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ORIGINAL ARTICLE

The use of box-traps for wild roe deer: behaviour, injuries and recaptures

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Abstract Tracking devices are commonly used to locate and monitor wild animals for studying spatial ecology and survival rates. There is growing interest in capture effects, partially to minimize the impact on the study species, but also for animal welfare reasons. This study aims to examine roe deer behaviour in box-traps, when restrained, when released and during recaptures to quantify injuries and deaths over a period of 41 years. We use data from 2911 captures from 926 individuals between 1973 and 2014. We recorded behaviour inside the box-traps over two seasons. We also recorded behavioural data from 671 catches of 346 individuals during six seasons to study habituation. Additionally, we discuss box-traps in relation to ethological theory and animal welfare. Over a 41-year period, one roe deer suffering from starvation was found dead in a trap (0.035%), which cannot be solely related to capture (*N* = 926). About 58% of all roe deer were recaptured at least once during their life time. There was a low prevalence of injuries (0.5% of the captures, *N* = 2911), and they occurred predominately to the nose or antlers in velvet (in males). During the first hour after capture, animals typically stand very tense between eating bouts. Thereafter, the deer tended to move more softly and exhibited resting behaviours (e.g. lying down). Overall, we conclude that this method of capture and handling had very low impact on the welfare or survival of roe deer, which also habituated to recapture over successive events.

Keywords Behaviour · Box-trap · Capture · Habituation · 3R's

Highlights

- We used data from 2911 captures from 926 individuals between 1973 and 2014.
- We recorded recaptures, injuries and behaviour during restraint in box-traps.
- About 58% of roe deer were recaptured during their life time.
- The estimated direct mortality and wounds was 0.035 and 0.5% respectively.
- Roe deer habituate to the capture and become calmer at consecutive captures.

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Determining the home-range, dispersal, movement, resource selection and survival of wild animals often involves the use of tracking devices. The fitting of such devices, often VHF or GPS collars in large animals, requires capture, some manner of restraint and handling. Typically, capturing wild animals causes stress and can potentially cause injuries, behavioural and physiological disorders and in some cases death (Arnemo et al. 2006; Iossa et al. 2007). To date several different methods have been used to capture different deer species such as drive nets (roe deer; Morellet et al. 2009), net guns (white-tailed deer; Jacques et al. 2009), remote drug delivery by darting (moose; Arnemo et al. 2006), netted cage traps (white-tailed deer; VerCauteren et al. 1999), drop-nets (mule deer; D'Eon et al. 2003), cannon nets (Hawkins et al. 1968), corrals (Rempel and Bertram 1975) and box-traps (roe deer; Heurich et al. 2012). Several variables should be taken into consideration when decisions about which capture and handling methods are used, as some methods are not suitable in adverse weather conditions, in differing habitat types and population sizes.

Evaluation of restraining traps is usually based on simple quantitative measures such as mortality and observed injuries of trapped animals (Anonymous 1998; Iossa et al. 2007). Various studies examine behavioural effects on captured animals by assessing alterations in movement, habitat choice and search for cover after being released (Jacques et al. 2009; Morellet et al. 2009). Behavioural analyses can generate useful information about expected injuries, indicating why and when these are likely to occur. In addition, animal behaviour while inside a trap analyses can provide important information about injury avoidance, and about behaviour and habituation. Habituation, in turn, can show waiting time and handling effects on animals (Andrade et al. 2001; Pearce 2008). In this study, we quantify physical injuries and behavioural indices in box-trapped wild roe deer, to evaluate animal welfare issues, with emphasis on 'refine' in the 3R's (Lindsjö et al. 2016) of a very common capture method (box-trapping).

Fearfulness can be defined as 'a basic psychological characteristic of the individual that predisposes it to perceive and react in a similar manner to a wide range of potentially frightening events' (Boissy 1995) and has been examined in several different restraint tests using a scale from calm to more agitating behaviour (Benhajali et al. 2010; Grandin 1997; Holl et al. 2010; Hoppe et al. 2010; Voisinet et al. 1997). When the capture or restraint method does not allow much movement, an 'exit speed test' has been shown to be useful (Gibbons et al. 2011). Learning, in the form of habituation or conditioning, can decrease the emotional response and hence fearfulness (Roberts 1988). However, prior negative experience can increase the reaction towards a specific stimulus (sensitization: Roberts 1988). Hence, an animal trapped recently might react more to handling than an animal that has waited in the trap for a certain period and that has calmed down after the initial surprise when the trap closed. Therefore, it is important to know if the focal animal changes its behaviour over time in a trap. In addition, ungulates quickly learn to avoid treatments and places they find aversive, which has been studied in 'aversive learning' situations (Rushen 1996). Both domesticated and wild ungulates show individual differences in how much they react to human handling and novelty (dairy cows: Gibbons et al. 2011; goats: Lyons et al. 1988; big horn sheep: Réale et al. 2000). Therefore, in this study, we expect to find individual differences in docility, which in turn might influence the probability of recapture of a specific animal. We also expect roe deer to habituate to the situation, which means that a specific roe deer should become more docile over time. However, if the roe deer instead find the trap and handling very aversive, we expect low recapture frequencies and also increasing levels of stress and struggling with increasing numbers of recaptures (Rushen 1996).

In the present study, information from 41 years of capturing roe deer in a standardized box-trap (see 'Methods') has been compiled. The roe deer were captured for ecological research studies. First, we account for general descriptive statistics about wounds, injuries, death and other observations made, based on 2911 capture events of 926 different individuals. Secondly, individual stress level was estimated by the same handler (LJ, author) with more than 40 years of experience in roe deer handling, based on animal behaviour during 671 catches of 346 individuals of known age, during six winter seasons. We used subjective indices of stress during handling and when released. Finally, in a smaller dataset, animals were continuously recorded inside and outside the trap and their different behaviours were quantified over time.

Methods

The roe deer is a small (20–30 kg) solitary ruminant with a low level of sexual dimorphism, classified as a concentrate selector, which can form temporal feeding groups during winter (Andersen et al. 1998). Roe deer can live for 8 to 10 years, for why a single individual can be captured several times during its life time. Ethical permission for handling roe deer have been approved since the mid-1990s by the Ethical Committee of Animal Experiments in Uppsala, Sweden, to all our predecessors studying this population and now more recently to PK (author) by permit numbers C289/2009, C302/2012 and C149/2015.

The Grimsö Wildlife Research Area (GWRA) covers 130 km^2 in south-central Sweden (59°40′ N, 15°25′ E). The study area mainly consists of intensively managed Scandinavian boreal forest, dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Temperatures normally range from −20 °C in winter up to 25 °C in summer, with an average annual precipitation of 670 mm. Regular hunting has been permitted in the area over most of the years that data was collected for this study, including hunting of marked animals for the last 20 years. The annual cull has been 5–150 animals. The study population of roe deer have been used for many different research projects throughout the years (Cederlund and Lindström 1983; Samelius et al. 2013); it has thus been intensively monitored, using capture-mark-recapture with the same type of box-trap since 1973.

During winter when natural food is scarce due to snow cover, the roe deer visit traps to access small portions of food, distributed at a regular basis, inside un-set traps. The same trap locations are used for many years to cause habituation. After some time—when animals show signs of visiting the traps on a regular basis—the box-trap is set in late afternoons, using a fine fishing line stretched between the floor and roof inside the trap, in the middle of the small pile of forage. When an animal enters the trap, eats and touches the fishing line, a pin is removed that releases the door that falls down behind the animal. The traps are checked in the mornings, and captured individuals are released after having been measured and marked. No anaesthesia is used. Still, some roe deer are caught repeatedly during their life time, sometimes on consecutive days. We captured roe deer at 16 different locations throughout the duration of the study. Each location contains two or three traps. The box-trap (approved by the Swedish Environmental Protection Agency: registered as 'L6 Rådjursfälla M/Öster Malma') and similarly designed traps are widely used in research projects in countries that receive snow in the winter (Heurich et al. 2012). Box-traps are constructed using Masonite boards for the side walls and door, while the roof and floor is composed of oil-tempered board and wooden bars (50 × 57 mm) in the short end front, opposite to the door (Supplementary 2). The minimum to maximum sizes are (length × width × height): 1300–1400 × 625–675 × 1300–1400 mm.

In total, 926 individuals were captured in this type of box-trap on 2911 different occasions, between 1973 and 2014. The box-traps were typically prepared for trapping during sun set, between 15.00 and 17.00. New forage (approx. 2 l 'Renfor') was placed inside the trap and the trap release mechanism set. 'Renfor' is a commercial pelleted product produced for semi-domestic reindeer and is widely used also for wild deer. It contains 11.4 MJ and 113 g crude protein per kg dry substance (88%), and is made of corn, milling by-products, sugar beet by-products, minerals, vitamins, fat and vegetable oils (manufactured in Sweden by Lantmännen). Animals were released between 08.00 and 10.00 in the next morning.

A typical handling procedure was initiated by one person walking calmly towards the closed trap. If a roe deer was trapped, two more people arrived within 1 min to assist with marking the animal. Within 2 min, the deer was restrained and taken out of the trap. Since the opposite side to the entrance is barred, animals stand directed towards the daylight with the back legs closest to the door (see picture in Supplement 2). When the door was opened, one person restrained the back legs and pulled the animal out of the trap while a second person restrained the front legs. We then placed the roe deer on a cover on the ground where the animal was marked and measured. We marked individuals on their first capture using one ear tag (designed for sheep) in each ear and fitted them with a VHF or GPS collars. We assessed individual age according to tooth wear and eruption that characterize less than 1-year-old individuals (Ratcliffe and Mayle 1992). Older individuals were aged too, but with less precision. Before releasing, we recorded animals' weight by tying a rope between the front and back legs and hanging them from a scale. Normally, this procedure took 2–3 min in total and the animals were released at the point of measurement. Individuals were only handled once per week. Any individuals that we caught more often were simply released by opening the door of the trap.

During handling and immediately after release, the handler L.J. (author) scored the animal's behaviour and perceived stress level. The score was based on several subjective and objective behavioural components such as screaming, struggling and kicking, heart and breathing rate during handling. In this paper, we use data from this scoring method collected during six consecutive winters from 2008/2009 to 2013/2014. The scale of the handling score ranged from 0 to 4 and the release score ranged from 0 to 2 (Table 1). The use of a subjective measure of calmness or stress is a commonly used method for describing behaviour (Benhajali et al. 2010; Le Neindre et al. 1995; Réale et al. 2000). During all captures, animals were handled by the same handling team lead by L.J. and he judged the subjective components of the data collection and has experience capturing roe deer in box-traps at GWRA for over 40 years.

To investigate recaptures, we only included animals that survived and remained in the trap area, i.e. did not disperse out of the GWRA for at least 1 month after the first capture event. To investigate dispersal, we used VHF or GPS positions. We thus excluded 11 individuals that were killed within less than 1 month from the first capture and we also excluded seven individuals that migrated within less than 1 month after the first capture. In a subset of roe deer captured during 2008–2013, we tested if behaviour at the first novel capture event differed between individuals that were never recaptured and those with one or several recaptures.

We video-recorded behaviours both inside and outside traps at three catch sites during 513 h from January 18 to March 15, 2011, and 530 h between January 9 and March 13, 2012. Behaviour was recorded in the traps by continuous colour recording in day light and by black-and-white IR sensors during night (Loke AB, Skinnskatteberg). A 12-V DVR hard drive was placed together with a battery, in concealed insulated styrofoam boxes at the trap site and connected to the three cameras. At each of the two investigated trap sites, two cameras were recording inside two of the box-traps, and one larger camera was recording outside the site. We used continuous recording to allow the roe deer to become habituated to the red light from the infrared cameras.

During this study, we employed an ethogram, which is a list of the behaviours or behavioural categories that an animal performed in the trap. The ethogram used was produced after scoring 12 different behavioural categories (Table 2). Initially, we recorded the number of transitions between lying down and standing, as well as the length of time it took until the animal started to eat and the length of time it took until the animal lied down for the first time. Next, we sampled 6 min/h (10% of the time) to explore behavioural differences over time. We analysed 14 recordings (113 h in total) of 11 individual roe deer, comprising four recordings of one individual, two recordings of another individual (but from two different years) and one recording each of the remaining nine individuals.

Table 1 Subjective measure of stress and struggling during handling and behaviour when the roe deer are released

Score	Behaviour during handling The subjective measurement on how the animals react on the handling situation	Behaviour when released How the animal act when leaving the site for the handling
0	Calm. No resistance. No kicking with legs. No screaming	Leaving the place slowly. Stops several times
1	Calm. Screams not more than ~twice. Almost no kicking	Run away, but stop after a short distance
2	Screaming and kicking some, but are calm between these occasions	Runs away without stopping until it cannot be seen any more
3	Stressed out. Are screaming and kicking more, but the animal can be handled	
4	Extremely stressed. Almost impossible to handle. Impossible to take proper measures	

To test if the methods were improved with time, we tested if the proportion wounds (mainly on antlers and nose), losses of ear tags, hair loss on neck as a result of a poorly fitted collar, legs in collar and death changed over time.

Statistical analyses

First, we analysed the behavioural observations from the films inside the traps. To determine if a specific type of behaviour changed with time spent in the box, we performed a Spearman's rank correlation. Second, we also analysed the behaviour during handling and release. A Pearson's rank correlation was used to investigate if the total number of captures, the number of captures per year and individual age were correlated. Thereafter, we performed two different ordered logistic regressions to test variables that affect (1) behaviour during handling and (2) behaviour during release. We fitted two sets of ordinal logistic regression models to explain variation in (1) behaviour at handling and (2) behaviour at release. Because individuals can habituate to repeated captures at both short and long-terms, we included the two-way interaction between the total number of captures (tot capt) and the number of captures experienced by an individual within a year (year capt). To take into account for intrinsic characteristics, we also included sex and age, as well as their two-way interaction with the total number of captures (tot capt) and the number of captures experienced by an individual within a year (year capt). Therefore, the most complex model explaining variation in behaviour included the four two-way interactions between the total number of captures (tot capt) and the number of captures experienced by an individual within a year (year capt), age and sex. The most complex model explaining variation in behaviour at release scores was similar.

We compared the most complex models (age × sex × captures per year × total number of captures) with all nested models using the Akaike's information criterion corrected for small sample size (AICc) and the model with the lowest AICc value reflects the best compromise between complexity and precision (Burnham et al. 2011). In addition, we used the parsimony principle, and among the most supported models (ΔAICc value differing by <2), we retained the model with the lowest number of parameters (K).

Third, we compared the behavioural scores at the first capture event between individuals with consecutive recaptures with those that were not recaptured, by performing a Mann-Whitney *U* test. Forth, we performed a Spearman's rank correlation on the proportion wounds over time. The statistical tests were performed in Statistica 12, Statsoft or in R (R Core Team, 2015).

Results

Out of 2911 captures of 926 individuals, between 1973 and 2014, one malnourished individual (ID116) was found dead in an unclosed trap. This female was marked 3 years earlier and estimated to be 5 years old at that time. When first recaptured (8 years old), she weighed 21 kg. Twenty-three days later, she was found dead and malnourished in a trap weighing 18.5 kg. Another death was a juvenile female (ID 71, 18 kg) that showed problems with balance and signs of illness when released. When checked 1 h later, she was found dead potentially due to myopathy (unconfirmed). This gives an estimated direct mortality of 0.035%, including ID116, or 0% if ID116 is excluded, and a total capture-related immediate mortality of 0.07 or 0.035%.

Reported injuries were predominately on animals' noses or the velvet of antlers and occurred in 0.5% of the trapped animals; however, such injuries are gender-specific since only males have antlers. Other reported injuries included hair loss at the neck, a front leg caught in fitted collars and lost ear tags. Hair loss is sometimes related to a fur-eating parasite *Damalinia cervi* (Aguirre et al. 1999), but can also be caused by wear of poorly constructed or fitted collars. When this was observed on recaptured animals, the collar was modified or removed. Some types of ear tag seemed to work less well and were repeatedly found on the ground near sheep fences, and this is a potential explanation for how ear tags are lost. Another reported problem was individuals with one front leg

Table 2 Ethogram developed for quantifying roe deer behaviour in box-traps. For the simplified Fig. 2, some behaviours are grouped. Rare behaviours are excluded from the figure

Behaviour	Description	Category in Fig. 2
Stand tense	The roe deer stands completely still and movements of head and ears are quick and the ears are often pointed in a direction and are pricked between movements	Stand tense
Stand relaxed	The roe deer stands still and moves head and ears in a soft slow way. Jaw movements, closed eyes and licking can be seen	Stand relaxed
Move soft	Movements of at least one leg or turn around in a soft manner. If touching the walls, it is soft	Exploration
Move hard	Fast movements or turn around where the roe deer bumps hard into the walls	
Exploration	Soft movements together with head movements and the nose almost touches part of the box or camera	Exploration
Head down	The head is low. We cannot see if the roe deer eats, explores the box or just stands still	Exploration
Eat	The head is either low, while eating food off the floor, or lifted when chewing.	Exploration
Self-groom	The roe deer grooms itself with mouth parts, typically on the back or the belly	Self-groom
Lie/head up	Ears similar to that in stand/soft	Lie
Lie/head low	Lies down with the head down close to the body or in rare cases in front of the body. Eyes can be closed	Lie
Ruminating	Slow jaw movements and regurgitation. When it occurs, the roe deer is standing	
Repeated movement	The behaviour is performed in a in a repetitive manner, from side to side or backwards and forwards	

caught in the collar which occurred on eight separate occasions, and five of these were found in the trap. In two cases, the collars were removed, in two cases, changed to another collar and in the final case, the animal was euthanized due to severe wounds. Two animals with a leg in the collar were shot during the hunting season and one was found dead. We found no change over time in proportion animals with any of the above reported injuries or problems including hair loss on neck and losses of ear tags (Spearman's rank correlation; $n = 40$, $r^2 = 0.02$, $p = 0.39$). However, the problem with one leg in the collar only occurred between 1980 and 1982.

Average handling score (behaviour at handling) for a first capture was 2.23 and for consecutive captures, it was 1.39. The selected model for behaviour at handling included four two-way interactions between the total number of captures (tot capt) and the number of captures experienced by an individual within a year (year capt), age and sex and an effect of id (Tables 3 and 4). The selected model for behaviour at release included a two-way interaction between the total number of captures and the number of captures experienced by an individual within a year and an effect of age (Tables 3 and 4). We found an effect of total number of recaptures, which means that individuals became habituated over time (Fig. 1, Tables 3 and 4). From the ordinal logistic regression for the handling score, we found an effect of the total number of captures, age and id. In addition, there were an interaction between the total number of captures, sex and age (Fig. 1, Table 4).

We found a very weak negative correlation between individual age and number of captures per year (Pearson's $r = -0.189$; $P < 0.001$) and a weak positive correlation between age and the total number of captures (Pearson's $r = 0.2243$; $P < 0.001$).

Out of 905 roe deer, 527 individuals (58%) were recaptured at least once during their lifetime and 378 individuals (42%) were never recaptured. In a subset of roe deer captured during 2008–2013 ($n = 152$), we found that 89% were recaptured at least once. The total amount of recaptures in this subset, including migrants and killed roe deer, was 66%. For all roe deer with a handling score on the first capture (we started in 2008), we found that behaviour at first capture did not differ between those that were not recaptured and those with one or several consecutive recaptures (Mann-Whitney U test; $U = 3542$, $Z = -26$, $n_{recap} = 100$, $n_{not} = 52$, $P = 0.79$).

In 11 out of 14 recordings we were able to observe the behaviour inside the trap, from capture to release (Supplementary material 1), and in another three recordings, only parts of the captures were filmed due to technical failure. Captured animals started to eat 126 s (median = 90 s) after the trap was closed, with an individual variation between 22 s and 7 min and 15 s.

The animals often changed position between standing up and lying down. On average, these shifts occurred ten times per night. Including only animals that laid down, there were on average 15 changes in position per night. Ruminating and

Table 3 Model selection outcome of an ordinal logistic regression procedure, of factors affecting (1) the behaviour at handling and (2) behaviour at release

Variable	Model	AIC_c	Δ AIC_c
Behaviour at handling (0–4)	*year capt × tot capt × sex × age + ∣ id∣*	1479.9	0
	year capt × tot capt × sex × age	1483.6	3.7
	year capt × tot capt × sex + age + ∣ id∣	1491.4	11.5
	Null model	1587.1	107.1
Behaviour at release (0–2)	age × year capt + tot capt × year capt	864.9	0
	age × sex + tot capt × year capt	865.9	1
	age + tot capt × year capt	866.3	1.4
	Null model	891.1	26.1

lying down was mainly observed after midnight (Fig. 2, Tables 5 and 6). Based on all recorded individuals, they laid down 35% of the time; when only the nine individuals that did lay down were included, the average was 54% (min = 23%, max = 69%). Two individuals, one male and one female that were caught for the first time changed weight from left to right front leg with a swinging head in a repetitive manner similar to 'weaving' which has been described in horses (Cooper et al. 2000). In addition, these two individuals also had high handling scores, 3 and 4, respectively. The male that scored 4 on handling also showed a very strong reaction when he was trapped and the door closed behind him. This individual jumped and turned so he landed on his side. Two individuals looked exhausted on recordings with the medial and lateral hoofs not pointing frontwards while standing but with an approximately 80° angle between them.

From recordings outside the traps (1043 h), we found that groups of on average 1.93 individuals (range = 1 to 7) visited trap sites for an average of 6.14 min ($N = 220$). Roe deer ate from the traps about 4.9 times for 14.5 s each time ($N = 25$). One roe deer escaped from the trap when the door was stuck and left an opening as low as 40 cm from the ground. However, this female re-entered the trap several times to eat the food, even with significant effort due to the small entrance.

Discussion

We show that box-trapping has very low levels of direct mortality and capture-related mortality (≤0.035%) compared to other methods using anaesthesia in ungulates or carnivores

Table 4 The output (regression coefficients, SE, *t* and *P*) from an ordinal logistic regression investigating the relationship between the release score and number of captures within a year (Year Captures), total number of captures in life (Total captures), gender (Sex), age in years (Age) and id number (Id) as a random factor

Variable	Value	Std. error	*t* value	*P* value
Year captures	−0.22	0.384	−0.56	0.57
Total captures	−0.67	0.176	−3.82	0.00013
Sex	−0.07	0.412	−0.16	0.87
Age	−0.72	0.339	−2.11	0.035
Id	0.00	0.001	−2.44	0.015
Year captures × Total captures	0.12	0.065	1.90	0.057
Year captures × Sex	−0.28	0.226	−1.22	0.22
Total captures × Sex	0.25	0.107	2.30	0.022
Year captures × Age	−0.11	0.197	−0.55	0.58
Total captures × Age	0.10	0.050	2.04	0.042
Sex × Age	0.44	0.206	2.13	0.035
Year captures × Total captures × Sex	−0.04	0.037	−1.03	0.3
Year captures × Total captures × Age	0.00	0.023	−0.14	0.8
Year captures × Sex × Age	0.05	0.116	0.46	0.6
Total captures × Sex × Age	−0.06	0.031	−1.99	0.047
Year captures × Total captures × Sex × Age	0.00	0.014	0.15	0.1
0|1	−6.23	0.210	−29.72	<0.0001
1|2	−4.28	0.230	−18.60	<0.0001
2|3	−2.33	0.255	−9.16	<0.0001
3|4	0.68	0.438	1.56	0.12

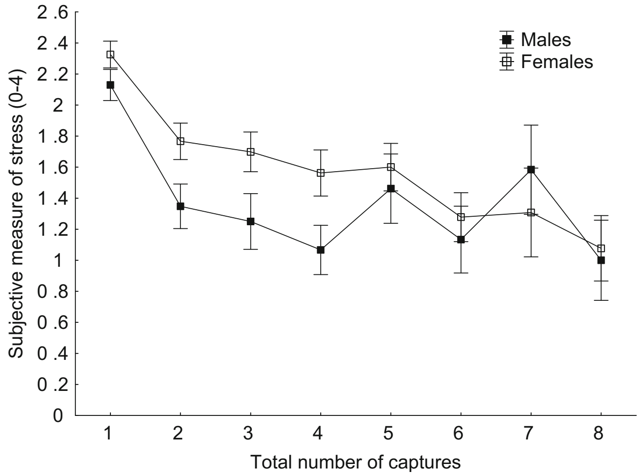

Fig. 1 The subjective measure of stress and struggling from 672 box-trapped roe deer (mean ± SE), based on the first 8 captures of 97 males (*filled squares*) and 113 females (*circles*) in 366 and 306 capture events respectively, during 2008 to 2014

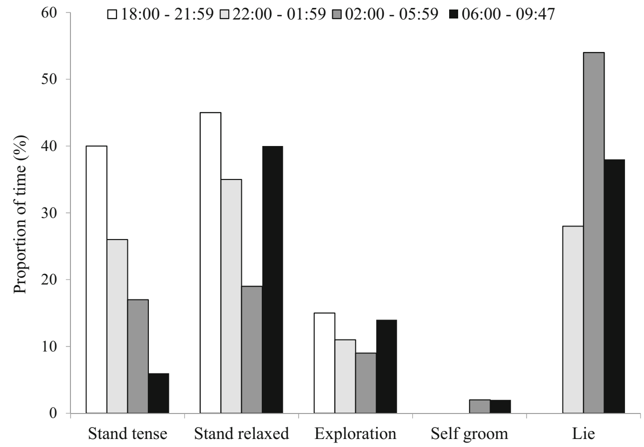

Fig. 2 The proportion of different behaviours of roe deer caught in box-traps, divided in to four hour periods, based on nine different individuals. Behavioural categories are described in Ethogram Table 2

(e.g. moose 0.7%, lynx 3.9%; Arnemo et al. 2006), or even compared to anaesthesia of domestic ungulates under more controlled conditions (e.g. horse 1.0%; Jones 2001). Box-traps also show lower mortality rates than other capture methods for roe deer such as drive nets (range from 1.3 to 4.2%; reviewed in López-Olvera et al. 2009). Box-traps in general seem to generate very low mortality rates and several traps in fact show 0% mortality (several species of carnivores, reviewed in Iossa et al. 2007; badgers, Byrne et al. 2015). We believe that one of the two dead roe deer in our study did not die as a direct result of the capture event; instead, the animal desperately searched for food in a fairly reliable food site. The female that was found dead in the trap was apparently malnourished, as she was thin and had started to lose weight 1 month prior to death. Winter starvation is a common cause of death among Nordic roe deer populations and usually ranges between 18 and 60% death rate per year, depending on age class, population density and winter severity (Cederlund and Lindström 1983; Aguirre et al. 1999; Kjellander 2000; Arbieu 2012). The second animal that died within an hour after release could potentially have died of post-release capture myopathy (Paterson 2007). Thus, it is likely that only one animal out of 926 individuals might have died as an immediate result of the trapping.

From domestic ungulates, it is known that response behaviour is influenced by previous experience in a certain situation. For instance, domestic sheep and cows have excellent memory of previous aversive handling (Grandin and Deesing 2014) and a calm and short handling time has a better chance of resulting in habituation than rough and prolonged handling. In our case, the first handling event included ear-tagging, measuring of body parts, fitting a collar and weighing, which took about 8 min in total. Subsequent recapture procedures only took approximately 2 min. Andrade et al. (2001) found that cows habituated to being placed in a handling crush, and that the habituation effect was strongest between the first and the second trial. In the present study, the largest change in response behaviour was found between the first and second time a roe deer was handled. Although the handling procedure differs between the first and consecutive captures, we cannot determine if the first capture procedure is worse (due to ear-tagging) or if it is simply due to the novel experience. However, the increased struggling behaviour present during first capture is demonstrated prior to ear-tagging. In addition, capture-experienced roe deer usually lay down in the trap when the handler approached, while animals captured for the first time almost always stood up and showed distress. In addition, we also found that a greater number of recaptures was related to a gradually decreasing handling score, even if the first event was excluded. That together led us to believe that the reason for an elevated stress response during the first novel capture event was a combination of ear-tagging and later habituation.

A major welfare issue for captured animals is wounding (Iossa et al. 2007). It is thus of major importance to identify when wounds do appear, how severe they are and how to avoid, prevent or minimize them. For this type of trap, wounds seem to appear when the roe deer are removed from the trap. Firstly, fresh blood is often evident on removal, and secondly, only one out of 14 roe deer filmed in a trap showed some behaviour that could result in wounding before removal. In this case, the roe deer jumped and fell on its back as the door closed. This was the first capture of a roe deer that scored a 4 for handling behaviour. An injury that occurs at the capture event is probably worse than if it occurs just before release when the animal can start to recover from stress. Wounds on antlers in velvet can be avoided or minimized if the capture period is ceased as the antlers start to grow longer, later in the season. However, this point in time can differ between populations (Andersen et al. 1998; Johansson 1996). One way to

Table 5 Spearman's rank correlation for proportion of activity over time, from catch to release for nine individuals

Behaviour	$r(X,Y)$	t	P	Change over time
Stand tense	−0.36	−4.00	0.00011	Decrease
Eat	−0.12	−1.25	0.21	No
Exploration	−0.10	−1.07	0.29	No
Head down	−0.07	−0.73	0.46	No
Soft movement	−0.19	−2.06	0.042	Decrease
Stand relaxed	−0.06	−0.66	0.51	No
Self-groom	0.32	3.50	0.0007	Increase
Lying/head up	0.39	4.44	<0.0001	Increase
Lying /head down	0.19	2.00	0.047	Increase
Hard movement	0.02	0.24	0.81	No

Table 6 Spearman's rank correlation for proportion of activity over time, from catch to release for nine individuals

Behaviour	$r(X,Y)$	t	P	Change over time
Stand tense	−0.36	−4.00	0.00011	Decrease
Eat	−0.12	−1.25	0.21	No
Exploration	−0.10	−1.07	0.29	No
Head down	−0.07	−0.73	0.46	No
Soft movement	−0.19	−2.06	0.042	Decrease
Stand relaxed	−0.06	−0.66	0.51	No
Self-groom	0.32	3.50	0.0007	Increase
Lying/head up	0.39	4.44	<0.0001	Increase
Lying/head down	0.19	2.00	0.047	Increase
Hard movement	0.02	0.24	0.81	No

avoid fall-related wounds during capture is to keep the floor of the trap in a non-slippery condition.

The use of anaesthesia is typically motivated by stress reduction (Teixeira et al. 2007) or to reduce the incidence of capture myopathy (Read et al. 2000). However, tranquilizing has not always been shown to improve survival (Letty et al. 2000), and one explanation can be the lack of control that can act as a stressor for the animal (Sapolsky 1982). Therefore, it has been suggested that the benefits of anaesthesia should override the cost of it (Dickens et al. 2010), which could be in the form of prolonged handling time and the risk of releasing a partly intoxicated, and therefore vulnerable, animal into a potentially hazardous environment (for example, roads, lakes or rivers with thin ice, large predators or other unpredictable threats that would be a threat even for unaffected animals). There are several reasons for why chemical immobilization of roe deer prior handling is not always to prefer. First, the roe deer are captured several hours before handling and the sedation could in fact only be applied after a second stressful event (the humans approaching the trap). Second, it would increase the total handling time substantially. Third, mortality rates as a direct effect of sedation (typically respiratory depression) seems generally to be higher than what we report here (Arnemo et al. 2006). However, this only applies for this specific method. Short-acting antipsychotic drugs given to roe deer during transport have shown to reduce stress (Montane et al. 2002).

Stereotypic behaviours are characterized by their repetitiveness and apparently functionless behavioural pattern (Mason 1991). Stereotypic behaviours have been shown in a variety of species and are known to be produced by frustration, stress, fear or restraint (Mason and Rushen 2006). Out of 11 roe deer, two individuals performed some kind of repetitive behaviour. They changed weight from the left to right front leg with a swinging head, in a repetitive manner similar to 'weaving' which has been described in horses (Cooper et al. 2000) and red deer (Pollard and Littlejohn 1996). These two individuals were caught for the first time and stayed standing during the entire trapped time, unlike the other capture-experienced animals that lay down several times. In addition, both were judged as stressed (3 and 4, respectively) during handling (Table 3). Neither of these two individuals was caught again during the remaining 2 months of the study. In two cases, we found that the medial and lateral hoofs were not pointing frontwards while standing, but were creating an approximate 80° angle. This posture indicates that these individuals were tired, probably due to stress. Also, the presence of stereotypic behaviours indicates bad welfare and should be documented when capture methods are evaluated. One way to avoid these behaviours is to release animals as soon as possible and to use alarmed traps such that trappers can be immediately alerted when traps are engaged (Larkin et al. 2003).

There is increasing interest in capture effects, primarily to minimize the impact on the study species, but also for pure animal welfare reasons (Powell and Proulx 2003; Iossa et al. 2007). Novelty itself is a strong stressor (Dantzer and Mormede 1983), and therefore, it is important that the roe deer are familiar with the un-set traps and are accustomed to feeding from them before they are actually trapped and restrained. Experiences from zoos show that ungulates habituate to specific procedures and react strongly when procedures are even slightly changed (Grandin and Johnson 2010). Therefore, keeping the procedure as constant as possible seems to be important and will probably increase animal welfare during recaptures. Providing food in the traps outside trapping season should increase the probability of recaptures, increase the number of animals trapped in the future and, according to theory, will almost certainly decrease the stress perceived by captured animals (Grandin and Deesing 2014). In conclusion, this type of box-trap has very low capture-related mortality and a relatively high recapture rate, but requires feeding in the traps even when traps are not used.

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