Effect of storage conditions on dispersal and short-term survival of translocated wild rabbits Oryctolagus cuniculus

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SHORT COMMUNICATION

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Effect of storage conditions on dispersal and short-term survival of translocated wild rabbits *Oryctolagus cuniculus*

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Restocking is a widespread management practice used to support wild populations of European rabbit *Oryctolagus cuniculus* which are jeopardised by habitat loss and disease outbreaks. However, rabbits are known to experience a high mortality just after release, which might be due to the handling stress induced by translocation, and particularly to storage condition between capture and release. In our study, we tested two soft treatments of storage in boxes, where rabbits were stored either alone or in groups of four or five, and we assessed both survival rates and maximum dispersal distances by radio-tracking 43 individuals during eight weeks after release. We also recorded data about the survival at the time of release for 11 other rabbits that either died before release or were not radio-equipped. Our study involved two similar experimental releases in 2001 and 2002 in distinct nearby study areas to assess the effect of storage condition. Rabbits were released in two subsequent batches at a few days interval. Overall cumulated survival over the first 10 days after capture was 61%, and 96% during the subsequent 46 days. There was no clear overall effect of the storage method used on early survival: all individuals stored in groups survived in the second experiment, but not in the first experiment, whereas early mortality was equal for individually stored rabbits in both experiments. Otherwise, there was no effect of sex and batch on survival. Maximum dispersal distances from the release sites ranged within 20-280 m, except for two rabbits that moved 1.1-1.4 km away. Dispersal after release depended on both experiment and batch, but neither on sex nor on storage condition. It is not possible to conclude from our results that storage condition is a critical factor determining release success in wild rabbit, at least not the soft treatments that we tested.

Key words: dispersal, Oryctolagus cuniculus, radio-tracking, restocking, storage conditions, survival, translocation stress

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Restocking is a commonly used practice in wildlife management, and particularly for European wild rabbit *Oryctolagus cuniculus* in France, Portugal and Spain. Wild rabbit is not a genuinely endangered species, but many populations are declining, primarily because of habitat destruction and epizootics of both myxomatosis (Trout et al. 1992) and rabbit haemorrhagic disease (Marchandeau et al. 1998, Marchandeau et al. 2000). The extent of the population decline is reflected in the French national bag records survey: 13.5 million rabbits in 1974/75, 6.4 million rabbits in 1983/84 and 3.2 million rabbits in 1998/99 (Arthur & Guénézan 1986, Marchandeau 2000). Thus, the populations are generally small and do not live up to the expectations of hunters, who therefore commonly resort to rabbit restocking despite the fact that restocking success is generally low due to heavy early mortality (Arthur 1989, Mauvy et al. 1991, Moreno et al. 1996, Calvete et al. 1997, Letty 1998, Letty et al. 2002). One explanation of the increased short-term mortality after translocation could be acute stress known to be rapidly induced by capture and handling in other mammals (Guthrie et al. 1967, Hamilton & Weeks 1985, Waas et al. 1999, Warburton et al. 1999).

We aimed at determining whether translocation stress was responsible for the early mortality in rabbit restocking. For instance, we previously found that the administration of tranquillisers between capture and transport did not increase release effectiveness (Letty et al. 2000). In this paper, we report the results of rabbit releases designed to assess the effect of storage conditions during translocation on short-term survival and dispersal of individuals. More precisely, we compared the fate of rabbits that were exposed to one of two different soft storage treatments in boxes, alone or in small groups, during translocation. We did this as the amount of stress due to translocation, and consequently the overall success of the release, might depend on storage conditions.

Material and methods

Study areas

We carried out two translocation experiments in 2001 and 2002 in Dompierre-sur-Yon (Vendée, western France) in two distinct release areas which were a few kilometres apart. The background landscape consisted mainly of a patchwork of pastures, but also of cereals fields, separated by hedgerows composed of natural shrubs, e.g. bramble *Rubus fruticosus*, hawthorn *Crataegus monogyna*, blackthorn *Prunus spinosa*, ash *Fraxinus excelsior*, privet *Ligustrum vulgare*, butcher's broom *Ruscus aculeatus*, common oak *Quercus robur* and hazel *Corylus avellana*. There were also a few woods and fallows in the areas. In each study area, several release warrens were made of a big pile of stumps covered with loam and branches. In the first study year (2001), warrens were constructed along an edge (350 m in length) between a meadow and an area of fallows and woods, while in the second study year (2002), warrens were built inside a 3-ha plot consisting of several adjacent cultivated and fallow strips. Weather conditions were typical of a temperate oceanic climate. The overall population density before the translocations was low (ca 0.5 rabbits ha^{-1}). No hunting occurred during either study year, but a few mammalian predators such as red fox *Vulpes vulpes*, mustelids *Mustelidae*, domestic dog *Canis familiaris*, and domestic cat *Felis catus* were present.

Capture and handling

We captured 54 rabbits (34 ♀, 20 ♂) using ferreting (Cowan 1984), i.e. rabbits were flushed out of their burrows and driven into nets. We ferreted several warrens, and thus several breeding groups, in each capture area. There were two successive translocation batches in each experiment. In 2001, we caught all the translocated rabbits in Notre-Dame-de-Monts (Vendée, western France); the first batch (10 ♀, 7 ♂) was caught on 12 February, and the second batch (15 ♀, 5 ♂) on 20 February. In 2002, the first batch (6 ♀, 3 ♂) was also caught in Notre-Dame-de-Monts on 29 January, but the second batch (3 ♀, 5 ♂) was caught in La-Petite-Boissière (Deux-Sèvres, western France) on 11 February.

All rabbits were weighed, sexed, vaccinated against rabbit haemorrhagic disease and myxomatosis (DERCUNIMIX ®, MERIAL, Lyon, France), and individually marked with ear tags. At the time of capture, the source populations were mainly composed of adults and subadults. Except for two juvenile females each weighing 350 g, body mass ranged within 1,210-1,870 g. Of the 54 full-grown rabbits released, 43 were also radio-equipped, using transmitters supplied with a loop antenna and a mortality sensor with a range of ca 1.5 km and weighing ca. 30 g, i.e. 2-3% of rabbit body mass. We used two transmitter models: TXP-1 (TELEVILT INTERNATIONAL ®, Lindesberg, Sweden) and TW-5 (BIOTRACK Ltd, Wareham, UK).

Storage treatments

To compare survival after release of rabbits that had been exposed to one of two different soft restraint treatments between capture and release, we used 1) individual storage (I) or 2) storage in groups of 4-5 rabbits/box (G). Rabbits were stored in wooden boxes riddled with holes, and there was less room per individual for I rabbits (box size: 29 × 16.5 × 14 cm) than for G rabbits (box size: 100 × 50 × 30 cm). I and G treatments were evenly distributed within each translocation batch (2001-1: 9/8; 2001-2: 11/9; 2002-1: 5/4; 2002-2: 4/4), and concurrently also within sex (♀: 18/16; ♂: 11/9). Each rabbit was given a piece of beet or apple as a source of wet food to limit dehydration during storage. Rabbits were transported by car for a journey of about one hour on the day of capture, and then, kept in boxes until release the following morning.

Release and monitoring

We split the rabbits into groups of 3-7 individuals, irrespective of sex, which were introduced in different release warrens. To avoid pseudo-replication, we mixed I and G rabbits within release groups. Moreover, to minimise any influence of prior familiarity among the rabbits, we were careful not to reunite all individuals caught in the same warren in either storage groups or release groups, just as we were careful not to reunite individuals from the same storage groups in the release groups. There were three release groups in each translocation batch, except for the second batch in 2002, which had only two groups. The groups were released in five warrens in 2001, but only in three warrens in 2002, so some release warrens were consecutively used twice.

The monitoring was the same for each translocation batch. During the first five days after translocation, the release warrens were fenced with wire mesh, so that rabbits were kept inside temporary pens for acclimatisation before they were released into the new environment. However, some rabbits succeeded in escaping from the pens before the fence was removed. Cabbage and corn were provided as food inside the pens. The monitoring consisted of several radio-tracking sessions conducted over two months after the release; the first two sessions occurred before the fence was removed.

Survival analysis

We performed the survival (φ) modelling on the basis of telemetry data following standard capture-mark-recapture (CMR) methods (Lebreton et al. 1992). We used the 'known fate' procedure of the software MARK 2.1 (White & Burnham 1999) to assess the significance of the different effects that may arise and interact. We modelled the effects on survival probabilities of sex (s), translocation experiment (e: 2001 or 2002), release batch (b: first or second one) and, of course, experimental treatment: restraint-storage condition in boxes for one day (r: I or G). We also accounted for the effect of the time elapsed since capture (t: date of monitoring), for each batch respectively, and we simplified it through a period pattern by grouping together consecutive intervals of time. We considered 15 monitoring occasions over 56 days from the capture dates, i.e. the event of release and 14 subsequent telemetry sessions. Once the main period of mortality was discovered, we particularly looked for interactions among the remaining factors during this critical period. Survival data from five I and three G females, which were not radio-equipped during the first experiment, were recorded only between capture and release inside pens (later fate unknown). Neither mortality induced by radio-collar nor signal loss were considered as true mortality, but only as 'losses on capture'. There were four such cases (three mortalities and one signal loss) during the first three weeks after capture, one in each sex-restraint category.

Model selection was achieved following a backward process leading from complex models to simplified models by comparison of Akaike's Information Criterion (AIC; Akaike 1973). For each model, AIC accounts for its relative deviance (DEV) and its number of estimated parameters (np), the best model having the lowest AIC value; MARK corrects AIC into AIC_c according to the effective sample size of the CMR data set (n-ess = 439). However, when two models have very similar AIC values (difference around 1 or 2), then the choice of a unique model could not be justified solely on statistical grounds, but should be also supported by biological understanding (Burnham & Anderson 1992). We also used the Likelihood Ratio Test (LRT) to assess specific assumptions as it allows the comparison between a baseline model and the more complex model within which it is nested, and which includes the tested effect.

Dispersal analysis

For each telemetry session, we measured, with an accuracy of ca 5 m, for all radio-tracked rabbits the linear distances between their diurnal resting places and their release warrens. Then, we studied dispersal by analysing the maximum distance of each individual from its

Table 1. Survival (φ) model selection based on data of translocated wild rabbits according to sex (s), restraint treatment (r), translocation experiment (e), release batch (b), time after capture (t; monitoring intervals) or period of time ('t0-10-56' covering two periods, the first 10 days (0-10) and the 46 subsequent days (10-56)); - indicates the overall baseline value; + the additive effects, and * the interaction. Number of estimated parameters (np), deviance (DEV) and Akaike's information criterion (AIC_c; n-ess = 439) are given. The selected models are in italics.

Survival model	np	DEV	AIC_c
φ s * r * e * b * t	240	65.01	1129.25
φ s * r * e * b	16	138.34	171.63
φ s * r * e * b * t0-10-56	32	97.71	166.91
φ (s * r * e * b) * t0-10 + t10-56	17	102.04	137.50
φ (r * e * b + s) * t0-10 + t10-56	10	105.82	126.33
φ (r * e * b) * t0-10 + t10-56	9	105.95	124.38
φ (r * e + b) * t0-10 + t10-56	6	107.34	119.54
*φ (r * e) * t 0-10 + t 10-56*	*5*	*107.47*	*117.61*
*φ (G 2002 - others) * t 0-10 + t 10-56*	*3*	*107.89*	*113.94*
φ (r + e) * t0-10 + t10-56	4	113.41	121.50
φ (e) * t0-10 + t10-56	3	115.24	121.29
φ (r) * t0-10 + t10-56	3	114.03	120.08
φ t0-10-56	2	115.91	119.94
φ -	1	158.41	160.42

release warren, using stepwise options in the general linear model (GLM) procedure of the software SYSTAT (SPSS Inc. 2000).

Results

Survival

We started the analysis from the saturated model 'φ s*r*e*b*t' (Table 1) and first simplified the effect of time elapsed since capture. The best period pattern, 't0-10-56', highlighted the first 10 days after capture during which 17 natural deaths occurred (out of the 18 deaths recorded by telemetry during both study years). Consequently, we focused the analysis on this first period to assess the effects of sex, restraint treatment, experiment, batch and of their interactions on survival. The model 'φ (r*e)*t0-10+t10-56' was first selected, but the interaction between restraint treatment and experiment during the first period amounted to a single significant difference between individuals stored in group boxes in 2002 and all the other rabbits (Table 2). Thus, the nested model 'φ (G2002-others)*t0-10+t10-56' was finally selected (LRT: $\chi^2_2 = 0.417$, $P > 0.8$). In fact, none of the eight rabbits stored in group boxes in 2002 died during the first period while the cumulated survival only reached 54% in the other categories of rabbits. During the subsequent period, the survival rate was very high in all categories of individuals (see Table 2), as expected in absence of translocation. Concerning the causes of death, there were three cases of spontaneous mortality during storage in boxes (1 juvenile I ♀, 1 I ♀ and 1 G ♂). After release, mortality was attributed in 12 cases to predation by mammalian carnivores, even though carcass scavenging after what could possibly have been a stress-related death was also suspected in some cases. Indeed, we also recorded three other cases of spontaneous mortality at the same time.

Dispersal

Among the 38 rabbits known to be alive after release from radio-tracking, eight individuals from the four batches (2 I ♂, 3 G ♂, and 3 I ♀) were not located outside their respective release warrens, mainly because

Table 2. Survival ($\hat{\varphi}$) estimates per day (mean and 95% CI) of wild rabbits over 56 days after translocation. Survival probabilities were derived from the model 'φ (r * e) * t0-10 + t10-56' (see Table 1), in which survival depends on time period (the first 10 days (0-10) or the 46 days after (10-56)), and also, for the first period only, on both restraint treatment and translocation experiment.

Survival estimates (per day)	$\hat{\varphi}$ (r * e) * t0-10		$\hat{\varphi}$ t10-56
Restraint \ Experiment	2001	2002	
Individual	0.945 (0.882 - 0.975)	0.923 (0.827 - 0.968)	0.999 (0.994 - 1.000)
Group	0.945 (0.884 - 0.975)	1.000 (0.999 - 1.000)	

Table 3. Maximum distance (in m; mean ± SD) from release warrens obtained by radio-tracking wild rabbits for 56 days after translocation, according to translocation experiment and release batch. Individuals (2) that moved further away than usual were excluded from the analysis.

	Maximum distance from warrens	
Batch/Experiment	2001	2002
1	172 ± 59 (9)	132 ± 34 (5)
2	128 ± 70 (8)	83 ± 62 (6)

they died rapidly, sometimes even before fences were removed. Two rabbits (1 I ♂ from the first batch in 2001, and 1 I ♀ from the second batch in 2002) early moved ca 1.1-1.4 km away from the release point, but they died soon after. We focused the analysis of maximum distance on the other 28 rabbits, which made moderate movements ranging within 20-280 m from their respective release warrens. We selected a model including only additive effects of the translocation experiment and of the release batch ($F_{2,25}$ = 3.639, P = 0.041). Movements were greater in 2001 than in 2002, and concurrently, in first batches than in second batches (Table 3). However, the effects of experiment and batch were not significant alone ($F_{1,26}$ = 3.183, P = 0.086; $F_{1,26}$ = 3.983, P = 0.057), and effects of storage conditions and sex were completely discarded ($F_{1,26}$ = 0.037, P = 0.850; $F_{1,26}$ = 1.377, P = 0.251).

Discussion

Survival

Early survival was affected by the disruption caused by the translocation, as already known in released wild rabbits (e.g. Calvete et al. 1997, Letty et al. 2002). However, there was almost no effect of storage conditions between capture and release on the early survival. Indeed, the very high early survival rate recorded in rabbits stored in group boxes in 2002 only concerned eight individuals, a small sample size which enhances the risk of demographic stochasticity. Moreover, the confidence interval of the estimate is very narrow, and then, as the estimate is located on a range boundary, any parameter which confidence interval does not include this range boundary is consequently significantly different from it. Therefore, we do not trust in an actual effect of storage conditions on early survival, especially as we cannot explain why such an effect would have been present in 2002, and not in 2001. It is clear that biochemical and physiological monitoring of rabbits undergoing such translocation tests would be very helpful in understanding the determinism of short-term survival after release. Otherwise, the absence of an effect of storage conditions is in accordance with a concurrent study in which we recorded almost no deleterious effect of translocation handling alone on early survival (Letty et al. 2003). Similarly, farmed rabbits were not known to be much affected by transport, contrary to cage changing, which is probably related to rabbit territorial behaviour (Finzi & Verità 1980, Verità & Finzi 1980). Then, based on our results we cannot conclude that storage condition during translocation is a critical factor for early survival in translocated wild rabbits, at least not under the environmental conditions of our study. Very likely the arrival in a completely unknown area is much more stressful than storage conditions for translocated rabbits, which may explain the high early mortality after release.

Dispersal

Storage conditions did not affect dispersal distances. We expected any differences in dispersal distance induced by the different storage treatments to arise early after release, and we would have detected such a difference when analysing the maximum distances recorded during the entire study period, because the most important movements of the translocated rabbits early after release were covered (Letty et al. 2002). Likewise, there was no effect of sex on maximum dispersal distance after release as previously recorded (Arthur 1989, Letty et al. 2002). The reduced dispersal distances of individuals from the second release batch, compared to the first batch in both years might be explained by some kind of conspecific attraction behaviour (e.g. Reed & Dobson 1993). However, we do not know if this movement behaviour reveals an actual social attraction among rabbits, or only the selection of a similar and suitable habitat. Concerning the habitat suitability hypothesis, we suspect that the precise location of the release warren partly determines subsequent dispersal movements according to the habitat characteristics of the immediate surroundings. Particularly, dispersal might depend on the availability in the landscape of resting places, e.g. warrens or low covers. For instance, in 2001, the smaller dispersal in the second batch than in the first batch may be explained by the fact that the release warrens used were on average closer to a fallow area used as resting place in the former case than in the latter. Similarly, the overall smaller dispersal in 2002 than in 2001 might be due to the closer vicinity of both cultivated and fallow strips in the former case than in the latter. Otherwise, in 2001, dispersal was greatly prevented in one direction by the meadow facing the release warrens, even though this was used as a foraging place (J. Letty et al., pers. obs.).

Overall dispersal after release was slightly smaller in this study than 1) in a study performed in a similar but somewhat more open landscape (Letty et al. 2002), and 2) in a Mediterranean area (Calvete et al. 1997), and also than natural dispersal (Cowan 1991).

Finally, storage conditions do not appear to be a critical factor in release success in the wild rabbit, at least not with the soft restraint treatments we used, and in winter releases. But, for instance, the higher temperatures occurring in summer releases, a higher density in group storage, a different kind of transportation box, or a longer storage duration might markedly affect the result. So, particular attention should be directed towards environmental quality in the release area, particularly towards predator control in order to improve early survival, and towards availability of suitable resting places in order to limit dispersal.

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