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Vaccination of free-living juvenile wild rabbits (*Oryctolagus cuniculus*) against myxomatosis improved their survival

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Abstract

For several decades, the populations of the European wild rabbit (*Oryctolagus cuniculus*) have declined, which is partly due to myxomatosis. Vaccination against this disease is expected to contribute to restoration of rabbit populations but the actual impact of myxomatosis is not well known and vaccination might have some negative effects. We analyzed the capture–mark–recapture data obtained in a 4-year field experiment (1991–1994) in a park near Paris, France wherein 300 out of 565 seronegative juvenile rabbits were vaccinated at first capture against myxomatosis with the nontransmissible Dervaximyxo SG33© vaccine. After accounting for weight at first capture, age-class (juvenile/adult), "trap-happiness" and season (spring/autumn) of the capture event, vaccinated rabbits had 1.8-fold greater odds of surviving than the unvaccinated rabbits. The average summer survival risk for vaccinated juveniles was 0.63 (±0.08 S.E.) whereas it was 0.48 (±0.08 S.E.) for unvaccinated juvenile rabbits.

Keywords: Infectious diseases; Capture–mark–recapture; Population management

1. Introduction

In southwestern Europe, wildlife managers consider vaccination against myxomatosis to be a way to restore wild-rabbit (*Oryctolagus cuniculus*) populations. This lagomorph has strong

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economic implications as a popular small-game species (Angulo and Villafuerte, 2003; Marchandeau, 2000) and is a prey of some endangered specialist predators (Ferrer and Negro, 2004; Iborra et al., 1990). Its major decrease in Europe has been recorded for several decades (Ferrer and Negro, 2004; Marchandeau, 2000) and is due partly to myxomatosis (as well as to habitat destruction, insufficient hunting management and rabbit hemorrhagic disease RHD). Myxomatosis is caused by a *Leporipoxvirus* that was introduced in France in 1952 where it induced >95% mortality (Giban, 1956). Typically, epidemics are in the summer or autumn but this pattern has spatiotemporal variations (Arthur and Louzis, 1988). Infected rabbits will show some clinical signs of acute blepharoconjunctivitis, swelling of the genital organs and dyspnoea. The protection of individuals that recovered from myxomatosis seems mostly to be cell-mediated (Kerr and McFadden, 2002) but maternally transferred antibodies provide a short-term immunity to kittens. Antibody seropositivity in the serum of older rabbits is used as an indicator of their immune status. The coevolution of the virus and its host led to the rapid selection of less-virulent strains and innately resistant rabbits (Fenner, 1983) halving the mortality risk (Ross et al., 1989). In many countries, the infection is now endemic.

Woodroffe (1999) pointed out that the vaccination of threatened species often failed to provide significant individual protection for two main reasons: (i) the lack of protective antibody response (either because of the type of vaccine or because of an inefficient vaccination protocol); (ii) the pathogen was just one in a succession of mortality factors. In the case of vaccination against myxomatosis, one single injection with the attenuated SG33 strain is suspected to induce just a short and only partially protective immune response (Bertagnoli et al., 1996), and might be immunosuppressive in young rabbits (Marlier et al., 2000). Also, the current impact of the myxoma virus on the survival of wild rabbits is not well known because it depends on the incidence of epidemics that vary in time and space (Williams et al., 1973), on the virulence of circulating virus strains and on the rabbits' level of innate and acquired immunity (Fenner, 1983). The myxoma virus is too widely present in wild-rabbit populations to consider its eradication to be a realistic objective. Thus, the main objective of vaccination against myxomatosis is to reduce its impact on the rabbit population at a reasonable cost. Calvete et al. (2004a) assessed the effect of rabbit vaccination in a wild population. However, those authors vaccinated individuals against both RHD and myxomatosis and did not control for the immune status (seropositive or seronegative) of the young rabbits. Their results have a low external validity because exposure (and seroprevalence) vary between years and populations. Moreover, because those authors excluded all data obtained during the first week after tagging from their radiotracking analysis, the global impact of vaccination might have been overestimated, due to potential short-term negative effects of vaccination (Calvete et al., 2004b).

We used capture–mark–recapture (CMR) models to test the impact of vaccination against myxomatosis with the SG33 strain (Saurat et al., 1978) on the survival of individual wild rabbits. First we took account of their immune status, age and sex (as possible confounders). Then we tested for a vaccination effect and investigated how this effect depends on epidemic intensity.

2. Material and methods

2.1. Study site and data collection

The Chèvreloup arboretum (48°50′N, 02°06′E) is a 200-ha park located close to Paris, France whose wild-rabbit population is not hunted but has no other peculiarity when compared to other populations. A 5-ha central study area with a high density of warrens was defined. Rabbits were

live-trapped with wire cage-traps during trapping sessions that were organized every 2–4 weeks between 1991 and 1994. One additional capture operation per warren was conducted each year in October using ferrets (*Mustela furo*) which force rabbits to flush out of their burrows into nets (Cowan, 1984). At its first capture, each animal was individually marked with reflecting ear-tags, as described by Marchandeau et al. (1998). This allowed us to plan about 30 resighting sessions per year from March to September (at dusk, when rabbits are more active). The sex and age of each animal were determined at its first capture by palpation of their apophyseal line, to distinguish juveniles (born in the present year) from adults (Watson and Tyndale-Biscoe, 1953). At each capture occasion, the animals were also weighed, which allowed us to infer with greater precision the age of all young (the growth of which is reported to be linear during the first 3 months of life; Marchandeau et al., 1995). And, lastly, at each physical capture a blood sample was taken on a strip of blotting paper to detect myxomatosis antibodies with an indirect immunofluorescence test (Chantal and Gilbert, 1996; Gilbert et al., 1989) for which sensitivity and specificity are, respectively, 90 and 100% when compared to an ELISA (enzyme-linked immunosorbent assay; Gelfi et al., 1999).

Myxomatosis was known to be present in the population, conversely to RHD (for which the first outbreak did not occur until 1995). Half the young was vaccinated at first capture with the nontransmissible attenuated strain of the Dervaximyxo SG33© vaccine (Saurat et al., 1978) in the springs of 1991 and 1992 and, for management reasons, two-thirds of them in the spring of 1993. Adults were not vaccinated.

2.2. Survival analysis

To estimate survival rates we used recent developments of the Cormack–Jolly–Seber (CJS) model $\Phi(t)p(t)$ (Cormack, 1964; Jolly, 1965; Seber, 1965), where both survival Φ and recapture p rates vary over time (reviewed in Lebreton et al., 1992). Indeed, the capture–mark–recapture (CMR) framework allows us jointly to calculate unbiased estimates of capture and survival probabilities (Nichols, 1992) between discrete capture occasions based on individual capture histories. In addition, one can specifically test for the effects of relevant biological factors (Lebreton et al., 1992) on survival and recapture rates. In our study, a reorganization of individual recapture histories was needed because numerous sessions were characterized by too few resightings or trappings. Thus, several sessions were pooled into a number of ''capture occasions''. Because only few captures took place in the beginning and at the end of each year, and because myxomatosis epidemics mainly occur in summer, we only considered all captures and resighting events between mid-April and the end of June, pooled in ''spring-capture occasions'', and those between mid-August and the end of October, pooled in ''autumn-capture occasions''. We thus studied the survival rates between ''spring'' and ''autumn'' capture occasions and between ''autumn'' and ''spring'' capture occasions. Because the vaccinations were only made in the springs of 1991–1993, the only young rabbits included in the analysis were those caught for the first time between mid-April and the end of Junes of those years. The vaccination effect is expected to be low or even nil for seropositive rabbits because they are still protected; also, high antibody titers can have negative effects on vaccinal response (Saurat et al., 1980). At their first capture, not enough juveniles were seropositive to retain satisfactory sample sizes and test for this hypothesis. Thus, they were excluded from the analysis and only young individuals that were seronegative at the time of their first capture were kept; in our data set, this was 300 vaccinated rabbits (152 males and 148 females) and 265 control animals (131 males and 134 females; Table 1). ''Weight at first capture'' and ''day of first capture'' (numbered from the 1

Table 1
Numbers of vaccinated and unvaccinated seronegative young rabbits first captured in spring between 1991 and 1993 in France

	Vaccinated	Unvaccinated
Year of first capture		
1991	131	127
1992	97	104
1993	72	34

Table 2
Individual covariates quartiles of vaccinated and unvaccinated seronegative young rabbits first captured between 1991 and 1993 in France

		Vaccinated	Unvaccinated
Weight at first capture (w; in g)	1st quartile	280	270
	Median	395	360
	3rd quartile	510	480
Day of first capture (d; numbered from the 1 January)	1st quartile	139	135
	Median	143	142
	3rd quartile	169	156

January) were similar between the vaccination and control groups (Table 2). The median ''day of first capture'' was 142 (corresponding to the end of May) and the median ''weight at first capture'' was 370 g (a little more than 1-month old; Table 2).

In CMR analysis, the first step is to find an initial general ''umbrella'' model that fits the data well (*i.e.*, with no serious departure from the CJS model basic assumptions; Lebreton et al., 1992). Such an umbrella model is then used as the starting point for the selection/testing of risk factors, potential confounders, and the effect of the intervention on the survival of the rabbits. We used U-CARE 2.0 (Choquet et al., 2003) to find the initial model with various goodness-of-fit (GOF) tests and MARK 3.1 (White and Burnham, 1999) to run the models and to obtain maximum-likelihood estimates of effects.

The two major violations of the CJS model that concerned us were ''transience'' (Pradel et al., 1997) and ''immediate trap-happiness'' (Pradel, 1993). When all animals are first captured as young (as at our vaccination intervention), transience becomes a true age effect that results in lower survival of young rabbits after a spring-capture occasion (rabbits typically are born in the spring) than after an autumn-capture occasion. Therefore, we used A2 to distinguish juveniles in their first spring/summer from older animals (''adults''; Table 3). ''Trap-happiness'' refers to a higher capture risk for animals captured at the previous trapping occasion than for animals not captured at the previous occasion, for example from learning that the bait in the trap tastes good (''trap-shyness'' instead would imply a learned dislike and subsequent avoidance of the traps).

We started with the simple model $\Phi(t)p(t)$, which had poor overall GOF ($P < 10^{-4}$). We then tried $\Phi(\mathrm{A2} \times t)p(t)$ to account (by the binary age-group variable A2) for transience, but P still was $<10^{-4}$. Adding the trap-happiness term [following the approach of Pradel (1993) and Schmitt et al. (2002)] brought the model $[\Phi(\mathrm{A2} \times t)p(m \times t)]$ up to $P = 0.015$ (deviance = 1566.00, with 11 identifiable parameters; $\chi^2_{\mathrm{GOF}} = 12.24$, d.f. = 4). Because this still was poor fit, we calculated a variance-inflation factor ($\hat{c}$). The $\hat{c}$ we used was the $\chi^2_{\mathrm{GOF}}/\mathrm{d.f.} = 12.24/4 = 3.06$ (Lebreton et al., 1992); we used $\hat{c}$ as the adjustment factor when calculating the

Table 3
Models parameters and abbreviation initials meanings

Notation	Description
Φ	Survival probability
p	Recapture probability
A2	Age-class (binary: young (rabbits during their first spring/summer) vs. adults)
t	Time (seven-level index for recapture events and survival periods through the two seasons per year across 4 years)
Sa	Season (binary: spring vs. autumn)
y	Year (four-level: 1991–1994)
m	Immediate trap-dependence (binary index on p: recapture when captured at the previous occasion vs. recapture when not captured at the previous occasion)
w	Weight at first capture (in g)
d	Day of first capture (number of days between the beginning of the year and the first capture)
s	Sex (binary: male vs. female)
v	Vaccination (binary: vaccinated vs. unvaccinated)
Ei	Intensity of myxomatosis epidemics during the year (binary: low vs. high)
$\hat{c}$	Variance-inflation factor
CJS	Cormack, Jolly, Seber
CMR	Capture, mark, recapture
GOF	Goodness-of-fit
QAICc	Corrected quasi-likelihood Akaike's information criterion
RHD	Rabbit hemorrhagic disease

"corrected quasi-likelihood Akaike's information criterion" (QAICc) that takes the extra-binomial variation into account (Anderson et al., 1994) and S.E.$_{\hat{c}}$ (Lebreton et al., 1992) in the subsequent models.

We realized that we could not add all potential confounders simultaneously to the starting model, because of data sparseness, and that even its multiplicative form had to be modified, because of parameter-identifiability problems with the fully time-dependent model (Pradel, 1993). So, we altered the umbrella model to the form: $\Phi(\mathrm{A2} + t)\, p(m + t)$.We then used a three-step sequential process in which we added and tested the effects of potential confounders (Table 3): season (spring/autumn; Sa), year (y), weight of first capture (w), day of first capture (d) and sex (s). We added Sa and y (after removing the seven-level index t with which Sa and y were collinear) in step 1, then w and d in step 2, and finally s in step 3. At each step, we tested four or five models in which the additional parameters were included in various additive or multiplicative forms. We did not test any three-way interactions (because of the sparseness of the data). We calculated the QAICc for each of the four or five models in the step, and then "selected" the model that had the fewest parameters and still had QAICc within "2" of the smallest QAICc of the models within the subset (Burnham and Anderson, 2003). That selected model then was the starting model for the next step (*i.e.*, for the next parameter subset to be tested). After these steps, our chosen model was $\Phi(\mathrm{A2} \times w)\, p(m + \mathrm{Sa})$ (seven identifiable parameters, deviance = 1534.20, QAICc = 515.50). The full set of the models tested and their deviances and QAICcs is available from the first author upon request.

At that point, we felt that we could test the effect of vaccination (v) on rabbit survival. We looked at adding v in four different additive or multiplicative forms (one of which had v in a three-way interaction), and used the same selection criteria as for the potential confounders. To the best model we found, we then tested an interaction between v and epidemic intensity (Ei). Ei was defined as a binary categorical variable: serological data show that high myxomatosis

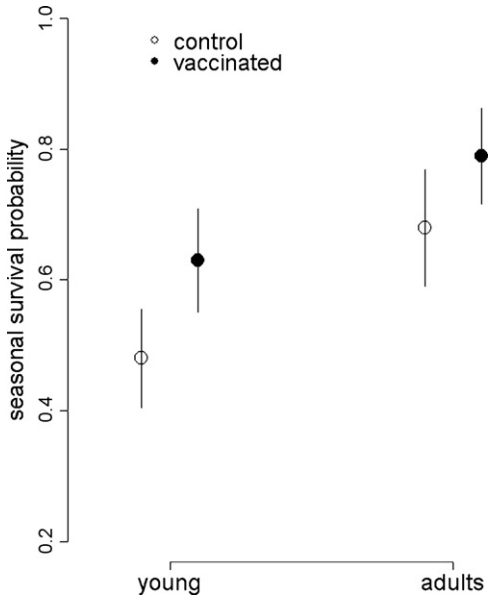

Fig. 1. Seasonal survival probabilities (±corrected S.E.) of young and adult rabbits between 1991 and 1994 in France under the selected model $\Phi(\mathrm{A2} \times w + v)\, p(m + \mathrm{Sa})$ with $\hat{c} = 3.06$.

epidemics occurred in 1991 and 1993 (∼90% of seropositive young at the end of the year) whereas epidemics were much lower in 1992 and 1994 (∼20% seropositive young at the end of the year).

The results of the selected model were examined both by the estimated survival probabilities and odds-ratio. The odds-ratio of vaccinated individuals is defined as $(\Phi(v)/(1 - \Phi(v))/(\Phi(c)/(1 - \Phi(c))$ (where c refers to control animals) and is estimated by the exponential of the v parameter of the selected model.

3. Results

Our selected model for the effect of vaccination on the survival of rabbits was $\Phi(\mathrm{A2} \times w + v)\, p(m + \mathrm{Sa})$. This model had eight identifiable parameters, deviance = 1520.91, and QAICc = 513.19. The vaccinated rabbits had 1.8-fold higher odds of surviving than the unvaccinated ones (after accounting for the effects of age group, weight at first capture, trap-happiness and season; seasonal survival probabilities are given in Fig. 1).

The effect of epidemic intensity on vaccination impact was not selected because the QAICc score of $\Phi(\mathrm{A2} \times w + v \times \mathrm{Ei})\, p(m + \mathrm{Sa})$ was 515.21 (10 identifiable parameters, deviance = 1514.56).

4. Discussion

4.1. Confounding effects and overdispersion

The seasonal and trap-happiness effects on our recapture rates may be respectively explained by the efficient capture operations with ferrets that took place every year in October (inducing the

higher recapture probability in autumn) and by the use of baited traps throughout the year (that might have caused immediate trap-happiness).

Young rabbits showed a lower survival rate than adults, which is a common trait in mammals (Caughley, 1966), that is also well documented in rabbits (Cowan, 1987; Wood, 1980). Moreover, the effect of *weight of first capture* on young-rabbit survival indicates that, as expected, young rabbits have a higher mortality rate during the first weeks of life (Cowan, 1987).

The $\hat{c}$ value was at the upper limit of what is usually found (Burnham et al., 1987; Lebreton et al., 1992). Pooling of the numerous trapping and resighting sessions into a few ''seasonal'' capture occasions could have had only a limited impact because the individual covariate *day of first capture* was not selected (although it undoubtedly induced part of the observed overdispersion of the data). Using such a high $\hat{c}$ value, due to the large extra-binomial variation, in conjunction with small sample sizes, severely limited the power of model selection to detect differences. For example, no sex effect on survival was detected, although males have higher mortality and disperse more (which means that they cannot be trapped in the original area) than females (Cowan, 1987, 1991; Künkele and Von Holst, 1996).

4.2. Impact of vaccination against myxomatosis on survival probability

Yet, this low statistical power did not ''hide'' the impact of vaccination of seronegative young rabbits on their survival probability. This result leads us to two main interpretations.

First, it suggests that a single injection of the SG33 vaccine has only limited negative effects, as argued by Marchandeau et al. (1995) who did not find any effect of vaccination on body growth rate on the same data set. Possible short-term negative effects of vaccination (Calvete et al., 2004b) did not suppress its positive impact on survival of seronegative juvenile rabbits.

Second, our experiment shows that myxomatosis still has a significative impact on survival of juvenile rabbits. It might still constrain the growth rate of some wild-rabbit populations (even though it is several decades after its introduction into Europe). In the studied population, on average the disease was responsible for the death of ∼15% of seronegative young rabbits during the summer. However, its impact might not be the same in every European or even French population and every year. First, it might depend on the level of epidemic intensity, which varies in time and over space (Williams et al., 1973). For example, in our field experiment, even if the model taking account for this effect was not selected (probably because of the low statistical power), its estimated parameters suggest that the mortality of young induced by the disease varied from ∼5% (during low epidemic intensity years; odds-ratio = 1.2) to ∼20% (during high epidemic intensity years; odds-ratio = 2.4). Disease impact might also depend on the virulence of the circulating virus strain, on the level of rabbit genetic resistance and on the proportion of naturally seropositive individuals (Fouchet et al., 2006).

From a population-management point of view, the objective of vaccination campaigns is not only to increase the individual survival rate of rabbits but above all to increase the numbers of rabbits. At this scale, the benefit of vaccination highly depends on the vaccination protocol. Firstly, the proportion of vaccinated rabbits is a key parameter and high proportions are very difficult to attain when the vaccination of an individual requires its capture. It could be increased by the use of a new generation of recombinant vaccines that would be administered orally (Messud-Petit and Bertagnoli, 2000) or even be transmissible (Torres et al., 2001). However, mainly for some economic and administrative reasons, these vaccines are still not available. Moreover, the efficacy of vaccine transmission still needs to be assessed at lower rabbit densities than those that were tested by Torres et al. (2001) on a highly populated island (±10 rabbits/ha).

Secondly, the time of vaccination is probably important. Indeed, campaigns might be more efficient just before the yearly epidemics because the immunity of vaccinated rabbits is waning and because numerous sensitive young might be born in this time lag. However, this optimum might be difficult to achieve in the field because the time at which the epidemics occur varies from one year to another (Arthur and Louzis, 1988; Dunsmore et al., 1971; Kerr et al., 1998).

Thus, many factors can reduce the impact and the benefit of vaccination campaigns. And of course, nobody should expect that it could be a substitute for other necessary management and conservation measures, such as habitat restoration or hunting regulation.

5. Conclusion

We demonstrated that, under the epidemiological conditions of our field experiment and after taking account for the effect of weight at first capture and age-class (juvenile/adult) on survival rate and for the effect of season (spring/fall) and ''trap-happiness'' on recapture rate, seronegative juveniles rabbits vaccinated against myxomatosis had a better average summer survival probability (0.63 ± 0.08 S.E.) than seronegative unvaccinated juveniles (0.48 ± 0.08 S.E.).

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References

Anderson, D.R., Burnham, K.P., White, G.C., 1994. AIC model selection in overdispersed capture–recapture data. Ecology 75, 1780–1793.

Angulo, E., Villafuerte, R., 2003. Modelling hunting strategies for the conservation of wild rabbit populations. Biol. Conserv. 115, 291–301.

Arthur, C.P., Louzis, C., 1988. la myxomatose du lapin en France: une revue. Rev. sci. tech. Off. int. Epiz. 7, 937–957.

Bertagnoli, S., Gelfi, J., Le Gall, G., Boilletot, E., Vautherot, J.-F., Rasschaert, D., Laurent, S., Petit, F., Boucraut-Baralon, C., Milon, A., 1996. Protection against myxomatosis and rabbit viral hemorrhagic disease with recombinant viruses expressing rabbit hemorrhagic disease virus capsid protein. J. Virol. 70, 5061–5066.

Burnham, K.P., Anderson, D.R. (Eds.), 2003. Model Selection and Inference: A Practical Information–Theoretic Approach. Springer-Verlag, New York.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., Pollock, K.H., 1987. Design and analysis methods for fish survival experiments based on release-recapture. Am. Fish. Soc. Monogr. 5.

Calvete, C., Estrada, R., Lucientes, J., Osacar, J.J., Villafuerte, R., 2004a. Effects of vaccination against viral haemorrhagic disease and myxomatosis on long-term mortality rates of European wild rabbits. Vet. Rec. 155, 388–392.

Calvete, C., Estrada, R., Osacar, J.J., Lucientes, J., Villafuerte, R., 2004b. Short-term negative effects of vaccination campaigns against myxomatosis and viral hemorrhagic disease (VHD) on the survival of European wild rabbits. J. Wildl. Manage. 68, 198–205.

Caughley, G., 1966. Mortality patterns in mammals. Ecology 47, 906–918.

Chantal, J., Gilbert, Y., 1996. Myxomatosis. In: OIE (Eds.), Manual of Standards for Diagnostic Tests and Vaccines. OIE, Paris, pp. 578–583.

Choquet, R., Remoulet, A.M., Pradel, R., Gimenez, O., Lebreton, J.-D., 2003. In: CEFE/CNRS (Eds.), U-Care User's Guide, Version 2.0. CEFE/CNRS, Montpellier. , http://ftp.cefe.cnrs.fr/biom/Soft-CR/Last_Update/.

Cormack, R.M., 1964. Estimates of survival from the sighting of marked animals. Biometrika 51, 429–438.
Cowan, D.P., 1984. The use of ferrets (*Mustela furo*) in the study and management of the European wild rabbit (*Oryctolagus cuniculus*). J. Zool. Lond. 204, 570–574.
Cowan, D.P., 1987. Patterns of mortality in a free-living rabbit (*Oryctolagus cuniculus*) population. Symp. Zool. Soc. Lond. 58, 59–77.
Cowan, D.P., 1991. The availability of burrows in relation to dispersal in the wild rabbit *Oryctolagus cuniculus*. Symp. Zool. Soc. Lond. 63, 213–230.
Dunsmore, J., Williams, R., Price, W., 1971. A winter epizootic of myxomatosis in subalpine south-eastern Australia. Aust. J. Zool. 19, 275–286.
Fenner, F.R.S., 1983. Biological control, as exemplified by smallpox eradication and myxomatosis. Proc. R. Soc. Lond. B 218, 259–285.
Ferrer, M., Negro, J.J., 2004. The near-extinction of two large predators: the super-specialists pay a price. Conserv. Biol. 18, 344–349.
Fouchet, D., Marchandeau, S., Langlais, M., Pontier, D., 2006. Waning of maternal immunity and the impact of diseases: the example of myxomatosis in natural rabbit populations. J. Theor. Biol. 242, 81–89.
Gelfi, J., Chantal, J., Phong, T.T., Boucraut-Baralon, C., 1999. Development of an ELISA for detection of myxoma virus-specific rabbit antibodies: test evaluation for diagnostic applications on vaccinated and wild rabbit sera. J. Vet. Diagn. Invest. 11, 240–245.
Giban, J., 1956. Répercussion de la myxomatose sur les populations de lapin de garenne en France. La Terre et la Vie 103, 179–187.
Gilbert, Y., Picavet, D.P., Chantal, J., 1989. Diagnosis of myxomatosis: development of an indirect immunofluorescence technique. Rev. sci. tech. Off. int. Epiz. 15, 323–335.
Iborra, O., Arthur, C.P., Bayle, P., 1990. Importance trophique du lapin de garenne pour les grands rapaces provençaux. Vie et Milieu 40, 177–188.
Jolly, G.M., 1965. Explicit estimates from capture–recapture data with both dead and immigration-stochastic model. Biometrika 52, 225–247.
Kerr, P., McFadden, G., 2002. Immune responses to myxoma virus. Viral Immunol. 15, 229–246.
Kerr, P.J., Twigg, L.E., Silvers, L., Lowe, T.J., Forrester, R.I., 1998. Serological monitoring of the epidemiology of myxoma virus to assess the effects of imposed fertility control to female rabbits on myxomatosis. Wildl. Res. 25, 123–131.
Künkele, J., Von Holst, D., 1996. Natal dispersal in the European wild rabbit. Anim. Behav. 51, 1047–1059.
Lebreton, J.-D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. 62, 67–118.
Marchandeau, S., 2000. Enquête nationale sur les tableaux de chasse à tir, saison 1998–1999. Le Lapin de garenne. Faune Sauvage 251, 18–25.
Marchandeau, S., Chantal, J., Portejoie, Y., Barraud, S., Chaval, Y., 1998. Impact of viral hemorrhagic disease on wild population of European rabbits in France. J. Wildl. Dis. 34, 429–435.
Marchandeau, S., Guénézan, M., Chantal, J., 1995. Utilisation de la croissance pondérale pour la détermination de l'âge de jeunes lapins de garenne (*Oryctolagus cuniculus*). Gibier Faune Sauvage/Game Wildl. 12, 289–302.
Marlier, D., Mainil, J., Boucraut-Baralon, C., Linden, A., Vindevogel, H., 2000. The efficacy of two vaccination schemes against experimental infection with a virulent amyxomatous or a virulent nodular myxoma virus strain. J. Comp. Pathol. 122, 115–122.
Messud-Petit, F., Bertagnoli, S., 2000. Le virus myxomateux: de l'agent pathogène au vecteur vaccinal. Virologie 4, 453–462.
Nichols, J.D., 1992. Capture–recapture models: using marked animals to study population dynamics. Bioscience 42, 94–102.
Pradel, R., 1993. Flexibility in survival analysis from recapture data: handling trap-dependence. In: Lebreton, J.-D., North, P.M. (Eds.), Marked Individuals in the Study of Bird Population. Birkhäuser Verlag, Basel, pp. 29–37.
Pradel, R., Hines, J.E., Lebreton, J.-D., Nichols, J.D., 1997. Capture–recapture survival models taking account of transients. Biometrics 53, 60–72.
Ross, J., Tittensor, A.M., Fox, A., Sanders, M.F., 1989. Myxomatosis in farmland rabbit populations in England and Wales. Epidemiol. Infect. 103, 333–357.
Saurat, P., Chantal, J., Ganière, J.-P., Gilbert, Y., Picavet, D., Lefort, C., 1980. La réponse immunitaire dans la myxomatose. Étude de la réponse humorale. Bull. Mens. Off. Natl. Chasse 12, 297–309.
Saurat, P., Gilbert, Y., Ganière, J.-P., 1978. Etude d'une souche de virus myxomateux modifié. Rev. Méd. Vét. 129, 415–451.

Schmitt, B.R., Schaub, M., Anholt, B.R., 2002. Why you should use capture–recapture methods when estimating survival and breeding probabilities: on bias, temporary emigration, overdispersion, and common toads. Amphibia-Reptilia 23, 375–388.

Seber, G.A.F., 1965. A note on the multiple recapture census. Biometrika 52, 249–259.

Torres, J.M., Sanchez, C., Ramirez, M.A., Morales, M., Barcena, J., Ferrer, J., Espuña, E., Pagès-Manté, A., Sanchez-Vizcaino, J.M., 2001. First field trial of a transmissible recombinant vaccine against myxomatosis and rabbit hemorrhagic disease. Vaccine 19, 4536–4543.

Watson, J.S., Tyndale-Biscoe, C.H., 1953. The apophyseal line as an age indicator for the wild rabbit, *Oryctolagus cuniculus* (L.). N. Z. J. Sci. Technol. 34, 427–435.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46, 120–138.

Williams, R.T., Dunsmore, J.D., Sobey, W.R., 1973. Fluctuations in the titre of antibody to a soluble antigen of myxoma virus in field populations of rabbits, *Oryctolagus cuniculus* (L.), in Australia. J. Hyg. Cambridge 71, 487–500.

Wood, D.H., 1980. The demography of a rabbit population in an arid region of New South Wales Australia. J. Anim. Ecol. 49, 55–79.

Woodroffe, R., 1999. Managing disease threats to wild mammals. Anim. Cons. 2, 185–193.