Use of the bait-marking method to estimate the territory size of scavenging birds: a case study on ravens Corvus corax

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We tested the applicability of the bait-marking method in ravens *Corvus corax* to estimate their territory size during the breeding season in Białowieża Forest, eastern Poland. We marked 57 carrion baits and six additional carcasses with a distinctive type of plastic marker. The baits were experimentally placed around seven raven nests at different distances. A total of 1,018 pellets and 1,193 droppings from seven target raven nests, six neighbouring raven nests and from the communal roost were checked for markers. Ravens used 89% of baits and carcasses. In total, 705 markers, corresponding to 40 different baits and carcasses, were recovered. As confirmed by marker-type recoveries, ravens fed on 63% of experimental baits and 76% of those exposed inside the estimated territory. The proportion of baits utilised by a raven pair, as well as the total number of recovered markers declined with increasing distance of the bait from the nest. The probability of ravens feeding on a bait significantly decreased with greater distance from the nest. Distance from the nest correctly explained 84.5% of variation in the use of carrion by ravens. A threshold of 2,040 m indicated a raven territory size of 13.1 km². Raven pairs utilised baits and carrion further away than 2,040 m only exceptionally. Habitat characteristics and snow cover did not affect bait use and marker recoveries. Bait-marking was revealed as an efficient, accurate and economic method to estimate the territory size of scavenging birds, as well as to collect information on their movements.

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Bait-marking has been a widely used technique to investigate spatial ecology and territorial behaviour of some mammalian species (review in Delahay et al. 2000), especially in carnivores using latrines, such as badgers *Meles meles* (Kruuk 1978, Cheeseman & Mallinson 1979, Cheeseman et al. 1981, Parish & Kruuk 1982, Thornton 1988, Roper & Lüps 1993, Stewart et al. 2001) and raccoon dogs *Nyctereutes procyonoides* (Ikeda et al. 1979, Ikeda 1984), but also in rodents (Andrzejewski & Babińska-Werka 1986). A similar approach (foil-ball method) was adopted to study the movements and home range of woodrats *Neotoma* sp., based on their habits of

collecting small objects and bringing them to their nests (Ireland & Hays 1969, Henke & Smith 2000). To our knowledge, only three comparable studies have focused on birds. One used the bait-marking method to estimate the foraging distances of jackdaws *Corvus monedula*, crows *Corvus corone* and rooks *Corvus frugilegus* at communal winter roosts (Schramm 1974). The second study was based on prey-marking to determine home ranges of tawny owls *Strix aluco* (Southern & Lowe 1968). A recent study by Wright et al. (2003) demonstrated that sheep carcasses baited with colour beads and placed at varying distances from a large roost was a very successful method to investigate the structure of raven *Corvus corax* communal roosts as information centres.

The advantages of the bait-marking method have been proven by comparing it with standard techniques in vertebrate ecology (e.g. Parish & Kruuk 1982, Henke & Smith 2000). Bait-marking showed high recovery rates (Ikeda 1984, Ikeda et al. 1979, Henke & Smith 2000, Wright et al. 2003) providing almost the same results as telemetry (Kruuk 1978, Cheeseman & Mallison 1979, Parish & Kruuk 1982, Roper et al. 1986). Standard techniques often include trapping and the attachment of tags or transmitters, thus involving certain risks for the animals (Knight & Call 1980, Kochert et al. 1983, Greenwood 1997, Kenward et al. 2002). This may lead to numerous problems if the target species is rare, endangered or protected by law, simply too small for carrying active tags, or if it inhabits impenetrable environments, where radio telemetry becomes quite a complicated task. Furthermore, the costs of telemetry in terms of money, time and manpower are relatively high. The bait-marking method might be a useful technique for bird species that regurgitate food at the nest or roost and exploit carrion to a certain extent. It may also represent a useful alternative to both territory mapping and nearest-neighbour distance method (e.g. Clark & Evans 1954, Gibbons et al. 1995), mainly in cases of low breeding densities and/or difficult habitats, where it is almost impossible to find all breeding pairs within a given area.

Ravens are known to be neophobic, intelligent and extremely difficult to trap, especially adult individuals (Knight & Call 1980, Engel & Young 1989, Heinrich 1988, 1990, 1995, Boarman & Heinrich 1999). Moreover, finding all their nests in a study plot is not an easy task in densely forested areas. They are rather opportunistic and their diet ranges from seeds to small vertebrates, being highly dependent on carcasses in northern latitudes (Heinrich 1990, Ratcliffe 1997, Boarman & Heinrich 1999, Selva et al. 2003). We decided to test the bait-marking method with ravens in Białowieża Forest because of

their scavenging habits and because of two special circumstances: telemetry studies on territorial pairs are not feasible, due to trapping difficulties; and in densely forested areas both mapping and nearest-neighbour distance methods are extremely time consuming and not always accurate. The bait-marking method in ravens should work assuming that 1) the exposed and marked carrion is accepted and utilised by ravens, 2) the markers are taken together with the flesh, and 3) the markers appear in raven pellets and droppings at the nesting places.

The main objectives of our study were: 1) to test the validity of the bait-marking method in birds, providing recommendations for future studies, 2) to estimate the territory size of ravens and investigate aspects of their spatial use of carrion, and 3) to check the accuracy of the bait-marking technique by comparing our results with those obtained from a parallel study by Müller (2001) on raven breeding densities following standard procedures.

Study area

Białowieża Forest covering ca. 1,450 km² and located in the Polish-Belarusian border land, is one of the best preserved forest ecosystems in lowland temperate Europe
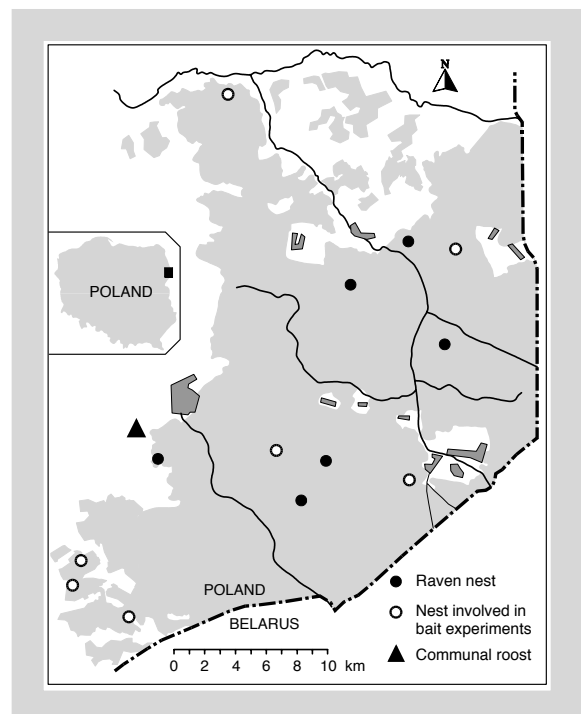

Figure 1. The study area in the Polish part of Białowieża Forest with indication of the locations of the raven nests, the nests involved in the marked bait trials (N = 7) and the communal roost.

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(Fig. 1). Our study was conducted in the Polish part of Białowieża Forest (52°30'-53°00'N, 23°30'-24°15'E; ca 600 km²), which includes Białowieża National Park (100 km²) and the commercial, exploited forest. The tree stands are dominated by oak *Quercus robur*, hornbeam *Carpinus betulus*, black alder *Alnus glutinosa*, Norway spruce *Picea abies*, and Scots pine *Pinus silvestris*. The ungulate community in Białowieża Forest consists of European bison *Bison bonasus*, moose *Alces alces*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus* and wild boar *Sus scrofa*. Large predators include lynx *Lynx lynx* and wolf *Canis lupus*. With 150 breeding species, the bird community is quite diverse, but species density is rather low (Tomiałojć & Wesołowski 1994). Detailed information on vegetation and vertebrate community is provided by Faliński (1986) and Jędrzejewska & Jędrzejewski (1998).

The climate of Białowieża Forest is transitional between continental and Atlantic types with clearly marked cold (November-March) and warm seasons. The mean temperature during the study period was 3.5°C. The minimum recorded daily temperature was -12.9°C and the maximum was 17.9°C. Mean annual precipitation in 2001 amounted to 500 mm. Snow cover persisted during 56 days from January to March 2001, with a maximum and mean snow depth of 13 and 3.1 cm, respectively.

Raven breeding density in Białowieża Forest was 13.8 pairs/100 km² in 1985-1994 (Pugacewicz 1997), declining to 6.0 pairs/100 km² in 2001 (Müller 2001). Raven nests are uniformly distributed and located mainly in the top of pines (Pugacewicz 1997, Müller 2001). Their breeding success is in general low; in 2001, 61% of raven pairs reared some young successfully (Müller 2001). Up to 74 subadult ravens were counted at the regular roost on the western edge of the forest in a pine stand close to a landfill site (see Fig. 1). The maximum size of a raven flock observed scavenging at carcasses in Białowieża Forest was about 50 individuals (Selva et al. 2003).

Material and methods

A total of 63 baits and carcasses were marked during the raven breeding season between 3 February and 23 May 2001. We experimentally placed 57 baits which consisted of ungulate entrails without rumen content (from bison, red deer and wild boar) obtained after hunting and culling activities (N = 20) or of dead chickens from a poultry farm (N = 37). Baits weighed either 20 (N = 19) or 10 kg (N = 38). In addition, five ungulate carcasses (one bison, two wild boar, one red deer and one cow),

found in the forest accidentally, and 40 chickens discarded close to a farm were also marked.

Each bait was marked with a distinctive type of marker, clearly different from the others. The markers were manually punched out of thin Polypropylene or Polyethylene foil and afterwards rubbed with the fingers to avoid them getting stuck in a pile. Standard markers had different shapes and colours and were 2.0-2.5 mm long. The 20- and 10-kg baits were provided with ca 8,000 (2.24 g) and 4,000 (1.12 g) markers, respectively. Markers were regularly scattered over the baits by hand. As ravens are known to be afraid of new and unknown objects (Heinrich 1988, 1995, Kotrschal et al. 2001), we tested whether ravens avoided taking the markers while eating flesh from the baits by providing 53 of the 57 experimental baits with a second type of larger marker. 'Large' markers were 3.0 mm large, round and of different colours. We buried 25 large markers separately one centimetre deep in the most attractive parts of each bait with the help of tweezers, to make them invisible to ravens.

The experimental baits were exposed around seven raven nests which were known to have good breeding success from previous investigations (N. Selva, pers. obs.; see Fig. 1). Baits for determining the territory of a given pair were exposed at sunrise at 3-day intervals, and left until depleted. The sites where the baits were placed followed a design to avoid habituation of ravens to the direction of bait exposition. The locations of baits and distances were measured with a Global Positioning System (GPS; Garmin 12). The first experimental bait was placed 1.0 km east of the nest. Each following bait was placed 300 m further away from the nest than the previous bait, and in a different direction clockwise. The first four baits were exposed in the main directions (east, south, west and north) and the following baits subsequently 45° clockwise from the location of the previous bait. Some baits (N = 29 pairs of baits) were placed at the same distance from the nest but in a different direction. The mean number of baits exposed at each nest was eight (range: 3-16). As more bait trials were conducted and more information became available about raven territory size, we reduced the amount of baits placed closest (1.0 km) to and farthest (i.e. 2.8, 3.1 and 3.4 km) from nests. Baits were inspected daily to record the tracks and signs of the scavenger species visiting the baits till complete consumption.

Raven pellets were collected every five days at the seven raven nests involved in the bait trials, and at six additionally found neighbouring nests which were occupied. Once per month, the roost of immature ravens was visited to collect pellets. Raven droppings at nests and the roost were also checked for markers on the site.

Table 1. Marker-type recoveries (in %) and total number of markers (of all types) recovered in relation to the place of marker retrieval. Markers were provided at baits (N = 57) and ungulate carcasses accidentally found (N = 6).

Place of marker retrieval	Marker-type recoveries			Number of markers recovered		
	Baits	Carcasses	All carrion	Baits	Carcasses	All carrion
Nests	59.6	33.3	57.1	646	7	653
Roost	0	33.3	3.2	0	10	10
Bait & carcasses	10.5	33.3	14.3	37	5	42
TOTAL	63.2	66.7	63.5	683	22	705

Pellets were carefully broken up and examined with a magnifier (©Eschenbach 6-10x). In total, 1,018 pellets (435 collected at the nests, 558 at the roost and 25 collected at carcasses) and 1,193 droppings (1,093 from nests, 100 from the roost) were checked for markers. 'Marker-type recoveries' were calculated as the percentage of baits whose markers were recovered in pellets or droppings; i.e., the portion of marker types retrieved from the total number of marker types provided. For every type of marker recovered, we calculated its 'recovery rate', defined as the percentage of markers of that type retrieved, from the total number of markers provided at the bait. The presence/absence of a given breeding pair, as determined by recoveries of the markers provided at baits and carrion located at different distances from the nest, was examined with a logistic regression analysis (Backhaus et al. 2000). We set the threshold at P = 0.5 in order to minimise the prediction error. This probability value is often taken as the cut-off level in studies of habitat use (e.g. Mladenoff et al. 1999). Data from all baits located up to 7,500 m from each of the 13 controlled nests were included in the analysis (N = 174). The significance level was set at 0.05.

To detect a possible influence of habitat characteristics on bait use by ravens, and thus in the recovery of markers, three habitat attributes were measured around bait locations. Tree density (number of trees/m²) was measured in a 400 m² (20 x 20 m) plot centred around the bait. The canopy cover was visually estimated at the bait location in a 10%-scale. In 4-ha plots centered at each bait, the main habitat type (farmland/opening/forest) was assigned using topographical maps (1:50,000). Moreover, presence and absence of snow on the day of bait exposition was recorded.

Results

Recovery of markers

Daily inspections of baits and carrion to register scavengers' tracks and signs, indicated that 89% (N = 56) of the experimental baits and marked carcasses were visited by ravens; 79% within the first 24 hours. The mean duration of complete bait-depletion by scavengers was 3.8 days. Baits weighing 20 kg lasted slightly longer (4.1 days) than 10-kg baits (3.7 days), although the differences were not significant (Mann-Whitney U-test: N_1 = 38, N_2 = 19, z = -0.266, P = 0.79). The presence of 15 scavenger species was recorded at the baits: raven, red fox *Vulpes vulpes*, buzzard *Buteo buteo*, dog *Canis familiaris*, jay *Garrulus glandarius*, magpie *Pica pica*, wild boar, raccoon dog, lesser-spotted eagle *Aquila pomarina*, wolf, pine marten *Martes martes*, white-tailed eagle *Haliaetus albicilla*, blackbird *Turdus merula*, cat *Felis catus*, and marsh harrier *Circus aeruginosus*. The raven was the most common scavenger at the experimental baits (86% of baits visited), followed by the red fox (40%).

A total of 705 markers were recovered (Table 1). No alteration of structure or colour was observed, and all markers were clearly assignable to their bait. Marker-type recoveries confirmed that ravens fed on 63.5% of baits and carcasses, and on 63.2% of experimental baits. Most markers were retrieved at the nests, whereas a small percentage was recovered at the roost and at the bait or carcass itself. Only 42 markers (6%) were recovered at the bait or carcass location, which means that 663 markers (94%) were transported by ravens, thus providing information on raven movements. Of the transported markers, 98.5% (N = 653 markers) were recovered at raven nests and 1.5% (N = 10 markers) at the communal roost of immature ravens (see Table 1). The percentage of marker-types recovered was significantly higher in pellets (N = 502 markers, 71.2%) than in droppings (N = 203 markers, 28.8 %; G-test, G = 18.56, df = 1, P < 0.001). On average, a marked pellet contained 4.40 markers and a dropping 1.53 markers. Markers of two different types were included in eight pellets, usually from baits exposed near in time (mean interval: 7.6 days), 24 days being the longest interval recorded.

The total number of markers of a certain type recovered from a single experimental bait varied between 1 and 114 and averaged 17.1 (Table 2). A total of 641 standard markers were recovered from 31 of the 53 baits

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Table 2. Comparison of recovery data for standard and large markers, provided together at 53 experimental baits. The recovery data include percentage of baits with recovered markers (marker-type recoveries), maximum number of markers of one type recovered from a single bait, mean number of markers of one type recovered from the total number provided (recovery rates), and number of markers retrieved (total, in droppings and in pellets).

| | Markers | |
Recovery data	Standard	Large
Marker-type recoveries (%)	58.5	13.2
Maximum number of markers of one type recovered	114	3
Mean recovery rates (%)	0.24	0.66
Total no. markers recovered	641	9
Number of markers recovered in droppings (N = 193)	190	3
Number of markers recovered in pellets (N = 457)	451	6

marked with both types, whereas only nine large markers were recovered from seven baits. Marker-type recoveries were significantly higher for standard (58.5%) than for large markers (13.2%; G-test, G = 30.92, df =1, P < 0.001). Large markers were always retrieved together with their corresponding standard marker. The number of standard and large markers recovered was higher in pellets than in droppings. Recovery rates of standard markers averaged 0.24 ± 0.45 (mean ± SD), and were lower than for large markers (0.66 ± 2.02; see Table 2). However, no statistical differences were found among recovery rates of either marker type at the same bait (Wilcoxon test: z = -1.058, P = 0.290). The mean recovery rates of markers from chicken (0.22%) and from ungulate entrail baits (0.45%) were statistically similar (t-test: t = 1.214, df = 34, P = 0.223). Differences in the weight of baits did not lead to statistically different mean recovery rates (t-test, t = 1.31, df = 55, P = 0.067). The presence of snow also did not affect the rates of marker recovery (Mann-Whitney U-test: N_1 = 12, N_2 = 45, z = -0.152, P = 0.879).

Territory size and spatial use of carrion

Recoveries of markers at nests showed that baits were utilised by a raven pair up to a maximum distance of 5,580 m. There were highly significant differences in the mean distance from the nest between baits whose markers were recovered (1,776 ± 871 m, mean ± SD) and baits whose markers were not recovered (4,305 ± 1,844 m; t-test: t = 8.087, df = 172, P < 0.001). The proportion of baits utilised by a raven pair (as confirmed by marker-type recoveries) declined with increasing distance of the bait from the nest (Fig. 2). Although the recovery rate was higher in markers provided at baits located closer to the nests, the correlation with the distance was not significant ($r_{Spearman}$ = -0.297, P = 0.079).

Logistic regression analysis showed that the distance from the bait to the nest was an excellent predictor of bait utilisation by ravens. Distance from the nest explained 84.5% of the variation in bait use by the corresponding raven pair. The probability of ravens feeding on a bait significantly decreased with longer distance from the nest (Intercept = 2.785, β = -0.002, SE = 0.0,
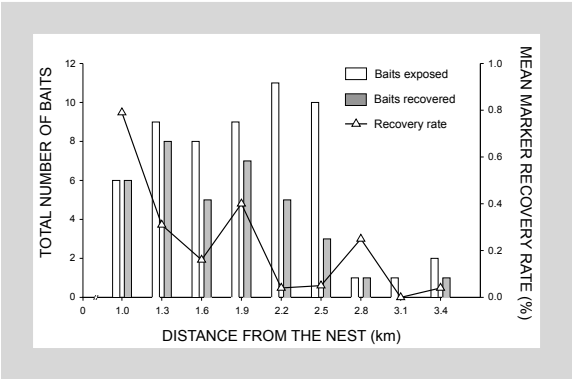

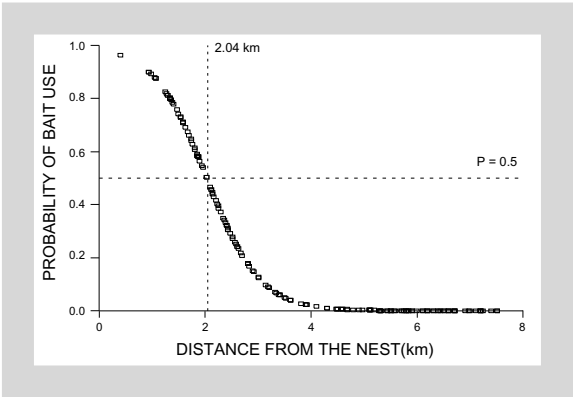Figure 2. Total number of marked baits involved in the trials (N = 57), number of these baits whose markers were recovered (marker-type recoveries), and mean recovery rate (in %) of markers in relation to the distance of the bait from the respective nest (in km).

Figure 3. Logistic regression curve (P = 1/(1+e $^{-2.785 + 0.002\ distance}$) indicating the probability of raven feeding on a bait (according to marker-type recoveries) in relation to the distance (in km) from the nest. The theoretical limit of the raven territory was set at P = 0.5.

$\chi^2 = 69.597$, $P < 0.001$). A threshold value of 2,040 m indicated the most probable edge of the main foraging area used by ravens (Fig. 3). Further away than 2,040 m, the probability that a raven pair visited and fed on a bait declined drastically. Data on marker recoveries from the pairs of baits placed at the same distance but in different directions agreed with the assumed round shape of raven territories. Nine pairs of baits came to lie within the estimated territorial area. Markers from the two baits of the pair were recovered in seven cases (78%), from only one of the baits in one case (11%), and from none in one case also (11%). From this fact and the known uniform distribution of breeding pairs, we estimated the raven territory size in Białowieża Forest to be 13.1 km². Baits located inside the estimated territory were used more frequently by the respective pair (77.8%), whereas the use of baits by the corresponding raven pair at longer distances was rather improbable (22.2%), and happened only on nine occasions, never exceeding 5,580 m. All these cases were related to the simultaneous presence of large flocks of immature ravens (44% of cases) and/or to large open habitats, mainly farmland (78%).

Inside raven territories, no differences in tree density and canopy cover were found between baits used and not used by the pair, according to marker recoveries (Mann-Whitney U-test, $N_1 = 17$, $N_2 = 28$, $z = -0.025$, $P = 0.980$ for canopy cover; $z = -0.099$, $P = 0.921$ for tree density). Outside the theoretical raven territory, i.e. further than 2,040 m from the nest, more of the baits used by the corresponding raven pair were situated in large open areas, although the differences were not significant (Mann-Whitney U-test, $N_1 = 105$, $N_2 = 9$, $z = -1.744$, $P = 0.081$ for canopy cover; $z = -1.576$, $P = 0.115$ for tree density). The mean marker recovery rate from baits situated in different habitat types ranged from 0.12% (SD ± 0.31) in forest openings to 0.19% (SD ± 0.39) inside the forest and 0.31% (SD ± 0.54) in open farmland.

The use of baits by two neighbouring pairs was documented on two occasions. These cases coincided with bait location at open landscapes and at the supposed territory borders. Only in one case, did flocks of immature ravens make use of an experimental bait that was placed close to a large ungulate carcass (a wolf kill), regularly visited by a raven flock. A total of 10 markers were recovered at the communal roost. These markers corresponded to two carrion baits: 40 chickens discarded close to a poultry farm 350 m from the roost and a cow exposed at a river valley inside the forest 14,900 m from the roost.

Discussion

Our study confirms the validity of the bait-marking method to estimate the territory size of ravens and also to investigate their movements. Our three initial assumptions were met and artificial bait exposing and plastic markers did not repel ravens in Białowieża Forest. Most markers were retrieved at the nests, and transported from the place of provisioning, thus providing information on both foraging area and behaviour. This technique may be applicable to other raven populations, as well as to other bird species, mainly raptors, which are known to scavenge to a certain extent. This method does not require any special equipment and it is relatively inexpensive. Moreover, it should not be labourious or time consuming. Although we conducted frequent visits to the nest in order to test the method, they could be reduced to one final control at the end of the breeding season, also to minimise possible disturbances. An additional visit in the middle of the breeding season is recommended to check whether the pair failed and trials should stop. The time interval between bait exposures, as well as the number and size of baits, should be estimated in relation to the scavenging efficiency of the target species, the bait depletion time and the other scavenger species present in the study area. In some cases, the habitat preferences of the species might be taken into account.

The bait-marking method seems very promising in species highly dependent on carrion and quite appropriate in the case of ravens, as also shown by Wright et al. (2003). Ravens are known to be highly efficient in discovering carcasses in cold climate regions (Heinrich 1990, Promberger 1992, Stahler et al. 2002, Selva et al. 2003). Of the exposed baits, 79% were visited by ravens in the first 24 hours. Their frequency of scavenging on the baits was quite similar to the data obtained by Selva et al. (2003) using bison carcasses. Only two baits (3.5%) were depleted by non-target species or immature ravens before the tested raven pair could discover it. Regarding the weight classes the data showed that 20-kg baits lasted slightly but not statistically longer than 10-kg baits. Although higher portions of indigestible contents in the bait, such as feathers, may lead ravens to produce more pellets, there were no differences in marker recoveries between bait types. The presence or absence of snow (contrast of flesh/blood) and the habitat characteristics (tree density and canopy) did not affect the use of carrion by ravens, and thus the effectiveness of the method. Our data also suggest that adult pairs have good knowledge of their territory and inspect it intensively. Raven territorial activity is at its peak in the breeding season (Boarman & Heinrich 1999, Delahay et al. 2000),

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so long-term or year-round surveys based on this method might result in different size of the raven foraging area.

The success of the bait-marking method lies in the excretory behaviour of the birds. Marker recoveries might be highly dependent on the number of pellets or droppings available at nests. We observed an enormous variation in the number of pellets (5-257) found at different raven nests. Even in the case of some pairs which reared up to five young, it was hardly possible to find pellets or even droppings under the nests. Thus, the number of marked pellets cannot reliably be used as an indicator of the intensity of raven activity at the bait. We recommend checking for markers not only in pellets, but also in droppings and even on branches that have fallen from the nests. Standard markers (ca 2 mm long) in large quantities (as a precaution against bait consumption by non-target species) are suggested and a proportion of 400 markers per kg of bait seems appropriate. On average, one marked pellet contained four markers, and 17 markers were retrieved from a single bait. Often, the markers were still squashed in small piles of two to five each when recovered, but counted as one, so the actual figures might be higher. The relatively high mean number of markers found in pellets indicated that when a raven fed on a marked bait, there was a high probability of recovering the markers at its nest.

At least 63% of marker types were recovered in pellets and droppings, and this figure increased to 76% when considering only the baits exposed inside the estimated raven territory. Wright et al. (2003) retrieved beads from all baited carcasses (100% marker type recovery), but no information was provided on the recovery rates. Data on marker retrieval from other studies are not always comparable, due to the different methodology. However, our marker type recovery results are quite similar to those obtained in raccoon dog studies, where the bait-marking method is considered a standard research technique: 88% (Ikeda 1984); and 9-69% (Ikeda et al. 1979). Studies on other mammals, such as woodrats (Henke & Smith 2000), and on birds (Southern & Lowe 1968, Schramm 1974) showed lower marker retrieval, 1-21% and 8-10%, respectively. The recovery rates of markers in our study were quite low, thus suggesting that other scavengers or non-target ravens ingested an important part of the bait, that many markers were not ingested, and/or that only a small part of the markers ingested by ravens were recovered.

Raven territory size estimated from the bait-marking method is in good agreement with the results from the parallel study by Müller (2001). Following standard procedures, Müller (2001) investigated the breeding density in plots and the nearest-neighbouring distances of raven pairs, obtaining a mean territory size of 13 km^2. The similar results obtained with the two methods illustrate the potential of bait-marking experiments in estimating main foraging areas of birds. A good correspondence between home-ranges obtained from bait-marking experiments and telemetry was also found in some studies on badgers (Kruuk 1978, Cheeseman & Mallison 1979, Parish & Kruuk 1982, Roper et al. 1986). Size of raven territories highly varies in relation to habitat, from 75 km^2 in the upland deer forest in Scotland (Ratcliffe 1997) to 24 km^2 in open grassland in Wales (Dare 1986) or 8 km^2 at coastal lines in California (Linz et al. 1992). Only few studies (Linz et al. 1992, Oggier 1986) provide data on the territorial area of individually marked ravens (telemetry or observations); most of them in rather open environments. To our knowledge, our study provides the first data on the territory size of breeding raven pairs in dense forests.

Interesting data on territorial and foraging behaviour, not only of breeding pairs but also of immature ravens, might also be obtained from bait-marking experiments (Wright et al. 2003). Marker recoveries at the communal roost indicated that immature ravens fed on a dead cow exposed at a river valley, almost 15 km from the roost. In Białowieża Forest, there was clear habitat separation between pairs and groups of immature ravens scavenging on bison carcasses. The immature birds fed in flocks and exclusively in open areas (Selva et al. 2003). We documented a territorial pair trespassing a neighbouring territory to feed on that same cow, 6 km from their own nest. Pairs might camouflage in these flocks to attend big food bonanzas, as territorial pairs give up defending carcasses inside their territories when the raven group size exceeds 20 individuals (Heinrich 1990). As determined by marker-type recoveries, incursions of pairs into neighbouring territories (outside the given threshold) and simultaneous use of some baits by two raven pairs, suggested some territory overlap in the breeding season. These cases of overlapping were mainly connected to large open habitats. Pellets with two types of markers could be explained by markers being retained in the gizzard for longer time, but also by the prevalence of caching in raven foraging behaviour. Although memory of cache sites declines after 14 days in ravens (Heinrich & Pepper 1998), we observed a raven cache being recovered after 24 days.

To sum up, the bait-marking technique may be applicable in studies of other raven populations and scavenging birds. In this first study, it has been proven to be an accurate and efficient method to investigate territory size and pair distribution during the breeding season, as well

as movements and foraging behaviour, especially of avian species which show some communal and gregarious behaviour. Further studies on this method are necessary to check its potential as a standard research procedure.

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