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# The strong and the hungry: bias in capture methods for mountain hares *Lepus timidus*

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Estimating density, age and sex structure of wild populations is a key objective in wildlife management. Live trapping is frequently used to collect data on populations of small and medium-sized mammals. Ideally, sampling mammal populations by live capturing of individuals provides a random and representative sample of the target population. Trapping data may, however, be biased. We used live-capture data from mountain hares *Lepus timidus* in Scotland to assess sampling bias between two different capture methods. We captured hares using baited cage traps and long nets on five study areas in the Scottish Highlands. After controlling for the effects of body size, individuals caught in traps were lighter than individuals caught using long nets, suggesting that the body condition of hares differed between the capture methods. This tendency may reflect an increased risk-taking of individuals in poorer body condition and less aversion to entering traps in order to benefit from eating bait. Overall, we caught more adult hares than juveniles and more female hares than males. Our results show that estimates of density and population structure of mountain hares using live-capture data could be affected by the capture method used. We suggest that live-capture studies employ more than one capture method and test for heterogeneity in capture probability to minimise potential bias and achieve reliable estimates of population parameters.

*Key words: body condition, cage trap, capture-recapture, Lepus timidus, long net, mountain hare*

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The management and sustainable harvest of wildlife populations should be based on a thorough understanding of population density, age and sex structure, and the demographic processes. Live capturing of wild animals to collect data on density and demography, to mark individuals and fit radio-tags or GPS-collars is one of the most widely used tools in wildlife research (e.g. Krebs et al. 1995, Korpimäki et al. 2003, Cavanagh et al. 2004, Flowerdew et al. 2004). As with all sampling methods, a fundamental assumption of live capture is that the trapped population is a representative sample of the target population (Conroy & Nichols 1996, Greenwood 1996, Crawley 2002). Any particular capture method may, however, give a biased sample due to differences in capture probability among size, age or sex classes, and may be influenced by body condition, suggesting that a sampling protocol should combine different sampling methods (Conroy & Nichols 1996, Greenwood 1996, Laves & Loeb 2006).

Sampling biases may have profound implications for the estimation of population size, age structure, body condition, disease screening or indeed the estimation of any life history parameter, and may misguide management, conservation or control strategies (Baker et al. 2001, Elphick 2008). The analysis of trapping data to estimate density or survival recognises the problem of non-random sampling, and methods that recognise individual, time and behavioural heterogeneity in capture probability are widely available (White & Burnham 1999, Amstrup et al. 2005). However, although trapping data are regularly used to estimate, for example, body condition, disease prevalence, dispersal and is also used to test ecological hypotheses, parameterize models, assess habitat quality and population viability, trapping bias tends to be ignored (Baker et al. 2001, Pearson et al. 2003).

Mountain hares *Lepus timidus* are widespread throughout their northern Palaearctic distribution, and although generally occurring at low densities in Fennoscandia and the European Alps, hares can be locally abundant with densities in excess of 200 $km^{-2}$ (Angerbjörn & Flux 1995, Mitchel-Jones et al. 1999). Mountain hares are an important prey species, and as a widespread and at times locally abundant herbivore they can play an important role in shaping vegetation and predator assemblages. They are an important game species throughout much of their distribution and are designated as a species of conservation concern in some areas (Mitchel-Jones et al. 1999).

In this article, we use live-capture data collected during our long-term studies of the role of parasites, nutrition and management on the demography and population dynamics of mountain hares in Scotland to assess differences in body condition and relative numbers of individuals caught using two different methods of capturing hares: 'live trapping' using baited cage traps and 'long-netting' where hares are driven into nets.

## Methods

### Field techniques

We collected live-capture data during two separate studies conducted during 2002 and 2005 on two private hunting estates managed for red grouse *Lagopus lagopus scoticus* shooting in the Central Highlands of Scotland (Table 1; see Newey & Thirgood (2004) and Newey et al. (2010) for site details). All study sites were in areas of heather moorland subject to rotational, managed burning to maintain a mosaic of different ages of heather *Calluna vulgaris* and legal predator control (including crows *Corvus corone*, red fox *Vulpes vulpes*, stoat *Mustela erminea* and weasel *Mustela nivalis*), and mountain hares were legally hunted on both estates.

We carried out trapping and long-netting concurrently during September-November in both years under licence from Scottish Natural Heritage. We conducted trapping during September-November to avoid disturbance to ground-nesting birds and to work around estate management activities. We caught mountain hares in double entry cage traps using a mixture of Tomahawk model 107 (Tomahawk Livetrap, Wisconsin, USA) and Tomahawk clones (Jeremy Dewhurst Ltd, Bankfoot, Scotland) and long nets (Rabbit & Net Accessories, Wick, Scotland). Traps were placed throughout each study area on active hare runs, baited with apple, set at dusk and checked at first light the following morning. Long-netting was conducted in the same study areas. We set two 100-m long and 1-m high nets in a wide 'U' shape over the crest of a hill or in a gully. A line of human beaters walked from ca 500 metres towards the nets, shouting and waving flags to drive hares in front of them and chasing them into the nets where the hares became entangled. On capture, each hare was sexed, aged (juvenile or adult based on identification of the epiphyseal notch (Broekhuizen & Maaskamp 1979)), weighed, hind-foot measured, fitted with a small uniquely numbered ear-tag (Monel #1, National Band & Tag Co., Kentucky, USA) and released at the site of capture.

### Data analysis

Assessing body condition of live animals under field conditions is difficult and the subject of debate on the validity of different measures and indices (Green 2001, Schulte-Hostedde et al. 2005). We followed Wauters et al. (2007) and used body mass and control for the effects of body size by including hind-foot length as a covariate in each analysis. We recaptured a portion of animals during the course of the study. However, due to the low recapture rate, we focused on the capture method and individual morphometrics at the time of first capture. We used different study areas in the two years and not all age

Table 1. Number of individual mountain hares, along with number of trap nights, age and sex category, caught using traps and long-nets on the five different study areas (D1-D3 and P1-P2).

| | Trapping | | | Long netting | | |
|---|---|---|---|---|---|---|
| Area | Number of trap nights* | Number of individuals | Age class (♀♀/♂♂) | Number of drives** | Number of individuals | Age class (♀♀/♂♂) |
| D1[1] | 320 | 36 | Adults: 27 (20/7) | 22 | 33 | Adults: 29 (22/7) |
| | | | Juveniles: 9 (7/2) | | | Juveniles: 4 (3/1) |
| D2[2] | 320 | 13 | Adults: 11 (8/3) | 10 | 20 | Adults: 13 (6/7) |
| | | | Juveniles: 2 (1/1) | | | Juveniles: 7 (4/3) |
| D3[2] | 160 | 20 | Adults: 12 (8/4) | 8 | 10 | Adults: 3 (2/1) |
| | | | Juveniles: 8 (2/6) | | | Juveniles: 7 (3/4) |
| P1[2] | 320 | 32 | Adults: 9 (5/4) | 6 | 4 | Adults: 4 (2/2) |
| | | | Juveniles: 23 (16/7) | | | Juveniles: 0 |
| P2[2] | 140 | 11 | Adults: 3 (0/3) | 8 | 11 | Adults: 8 (3/5) |
| | | | Juveniles: 8 (5/3) | | | Juveniles: 3 (3/0) |
| Total (%) | Adults females = 41 (36%) | | | Adults females = 35 (45%) | | |
| | Adult males = 21 (19%) | | | Adult males = 22 (28%) | | |
| | Adults = 62 (55%) | | | Adults = 57 (73%) | | |
| | Juvenile females = 31 (28%) | | | Juvenile females = 13 (17%) | | |
| | Juvenile males = 19 (17%) | | | Juvenile males = 8 (10%) | | |
| | Juveniles = 50 (45%) | | | Juveniles = 21 (27%) | | |

[1] 2002 trapping data (Newey & Thirgood 2004);
[2] 2005 trapping data (Newey et al. 2010).
* Number of trap nights: Number of traps set each evening x the number of nights that traps were set.
** Number of drives: The number of long-netting attempts. One drive used 200 m of net and 2-6 beaters.

and sex categories were represented in all five study areas (see Table 1); we were therefore unable to assess statistically year and area differences. So we used Generalised Linear Mixed-Effect Models (GLMMs) and included area as a random term in each model. Our analysis thus focuses on the effects of method of capture, age and sex on body condition and proportion of animals caught. We used a GLMM with a Gaussian error term and identity link function to assess the effects of method of capture, age and sex on body condition, and a GLMM with binomial errors and logit link to assess the effect of method of capture, age and sex on the proportion of animals caught. We entered all factors, their second order interactions and covariates into each GLMM, and terms were sequentially removed from the full model by step-wise deletion of the least significant terms. We used Likelihood-ratio tests to assess whether removing a term improved the model fit or not. Non-significant terms we removed, whereas significant terms we retained in the model. Data analysis was conducted using R (version 2.12.2, R Development Core Team 2010) and package lme4 (version 0.99; Bates & Maechler 2010).

## Results

In total, we captured 190 individual hares in 2002 and 2005 using traps and long nets on the five different study areas in Central Scotland (see Table 1). After controlling for body size, method of capture and age were the only terms retained in the model (in order of removal from full model: Method*Age: $\chi^2_1 = 0.19$, $P = 0.67$; Method*Sex: $\chi^2_1 = 1.35$, $P = 0.24$; Sex*Age: $\chi^2_1 = 3.17$, $P = 0.08$; Sex: $\chi^2_1 < 0.01$, $P = 0.99$), and they had a significant effect on body mass; on average, individuals caught in long nets were significantly heavier than individuals caught in cage traps (estimate = 0.13 kg; SE = 0.05, t = -2.58), and juveniles were significantly lighter than adults (estimate = -0.37 kg; SE = 0.06, t = -6.45). Age, sex, method and the age*method interaction were retained in the model (in order of removal from full model: Age*Sex: $\chi^2_1 = 0.01$, $P = 0.76$; Sex*Method: $\chi^2_1 = 0.15$, $P = 0.70$). Age, sex and the age*method interaction had significant effects on the proportion of females and juveniles caught, indicating that adults were more likely to be caught than juveniles (logit $\text{estimate}_{\text{juveniles}} = -0.99$, SE = 0.26, z = 3.85, $P < 0.001$), females were more likely to be caught than were males (logit $estimate_{males}$ = -0.53, SE = 0.15, z = -3.50, P < 0.001) and juveniles were less likely to be caught in nets than in traps (logit $estimate_{traps}$ = 0.78, SE = 0.32, z = 3.3, P = 0.02).

## Discussion

Live-capture of small to medium-sized mammals is a commonly used method in wildlife research. Inference from and effective use of live-capture data assumes that all individuals in the target population are equally likely to be captured. Whilst methods for estimating survival and density from capture-recapture data have long recognised individual differences in capture probability and a suite of methods, which incorporate individual heterogeneity into the analysis, have been developed (White & Burnham 1999, Amstrup et al. 2005); most other applications of live capture generally ignore heterogeneity or capture bias. Using data at first capture from two fundamentally different methods of capturing mountain hares, we present evidence that body condition at first capture differs significantly between capture method and age, and that the number of individuals caught at first capture differs between age, sex and with the interaction between age and method.

Mountain hares accumulate body fat over the winter, thereby attaining maximum fat reserves and body condition in February, coinciding with the onset of the breeding season, and they have least body fat in August at the end of the breeding season (Merwe & Racey 1991). Mountain hares, in particular females, preferentially graze on grasses, only switching to bulk browsing of more woody species, such as heather during winter when grazing is limited (Hulbert et al. 2001). The dietary change from grazing to browsing occurs at the end of the summer, when grass production declines, and it is associated with the digestive constraints related to a lower quality diet (Hulbert et al. 2001, Iason & Van Wieren 2006). The switch to a lower quality diet and minimum body condition at the end of the breeding season is associated with a peak in hare mortality at the onset of the winter, which particularly affects juveniles (Iason 1989).

Mountain hares and snowshoe hares *Lepus americanus* both forage to minimise risk, balancing the needs to feed against the risk of exposure to predation (Boutin 1984, Hulbert et al. 1996). Snowshoe hares in poorer body condition are more likely to be predated than hares in better condition through state-dependent risk taking where individuals are likely to forage in a more risk-prone manner with worsening body condition (Murray 2002). The data we used were collected during September-November which coincides with the period of greatest nutritional stress in mountain hares. The lower body condition of individuals caught in traps may reflect increased risk taking and willingness to enter baited traps, possibly to benefit from the bait. Not surprisingly, juveniles caught in early winter were, even after controlling for body size, lighter than were adults, and potentially less risk averse, accounting for the higher proportion of juveniles caught in traps. Although an alternative hypothesis to account for the high proportion of juveniles caught in traps compared to long nets may be the use of borrows by juveniles to escape while being chased during long-netting (Flux 1970). The energetic and nutritional costs of breeding means that females also attain the lowest body condition in early winter, however, although a greater proportion of females were caught in traps, we found no statistical evidence that females are more likely to be caught in traps than males.

The bias towards females in the trapped population that we report is consistent with the results of other studies. Thus, Flux (1970) reports consistently more females than males in samples of shot (males = 46.6%) and snared (males = 45.3%) mountain hares, but he also reports appreciable seasonal variation in the sex bias with the proportion of males in the samples declining over the course of the breeding season with decreasing mating behaviour from 55% during the mating season to 35% after the mating season, but with an approximately 1:1 sex ratio in samples shot in early winter. The proportion of juveniles in samples of shot mountain hares ranged from 21.7% in August to 55.3% in December (Flux 1970). Sex and age bias has also been reported for brown hares *Lepus europaeus*; a greater proportion of females (N = 32) than of males (N = 10) was caught in long nets compared to cage traps, and a greater proportion of juveniles was caught in non-baited traps (40%) (but where the bottom of the trap was lined with straw) than in long nets (17%; Smith et al. 2004). The consistent pattern in the proportion of different age and sex groups caught by live trapping with baited and non-baited traps and long-nets is intriguing and highlights the importance of understanding method bias in wildlife trapping studies, but different methodologies, lack of metadata and problems of ensuring a non-biased age and sex population baseline structure make direct comparison between these studies impossible.

Statistical inference is particularly challenging in ecology. Statistical populations are not the same as biological populations; even defining a study population may be impossible and whilst statistical methods can deal with random error, systematic error or bias, is more problematic and sampling regimes should aim to minimise bias (Greenwood 1996, Krebs 1999). In this article, we show that live-capture of mountain hares using cage traps results in a sample of individuals biased towards poor body condition which, as well as resulting in low estimates of population body condition, over-samples juveniles and females, at least when trapping in early winter when juveniles and females are likely in poor body condition and less risk adverse. When using capture-recapture data for density estimation these biases can and should be investigated, and, if necessary, allowed for in the analysis by using an appropriate model that accounts for heterogeneity in capture probability, inclusion as covariates or a stratified analysis (Amstrup et al. 2005). In other applications of live-capture data, the way to manage bias is less clear and investigators should aim at minimising the bias by using more than one method of capture and apply caution when interpreting the results from possibly biased samples of individuals.

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