems in ecology, especially in the field of animal populations. On the other hand, long-term agronomic monitoring (agricultural pests), sanitary monitoring (diseases) and monitoring related to the knowledge and protection of biodiversity (fauna and flora conservatories and associations) are a mission for many regional organizations, with which intersectoral collaborative research is possible.

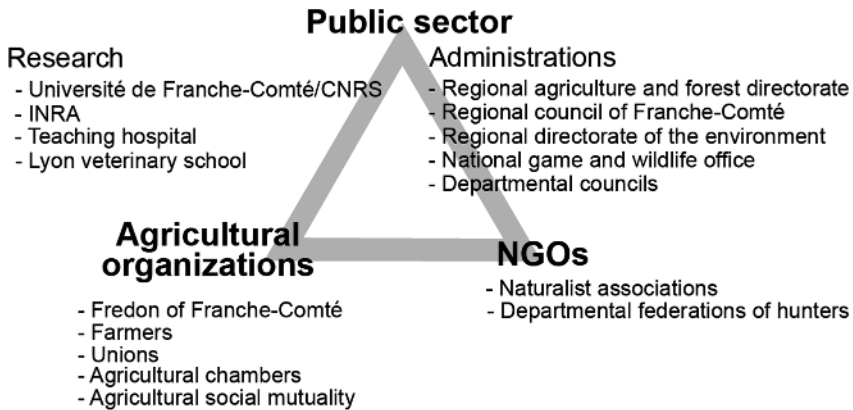


Figure 1.20. Professional sectors involved in the research

Since the will to last is not guaranteed by institutions, the critical question of persistence over time arises. It is, therefore, based on the question of the humans that pursue it. This structural problem was already raised in the last century: “Most long-term studies are still from Europe and the USSR² while North American series cover mainly the few years needed for a doctoral thesis” (Hansson and Henttonen 1988). We cannot provide any examples of long-term continuity provided by a succession of short contracts. The accelerated turnover of positions in administrations, short fixed-term contracts and the annualization of budgets, for example, make program continuity beyond a few years problematic. Duration here implies the personal commitment of several generations of researchers and their partners over several decades, and their tiling is essential. We cannot avoid

2 Author’s note: where permanent positions were the most common situation.

providing here a few decisive *ad hominem* examples of statutory positions whose persistence and synergy over the long term have allowed the continuity of the work. Pierre Delattre was the initiator of the research in 1979, especially the studies on the common vole and the community of small mammals of similar size. As a researcher at INRAE, he had a permanent position that enabled him to collect basic data for more than 10 years, without publishing on these data (the first international article was published in 1992). He was thus able to lead part of the research, ensure the continuity of the fieldwork and seek funding until his retirement in 2006 (28 years). Patrick Giraudoux, then a high school biology-geology teacher, joined the team in 1987 and was recruited as an associate professor at the University of Burgundy in 1992, thus with permanent status. He retired in 2019. Trained in Pierre Delattre's team as a PhD student, he took charge, from the beginning, of the scientific animation of a complementary part of the long-term research and continues to do so under the status of emeritus professor (35 years as of 2021). Michel Habert was director of the Regional Plant Protection Service of Franche-Comté (Ministry of Agriculture) until 2002 (over 30 years) and his successor, Philippe Guillemard, until 2017 (15 years). Denis Truchetet, agricultural engineer, was trained in 1989 by Pierre Delattre and Patrick Giraudoux on the subject, and joined the Plant Protection Service from 1995 to 2015 (20 years). During this period, he was the vertebrate pest expert for the Ministry of Agriculture. Régis Defaut, technician, joined Fredon in 1989 and was the main point of contact between this organization and the researchers and the leading figure behind experiments conducted with the cattle breeders, until his death in 2008 (20 years). Geoffroy Couval joined Fredon in 2006 as an environmental engineer (16 years to date) and has been, since 2014, in a liaison position (time shared between Fredon and university) and technical reference point for voles for the Fredon France network. All of these people, who regularly met in the field for joint work and to compare their experiences, formed the core group that made it possible to continue collecting data and conducting research over the long term, even during periods of funding shortfall.

KEY POINTS. –

The composition and structure of the landscape, determined by the socio-economic constraints on the socioecosystem, determine the dynamics of vole populations.

The details of the causes of fluctuations in abundance are still poorly understood, but they appear to be multifactorial, embedded in a systemic conceptual model, and hierarchical across space and time scales. They include the proportion of optimal habitats in the landscape, predation and disease, possibly combined with stress.

Changes in practices, based on systemic hypotheses derived from long-term observational (eco-epidemiological) studies, constitute quasi-experiments, that is tests of the validity of these hypotheses. This eco-epidemiological approach is at the heart of the adaptive management of vole populations and their effects on other components of the system.

Non-conceptual modeling does not allow the system to be modeled in its entirety. It does, however, make it possible to explore certain local sub-systems when they are framed (in space and time) by observational studies, to verify the theoretical sufficiency of certain hypotheses, to make certain hidden assumptions explicit and to estimate the possible values of certain non-measurable variables by inverse resolution.

The relevant space and time scales (several tens of thousands of square kilometers and several decades) for understanding the combined functioning of prey and predator populations and human societies are beyond the means of observation of researchers alone. Multisectoral partnerships make it possible to study such systems. They are facilitated by the establishment of consortia that coordinate sectors (including government agencies) around management issues. The selection and long-term professional stability of people motivated by such studies and multidisciplinary are indispensable.

Multifactoriality requires multidisciplinary to varying degrees. It can only be coherent if a shared question is answered first. Here: what are the mechanisms and consequences (proximal and ultimate) of regional outbreaks of grassland rodents?

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