Assessing the breeding season diet of goshawks *Accipiter gentilis*: biases of plucking analysis quantified by means of continuous radio-monitoring

Christian Rutz

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.

Abstract

Plucking analysis is a standard method for assessing the breeding season diet of goshawks *Accipiter gentilis*. Results may be biased, however, due to differences in the detectability of remains of certain prey species and to selective prey transportation by hawks. This study investigated prey choice of three goshawk breeding pairs in the city of Hamburg, Germany, during 1997–99. Predation data obtained by continuous radio-monitoring of the adult males were used to quantify biases of simultaneous plucking analyses, which were conducted in the nesting territories of the corresponding breeding pairs. A comparison of estimated average food requirements with actual biomass intake observed in two of the monitored goshawks (with sufficient sample sizes) indicated that it was possible to record virtually all kills that occurred during tracking sessions. Therefore, radio-tracking data could be used to evaluate the accuracy of plucking analysis. Comparisons showed that the proportions of small birds and of feral pigeons *Columba livia f. domestica* were underestimated by the scanning method by 10% and 13%, respectively. The latter finding was unexpected as pigeons have large, conspicuously coloured feathers that are easy to detect. However, as goshawks plucked large prey more thoroughly at the capture site than smaller prey, a comparatively small number of their feathers were present in the nesting areas. This source of bias in plucking analysis has passed unnoticed in previous studies. It may have important implications for the interpretation of results of future projects that aim to estimate predation rates in goshawks and other bird-eating raptor species.

Key words: northern goshawk, *Accipiter gentilis*, plucking analysis, continuous radio-tracking, diet choice

INTRODUCTION

The feeding ecology of the goshawk *Accipiter gentilis* has been the subject of thorough investigation during the past decades (reviewed in Cramp & Simmons, 1980; Fischer, 1995; Squires & Reynolds, 1997). A wide range of different methods have been used to document the food habits of this raptor, including: direct observations at nest sites from hides (Holstein, 1942; Schnell, 1958; Sulkava, 1964; Boal & Mannan, 1994; Mañosa, 1994), video-monitoring (Grønnesby & Nygård, 2000), nest-surveys (Sulkava, 1964; Mañosa, 1994), caging of young in the nest (Höglund, 1964; Sulkava, 1964), pellet analysis (Brüll, 1984; Mañosa, 1994) and stomach analysis (Bittera, 1916; Höglund, 1964). Additionally, systematic radio-monitoring has been used for assessing predation by goshawks in the non-breeding season (Kenward, 1977, 1979; Ziesemer, 1983; Widén, 1987; Tornberg & Colpaert, 2001).

The technique used most often, however, is plucking analysis, in which a defined area of the nesting territory is scanned systematically for prey remains (e.g. Sulkava, 1964; Opdam *et al.*, 1977; Brüll, 1984; Toyne, 1998). Pluckings are comparatively easy to find by this method during the breeding season as the provisioning adults carry prey to the nest site and remove feathers and hair before feeding their young (Brüll, 1984; Fischer, 1995; Squires & Reynolds, 1997). However, diet lists that are obtained by remnant-scanning are suspected to be biased for several reasons (reviewed by Sulkava, 1964; Newton & Marquiss, 1982; Bijlsma, 1997; Toyne, 1998).

There are two main sources of bias: (1) researchers may detect large and pale prey remains more easily than small or dark items (Errington, 1932; Opdam *et al.*, 1977; Ziesemer, 1981; Newton & Marquiss, 1982); (2) prey delivered to the nest may be an unrepresentative sub-sample of the actual diet (Newton & Marquiss, 1982; Bijlsma, 1997). Small prey may not be worth carrying to the nest if its energetic value lies below a certain threshold (load–size effect: Stephens & Krebs, 1986; Sonerud, 1992). On the other hand, some prey can be too heavy for transportation (Schnurre, 1934; Sulkava, 1964) and might get lost between successive transport flights as a result of scavenging (Kenward, 1977; Kenward,

E-mail: Christian.Rutz@zoo.ox.ac.uk

Table 1. Summary of radio-tracking information for three adult male goshawks *Accipiter gentilis* monitored in the city of Hamburg in the period 1997–99. Data of simultaneous plucking analyses are also given. Prey weights are presented as means $\pm$ 1 SD

	Male-1[a]	Male-2	Male-3	Pooled data
Year of data collection	1997	1998	1999	–
Nest site habitat	Public park	Hospital ground	Cemetery	–
Age of breeding male	4	3	$\geq$ 5	–
Juveniles in year of data collection	3	3	4	–
Trapping date	16 Feb	22 Feb	16 Apr	–
Monitoring period[b]	18 Feb–12 Jul	26 Feb–15 Jul	25 Apr–13 Jul	–
Tracking sessions	30	33	14	77
Total tracking time (hours)	371	333	154	858
Standard radio-fixes	1980	1940	871	4791
Total no. of identified prey	138	109	77	324
No. of radio-tracking prey[c]	69	36	17	122
of which feral pigeons	24	18	9	51
Prey weight (radio-tracking) (g)[c]	190 $\pm$ 103	289 $\pm$ 224	220 $\pm$ 94	223 $\pm$ 153
Prey weight (corrected scanning data) (g)[d]	219 $\pm$ 120	340 $\pm$ 301	216 $\pm$ 161	262 $\pm$ 220

[a] Abbreviations used for the individual males are the same as in the text.
[b] Data collection ended when the tail feather with the transmitter-unit was moulted.
[c] Dataset (R) according to nomenclature of Fig. 1.
[d] Dataset (S-[R,S]) according to nomenclature of Fig. 1.

Marcström & Karlbom, 1981; Ziesemer, 1981, 1983). Selective plucking of prey at capture sites before transportation to the nesting territory can also result in biased diet estimates (see Sulkava, 1964; Sodhi, 1992).

Explicit quantitative investigations of biases inherent in different methods of diet analysis have been reported for eagles (Real, 1996; Seguin *et al.*, 1998), harriers (Simmons, Avery & Avery, 1991; Redpath *et al.*, 2001) and falcons (Oro & Tella, 1995; Jenkins & Avery, 1999). So far, five studies have addressed methodological problems of assessing goshawk diets (Sulkava, 1964; Kenward *et al.*, 1981; Ziesemer, 1981, 1983; Mañosa, 1994; Grønnesby & Nygård, 2000). Sulkava (1964), Mañosa (1994) and Grønnesby & Nygård (2000) tried to establish the accuracy of plucking analysis by continuously observing prey deliveries at nests. Although it is often assumed that results obtained by direct observation are the least biased (Marti, 1987; Mañosa, 1994; Oro & Tella, 1995), such data will still be inaccurate if an unrepresentative cross-section of the diet is transported to the nest site. The only method that potentially circumvents both of the main sources of bias is systematic or continuous radio-monitoring (see Sonerud, 1992).

Kenward *et al.* (1981) compared kills found by radio-monitoring with diet lists obtained by stomach analyses, and Ziesemer (1981, 1983) used radio-tracking data to investigate possible errors of the scanning method for assessing predation rates in wintering rural goshawks. The present study followed the latter approach and applied it for the first time to breeding individuals. Three radio-tagged male goshawks were monitored continuously during half- and full-day tracking sessions in the city of Hamburg, Germany. A comparison of observed biomass intake with an estimate of average food requirements indicated that it was possible to record virtually all their kills during monitoring sessions. This justified the use of radio-tracking results for estimating biases in prey lists, which had been compiled simultaneously by scanning

the nesting territories of the corresponding pairs for pluckings. Prey selection of the goshawks investigated is described in detail elsewhere (Rutz, 2001; Rutz, in press).

METHODS

Study area and subjects

The study was carried out from 1997–99 in the city of Hamburg, Germany (53°34′N, 9°59′E). In each year, prey choice of a single urban goshawk pair was investigated during the breeding season (Table 1). All 3 pairs successfully raised young in the year of data collection. Hatching dates were calculated from weights and wing lengths of nestlings at the time of ringing (Kenward, Marcström & Karlbom, 1993; tabulated values from Bijlsma, 1997). For a detailed description of nest sites and breeding individuals see Rutz (2001).

Radio-tracking

The males of the 3 breeding pairs were trapped near the nest using spring-net traps (Karlbom, 1981) and instrumented with 16-g, tail-mounted radio-transmitters (TW-3 1/2-AA, 150 MHz-band, Biotrack Ltd, Dorset, U.K.; for tagging method see Kenward, 1978). Tags were equipped with activity-sensing switches that altered the pulse rate of the radio-signal according to the activity of the birds (Kenward, 1987). It was possible to distinguish between perching, inter-perch flight, soaring and plucking by signal interpretation without seeing the tagged hawk itself.

Birds were tracked continuously for half or full days (from dawn to dusk) at least once a week. Data were collected on all weekdays and during daylight hours to control for possible changes in goshawk hunting behaviour resulting from different levels of human disturbance. Fixes
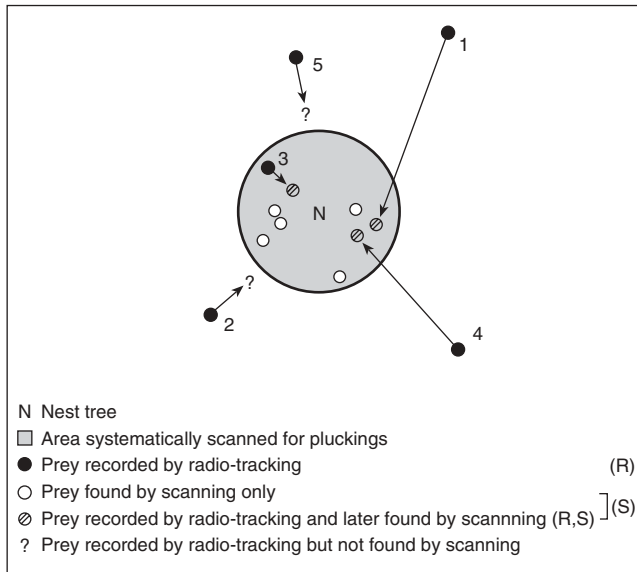
Fig. 1. Different datasets used to estimate the accuracy of plucking analysis for assessing the breeding season diet of goshawks *Accipiter gentilis* in the city of Hamburg. Nest of a breeding pair (N) and all prey collected during a hypothetical sampling day are shown. The male of the pair was radio-tagged and monitored continuously from dawn to dusk to record all its kills ([R]; kills 1–5). At the end of the tracking session, the inner nesting area (circle around nest with radius *r* = 100 m; grey shaded area) was systematically scanned for prey remains (S). Some prey recorded during radio-tracking were also individually identified as pluckings by comparing feather samples ([R,S]; kills 1, 3 and 4). Not all prey collected by radio-monitoring were also found by scanning (' ?'; kills 2 and 5) and vice versa (open circles). All prey in the scanning area (S) were removed at the end of the day to avoid counting items twice. Proportions in the figure not to scale.

were made at 10-min intervals by cross-triangulation (Kenward, 1987) or by homing in on the bird (White & Garrott, 1990) using a portable M-57 receiver (Mariner Radar Ltd, Suffolk, U.K.) and a 3-element hand-held Yagi antenna.

Usually hawks were followed by an observer on a bicycle. Occasionally, when birds travelled distances >1.5 km, they were searched for using a car with a roof-mounted dipole antenna. Compared to rural goshawks, the individuals in this study were remarkably tolerant towards human disturbance. It was possible to approach perched hawks as close as 20 m without disturbing them (Rutz, 2001). The tameness of the goshawks, together with the good infrastructure of the city, made it possible to keep in close contact with the tagged birds. Fifty-two per cent of all standard fixes (*n* = 4791) were based on direct observations.

Feeding hawks were located precisely (Kenward, 1979; Ziesemer, 1981, 1983; Widén, 1987; Tornberg & Colpaert, 2001). The duration of plucking was timed to the nearest minute. After goshawks flew off, their prey was identified from plucking remains (prey recorded by radio-monitoring henceforth referred to as [R]; see Fig. 1 for a

detailed illustration of the sampling protocol). Feathers of killed birds were collected and compared to fresh feathers of the same species that were found with the scanning method (see below) on the same day. Careful comparisons regarding feather position, coloration, length and general appearance allowed identification of individual pluckings as prey that had been recorded during the preceding radio-tracking session (prey recorded by radio-tracking and later found by scanning, [R,S]). Data on distance of kills from nests are given in Rutz (2001).

Plucking analysis

Pluckings were collected in the nesting territory at the end of each radio-tracking session. The ground was scanned systematically (Marti, 1987; Bijlsma 1997) covering an area of *c*. 3 ha (100 m-radius around the nest; prey found by scanning, [S]). The size of the sampled area was sufficient as nest stands of urban-breeding goshawk pairs are remarkably small and the majority of remains can be found very close to the nests.

Three precautions were taken to avoid double-counting of prey items: (1) all prey remains were removed after counting (Bijlsma, 1997); (2) primaries, secondaries and rectrices were collected, counted and compared in an attempt to separate scattered feathers of different individuals from the same species (Sulkava, 1964; Opdam *et al*., 1977; Reynolds & Meslow, 1984; Bijlsma, 1997); (3) bones and pellets were omitted from the analysis (see also Widén, 1987), as the numbers of individuals identified from these remains were lower than the corresponding values obtained from pluckings for all recorded prey species (see Sulkava, 1964; Grønnesby & Nygård, 2000). Single feathers were not recorded as they may have come from moulting birds (Boal & Mannan, 1994).

Data collection was restricted to the time periods of radio-tracking (Table 1). Ninety-five per cent of all prey items used in the diet analysis were identified to the species level. The remaining prey were at least seen when hawks carried them to the nest site. They were categorized as being smaller or larger than the size of a blackbird *Turdus merula* (see footnotes in Table 2). Unidentified prey (*n* = 24) were considered in the description of plucking behaviour and prey transportation, but omitted from all analyses regarding diet composition. During radio-tracking sessions, only prey killed by the tagged males were recorded (R). In contrast, the plucking list (S) potentially contained prey delivered to the nest site by both sexes. It also included kills from days with no radio-tracking sessions.

Prey weights

Prey weights were taken from Dietrich (1982), März (1987), Collar (1997) and Toyne (1998), and weight classes were adopted from Toyne (1998). Killed birds were classified as adults, fledglings and nestlings according to the growth stage of their feathers, using definitions from Newton & Marquiss (1982) with minor modifications

(see Rutz, 2001). The mass of fledglings and juvenile mammals was calculated as being two-thirds of the adult weight (Opdam, 1975; Newton & Marquiss, 1982; Toyne, 1998). Nestlings were assigned a weight of one-third of the corresponding adult weight (see Grønnesby & Nygård, 2000).

Average daily biomass requirements

The average daily food consumption (for simplicity, food is conservatively assumed to be pure meat) of goshawks is *c*. 130 g for males, 190 g for females (Kenward *et al*., 1981) and 200 g for juveniles (Heinroth, 1927; Uttendörfer, 1939). This gives an average daily meat requirement per pair of 320 g for the time before hatching of young ($= 1$ male$_{ad.} + 1$ female$_{ad.}$) and of 920 g for the period after hatching ($= 1$ male$_{ad.} + 1$ female$_{ad.} + 3$ juvs.). Assuming that goshawks can use *c*. 75% of the biomass of killed prey (in birds: feathers + skeleton $\sim 16\%$ of body weight; Bezzel & Prinzinger, 1990; see also Brody, 1945), average daily biomass requirements for the 2 periods can be estimated as being 425 g and 1225 g, respectively.

As all values from Kenward *et al*. (1981) refer to Scandinavian individuals, which are *c*. 25% heavier and live in a much harsher environment than birds from Western Europe (Fischer, 1995), the above figures were rescaled. It was estimated that the investigated hawks needed on average 15% less biomass than their larger Scandinavian counterparts, yielding corrected average daily biomass requirement figures of 360 g and 1040 g, respectively. This reduction was derived from the scaling relation between body mass and standard rate of metabolism (Bezzel & Prinzinger, 1990; McNab, 2002). Test results for both sets of predicted values are reported. Biomass intake was computed for full days only, on which all prey items could be identified to species level.

Data analysis

As a first step, estimated average biomass requirements (see above) were compared to observed daily biomass intake to measure the accuracy of radio-monitoring for assessing diets of the tagged males.

Radio-tracking data (R) were then used to investigate potential biases of the scanning method. Diet composition was analysed for prey species and prey weight. For each category, 4 comparisons were made (see Fig. 1):
(1) (R) *vs* (R,S) was considered to be the most direct and powerful test of the accuracy of plucking analysis. However, as the 2 samples were statistically dependent (all [R,S]-prey were also included in the [R]-sample), only a qualitative comparison was made;
(2) in (R-[R,S]) *vs* (R,S), samples were rendered 'independent' by excluding all (R,S)-prey from the radio-tracking list (R);
(3) (R) *vs* (S) investigated discrepancies between the complete scanning dataset and prey choice of males, as measured by (R). Again, no statistics could be applied, because (S) contained (R,S)-prey;

(4) (R) *vs* (S-[R,S]) was an attempt to make the plucking list (S) 'independent' of the radio-tracking data (R).

For (2) and (4), distributions were compared with χ^2-tests on contingency tables. Testing was assumed to be secure at $\alpha = 0.01$, when the average expected frequency was at least 10.0. In 1 case ([R-(R,S)] *vs* [R,S] for prey species), the average expected frequency was 6.1, and it was therefore tested at a significance level of $\alpha = 0.05$ (Zar, 1999). Note that the samples (S) and (S-[R,S]) may also have contained kills of the females.

As both diet lists ([R] and [S]) were sampled by the same observer, the accuracy of (S) was biased: it is most likely that some pluckings were found only by scanning, because they had been expected on the basis of that day's radio-tracking results. However, as this same-observer bias made the lists (R) and (S) more similar to each other, it was conservative for detecting a difference. Conversely, comparing (R) *vs* (S-[R,S]) slightly biased in favour of recording a difference, because an unbiased observer would presumably have missed some (R,S) (i.e. too much [R,S] was removed from [S]).

Weight and duration data did not follow normal distributions. In all but 1 case, standard transformations failed to normalize data and non-parametric tests were applied (1-sample Wilcoxon signed rank test; Mann–Whitney *U*-test, adjusted for ties Spearman rank correlation; Kruskal–Wallis ANOVA). One comparison could be made with a *t*-test on log-transformed data. All tests were 2-tailed, and results were considered significant at $\alpha = 0.05$. Throughout, the results are presented as arithmetic means with standard deviations ($\bar{x} \pm 1$ SD) (even in the context of non-parametric statistics).

In a strict statistical sense, the samples obtained by different methods in this study cannot be independent, because prey in both samples were killed by the same 3 individuals. However, the approach used in this paper is the only way of handling this type of data for bias estimations (see also Simmons *et al*., 1991; Oro & Tella, 1995; Real, 1996; Seguin *et al*., 1998; Jenkins & Avery, 1999; Redpath *et al*., 2001).

RESULTS

Accuracy of radio-monitoring for recording kills

In male-1, daily biomass intake was significantly higher after young had hatched (727 ± 303 g, $n = 6$ days) than in the time before (399 ± 147 g, $n = 11$; *t*-test on log-transformed data: $t_{15} = -3.158$, $P = 0.006$). There was no significant difference between the median biomass intake observed during radio-monitoring and predicted daily food requirements in both time periods (one-sample Wilcoxon signed rank test [values for comparisons with rescaled biomass estimates in brackets]: before hatching, $n = 11$, $T_+ = 23.5$ [39.0], $P = 0.424$ [0.625], NS; after hatching, $n = 6$, $T_+ = 1.0$ [2.0], $P = 0.059$ [0.093], NS). For male-2, no significant difference was found between observed (614 ± 708 g) and estimated biomass intake for the time before hatching (one-sample Wilcoxon signed

Table 2. Diet of goshawks *Accipiter gentilis* breeding in the city of Hamburg (1997–99). Data were collected by continuous radio-monitoring of three adult males (R) and by systematically scanning nest sites of the corresponding pairs for prey remains at the end of tracking sessions (S). Some items were found by both methods (R,S). Datasets (R-[R,S]) and (S-[R,S]) mentioned in the text were obtained by excluding all (R,S)-prey from the lists (R) and (S), respectively. For methodological details see Fig. 1 and text. Diet lists of the three individuals and pairs were pooled. Data were classified by: (a) prey species; (b) body weight (g)

Dataset	Prey recorded by radio-monitoring tagged males (R)		Prey found by scanning nest sites of the pairs (S)		Prey recorded by radio-tracking and later found by scanning (R,S)	
Classification	*n*	%	*n*	%	*n*	%
(a) Feral pigeon	51	42	78	33	9	29
Other pigeons	1	1	12	5	1	3
Magpie	17	14	41	18	5	16
Jay	6	5	10	4	3	10
Starling	7	6	13	6	3	10
Blackbird	8	7	34	15	5	16
Other small birds[a]	16	13	8	3	1	3
Other large birds[b]	5	4	18	8	1	3
Rabbit	8	7	17	7	3	10
Other mammals	3	2	2	1	0	0
(b) 0–40 (i)	0	0	4	1	0	0
41–80 (ii)	19	16	30	13	8	26
81–160 (iii)	28	23	50	22	6	19
161–320 (iv)	71	58	127	55	14	45
321–2000 (v)	4	3	22	9	3	10
Total	122	100	233	100	31	100

[a] Birds ≤ blackbird in size, which were not identified to species level (*n* = 15), were assigned a weight of 90 g.
[b] Birds > blackbird in size, which were not identified to species level (*n* = 3), were assigned a weight of 200 g.

rank test: $n = 7$, $T_+ = 13.0$ [13.0], $P = 0.933$ [0.933], NS). These results indicated that radio-monitoring gave reliable diet lists (R). A similar test for the time after hatching was impossible for male-2, because a high proportion of days with at least one unidentified prey item resulted in an insufficient sample size ($n = 2$ days). For the same reason, data from male-3 could not be used. There was, however, no significant difference in the number of kills (identified and unidentified pooled) recorded per full day for the three hawks (Kruskal–Wallis ANOVA: $n_{male-1} = 21$, $n_{male-2} = 16$, $n_{male-3} = 6$, $H_2 = 3.320$, $P = 0.190$, NS).

Plucking behaviour and transportation of prey

In 98% of all unambiguous cases ($n = 136$; data pooled across birds), hawks started plucking at or near the capture site. Duration of plucking showed a highly significant positive correlation with prey weight (Spearman rank correlation: $n = 91$, $r_s = 0.633$, $P < 0.001$). In particular, hawks plucked adult feral pigeons *Columba livia f. domestica* (estimated body weight = 300 g) for significantly longer (66 ± 70 min, $n = 45$) than all lighter prey (14 ± 18 min, $n = 45$; Mann–Whitney *U*-test, adjusted for ties: $U = 242.0$, $P < 0.001$). Visual inspection of pluckings at capture sites further confirmed that hawks prepared large prey more thoroughly than small prey. In 86% of 124 cases, goshawks flew off with their kill in

the direction of the nest site. Less than a third ($n = 31$) of these transported prey items were found with the scanning method at the end of tracking sessions (Table 2). Only a few recorded prey were consumed at or near the site of the kill ($n = 13$; instances where the hawk was disturbed were excluded). Considering only the sample of identified items, consumed prey (277 ± 70 g, $n = 9$) were significantly heavier than transported kills (222 ± 166 g, $n = 97$; Mann–Whitney *U*-test, adjusted for ties: $U = 268.5$, $P < 0.05$).

Accuracy of plucking analysis

Prey species

The apparent similarity between the datasets (R,S) and (S) (see Table 2a) indicated that (R,S) was a representative sub-sample of the plucking list (S). Scanning gave a biased picture of actual prey choice ([R] *vs* [R,S]; Table 2a). The largest discrepancies were found for the proportions of feral pigeons and 'small birds'. Scanning underestimated their contribution by 13% and 10%, respectively. On the other hand, the proportions of blackbirds and jays *Garrulus glandarius* were overestimated by plucking analysis (9% and 5%, respectively). There was a significant difference in the frequency distributions of prey species for the corrected radio-tracking dataset and the (R,S)-sample ([R-(R,S)] *vs* [R,S]; χ^2-test: $\chi^2_9 = 18.361$,

$P < 0.05$; Table 2a). Comparing (R) *vs* (S) revealed discrepancies > 5% for the same prey species as (R) *vs* (R,S) (except for jays), which also pointed in the same direction and were of similar magnitude (see above; Table 2a). Again, the contributions of feral pigeons and 'small birds' were smaller in the plucking list (9% and 10%, respectively). Diet composition was significantly different between methods ([R] *vs* [S-(R,S)]; χ^2-test: $\chi^2_9 = 23.983$, $P < 0.01$; Table 2a). Proportions of feral pigeons killed by individual males during radio-monitoring sessions did not show significant differences (χ^2-test: $\chi^2_2 = 3.259$, $P = 0.196$, NS; Table 1). This demonstrated that the above comparisons were robust despite the comparatively small sample size of only three investigated pairs and the necessity to pool data across subjects.

Prey weight

For all three individuals there was no statistically significant difference in median prey weights, as calculated from items found by radio-monitoring and scanning, respectively ([R] *vs* [S-(R,S)]; Mann–Whitney *U*-tests, all adjusted for ties: male-1: $n_R = 69$, $n_{S-(R,S)} = 69$, $U = 2034.5$, $P = 0.131$, NS; male-2: $n_R = 36$, $n_{S-(R,S)} = 73$, $U = 1290.0$, $P = 0.875$, NS; male-3: $n_R = 17$, $n_{S-(R,S)} = 60$, $U = 432.5$, $P = 0.335$, NS; pooled data: $n_R = 122$, $n_{S-(R,S)} = 202$, $U = 11660.5$, $P = 0.406$, NS; Table 1). The distribution of prey over five weight classes was similar for the two methods ([R] *vs* [R,S]; Table 2b). Scanning overestimated the contribution of prey in the second lowest class (ii) by 10% and underestimated that of items in class (iv) by 13%. Weight distributions of the corrected monitoring dataset and the (R,S)-sample differed significantly ([R-(R,S)] *vs* [R,S]; χ^2-test: $\chi^2_3 = 9.432$, $P < 0.05$; Table 2b). Proportions were very similar in the samples (R) and (S) (Table 2b). There was no significant difference between distributions obtained by the two sampling methods ([R] *vs* [S-(R,S)]; χ^2-test: $\chi^2_4 = 7.871$, $P = 0.096$, NS; Table 2b).

DISCUSSION

Accuracy of radio-monitoring for recording kills

A comparison of estimated average food requirements with actual daily biomass intake observed in two of the monitored goshawks indicated that it was possible to record virtually all kills made by these individuals during radio-tracking sessions. Note that even the corrected estimates derived in the methods section were probably too high for two reasons: (1) it was assumed that males had to provide all the food. Females may, however, continue hunting in the early phases of the breeding season (Opdam, 1975) and join food provisioning again from the middle of the nestling period (e.g. Siewert, 1933; Schnell, 1958; Grønnesby & Nygård, 2000; Dewey & Kennedy, 2001); (2) estimates were higher than values obtained in the field

by direct observation at nest sites (Holstein, 1942) and caging of young (Sulkava, 1964).

Owing to the excellent observation conditions in Hamburg it was possible to follow this highly agile predator closely during its hunting flights. Urban environments seem to be ideal study areas for continuous radio-monitoring of short-stay perch hunters (see also Sodhi, 1992). In contrast, following nesting *accipiters* closely as they hunt in rural settings is almost impossible (Newton, 1986). There were only a few incidents where a missed kill was suspected ($n = 9$; duration of radio-signal indicating plucking: 10 ± 5 min). Even when the radio-signal indicated foraging but the hawk flew off before a precise location was determined, kills could be recorded by directly heading towards the nest site and observing a plucking hawk, prey-transfer between adults, or feeding of young.

From the quantitative results and additional observational data, it is therefore concluded that all goshawk prey of the size of a blackbird (100 g) and larger were recorded accurately by radio-monitoring. Any missed prey were probably swallowed entirely without plucking (see Sládek, 1963; Höglund, 1964). Thus, radio-tracking diet lists in the present study seem to be slightly more accurate than those compiled by Kenward *et al.* (1981) and Ziesemer (1983), who inferred from their analyses that they failed to record some killed birds of thrush-size and smaller.

Biases of plucking analysis

The radio-tracking data showed that the proportions of 'small birds' and feral pigeons were underestimated by the scanning method (comparison [R] *vs* [R,S]). The first result is in agreement with the general idea of an observer bias (e.g. Errington, 1932; Opdam, 1975; Newton & Marquiss, 1982) and is supported by data from Ziesemer (1981, 1983), but the latter finding was quite unexpected. It seems to contradict the conclusions by Ziesemer (1981, 1983) that scanning is biased in favour of large and pale-coloured prey (e.g. pigeons), whereas the proportion of small and dark prey (e.g. thrushes) is underestimated.

A possible explanation for the contradictory results is the status of the investigated hawks. Ziesemer's birds were non-breeding individuals that consumed their prey at or near the capture site (see also Kenward, 1977). In contrast, the hawks studied in Hamburg were breeding males that had to transport kills to their families. Energetic costs for carrying prey to the nest site can be reduced by processing the kill before transportation (Sodhi, 1992; Korpimäki, Tolonen & Valkama, 1994; for a theoretical analysis see Rands, Houston & Gasson, 2000). Plucking of feathers (or fur) will not only reduce the mass of an item, but it can also considerably improve its aerodynamics.

The proportional reduction in flight costs by discarding feathers will be an increasing function of prey weight because of an almost linear relationship between feather weight and body weight (Brody, 1945). For example, by completely plucking a feral pigeon (300 g) a goshawk may

reduce its flight costs by about 2.2%, whereas by preparing a blackbird (100 g) it will only save about 0.9% of energy (computed by the method of Masman & Klaassen, 1987; see also Sodhi, 1992). Energetic costs involved in plucking are lower than costs of unloaded flight (Warkentin & West, 1990). The degree to which plucking can reduce drag is harder to quantify (see Rands *et al.*, 2000, and literature cited therein). Rands *et al.* (2000) developed a series of optimization models of prey processing for central place foragers. According to one of their models, the amount of plucking should increase with increasing prey weight for a given distance from the nest. However, a detailed interpretation of the data from the viewpoint of optimal foraging theory is beyond the scope of this technical report and will be presented elsewhere.

In fact, goshawks plucked large prey (e.g. feral pigeons) longer and more thoroughly than smaller prey (e.g. blackbirds) before they brought them to the nest site. This behaviour may account for the unexpected underestimation of feral pigeon pluckings; although this species has conspicuous feathers, only a comparatively small proportion of them appeared in the nesting territories and could be found during systematic searches. Intermediate-sized items like blackbirds were delivered unplucked and found during scanning, probably because of their comparatively large feathers. Their overestimation in the plucking list might be an artefact attributable to the unit-sum constraint inherent in proportional data (Aebischer, Robertson & Kenward, 1993). At the other extreme, small prey were delivered to the nest unplucked, but were either swallowed entirely (e.g. Sládek, 1963; Höglund, 1964) or if they were plucked, remains were hard to detect because of their smallness and crypticity (Opdam *et al.*, 1977; Ziesemer, 1981, 1983). It is very likely that some remains were found only by scanning, because the plucking hawk was located in the nesting area with the help of radio-telemetry. Therefore, the underestimation of small prey in plucking lists will be even greater in unaided scanning studies.

It is well known that goshawks process prey items away from the nest site and sometimes deliver perfectly plucked prey (e.g. Brüll, 1984; März, 1987; Bijlsma, 1997). Brüll (1984) interpreted this behaviour as an attempt by the birds to reduce the weight of their prey. In agreement with the findings of the present study Sulkava (1964) reported that plucking effort of goshawks varies with prey weight. Large prey were plucked more thoroughly in his study area than small prey. He was the first to suspect that this behaviour might result in biases in diet lists obtained by the investigation of prey remains near nest sites (see also Bijlsma, 1997). Sulkava's comparison of observational data with prey found during nest surveys highlighted some biases, but was ambiguous as a result of small sample sizes.

Mañosa (1994) did not find a significant difference between data collected by direct observation and data from plucking analysis. He pooled pigeons across species and obtained similar proportions with both methods (18.9% and 15.8%, respectively). In fact, in the present study, the comparison of the samples (R) with (S) also

showed that the proportions of pooled pigeons were similar (43% and 38%, respectively). 'Other pigeons' were woodpigeons *Columba palumbus* ([R]: $n = 0$, [S]: $n = 7$) and collared doves *Streptopelia decaocto* ([R]: $n = 1$, [S]: $n = 5$). Woodpigeons, which are considerably heavier than feral pigeons, were presumably caught and plucked by females in the vicinity of the nests. Therefore, prey choice of the females could have partly compensated for the underestimation of pigeons killed by their mates in the plucking list (S).

Newton & Marquiss (1982) showed that more small and fewer large items were found near sparrowhawk *Accipiter nisus* nests than away from nests. They hypothesized that this result was due to diet segregation between the sexes, with males killing smaller prey than females (see also Opdam, 1975). It may be, however, that males plucked large items more intensively before transporting them to the nest site. A comparison with the methodological studies on other raptor species quoted in the introduction of this paper is problematic, as other species have quite different feeding habits to the goshawk. It should be noted, however, that Jenkins & Avery (1999) did not find an underestimation of larger birds in the list of prey remains collected for peregrine falcons *Falco peregrinus*.

Selective transportation of prey items can also affect the accuracy of diet analysis (Sulkava, 1964; Sonerud, 1992). Several raptor species have been shown to transport large prey to the nesting territory and to consume small prey at the capture site (Rudolph, 1982; Masman *et al.*, 1986; Bull, Henjum & Rohweder, 1989; Sonerud, 1989). Using the sample of recorded prey of known weights, no evidence was found for such a load–size effect in the monitored goshawks (see also Korpimäki *et al.*, 1994). However, it cannot be ruled out that some small prey had been consumed by the males at the capture sites before the kills were recorded (see above).

Management implications

Estimates of raptor diets are crucial for developing rigorous management strategies (e.g. Reynolds *et al.*, 1992). Some studies on goshawk predation completely relied on scanning data to describe diet composition (e.g. Uttendörfer, 1939; Opdam *et al.*, 1977; Brüll, 1984, and literature cited therein). The present investigation has pointed to a potential source of bias in plucking analyses that has passed unnoticed in previous work: namely the selective processing of prey away from the nest site. This behaviour may severely affect the robustness of conclusions that are drawn from plucking data even if large numbers of breeding pairs are monitored over several years.

The contradictory results of studies on different raptor species and the importance of the subject for conservation biology make replications of the approach presented in this paper highly desirable. As continuous radio-monitoring is laborious, however, an alternative method is proposed: it is recommended that researchers who are using plucking analysis to assess raptor diets count the numbers of main

feathers of plucked birds. These numbers can be used as an indirect measure of the effort with which items have been prepared away from the nest. These data could then be correlated with prey weights to investigate size-dependent plucking behaviour quantitatively.

Results supporting the general findings of this study would mean that a fresh reinterpretation of the large body of existing data on diets of diurnal raptors is needed. Furthermore, future projects on goshawks and other bird-eating raptor species would have to use either continuous radio-monitoring as the most accurate technique available or, in the absence of a load–size effect, systematic observation at nests (with hide or camera). If the amount of time required for obtaining sufficiently large sample sizes with these methods is prohibitive, researchers should at least compute correction factors for plucking lists from baseline data collected in pilot studies.

Acknowledgements

REFERENCES

Aebischer, N. J., Robertson, P. A. & Kenward, R. E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**: 1313–1325.

Bezzel, E. & Prinzinger, R. (1990). *Ornithologie*. Stuttgart: Eugen Ulmer.

Bijlsma, R. G. (1997). *Handleiding veldonderzoek roofvogels.* Utrecht: KNNV Uitgeverij.

Bittera, J. v. (1916). Über die Nahrung des Habichts und Sperbers. *Aquila* **22**: 216–217.

Boal, C. W. & Mannan, R. W. (1994). Northern goshawk diets in ponderosa pine forests on the Kaibab Plateau. *Stud. Avian Biol.* **16**: 97–102.

Brody, S. (1945). *Bioenergetics and growth.* New York: Reinhold.

Brüll, H. (1984). *Das Leben europäischer Greifvögel.* 4th edn. Stuttgart: Gustav Fischer.

Bull, E. L., Henjum, M. G. & Rohweder, R. S. (1989). Diet and optimal foraging of great gray owls. *J. Wildl. Manage.* **53**: 47–50.

Collar, N. J. (1997). Family Psittacidae (parrots).In *Handbook of the birds of the World* **4**. *Sandgrouse to cuckoos*: 280–477. del Hoyo, J., Elliott, A. & Sargatal, J. (Eds). Barcelona: Lynx.

Cramp, S. & Simmons, K. E. L. (1980). *Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic* **II**. Oxford: Oxford University Press.

Dewey, S. R. & Kennedy, P. L. (2001). Effects of supplemental food on parental-care strategies and juvenile survival of northern goshawks. *Auk* **118**: 352–365.

Dietrich, J. (1982). *Zur Ökologie des Habichts – Accipiter gentilis – im Stadtverband Saarbrücken.* Diplomarbeit, Universität des Saarlandes.

Errington, P. L. (1932). Technique of raptor food habits study. *Condor* **34**: 75–86.

Fischer, W. (1995). *Die Habichte. Die Neue Brehm-Bücherei* **158**. 3rd edn. Magdeburg: Westarp Wissenschaften.

Grønnesby, S. & Nygård, T. (2000). Using time-lapse video monitoring to study prey selection by breeding goshawks *Accipiter gentilis* in central Norway. *Ornis Fenn.* **77**: 117–129.

Heinroth, O. (1927). *Die Vögel Mitteleuropas* **2**. Berlin: Behrmüller.

Höglund, N. H. (1964). Über die Ernährung des Habichts (*Accipiter gentilis* Lin.) in Schweden. *Viltrevy* **2**: 271–328.

Holstein, V. (1942). *Duehøgen.* Copenhagen: Hirschsprung.

Jenkins, A. R. & Avery, G. M. (1999). Diets of breeding peregrine and lanner falcons in South Africa. *J. Raptor Res.* **33**: 190–206.

Karlbom, M. (1981). Techniques for trapping goshawks. In *Understanding the goshawk*: 138–144. Kenward, R. E. & Lindsay, I. M. (Eds). Oxford: International Association for Falconry and Conservation of Birds of Prey.

Kenward, R. E. (1977). Predation on released pheasants (*Phasanius colchicus*) by goshawks (*Accipiter gentilis*) in central Sweden. *Viltrevy* **10**: 79–112.

Kenward, R. E. (1978). Radio transmitters tail-mounted on hawks. *Ornis Scand.* **9**: 220–223.

Kenward, R. E. (1979). Winter predation by goshawks in lowland Britain. *Br. Birds* **72**: 64–73.

Kenward, R. E. (1987). *Wildlife radio tagging.* London: Academic Press.

Kenward, R. E., Marcström, V. & Karlbom, M. (1981). Goshawk winter ecology in Swedish pheasant habitats. *J. Wildl. Manage.* **45**: 397–408.

Kenward, R. E., Marcström, V. & Karlbom, M. (1993). Post-nestling behaviour in goshawks, *Accipiter gentilis*: I. The causes of dispersal. *Anim. Behav.* **46**: 365–370.

Korpimäki, E., Tolonen, P. & Valkama, J. (1994). Functional-responses and load–size effect in central place foragers – data from the kestrel and some general comments. *Oikos* **69**: 504–510.

Mañosa, S. (1994). Goshawk diet in a Mediterranean area of north-eastern Spain. *J. Raptor Res.* **28**: 84–92.

März, R. (1987). *Gewöll– und Rupfungskunde.* 3rd edn. Berlin: Akademie.

Marti, C. D. (1987). Raptor food habits studies. In *Raptor management techniques manual*: 67–80. Giron Pendleton, B. A., Millsap, B. A., Cline, K. W. & Bird, D. M. (Eds). Washington, DC: National Wildlife Federation.

Masman, D., Gordijn, M., Daan, S. & Dijkstra, C. (1986). Ecological energetics of the kestrel: field estimates of energy intake throughout the year. *Ardea* **74**: 24–39.

Masman, D. & Klaassen, M. (1987). Energy expenditure during free flight in trained and free-living Eurasian kestrels (*Falco tinnunculus*). *Auk* **104**: 603–616.

McNab, B. K. (2002). *The physiological ecology of vertebrates. A view from energetics.* London: Comstock, Cornell University Press.

Newton, I. (1986). *The sparrowhawk.* Calton: T. & A.D. Poyser.

Newton, I. & Marquiss, M. (1982). Food, predation and breeding season in sparrowhawks (*Accipiter nisus*). *J. Zool. (Lond.)* **197**: 221–240.

Opdam, P. (1975). Intra- and interspecific differentiation with respect to the feeding ecology in two sympatric species of the genus *Accipiter. Ardea* **63**: 30–54.

Opdam, P., Thissen, J., Verschuren, P. & Müskens, G. (1977). Feeding ecology of a population of goshawk *Accipiter gentilis. J. Ornithol.* **118**: 35–51.

Oro, D. & Tella, J. L. (1995). A comparison of two methods for studying the diet of the peregrine falcon. *J. Raptor Res.* **29**: 207–210.

Rands, S. A., Houston, A. I. & Gasson, C. E. (2000). Prey processing in central place foragers. *J. theor. Biol.* **202**: 161–174.

Real, J. (1996). Biases in diet study methods in the Bonelli's eagle. *J. Wildl. Manage.* **60**: 632–638.

Redpath, S. M., Clarke, R., Madders, M. & Thirgood, S. J. (2001). Assessing raptor diet: comparing pellets, prey remains, and observational data at hen harrier nests. *Condor* **103**: 184–188.

Reynolds, R. T., Graham, R. T., Reiser, M. H., Bassett, R. L., Kennedy, P. L., Boyce, D. A., Goodwin, G., Smith, R. & Fisher, E. L. (1992). *Management recommendations for the northern goshawk in the southwestern United States. General Technical Report RM–217.* Fort Collins, CO: USDA Forest Service.

Reynolds, R. T. & Meslow, E. C. (1984). Partitioning of food and niche characteristics of coexisting *Accipiter* during breeding. *Auk* **101**: 761–779.

Rudolph, S. G. (1982). Foraging strategies of American kestrels during breeding. *Ecology* **63**: 1268–1276.

Rutz, C. (2001). *Raum-zeitliche Habitatnutzung des Habichts – Accipiter gentilis – in einem urbanen Lebensraum.* Diplomarbeit, Universität Hamburg.

Rutz, C. (In press). Breeding season diet of northern goshawks *Accipiter gentilis* in the city of Hamburg, Germany. *Corax.*

Schnell, J. H. (1958). Nesting behavior and food habits of goshawks in the Sierra Nevada of California. *Condor* **60**: 377–403.

Schnurre, O. (1934). Zwei Habichtsbruten in gegensätzlichen Landschafts formationen. *Mitt. Ver. Sächs. Ornith.* **4**: 99–109.

Seguin, J.-F., Bayle, P., Thibault, J.-C., Torre, J. & Vigne, J.-D. (1998). A comparison of methods to evaluate the diet of golden eagles in Corsica. *J. Raptor Res.* **32**: 314–318.

Siewert, H. (1933). Die Brutbiologie des Hühnerhabichts. *J. Ornithol.* **81**: 44–94.

Simmons, R. E., Avery, D. M. & Avery, G. (1991). Biases in diets determined from pellets and remains: correction factors for a mammal and bird-eating raptor. *J. Raptor Res.* **25**: 63–67.

Sládek, J. (1963). Beitrag zur Nahrungsökologie des Hühnerhabichts in der Tschechoslowakei. *Zool. Listy* **12**: 98–106.

Sodhi, N. S. (1992). Central place foraging and prey preparation by a specialist predator, the merlin. *J. Field Ornithol.* **63**: 71–76.

Sonerud, G. A. (1989). Allocation of prey between self-consumption and transport in two different-sized central place foragers. *Ornis Scand.* **20**: 69–71.

Sonerud, G. A. (1992). Functional responses of birds of prey: biases due to the load–size effect in central place foragers. *Oikos* **63**: 223–232.

Squires, J. R. & Reynolds, R. T. (1997). Northern goshawk (*Accipiter gentilis*). In *The birds of North America* **298**: 1–32. Poole, A. & Gill, F. (Eds). Washington, DC: The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union.

Stephens, D. W. & Krebs, J. R. (1986). *Foraging theory.* Princeton, NJ: Princeton University Press.

Sulkava, S. (1964). Zur Nahrungsbiologie des Habichts. *Aquilo Ser. Zool.* **3**: 1–103.

Tornberg, R. & Colpaert, A. (2001). Survival, ranging, habitat choice and diet of the northern goshawk *Accipiter gentilis* during winter in northern Finland. *Ibis* **143**: 41–50.

Toyne, E. P. (1998). Breeding season diet of the goshawk *Accipiter gentilis* in Wales. *Ibis* **140**: 569–579.

Uttendörfer, O. (1939). *Die Ernährung der deutschen Raubvögel und Eulen und ihre Bedeutung in der heimischen Natur.* Melsungen: Neumann-Neudamm.

Warkentin, I. G. & West, N. H. (1990). Ecological energetics of wintering merlins *Falco columbarius. Physiol. Zool.* **63**: 308–333.

White, G. C. & Garrott, R. A. (1990). *Analysis of wildlife radio-tracking data.* London: Academic Press.

Widén, P. (1987). Goshawk predation during winter, spring and summer in a boreal forest area of central Sweden. *Holarct. Ecol.* **10**: 104–109.

Zar, J. H. (1999). *Biostatistical analysis.* 4th edn. New Jersey: Prentice Hall.

Ziesemer, F. (1981). Methods of assessing goshawk predation. In *Understanding the goshawk*: 144–150. Kenward, R. E. & Lindsay, I. M. (Eds). Oxford: International Association for Falconry and Conservation of Birds of Prey.

Ziesemer, F. (1983). *Untersuchungen zum Einfluβ des Habichts (Accipiter gentilis) auf Populationen seiner Beutetiere. Beiträge zur Wildbiologie* **2**. Doktorarbeit, Universität Kiel.