Detectability and disappearance of ungulate and hare faeces in a European temperate forest

Jörn Theuerkauf[1], Sophie Rouys[2] & Włodzimierz Jędrzejewski[3]

[1] *Museum and Institute of Zoology, Polish Academy of Sciences, ul. Wilcza 64, PL-00-679 Warsaw, Poland (e-mail: jtheuer@miiz.waw.pl)*
[2] *Conservation Research New Caledonia, B.P. 2549, 98846 Nouméa Cedex, New Caledonia (email: rouys@ifrance.com)*
[3] *Mammal Research Institute, Polish Academy of Sciences, PL-17-230 Białowieża, Poland (email: wjedrzej@bison.zbs.bialowieza.pl)*

We counted droppings of ungulates and hare on transects in order to assess (1) seasonal changes in detectability and disappearance of pellet groups, (2) whether the detectability varies according to the forest type, and (3) the degree of misidentification between pellets of roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*). The summer decrease in detectability of pellet groups was the most important factor for all species but European bison (*Bison bonasus*). Detectability did not significantly depend on forest type. In summer, decay reduced significantly the dropping density of red deer, roe deer, wild boar (*Sus scrofa*) and European hare (*Lepus europaeus*) but not those of bison and moose (*Alces alces*). Misidentification of roe and red deer droppings did not influence much density estimates of red deer but resulted in an important overestimation of roe deer in areas were roe deer were much less common than red deer.

Introduction

Counts of faecal pellet groups are commonly used to indirectly estimate ungulate densities (Mayle *et al*. 1999). The accuracy of estimates obtained with this method depends on factors such as decay and defecation rates as well as pellet detectability. Defecation and decay rates of ungulates and hare are known to vary according to diet, rainfall, temperature and evaporation (Mayle & Peace 1999, Mayle *et al*. 1999, Murray *et al*. 2005). The most accurate method to estimate pellet densities is therefore to remove and count pellet groups after a defined time of exposition (which should be short enough for decay not

to significantly influence results) in sample plots and subsequently calculate animal densities by taking into account also daily defecation rates of each species (Mitchell & McCowan 1984, Mitchell *et al*. 1985, Prokešová *et al*. 2006). A less labour-intensive method is to estimate "standing crop" pellet density on transects (Marques *et al*. 2001, Campbell *et al*. 2004). This method, however, additionally requires information on disappearance rates in order to calculate absolute densities (Aulak & Babińska-Werka 1990, Mayle & Peace 1999, Hemami & Dolman 2005). Another factor that affects the accuracy of pellet density estimates, and especially the "standing crop" method, is the detectability of pellet

---

groups, which depends both on the observer and on the ground cover. Despite its importance for transect counts, the detectability of pellet groups has been given little attention. Lehmkuhl *et al.* (1994) and Persson (2003a, 2003b) estimated the detectability of red deer (*Cervus elaphus*) and moose (*Alces alces*) by monitoring pellet groups placed in sample plots. They found that the detectability was high only in spring, when there was neither snow nor dense vegetation at ground level. Pellet group surveys have been found reliable in estimates of habitat use by deer (Guillet *et al.* 1995, Weckerly & Ricca 2000). To assess habitat use from ungulate pellet counts done at different times of years, it is therefore necessary to take into account seasonal changes in detectability. Habitat type can also affect pellet detectability (Harestad & Bunnell 1987, Persson 2003a, 2003b), which would influence any assessment of habitat use based on pellet counts. Finally, visibility depends on the size of pellets, so the density of species with smaller pellets can be underestimated as compared with that of larger species (Hemami *et al.* 2005). Our aims were to assess (1) seasonal changes in detectability and disappearance of pellet groups, (2) whether the detectability varies according to the habitat type, and (3) the degree of misidentification between pellets of roe and red deer.

Study area and methods

The Białowieża Forest is a forest complex of 1450 km² (52°30´–53°00´N, 23°30´–24°15´E) that straddles the Polish–Belarussian border. The Polish side of the Białowieża Forest consists of the Białowieża National Park (100 km²) and a commercial forest (480 km²), in which logging, reforestation, and hunting occur. The central part of the national park is a strict reserve (50 km²), which has been protected for 85 years. An area of 50 km² surrounding the strict reserve became protected in 1996 (buffer zone between the strict reserve and the commercial forest). The study area is a lowland forest (altitude 134–202 m) in the transition zone between the boreal and temperate climates (Mitchell & Cole 1998). The mean daily temperature is –5 °C in January and 18 °C in July. During the 3 years of our study

(from July to June), snow cover persisted for 71, 60 and 96 days, and annual precipitation was 500, 704 and 601 mm, respectively. Mean spring animal densities in the study area during the period of this study ranged from 2.9 to 4.6 red deer, 1.2 to 3.2 roe deer (*Capreolus capreolus*) and 2.2 to 4.3 wild boar (*Sus scrofa*) km⁻² (Jędrzejewski *et al.* 2007).

We grouped the 19 vegetation types occurring in the Białowieża Forest (Kwiatkowski 1994) into 5 forest types mainly according to the trophic conditions and soil humidity: (1) eutrophic fresh deciduous forests (19% of the Białowieża Forest and 17% of transect area), (2) eutrophic humid deciduous forests (21% and 26%), (3) oligotrophic to mesotrophic mixed bog forests and eutrophic wet deciduous flood-plain forests (18% and 18%), (4) oligotrophic fresh to humid mixed forests (12% and 16%), and (5) oligotrophic to eutrophic dry forests (29% and 23%). Forest types 2 and 3 (humid and wet forests) have an abundant spring geophyte ground vegetation. In summer, forest type 3 has the densest ground vegetation, whereas the other forest types have sparse ground cover, especially the oligotrophic and dry forests (type 4 and 5). To assess detectability in winter after snowmelt, we pooled forest types 2 and 3 (dense ground cover) to compare them with types 1, 4 and 5 (sparse cover), whereas we analysed all 5 types separately in summer.

In 1997–1999, we counted all pellet groups or droppings (that were still attributable to a species) of red deer, roe deer, moose, wild boar, European bison (*Bison bonasus*), and hare (*Lepus europaeus*) that we could see while walking slowly on 16 transects that were about 10 km long each (one transect could be walked in one working day). We used transects because our study area was large and we needed a method that allowed us to cover the largest area possible. These transects were representative of the habitat types found in the study area. In 1997 and 1998, we sampled 4 of these transects four times per year (after snowmelt, in late spring/early summer, in mid/late summer, and in autumn). In 1999, these 4 transects were sampled only after snowmelt. In 1998 and 1999, we also sampled the other 12 transects.

We define a dropping or pellet group as a pile of faeces defecated by one animal at one time.

For simplification, we use the term droppings to refer to pellet groups and other droppings. We walked transects by following a compass bearing through the forest. We walked preliminary transects (115 km) in March 1997 to assess which width of a transect would be optimal. On these transects, we applied distance sampling (Buckland *et al*. 1993) to estimate the visibility of droppings of all species in relation to their distance to the transect line. The detectability of droppings was more than halved when droppings were farther than 50 cm from each side of the transect line (as compared with when they were on the transect line). We therefore decided to use a 1-m-wide strip transect. To reduce a potential observer bias (Ringvall *et al*. 2000), in the analyses we used transect data collected by only one observer.

In the 19th century, Russian foresters subdivided the forest into square compartments (side length 533 m on average, SD = 32 m). As the boundaries between forest compartments are marked (by roads, forest lanes or colour markings), we used the compartments to split each of the 16 transects (which went perpendicular through the compartments) into 19 sectors (each on average 533 m long) and noted separately the numbers of droppings for each species obtained for each sector. A transect sector was therefore the sample unit. We calculated the proportion of forest types in each transect sector (of 1 m width) based on Kwiatkowski's (1994) vegetation map entered into a geographic information system. Although transect sectors sometimes included different habitat types, it would have been too time consuming to record each change in habitat so we only recorded the numbers of droppings in each sector and then analysed the habitat component with our GIS. We therefore calculated the mean of dropping density (d) for the habitat k by weighting the dropping density of each transect sector (i) with the proportion of the given habitat (p^k) in this transect sector:

$$\overline{d}^k = \frac{\sum p_i^k d_i}{\sum\limits_{i=1}^{n} p_i^k}$$

If a given habitat represented for example 27% of the transect sector line, the weighting factor was 0.27. If a second habitat type represented the other 73% of the transect sector, its weighting factor was then 0.73. The sum of weighting factors of all habitat types in a given transect sector was therefore always 1 because the number of transect sectors was the sample size. We calculated weighted means and their variation using the weighting function in SPSS 11 for Windows.

To assess the proportion of droppings detected, we estimated, simultaneously with the transect counts, the dropping density in sample plots in 100 km of the transects (4 transects one time per year over two years, 2 transects one time in one year). To that effect, 2–4 persons carefully searched the ground for droppings, including those which were under vegetation or litter, in 4 square sample plots (50 m² each) in each of the 19 transect sectors along the transect line and spaced at 100-m intervals (76 plots per transect). In each plot, we counted droppings of each species and measured their fresh weight (20 plots could be done in one working day). We considered that a dropping was inside the sample plot (or the strip transect) if its centre was inside the sample area. In sample plots, we weighed all pellets that were inside the plot and discarded all pellets outside, regardless of whether a pellet belonged to a pellet group that was considered as being inside or outside. This procedure allowed us to assess if the weight of droppings and therefore their amount in the sample plot correlated with our estimates of the number of droppings. We pooled the data of the 4 plots examined in each transect sector (total surface 200 m²) and compared the dropping density (per 1000 m²) with that obtained during the strip transect count in that transect sector (surface 533 m² on average). The plots were therefore examined only in a part of the strip transects. This adds a certain spatial variation, but as we based the analyses on a large sample area (38 000 m² in plots, over 100 000 m² for strip transects), it may have increased the variation but not the mean of detectability.

To avoid problems due to division by zero, we first calculated means and standard deviations for strip transects (subscript T) and sample plots (subscript P) independently and then estimated the detectability (subscript D) as the mean

density on strip transects divided by the mean density in sample plots. We calculated confidence intervals for mean detectability based on standard deviations estimated as follows (modified from Goodman 1960):

$$SD_D = \sqrt{\frac{SD_T^2 \times SD_P^2}{\overline{x}_P^4} + \frac{\overline{x}_T^2 \times SD_P^2}{\overline{x}_P^4} + \frac{SD_T^2}{\overline{x}_P^2}}$$

We estimated disappearance rates by testing which regression model best described the decrease in dropping density after the first count of each year (after snowmelt). The disappearance rate that we calculated, therefore, does not include only the decay of droppings but also the increased production of droppings due to the birth of young deer in late spring/early summer.

To assess potential identification mistakes between droppings of young red deer and those of roe deer, we counted animals seen during pellet counts on transects. We then calculated the proportion of roe deer among deer (roe and red deer) that the strip transect observer saw during transects in 1997–1999 and compared it with that of the simultaneous dropping counts. In the strict reserve, the proportion of roe deer was similar in winter (4 of 99 deer on 41 km of transect) and summer (4 of 115 deer on 112 km of transect) and was about 4%. During a driving census of 11 km² in the strict reserve (unpublished report by W. Jędrzejewski, H. Okarma and K. Schmidt, Mammal Research Institute, Białowieża, 1997), the proportion of roe deer was also 4% (11 of 290 deer). Our estimate of the proportion of roe deer by the number of animals seen on transects therefore seems to be sufficiently accurate to assume that it is representative of the proportion of roe and red deer. In the buffer zone of the national park and the commercial forest, 24% of deer observed in both winter (20 of 83 deer on 199 km of transect) and summer (25 of 105 on 414 km of transect) were roe deer.

As detectability and disappearance rates of roe and red deer were different, we could not just compare the proportions of dropping densities with those of animal densities. We therefore assessed the proportion of misidentified droppings by calculating dropping density using the equations of dropping disappearance and detecta-

bility with varying values of misidentification (red deer dropping density +x and roe deer dropping density –x) simultaneously until the proportion of roe deer dropping density and red deer dropping density was equal to the proportion of roe deer density and red deer density seen on transects. The proportion of misidentified red deer droppings was then x divided by the density of droppings considered as red deer and the proportion of misidentified roe deer was x divided by the density of droppings considered as roe deer. Defecation rates of roe deer in western Europe are 14–20 per day and those of red deer 19–25 per day (Mitchell & McCowan 1984, Mitchell *et al.* 1985, Dobiáš *et al.* 1996). However, we did not have any information about defecation rates of these species in the Białowieża Forest. We therefore did not consider differences in defecation rates for our estimates of misidentification.

Results

The number of droppings found in plots highly correlated with their weight (Table 1). We therefore considered that our estimates of the number of droppings were representative of dropping densities. The number of pellet groups found on transects and in plots also correlated but for red deer, roe deer, wild boar and hare the density was lower on strip transects than in plots (Table 1).

Logarithmic ($y = b_1 \ln(x) + b_0$) and inverse ($y = b_1 x^{-1} + b_0$) regression models best explained the decrease in dropping density in plots and transects as well as in detectability (Fig. 1). We chose inverse regression models because the logarithmic models produced negative values for the months of autumn. For red deer and wild boar, the detectability on strip transects in March/April was 99% and 94%, respectively, of that in plots but detectability on transects decreased until the end of summer (Fig. 1). The detectability of roe deer droppings on transects in March/April was only 47%. Besides the decrease in detectability, the dropping density of red deer, roe deer and wild boar decreased because of disappearance throughout summer (*see* decrease of droppings in plots in Fig. 1). The inverse regression equations (y for density, x for months after 1 April) for transects, plots, and detectability (subscripts

Table 1. Weight (in g) and numbers (nb) of droppings per 1000 m² on strip transects and plots (*n* = 190 transect sectors) compared with Spearman's correlation coefficients (r_S) in the Białowieża Forest, from 1997 to 1999.

	Red deer		Roe deer		Moose		Wild boar		Bison		Hare	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Weight in plots	1253	113	51	8	105	35	288	59	268	140	6	2
r_S (weight, nb in plots)	0.86***		0.98***		1.00***		0.99***		1.00***		1.00***	
Nb in plots	25.5	1.8	3.5	0.4	0.5	0.2	3.7	0.6	0.3	0.1	5.5[1]	1.6
r_S (nb in plots, nb on transects)	0.57***		0.32***		0.33***		0.51***		0.18*		0.19**	
Nb on strip transects	14.7	1.4	1.1	0.2	0.5	0.1	3.0	0.4	0.3	0.1	0.3[2]	0.1

[1] nb of pellets, [2] nb of pellet groups, *P = 0.013, **P = 0.010, ***P < 0.001
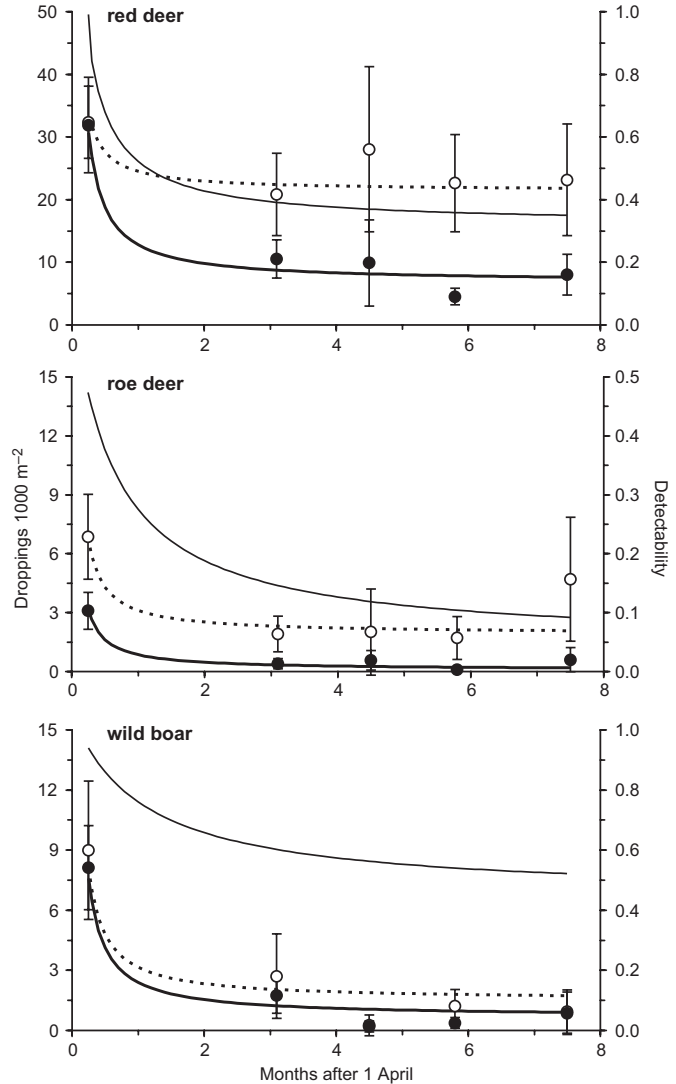

Fig. 1. Mean densities (with 95% confidence intervals for each age class) of red deer, roe deer and wild boar droppings estimated simultaneously on strip transects (filled circles, regression line bold continuous) and in plots (open circles, regression line bold dashed) and the detectability (continuous line) of droppings as (density on transects) (density in plots)⁻¹, on 190 transect sectors in the Białowieża Forest, on 9 occasions between 1997 and 1999. To make the figure easier to read, counts done in the same months were pooled to calculate means (regressions were not affected by this pooling).

T, P and D, respectively) were: red deer: $y_T = 5.96x^{-1} + 6.8$, $y_P = 3.09x^{-1} + 21.4$, $y_D = 0.149x^{-1} + 0.34$; roe deer: $y_T = 0.77x^{-1} + 0.1$, $y_P = 1.19x^{-1} + 1.9$, $y_D = 0.108x^{-1} + 0.11$; wild boar: $y_T = 1.73x^{-1} + 0.7$, $y_P = 1.64x^{-1} + 1.5$, $y_D = 0.121x^{-1} + 0.55$ (all $P \leq 0.001$). In autumn, especially in November, dropping densities seemed to increase again (Fig. 1). However, the increase was not strong as falling leaves concealed droppings.

Dropping densities of red deer, roe deer, and wild boar were high enough to compare their detectability on transects in different habitat types. After snowmelt, the detectability was not lower in habitats with spring ground vegetation than in the other habitat types (Table 2). Although there seems to be some differences in detectability among habitats in summer, the differences were not consistent for the three species. If detectability in a specific forest was lower, detectability of droppings of all species should have been lower in that forest type. However, this was not the case and there were no differences (confidence intervals largely overlapped) among forests. We therefore could not detect any differences in detectability of droppings in different forest types.

All bison droppings could be detected and the dropping density did not significantly decrease after 1 April, both in plots ($P = 0.281$) and on transects ($P = 0.104$). The detectability of moose droppings decreased during summer as the dropping density decreased on transects ($y_\mathrm{T} = 0.24x^{-1} + 0.2$, $P = 0.001$) but not in plots ($P = 0.251$). The hare dropping density decreased both on transects ($y_\mathrm{T} = 0.23x^{-1}$, $P < 0.001$) and in plots ($y_\mathrm{p} = 3.19x^{-1} + 1.3$, $P < 0.001$) and were not comparable since we had to count the number of single pellets in plots as pellet groups were not distinguishable.

When using pellet counts to calculate (corrected for detectability and disappearance) the proportion of roe deer among deer, the proportion was 6% in March/April in the strict reserve and 28% in the buffer zone and commercial forest. Direct observations yielded proportions of 4% and 24%, so we probably mistook about 0.8% of red deer droppings for roe deer droppings. Since roe deer density and detectability of their droppings are lower than those of red deer, especially in the strict reserve, this corresponded however to 35% of roe deer droppings in the strict reserve and 4% of roe deer droppings in the rest of the study area. In summer, we counted on average 2.6% (range 1.5%–3.5%) of red deer droppings as those of roe deer (corresponding to 88% of roe deer droppings in the strict reserve and 17% of roe deer droppings in the rest of the study area).

Discussion

In our study, the decrease in dropping density throughout the year was mainly related to a decrease in the detectability of droppings, especially for red deer, roe deer and wild boar. This decrease was less important for large species such as moose and bison. The detectability of hare pellet groups on line transects was too low to allow for a reasonable density estimate. Hare dropping densities should rather be estimated in plots (e.g. Murray *et al.* 2005, Homyack *et al.* 2006) as pellet groups cannot be easily distinguished from each other and counting single pellets while walking a transect is too time-consuming. While it was possible to detect nearly

Table 2. Mean detectability as (density on transects) (density in plots)$^{-1}$ with 95% confidence intervals of red deer, roe deer and wild boar droppings (*n* = 190 transect sectors) in winter after snowmelt (March/April) and summer (May–October) in different forest types of the Białowieża Forest, from 1997 to 1999 (a confidence interval that does not include the value 1 indicates a reduced detectability).

Period	Forest type	Red deer	Roe deer	Wild boar
Winter	1, 4 and 5 (dry, fresh or oligotrophic, *n* = 31.21)	1.0 ± 0.3	0.47 ± 0.27	0.9 ± 0.5
	2 and 3 (wet-humid, *n* = 22.79)	1.0 ± 0.4	0.37 ± 0.29	0.9 ± 0.7
Summer	1 (fresh eutrophic, *n* = 25.76)	0.3 ± 0.2	0.07 ± 0.19	0.5 ± 1.1
	2 (humid eutrophic, *n* = 38.72)	0.3 ± 0.2	0.05 ± 0.09	0.4 ± 0.5
	3 (wet, *n* = 20.56)	0.2 ± 0.1	0.11 ± 0.22	1.0 ± 3.5
	4 (humid-fresh oligotrophic, *n* = 21.00)	0.4 ± 0.2	0.14 ± 0.31	0.8 ± 2.7
	5 (dry, *n* = 29.96)	0.6 ± 0.5	0.03 ± 0.15	0.5 ± 2.0

Forest types: 1 = eutrophic fresh deciduous forests, 2 = eutrophic humid deciduous forests, 3 = oligotrophic to mesotrophic mixed bog forests and eutrophic wet deciduous flood-plain forests, 4 = oligotrophic fresh to humid mixed forests, 5 = oligotrophic to eutrophic dry forests.

all droppings of red deer, wild boar, moose and bison just after snowmelt, the detectability of roe deer droppings was only about 50% on transects (Fig. 1). It is therefore necessary to apply a correction factor for roe deer dropping density even in spring.

While transect counts were the most efficient method for the four larger species, roe deer pellet counts along transects were verging on inaccuracy. Habitat, however, did not influence the detectability of droppings much. As in our study, Lehmkuhl *et al.* (1994) and Persson (2003a, 2003b) observed a high detectability of red deer and moose pellet groups after snowmelt. Lehmkuhl *et al.*'s (1994) study took place in coastal forests of Washington with little snow and mild winters, where in April the detection rate was still more than 90%. In our study area the detectability was even higher maybe because winters are colder and there is little decay during winter. The end of winter is therefore the best moment for estimates of dropping density (Mitchell *et al.* 1985, Aulak & Babińska-Werka 1990, Welch *et al.* 1990). However, if information about dropping density in summer is also required, it is necessary to assess the detectability of droppings and to correct transect counts. We therefore recommend calibrating the density estimates obtained on transects by sampling a part of the study area both by plots and transects. Knowing the detectability will then allow the sampling of a much larger area to assess habitat use.

Disappearance of droppings was only the second factor that lowered their density. The highest disappearance was from April to June. Later in the year, droppings disappeared at a lower rate. The reasons for this reduction in disappearance are probably the birth of young deer in June/July (increased defecation) and the usually dry weather from August to October in our study area (reduced decay). These two factors probably explain the small variation in dropping density from June to November. We therefore recommend avoiding the period of rapid change in dropping density and using the period after snowmelt to assess winter habitat use and the period from mid summer to autumn for summer habitat use.

In summer, droppings of young red deer can be mistaken for droppings of roe deer, even by an experienced observer. We estimated that we incorrectly identified only a small proportion of red deer droppings as those of roe deer in summer. We therefore consider that our estimates of red deer density were not much affected by such mistakes. However, in some parts of our study area only 4% of individuals of the two deer species were roe deer and their density estimates by dropping counts would be highly overestimated if not corrected. Defecation rates of roe deer are usually about 25% lower than defecation rates of red deer (Mitchell & McCowan 1984, Mitchell *et al.* 1985, Dobiáš *et al.* 1996). We did not consider differences in defecation rates in our study, but if this is also true in our study area, the values of misidentification would accordingly be higher. However, this would only reinforce our conclusions that misidentification between roe and red deer in summer (when young red deer are born) is an important source of error when the smaller species is much less common. We recommend checking proportions of species that have similar droppings by direct counts of animals in order to detect potential errors. Another solution, but much more labour-intensive, would be to identify species for example by near infrared reflectance spectroscopy of the faeces as Tolleson *et al.* (2005) successfully did for red and fallow deer (*Dama dama*) droppings.

Acknowledgements

References

Aulak, W. & Babińska-Werka, J. 1990: Estimation of roe deer density based on the abundance and rate of disappearance of their faeces from the forest. — *Acta Theriol.*

35: 111–120.

Buckland, S. T., Anderson, D. R., Burnham, K. P. & Laake, J. L. 1993: *Distance sampling: estimating abundance of biological populations.* — Chapman & Hall, London, U.K.

Campbell, D., Swanson, G. M. & Sales, J. 2004: Comparing the precision and cost-effectiveness of faecal pellet group count methods. — *J. Appl. Ecol.* 41: 1185–1196.

Dobiáš, K., Paustian, K. H. & Tottewitz, F. 1996: Untersuchungen zur Bestandeshšhe und Dynamik der Schalenwildpopulationen in der Schorfheide. — *Beiträge zur Jagd- und Wildforschung* 21: 57–62.

Goodman, L. A. 1960: On the exact variance of products. — *J. Amer. Statist. Assoc.* 55: 708–713.

Guillet, C., Bergstrom, R., Cederlund, G., Bergstrom, J. & Ballon, P. 1995: Comparison of telemetry and pellet-group counts for determining habitat selectivity by roe deer (*Capreolus capreolus*) in winter. — *Gibier Faune Sauvage* 12: 253–269.

Harestad, A. S. & Bunnell, F. L. 1987: Persistence of black-tailed deer fecal pellets in coastal habitats. — *J. Wildl. Manage.* 51: 33–37.

Hemami, M. R. & Dolman, P. M. 2005: The disappearance of muntjac (*Muniacus reevesi*) and roe deer (*Capreolus capreolus*) pellet groups in a pine forest of lowland England. — *Eur. J. Wildl. Res.* 51: 19–24.

Hemami, M. R., Watkinson, A. R. & Dolman, P. M. 2005: Population densities and habitat associations of introduced muntjac *Muntiacus reevesi* and native roe deer *Capreolus capreolus* in a lowland pine forest. — *For. Ecol. Manage.* 215: 224–238.

Homyack, J. A., Harrison, D. J., Litvaitis, J. A. & Krohn, W. B. 2006: Quantifying densities of snowshoe hares in Maine using pellet plots. — *Wildl. Soc. Bull.* 34: 74–80.

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B. & Kowalczyk, R. 2007: Territory size of wolves *Canis lupus*: linking local (Białowieża Primeval Forest, Poland) and Holarctic-scale patterns. — *Ecography* 30: 66–76.

Kwiatkowski, W. 1994: Vegetation landscapes of Białowieża Forest. — *Phytocoenosis* 6 *(N.S.) Suppl. Cartographiae Geobotanicae* 6: 35–87.

Lehmkuhl, J. F., Hansen, C. A. & Sloan, K. 1994: Elk pellet-group decomposition and detectability in coastal forests of Washington. — *J. Wildl. Manage.* 58: 664–669.

Marques, F. F. C., Buckland, S. T., Goffin, D., Dixon, C. E., Borchers, D. L., Mayle, B. A. & Peace, A. J. 2001: Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. — *J. Appl. Ecol.* 38: 349–363.

Mayle, B. A. & Peace, A. J. 1999: Recent progress in determining deer population size: factors influencing faecal pellet group decay. — In: Zomborszky, Z. (ed.), *Advances in deer biology*: 57–62. Proceedings of the 4th International Deer Biology Congress, 1998, Kaposvár, Hungary.

Mayle, B. A., Peace, A. J. & Gill, R. M. A. 1999: *How many deer? A field guide to estimating deer population size.* — Forestry Commission, Edingburgh, U.K., Field Book 18.

Mitchell, B. & McCowan, D. 1984: The defecation frequencies of red deer in different habitats. — *Ann. Rep. Inst. Terrestr. Ecol.* 1983: 15–17.

Mitchell, B., Rowe, J. J., Ratcliffe, P. R. & Hinge, M. D. C. 1985: Defecation frequency in roe deer (*Capreolus capreolus*) in relation to the accumulation rates of faecal deposits. — *J. Zool.* 207: 1–7.

Mitchell, F. G. J. & Cole, E. 1998: Reconstruction of long-term successional dynamics of temperate woodland in Białowieża Forest, Poland. — *J. Ecol.* 86: 1042–1059.

Murray, D. L., Roth, J. D., Ellsworth, E., Wirsing, A. J. & Steury, T. D. 2002: Estimating low-density snowshoe hare populations using fecal pellet counts. — *Can. J. Zool.* 80: 771–781.

Murray, D., Ellsworth, E. & Zack, A. 2005: Assessment of potential bias with snowshoe hare fecal pellet-plot counts. — *J. Wildl. Manage.* 69: 385–395.

Persson, I.-L. 2003a: *Moose population density and habitat productivity as drivers of ecosystem processes in northern boreal forests.* — Ph.D. thesis, Swedish University of Agricultural Sciences, Umeå, Sweden.

Persson, I.-L. 2003b: Seasonal and habitat differences in visibility of moose pellets. — *Alces* 39: 233–241.

Prokešová, J., Barančeková, M. & Homolka, M. 2006: Density of red and roe deer and their distribution in relation to different habitat characteristics in a floodplain forest. — *Folia Zool.* 55: 1–14.

Ringvall, A., Patil, G. P. & Taillie, C. 2000: A field test of surveyors' influence on estimates in line transect sampling. — *For. Ecol. Manage.* 137: 103–111.

Tolleson, D. R., Randel, R. D., Stuth, J. W. & Neuendorff, D. A. 2005: Determination of sex and species in red and fallow deer by near infrared reflectance spectroscopy of the faeces. — *Small Ruminant Res.* 57: 141–150.

Weckerly, F. W. & Ricca, M. A. 2000: Using presence of sign to measure habitats used by Roosevelt elk. — *Wildl. Soc. Bull.* 28: 146–153.

Welch, D., Staines, B. W., Catt, D. C. & Scott, D. 1990: Habitat usage by red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer in a Scottish sitka spruce plantation. — *J. Zool.* 221: 453–476.