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Can distance sampling and dung plots be used to assess the density of mountain hares *Lepus timidus*?

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We evaluated distance sampling and dung plots as cost-effective methods of estimating the density of mountain hares *Lepus timidus* on moorland in the Scottish Highlands. We compared density estimates derived from these techniques to those derived from labour-intensive capture-recapture techniques. Distance sampling and capture-recapture techniques produced comparable density estimates at medium and low hare densities. Density estimates derived from distance sampling were higher than those derived from capture-recapture in high-density hare populations. Both distance sampling and capture-recapture techniques gave wide confidence intervals at high hare density. Histograms of perpendicular sighting distances showed that a large proportion of hares were seen on or close to the transect line and that there was a rapid fall off in detection rates with distance. This finding indicated that hare behaviour may lead to problematic survey design and may reduce the precision of density estimates. The collection of accurate distance sampling data was particularly problematic when hare density was high. In contrast, in low-density hare populations, considerable sampling effort was required to obtain sufficient sightings of hares to reliably estimate density. Dung plots provided a relative index of abundance that successfully ranked populations of mountain hares in order of increasing density as determined by distance sampling and capture-recapture techniques. With careful study design, distance sampling provides a good compromise between accuracy, precision and effort in estimating the density of mountain hares. The use of dung plots is a rapid alternative when only estimates of relative abundance are required.

Key words: capture-recapture, density estimation, distance sampling, dung plots, mountain hare

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Reliable estimation of population density is the corner stone of most ecological research. Methodological texts all suggest that census techniques must be tailored to the species in question and to the level of precision required in each study (Sutherland 1996, Krebs 1999, Southwood & Henderson 2000). Distance sampling techniques, where density estimates are derived from the distribution of sighting distances of individual animals from transect lines, have become widely used in recent years with the development of more powerful computers and the software package DISTANCE (Thomas, Laake, Derry, Buckland, Borchers, Anderson, Burnham, Strinderberg, Hedley, Burt, Marques, Pollard & Fewster 1998). The reliable use of distance sampling is bound by three critical assumptions (Buckland, Anderson, Burnham, Laake, Borchers & Thomas 2001): 1) all individuals are detected on the transect line; 2) individuals are detected before they move appreciably in relation to the observer; and 3) measurements of distance from the transect line are accurate. Violation of these assumptions can seriously compromise the accuracy and precision of density estimates. If these assumptions are met, the histogram of perpendicular sighting distances should possess a shoulder near the transect line, i.e. detection is certain near the transect line and stays nearly certain for some distance, if good estimates are to be obtained. Several studies have evaluated the reliability of density estimates derived from distance sampling and have found that the technique performs well for a variety of taxa (Southwell 1994, Endsign, Angermeier & Doloff 1995, Mandujauno & Gallina 1995, Casagrande, Beissinger & Steven 1997, Focardi, Isotti & Tinelli 2002).

As part of a study investigating the population dynamics of mountain hares *Lepus timidus* we were confronted with the problem of estimating density. Mountain hare densities have been estimated using capture-recapture techniques, but such studies require considerable investments in time and resources (Flux 1970, Hewson 1976a, Angerbjörn 1986). Less intensive census techniques such as vantage point counts, line transects and total counts using dogs have also been used for mountain hares, as have indirect methods based on dung plots (Flux 1970, Watson & Hewson 1973, Angerbjörn 1983, Hewson 1989, Gilbert, Norman, Laurenson, Reid & Hudson 2001). These studies did not, however, evaluate the effectiveness of the alternative census methods. Similar census techniques have been applied to brown hares *Lepus europaeus* in farmland in the UK (Barnes, Tapper & Williams 1983, Barnes & Tapper 1985) and snowshoe hares *Lepus americanus* in the boreal forests of North America (Boulanger & Krebs 1994, 1996, Krebs, Gilbert, Boutin & Boonstra 1987, Krebs, Boonstra, Nams, O'Donoghue, Hodges & Boutin 2001). Langbein, Hutchings, Harris, Stoate, Tapper & Wray (1999) compared direct and indirect methods to estimate brown hare density and concluded that distance sampling offered the best compromise between accuracy and efficiency.

With careful planning, sufficient effort, a short sampling period and a reliable method of marking, the assumptions of capture-recapture methods can be effectively met and a sufficient number of animals trapped to generate reliable estimates (Krebs 1999). Capture-recapture methods are labour intensive, however, and are also intrusive to the study animals. Because of these logistic and welfare considerations, capture-recapture techniques are usually limited to detailed ecological research rather than as a quick method for assessing abundance. Distance sampling offers a potentially useful technique for estimating mountain hare density as counts from line transects are both less intrusive and labour intensive than capture-recapture techniques, offer the advantage of being able to quickly cover large study areas, and allow estimates of precision to be attached to density estimates. In this paper we test the use of distance sampling methods to estimate densities of mountain hares in the Scottish Highlands. We compare density estimates derived from distance sampling with those derived from capture-recapture techniques on mountain hare populations of high, medium and low densities. Estimates of population density may not be required for all research or management purposes, and in some cases an index of relative abundance may be sufficient (Krebs 1999). Indirect surveys of animal abundance may be cheaper and easier to perform than direct counts of the animals themselves. Ideally such an index of abundance will be monotonically correlated with density such that a doubling or halving of the index represents a doubling or halving of the population. We also assess the use of dung plots as an indirect index of the abundance of mountain hares.

Methods

Study areas

The study was conducted during March-May 2000 and 2001 and August-September 2000 on four moorlands managed for red grouse *Lagopus lagopus scoticus* in the Central Highlands of Scotland. The four study areas ranged in altitude from 300 to 950 m a.s.l., and the moors were subject to rotational burning and consisted of a mosaic of different age stands of heather with grass and lichen communities above 600 m a.s.l.. The study sites varied in size from 4 to 6 km^2 and were demarcated by

Table 1. Census method used at each of the four sites in the Central Highlands during the study period.

Year	Time of year	Site	Distance sampling (No. of transects)	Capture-recapture (No. of traps x No. of nights)	No. of dung plots
2000	Spring	A1	4	20 x 7	-
2000	Autumn	A1	4	40 x 5	30
2000	Autumn	B	4	40 x 5	30
2000	Autumn	C	4	40 x 5	30
2001	Spring	A2	4	20 x 7	50
2001	Spring	B	4	-	50
2001	Spring	C	5	-	50

natural features. The study areas were chosen to represent high (A1 & A2), medium (B) and low (C) hare density. We used capture-recapture and distance sampling techniques to estimate mountain hare densities and dung plots as an index of relative mountain hare abundance. The census methods used in each study area in each time period are summarised in Table 1.

Distance sampling

The theory and assumptions of distance sampling and practical aspects of survey design are described by Buckland et al. (2001). A grid of parallel transect lines spaced 500 m apart was randomly placed over each of the four study areas. Transect lines were 1.5-2.5 km in length and were orientated in parallel to the altitude gradient. If too few encounters were obtained, we undertook replicate counts or placed additional transects equidistant between the original transects. Transect lines were traversed on foot by one observer (SN). Adjacent transect lines were not surveyed on the same day to minimise repeat counts of the same animals. Hares tend to flush up-hill, and we therefore conducted counts travelling down-hill whenever there was an appreciable altitude gradient (A1 & A2). We used a GPS to navigate on the transects. During 2000, we estimated sighting distances by eye to the nearest 10 m, whereas in 2001 we used a laser range finder to obtain exact distances. During both years, the sighting angle was measured using a compass. Data were analysed using DISTANCE 3.5 (Thomas et al. 1998). Sighting distances and angles were transformed to perpendicular distances prior to analysis. In 2000, sighting distances were estimated by eye; therefore perpendicular distances were pooled prior to analysis to improve the shape of the distance histogram and model fit. In 2001, distance data were measured precisely and were analysed without pooling. Data sets were subjected to truncation before analysis to remove the greatest 5-15% of the perpendicular distances. Candidate models were chosen and tested against the data once a suitable distance histogram had been obtained. Model selection was based on minimum AIC score and Chi-squared goodness-of-fit tests, and special attention was paid to the model fit close to the transect line where a good fit is crucial. Where transects were counted more than once in one sampling period, density was post-stratified by replicate where the detection function was estimated globally. Similar techniques were used for moor C in 2001 after repeated counts failed to obtain sufficient sightings to reliably fit a detection function. Data for 2000 and 2001 were pooled to generate a detection function and density was post-stratified by year.

Capture-recapture

The theory and assumptions of capture-recapture techniques and practical aspects of survey design are reviewed by Otis, Burnham, White & Anderson (1978), White, Anderson, Burnham & Otis (1982) and Pollock, Nichols, Brownie & Hines (1990). We trapped at site A1 during April-May 2000 and at site A2 from April to May 2001. We placed 20 cage traps in a grid on hare runs with 75 m spacings, and moved the traps at intervals of 5-7 days. We trapped for five consecutive nights at sites A1, B and C during autumn 2000. We set 36 cage traps on a six by six grid with 75 m spacings, which gave four traps per home range as suggested by White et al. (1982) assuming a hare home range size of 10 ha (Hewson & Hinge 1990, Hulbert, Iason, Elston & Racey 1996). Four additional traps were randomly placed on the grid each evening to give two traps at four stations. The traps were locked open and pre-baited for one night prior to trapping, and were set at dusk and checked at dawn. New captures were sexed, weighed, the hind foot length measured and tagged in each ear with individually numbered poultry wing tags. Recaptured hares were identified and released. The long trapping periods used on A1 in spring 2000 and A2 in spring 2001 made it impossible for us to assume that the hare populations were closed. We used the trapping data from the first seven consecutive days of trapping and treated these as closed samples. Data gathered during autumn 2000 were assumed to come from closed populations given the short duration of the trapping period. Data were analysed using CAPTURE (Rexstad & Burnham 1991). We follow Boulanger & Krebs (1994, 1996) and used the

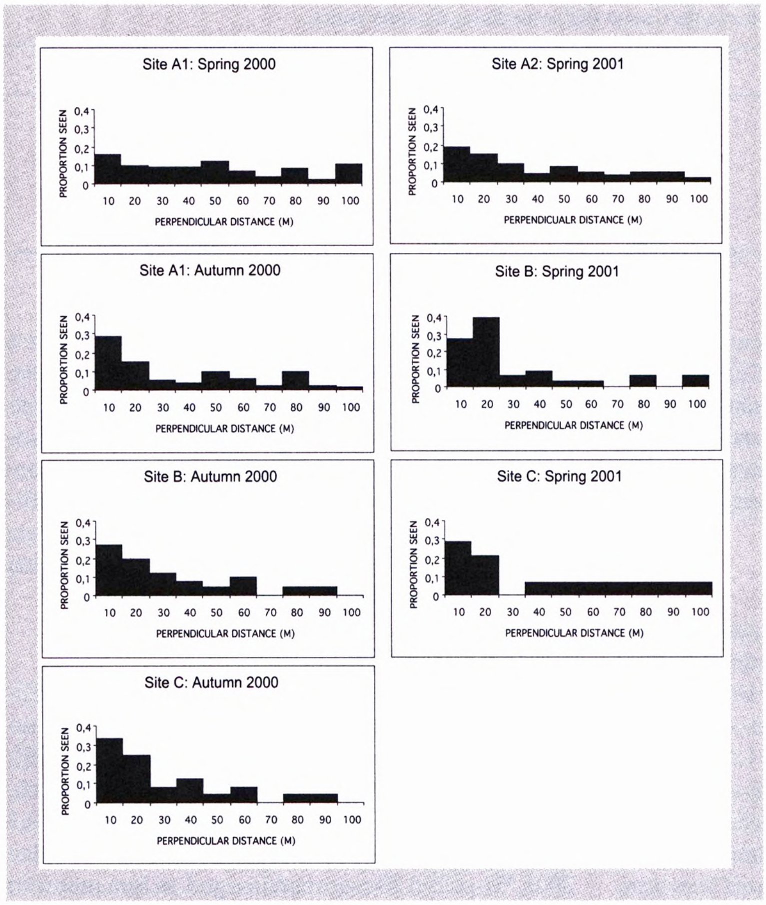

Figure 1. Histograms of perpendicular sighting distances for mountain hares on transects in the Central Highlands, Scotland.

Jack-knife estimator of $M_{(h)}$. In addition, we also used Chao's estimator for $M_{(h)}$ which is known to perform well on small data sets (Chao 1988, 1989). By using the same estimators to compare sites we aimed to avoid introducing further bias inherent to each estimator. CAPTURE abundance estimates were converted to density estimates by adding half the diameter of estimated home range size to the sides of the trapping grid to give the effective area of the trapping grid and then dividing the abundance estimates by this area (Krebs 1999).

Dung plots

The use of dung plots to give indices of relative abundance is reviewed by Putman (1984). Dung density can provide a simple index of density, and assuming constant defecation and accumulation rates in conjunction with a standardised sampling regime can be used as relative measures of population density. Dung counts have been calibrated against capture-recapture estimates to calculate densities of snowshoe hares by Krebs et al. (1987, 2001). Long, thin quadrats are commonly used for dung plots and allow a single observer to search efficiently. We determined the optimal plot size of 0.5 x 6.0 m by examining the variance in dung density from plots of increasing length and width as described by Krebs et al. (1987). Dung plots were randomly placed in a 1-km^2 block centred on the trapping grid in each study area. We sampled 30 plots in 2000 and 50 plots in 2001 and recorded the number of pellets found.

Results

Distance sampling

Histograms of perpendicular sighting distances exhibited a narrow shoulder indicating that a large proportion of hares were detected on the transect line, and that detection fell rapidly with distance (Fig. 1). We therefore first considered models based on the half normal key-term with a cosine expansion term and then models based on the hazard rate key-term with cosine or simple polynomial expansion term. The half normal and hazard rate models are known to perform well with data that show a rapid fall in detection (Buckland et al. 2001). Density estimates based on the hazard rate key-term yielded the lowest AIC score, but generally gave a poor fit close to the transect line. These models gave high estimates with wide confidence intervals (Table 2). Models using the half normal key-term yielded marginally higher AIC scores than the hazard rate models, but gave a better fit close to the transect line. Half normal models produced low estimates with narrower confidence intervals (see Table 2).

Capture-recapture

Density estimates from Chao's estimator were higher with wider confidence intervals compared to the Jack-knife estimator (Table 3). Density estimates for both the Jack-knife and Chao's estimators were similar to density estimates derived from distance sampling, and ranked the study areas in the same order of increasing density (Fig. 2). Capture-recapture gave lower density estimates than distance sampling at site A1 in autumn

Table 2. Details of distance analysis of mountain hares in the Central Highlands during the study period. The abbreviations used are: Key = key-term with HN = half-normal and HZ = hazard rate; E = expansion term with HM = Hermite, CS = cosine and SP = simple polynomial; AIC = Akaike's Information Criteria; ESW = effective strip width; D = density; LCL = lower 95% CL; UCL = upper 95% CL; CV = coefficient of variation; and P = probability (χ^2).

Time of year	Site	Key	E	AIC	ESW	D	LCL	UCL	CV	P
Spring 2000	A1	HN	CS	362	97	0.39	0.27	0.56	0.16	0.89
	A1	HN	HM	362	97	0.39	0.27	0.56	0.19	0.90
	A1	HZ	CS	363	100	0.38	0.25	0.56	0.19	0.90
	A1	HZ	SP	363	100	0.38	0.25	0.56	0.19	0.90
Autumn 2000	A1	HN	CS	187	34	1.54	0.96	2.48	0.21	0.12
	A1	HZ	CS	186	24	2.18	0.65	7.32	0.67	0.19
	A1	HZ	SP	186	24	2.18	0.65	7.32	0.67	0.19
	B	HN	CS	156	49	0.43	0.32	0.59	0.15	0.75
	B	HN	HM	157	55	0.38	0.28	0.51	0.14	0.57
	B	HZ	CS	156	42	0.50	0.30	0.85	0.27	0.74
	B	HZ	SP	156	42	0.50	0.30	0.85	0.27	0.74
	C	HN	CS	85	50	0.11	0.08	0.15	0.15	0.29
	C	HN	HM	83	41	0.13	0.09	0.20	0.18	0.50
	C	HN	CS	82	33	0.16	0.11	0.25	0.21	0.71
	C	HZ	SP	82	28	0.19	0.09	0.42	0.39	0.78
Spring 2001	A2	HN	HM	1012	76	0.88	0.67	1.16	0.12	0.00
	A2	HN	CS	1005	56	1.20	0.88	1.64	0.15	0.07
	A2	HN	CS	1004	56	1.19	0.89	1.61	0.14	0.12
	A2	HZ	SP	1002	46	1.45	0.87	2.41	0.26	0.21
	A2	HZ	CS	1002	46	1.45	0.87	2.41	0.26	0.21
	B	HZ	CS	384	28	0.69	0.27	1.75	0.49	0.13
	B	HZ	SP	384	28	0.69	0.27	1.75	0.49	0.13
	B	HN	CS	388	48	0.40	0.22	0.71	0.27	0.17
	B	HN	HM	404	99	0.19	0.11	0.33	0.23	0.00
	C	HN	CS	366	18	0.16	0.07	0.35	0.40	0.23
	C	HN	CS	372	51	0.05	0.04	0.07	0.12	0.48
	C	HN	HM	374	64	0.04	0.04	0.05	0.08	0.12

2000 and site A2 in spring 2001. Differences between estimates of density between sites as determined by capture-recapture were smaller than the differences identified by distance sampling and were suggestive of trap saturation at site A1 in autumn 2000 and at site A2 in spring 2001.

Dung plots

Mean dung density was closely related to mountain hare density estimated by capture-recapture and distance sampling and was in accordance with our subjective ranking (see Fig. 2). There was good differentiation between high and low density areas during spring in both years, but in autumn 2000 there was overlap between the medium and high density areas.

Comparison of methods

Although the different techniques gave different density estimates, the rank order of sites was consistent, and mean dung density showed a consistent relationship with the estimated hare densities (see Fig. 2). Estimates from distance sampling were higher than those derived from capture-recapture at the high-density sites. While the density estimates were all comparable, the precision was dependant on both the analysis used and the density, but our data do not allow us to identify whether the poor precision at the two high-density sites was density dependant or site dependant as both high-density sites were steep hillsides with complex topography.

Table 3. Capture-recapture estimates of mountain hare density (hares ha-1) with 95% confidence limits.

Year	Season	Site	Samples (Individuals)	Total individuals (M_{t+1})	Total captures (N)	Jack-knife density M(h)	Chao density M(h)
2000	Spring	A1	7	18	25	0.33 (0.22-0.55)	0.36 (0.20-1.04)
2000	Autumn	A1	5	23	35	0.51 (0.42-0.77)	0.52 (0.40-0.92)
2000	Autumn	B	5	14	21	0.29 (0.24-0.49)	0.31 (0.25-0.66)
2000	Autumn	C	5	8	12	0.17 (0.14-0.37)	0.22 (0.14-0.74)
2001	Spring	A2	7	23	44	0.48 (0.40-0.74)	0.51 (0.40-0.95)

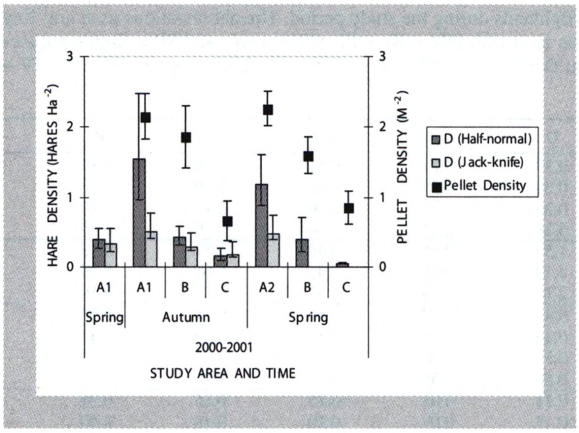

Figure 2. Density estimates for mountain hares in the Central Highlands derived from line transects (half-normal estimator) and capture-recapture (Jack-knife estimator) and an index of abundance derived from dung density. The estimates are shown with 95% confidence intervals.

Discussion

Distance sampling

Examination of the perpendicular distance histograms suggested that only hares close to transects were detected with certainty, and that a large proportion of hares were either evading detection further away from the transects or moving away from the transects prior to detection. The rapid fall in detection might be explained either by the behaviour of hares or the inaccurate measurement of sighting distances and angles. Our experience suggests that hares in areas of tall heather or uneven terrain often do not flush until an observer is within five metres, and this behaviour could account for the narrow shoulder of the distance histogram. Distance histograms with a sharp decline in the detection probability are known to be problematic to analyse and can lead to inaccurate estimates of density (Buckland et al. 2001).

The large proportion of hares seen close to transects suggest that the assumption that all animals on transects be detected with certainty was met. It is difficult from our data to assess the assumption of the accuracy of measurements. Although the frequency plots do not highlight a problem with animal movement it was not possible to assess the significance of animal movement prior to detection. Movement of hares was often the detection cue, and this characteristic is likely to lead to a positive bias in sighting distances and a corresponding negative bias in density estimates.

High hare densities created a number of methodological problems for distance sampling. It became difficult with increasing density to remember which hares had been recorded and to remember sighting locations. Such 'counting saturation' is likely to detract from the accuracy of data and may introduce bias if certain categories of detection cue or distance category are systematically ignored. With increasing density, hares are also disturbed by the observer and are more likely to flush or alert other individuals. Although hares are generally solitary, they do occur in small groups when feeding, and large groups of up to 100 hares may occasionally occur (Hewson 1990). This poses further problems as groups are more likely to be seen than singletons. The occurrence of groups where animals are recorded as individuals can lead to pronounced spikes in the perpendicular distance histograms. Buckland et al. (2001) suggest that in these circumstances groups should be treated as the unit of analysis. This is difficult in practice with mountain hares, as the groups are difficult to rigorously define.

Transect lines should encompass as much of the underlying variability as possible which in mountainous terrain generally means that transects should run parallel to the prevailing altitude gradient, i.e. perpendicular to the contour lines. Hares are highly aggregated in their distribution and will move in response to the prevailing weather (Hewson 1962). Flushing behaviour of hares also changes with season, weather and as a result of human disturbance or the presence of predators (Flux 1970). These behavioural characteristics make direct counting of hares problematic and good survey design important. Our survey design comprised a grid of parallel transect lines laid at random over each study area. This design, in combination with the need to conduct transects down-hill, meant that we were only able to survey a small number of transects per survey. As a result, our density estimates were susceptible to the effects of sampling noise caused by either one transect yielding unusually high or low sightings or the movement of hares. A larger number of shorter transects might represent a better survey design.

Capture-recapture

We were confident that the hare populations were effectively closed with very few births, deaths, immigration or emigration during the sampling periods of five or seven days trapping. Concurrent radio tracking demonstrated that no study animals died or left the study area over the time period used in obtaining the density estimates (S. Newey, unpubl. data). Though we cannot ignore the possibility that some hares died or left the study area, we were confident that such events were rare. Animals were tagged in both ears, and we have no indication that tag loss was a problem during the trapping period. The use of metal ear tags meant that tags were easy to read, and we are confident that recoveries were recognised and correctly identified.

The reliable estimate of density from capture-recapture methods is also dependant on obtaining sufficiently large sample sizes. The number of traps used in our study was largely determined by logistic constraints, and was fewer than suggested by White et al. (1982), who recommend a trapping grid comprising of r rows and c columns such that $r + c > 25$. White et al. (1982) also recommend the use of four traps per individual home range. Given a mountain hare home range of 10 ha (Hewson & Hinge 1990, Hulbert et al. 1996), an ideal trapping design would include a trap spacing of 90 m compared to the 75 m spacing we used.

Differences between density estimates derived from distance sampling and capture-recapture sampling were most likely due to the small number of traps and the low capture rates which reduced the precision of density estimates. The small number of traps may also have lead to trap saturation, particularly at the high-density sites and during the autumn trapping periods. Furthermore, as only a small portion of each study area was trapped, the capture-recapture estimates may not apply to the areas covered by distance sampling. Density estimates were based on an estimate of the effective trapping area of the trap grid. The addition of half the estimated home range size to the trap grid fails to take into account the seasonal or density-dependant changes in ranging behaviour of the hares.

Dung plots

Mean dung density was closely related to hare density estimated by distance sampling or capture-recapture methods. This was particularly apparent during spring 2001, but whether this was due to the larger sample size or represents a seasonal effect is not clear. Defecation rates and dung decomposition rates of mountain hares vary with time of day, season, habitat and substrate (Hewson 1989). In addition, the habitat use and diet of mountain hares vary with population density and with the presence of other herbivores (Hewson 1976b). Despite these potential problems, our results suggest that with sufficient sampling intensity and standardised sampling regimes, dung plots can offer a quick yet reliable index of relative abundance.

Recommendations

With careful study design, distance sampling offers a good compromise between accuracy, precision and effort as a technique to estimate the density of mountain hares. Distance sampling can give accurate density estimates across a range of hare densities, although there are methodological problems associated with hare behaviour, particularly at high density. Discrepancies between density estimates derived from distance sampling and from capture-recapture techniques at high density are more likely the result of underestimation by capture-recapture due to trap saturation than overestimation by distance sampling, as suggested by the increase in dung density with increasing distance sampling estimates. A further difficulty is that density estimates at low hare densities are only possible by pooling survey data that require unverifiable assumptions about detection functions. However, distance sampling is considerably less labour intensive in comparison to capture-recapture techniques and offers a cost-effective method for estimating mountain hare density when a high degree of precision is not critical. Dung plots are a rapid and reliable alternative technique where estimates of relative mountain hare abundance are all that are required.

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References

Angerbjörn, A. 1983: Reliability of pellet counts as density estimates of mountain hares. - Finnish Game Research 41: 13-20.

Angerbjörn, A. 1986: Reproduction of mountain hares in relation to density and physical condition. - Journal of Zoology, London, 208: 559-568.

Barnes, R.F.W. & Tapper, S. 1985: A method for counting hares by spotlight. - Journal of Zoology, London, 206: 273-276.

Barnes, R.F.W., Tapper, S.C. & Williams, J. 1983: Use of pastures by brown hares. - Journal of Applied Ecology 30: 179-185.

Boulanger, J.G. & Krebs, C.J. 1994: Comparison of capture-recapture estimators of snowshoe hare populations. - Canadian Journal of Zoology 72: 1800-1807.

Boulanger, J.G. & Krebs, C.J. 1996: Robustness of capture-recapture estimators to sample biases in a cyclic snowshoe hare population. - Journal of Applied Ecology 33: 530-542.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. 2001: Introduction to Distance Sampling: Estimating abundance of biological populations. - Oxford University Press, 432 pp.

Casagrande, D.G., Beissinger, S.R. & Steven, R. 1997: Evaluation of four methods for estimating parrot population size. - Condor 99: 445-457.

Chao, A. 1988: Estimating animal abundance with capture frequency data. - Journal of Wildlife Management 52: 295-300.

Chao, A. 1989: Estimating population size for sparse data in capture-recapture experiments. - Biometrics 45: 427-438.

Endsign, W.E., Angermeier, P.L., & Doloff, C.A. 1995: Use of line transect methods to estimate abundance of benthic stream fishes. - Canadian Journal of Fisheries and Aquatic Sciences 52: 213-222.

Flux, J.E.C. 1970: Life history of the mountain hare in north-east Scotland. - Journal of Zoology, London, 161: 75-123.

Focardi, S., Isotti, R. & Tinelli, A. 2002: Line transect estimates of ungulate populations in a Mediterranean forest. - Journal of Wildlife Management 66: 48-58.

Gilbert, L., Norman, R., Laurenson, K.M., Reid, H.W. & Hudson, P. J. 2001: Disease persistence and apparent competition in a three-host community: an empirical and analytical study of large-scale, wild populations. - Journal of Animal Ecology 70: 1053-1061.

Hewson, R. 1962: Food and feeding habits of the mountain hare. - Proceedings of the Zoological Society of London 139: 515-526.

Hewson, R. 1976a: A population study of mountain hares in north-east Scotland from 1956-1969. - Journal of Animal Ecology 45: 395-414.

Hewson, R. 1976b: Grazing by mountain hares, red deer and red grouse on heather moorland in north-east Scotland. - Journal of Applied Ecology 13: 657-666.

Hewson, R. 1989: Grazing preferences of mountain hares on heather moorland and hill pastures. - Journal of Applied Ecology 26: 1-11.

Hewson, R. 1990: Behaviour, population changes and dispersal of mountain hares in Scotland. - Journal of Zoology, London, 220: 287-309.

Hewson, R. & Hinge, M.D.C. 1990: Characteristics of the home range of mountain hares. - Journal of Applied Ecology 27: 651-666.

Hulbert, I.A.R., Iason, G.R., Elston, D.A. & Racey, P.A. 1996: Home-range sizes in a stratified upland of two lagomorphs with different feeding strategies. - Journal of Applied Ecology 33: 1479-1488.

Krebs, C.J. 1999: Ecological Methodology. - Longmans, 620 pp.

Krebs, C.J., Gilbert, B.S., Boutin, S. & Boonstra, R. 1987: Estimation of snowshoe hare population density from turd transects. - Canadian Journal of Zoology 65: 565-567.

Krebs, C.J., Boonstra, R., Nams, V., O'Donoghue, M., Hodges, K.E. & Boutin, S. 2001: Estimating snowshoe hare population density from pellet plots: a further evaluation. - Canadian Journal of Zoology 79: 1-4.

Langbein, J., Hutchings, M.R., Harris, S., Stoate, C., Tapper, S.C. & Wray, S. 1999: Techniques for assessing the abundance of Brown Hares. - Mammal Review 29: 93-116.

Mandujano S. & Gallina, S. 1995: Comparison of deer censusing methods in tropical dry forest. - Wildlife Society Bulletin 23: 180-186.

Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. 1978: Statistical inference from capture data on closed animal populations. - Wildlife Monographs 62: 1-135.

Pollock, K.H., Nichols, J.D., Brownie, C. & Hines, J.E. 1990: Statistical inference for capture-recapture experiments. - Wildlife Monographs 107: 1-97.

Putman, R.J. 1984: Facts from faeces. - Mammal Review 14: 79-97.

Rexstad, E. & Burnham, K.P. 1991: User's guide for interactive program: CAPTURE - Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, 29 pp.

Southwell, C. 1994: Evaluation of walked line transect counts for estimating macropod density. - Journal of Wildlife Management 58: 348-356.

Southwood, R. & Henderson, P.A. 2000: Ecological Methods. - Blackwell Science, 575 pp.

Sutherland, W.J. 1996: Why Census? - In: Sutherland, W.J. (Ed.); Ecological Census Techniques: A Handbook. - Cambridge University Press, pp. 1-10.

Thomas, L., Laake, J.L., Derry, J.F., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Strinderberg, S., Hedley, S.L., Burt, M.L., Marques, F.F.C., Pollard, J.H. & Fewster, R.M. 1998: DISTANCE 3.5. - Research Unit for Wildlife Population Assessment, University of St. Andrews, UK.

Watson, A. & Hewson, R. 1973: Population densities of mountain hares on western Scottish and Irish moors and Scottish hills. - Journal of Zoology, London, 170:159

White, G.C., Anderson, D.R., Burnham, K.P. & Otis, D.L. 1982: Capture-recapture and removal methods for sampling closed populations. - Los Alamos National Laboratory, USA, 235 pp.