Zoological Studies **48**(2): 215-222 (2009)

Zoological Studies

Seasonal Changes in the Avian Diet of Breeding Sparrowhawks *Accipiter nisus*: How to Fulfill the Offspring's Food Demands?

Małgorzata Bujoczek* and Michał Ciach

Department of Forest Zoology and Wildlife Management, Faculty of Forestry, Agricultural University, al. 29 Listopada 46, Kraków 31-425, Poland

(Accepted July 14, 2008)

Małgorzata Bujoczek and Michał Ciach (2009) Seasonal changes in the avian diet of breeding Sparrowhawks *Accipiter nisus*: how to fulfill the offspring's food demands? *Zoological Studies* **48**(2): 215-222. During the 2002-2006 breeding seasons, changes in the diet of Sparrowhawks *Accipiter nisus* were studied in the Carpathian Mountains (southeastern Poland). Material (1592 prey items) from 4 periods of the breeding cycle was analyzed. Among 61 identified bird taxa, *Turdus philomelos*, *Sylvia atricapilla*, *T. merula*, *Fringilla coelebs*, *Erithacus rubecula*, and *Parus major* dominated and comprised 41% of the total number of prey. *Turdus merula*, *T. philomelos*, and *Garrulus glandarius* comprised 42% of the total biomass. Prey items varied in weight from 5 to 485 g. Typical prey of Sparrowhawk males (≤ 35 g) dominated, and their proportion in the diet increased from 55% to 77% during the breeding season. Typical prey of females (> 120 g) were caught to a greater extent (21%) in the 1st period only, and their proportions (to 2%) of the diet significantly decreased in the next periods. With respect to the total biomass, large birds dominated in the 1st period only (54%). The percentage of small- and medium-sized birds in the total biomass increased as the season progressed. In successive periods of the breeding season, the ratio of the number of prey to its biomass significantly increased. Despite females resuming hunting activities in the nestling and post-fledgling periods, there was no increase in the mean body weight of avian prey supplied to the young. However, there was a marked increase in the number of prey items found at the nest. It was concluded that with the high food demands of the rapidly growing Sparrowhawk nestlings, it is more efficient to more-frequently catch small birds than to less-frequently catch larger birds. This might decreases the parents' time and/or energy expenditures for feeding nestlings.
http://zoolstud.sinica.edu.tw/Journals/48.2/215.pdf

Key words: Food composition, Prey choice, Dietary change, Successful attack profit.

Birds are the basic component of the Sparrowhawk's diet, composing up to 97% of the total biomass of prey caught (Glutz v. Blotzheim et al. 1971, Newton 1973, Opdam 1979, Cramp and Simmons 1980, Jędrzejewska and Jędrzejewski 1998). Prey choices (species composition, number, and mass) change as the breeding season progresses (Tinbergen 1946, Newton 1973 1978, Opdam 1975, Eldegard et al. 2003), and also differ between both individual pairs and populations (Schnurre 1956 1957, Eldegard et al. 2003). These differences depend on the availability of particular prey in the environment (Opdam 1979, Marquiss and Newton 1982, Jędrzejewska and Jędrzejewski 1998), on changes in food requirements in different phases of the breeding season, and on brood size (Newton 1973, Geer 1978, Eldegard et al. 2003), as well as on the sex and age of the parent (Mueller and Berger 1970, Opdam 1975, Newton 1978 1986, Eldegard et al. 2003).

Sexual dimorphism influences the size of prey caught by both parents (Reynolds 1972, Newton 1973 1978 1986, Ortlieb 1987). Male Sparrowhawks are mainly responsible for providing

*To whom correspondence and reprint requests should be addressed. E-mail:bujoczek.m@gmail.com

food for the nestlings. Females are much larger than males, and only periodically join in the hunting, mainly during the late nestling and post-fledgling period (Newton 1973, Ortlieb 1987, Cramp and Simmons 1980, Eldegard et al. 2003). The female's contribution to hunting may vary considerably between populations and habitats (Newton 1978, Eldegard et al. 2003). However, hunting by the female during the breeding season enables a pair to broaden the range of prey taken, and increase both the average size of items taken and the overall food supply (Newton 1978, Cramp and Simmons 1980).

Hunting by both parents during the courtship and nest building period results in an increase in the prey mass. During the incubation and brooding periods, when the female does not hunt, the mean prey mass decreases. Resumed hunting activity by females in the late nestling and post-fledgling periods leads to another increase in prey mass (Newton 1978 1986). The aim of this paper was to describe changes in the composition of the avian prey of Sparrowhawks as the breeding season progresses. We refer to the hypothesis that prey size increases after females resume hunting during the nestling and post-fledgling periods.

MATERIALS AND METHODS

Study area

This study was conducted in woodlands of the Pogórze Przemyskie foothills (western Carpathian Mountains, southeastern Poland). The area is located at 250-600 m in elevation in a moderately warm, but continental, climatic zone. Forests cover 64% of the area, including Carpathian beech forests *Dentario glandulosae-Fagetum*, mixed lime-oak-hornbeam forests *Tilio-Carpinetum*, and *Dryopterido dilatate-Abietetum* fir forests (Bylicka 2004). Farmlands, river valley habitats, and built-up areas cover the rest of the terrain.

All Sparrowhawk territories were dominated by forested habitats. Nests were located in similar habitat types in fir-beech forests, where silver fir *Abies alba* dominated. However, it was possible for all pairs to hunt in different habitat types. The area surrounding the territories consisted of a mosaic of forests, meadows, arable fields, and built-up areas. The distance from the nests to fields and meadows varied from 50 to 600 m, and to built-up areas from 150 to 1500 m. Two of the nests were located near the San River.

Field methods and materials

The study was carried out during the 2002-2006 breeding seasons. The area surrounding 13 nests of 6 Sparrowhawk pairs was surveyed during the entire breeding season from the beginning of courtship until the fledglings left the vicinity of their nests. Plucking places, usually stumps of cut trees or fallen logs, branches, and nests from previous seasons, were examined. Feathers, legs, bills, and other prey remains were collected within a 150 m radius of the nests. When remains of 1 species were collected during nest control in a single period, the minimum number of prey killed was estimated according to the number of wing or tail feathers. All prey remains were thoroughly removed to avoid repetitive counting. The method of prey remains analysis allowed a high percentage of prey to be identified to the species or genus level (Huang et al. 2006).

Prey remains found near a nest represent a sample, which exemplifies the diet composition of the studied Sparrowhawks (Tinbergen 1946, Selås 1993, pers. obs.). Studies on Goshawks *Accipiter gentilis* showed that large prey may be plucked near the place of capture (Rutz 2003), leaving few feathers near the nest. Thus they may be underestimated in analyses based on remains found near the nest. Some small birds items plucked in the territory could probably be missed as well, due to difficulties in finding their small feathers. In contrast to Newton and Marquiss (1982), we found remains of small, as well as large, prey in the vicinity of the nest. We assume that the proportion of large prey plucked near the place of capture and small prey found near the nest was stable within the entire breeding season. However, we could not exclude the possibility that plasticity exists in the way parents process prey during the season. Prey processing may be related to food demands, and parents may tend to bring more unplucked prey to the nest site later in the season when food demand is high. However, this potential plasticity in the way parents process prey needs to be verified in empirical studies.

During 5 seasons with a total of 252 controls (Table 1), 1592 individual prey remains were found. The number of prey items in each control ranged from 1 to 32 (mean, 6.3) individuals. The species or genus of 96% (1522 items) of the total number of remains were identified.

Female hunting activities influence the number and weight of prey delivered to the nest (Newton 1986). During our inspections of nests and territories, we found that as incubation and nestling brooding ended, females resumed hunting. Direct observations of changes in female activity (hunting or delivering food) as the breeding season progressed were recorded at 10 nests (Table 1).

Data analyses

The dates of the 1st (Mar. 20) and last (Aug. 16) control, when Sparrowhawks were observed in their territories, were respectively taken as the beginning and end of the research season. Based on characteristic traits of the Sparrowhawk' s breeding biology, the season was divided into 4 periods: (1) courtship and nest building (from return to the breeding territory to the end of nest building or repair, and both males and females hunt; 45 d); (2) incubation and brooding (when only males hunt and deliver food to the female and nestlings; 30 d); (3) nestling stage (when nestlings remain in the nest, and females may resume hunting, i.e., both parents hunt; 45 d); and (4) post-fledgling stage (when birds move from the nest to branches and eventually leave the nest area, becoming independent, and both parents may hunt; 30 d) (Cramp and Simmons 1980, Newton 1986, Ortlieb 1987, pers. obs.).

For each individual period, the number of prey was totaled, and 3 individual categories were distinguished on the basis of prey body weight: small birds (weighing ≤ 35 g), which are typically within a male's grasp; medium (35-120 g), which are common within the grasp of both sexes; and large birds (> 120 g), which are typically within a female's grasp. The mean body masses of prey species were determined according to Cramp and Simmons (1980), based on data from Central European populations.

In the literature, hunting efficiency is defined as the ratio of the number of successful attacks (ending in prey capture) to the total number of attacks undertaken (Wakeley 1974, Temeles 1986). Hunting effort is described as the proportion of budget time spent in flight-hunting or as the number of prey items delivered to the nest per time unit (Tolonen and Korpimäki 1994). Both terms are based on attack decisions and success, and are a

Table 1. Years, study dates, and the number of controls carried out in the nest area of the Sparrowhawk *Accipiter nisus* and the recorded changes in activity of the female (+, the female's hunting activity resumed after the incubation period; ?, a female's absence from the nest but no proof of hunting)

Nest area	Years	Study date	Number of controls	Change in the female's activity
Dylągowa	2002	18 May - 14 July	20	?
Dylągowa	2003	20 Mar. - 16 Aug.	37	+
Dylągowa	2004	31 Mar. - 17 July	33	+
Nienadowa		30 May - 10 Aug.	20	+
Dylągowa	2005	26 Mar. - 23 July	23	+
Nienadowa		7 Mar. - 24 July	13	+
Dąbrówka Starzeńska		6 Apr. - 23 July	15	+
Dylągowa	2006	30 Mar. - 29 July	21	+
Nienadowa		2 Apr. - 12 May	5	?
Dąbrówka Starzeńska		4 Apr. - 29 July	21	+
Reszów		9 Apr. - 29 July	23	+
Harta		8 Apr. - 4 July	13	+
Wybrzeże		27 May - 4 July	8	?
		Total	252	

function of prey vulnerability (Quin and Cresswell 2004). Sarasola and Negro (2005) described successful hunting based on the number of prey captured per energy unit. Attack (or hunting) success results in prey capture which brings a profit to the predator that can be measured in mass or energy units obtained per event. Therefore, we introduce the term, successful attack profit, which is the mass of prey obtained in a successful attack.

Changes in the number and mass of prey caught during the breeding season are represented by the K coefficient: $K = (N/M)*100$, where N is the number of birds caught in an individual period of the breeding season and M is their mass in grams. This coefficient calculated for each Sparrowhawk pair determined the number of prey needed to obtain 100 g of food. It represents the successful attack profit which is seen as the mean body weight of prey caught during a single successful attack. A lower K coefficient value indicates a higher profit from a successful attack. Theoretically, K values range from > 0 to infinity. However, they are limited by the masses of the largest and smallest potential prey of a particular predator.

To avoid the problem of pseudo-replication, where single pair hunting in a special way for several seasons can bias the overall results, mean K coefficients based on individual nests, recalculated from all seasons, were used as observation units. One-way ANOVA was applied to compare K coefficient values between subsequent periods. The error variance in the K coefficient was equal in subsequent periods (Levene's test of equality of error variance, $p = 0.3$). Changes in the proportion of prey categories between the 4 periods were tested by G-test according to Zar (1999).

RESULTS

Diet composition

Among the prey remains, 61 bird taxa were identified. Song Thrush *Turdus philomelos*, Blackcap *Sylvia atricapilla*, Blackbird *T. merula*, Chaffinch *Fringilla coelebs*, Robin *Erithacus rubecula*, and Great Tit *Parus major* were the most numerous, comprising 41.2% of the total number of items. The next 45 taxa were rarely caught, and each comprised < 5.0% of the total number of prey. The next 10 taxa were caught even less frequently, and each comprised < 0.1% of the total number of prey (Appendix). Thrushes (Turdidae, 24.1%), finches (Fringillidae, 18.3%), warblers (Sylviidae, 13.4%), and tits (Paridae, 10.9%) dominated the diet. In terms of the total biomass, Blackbirds, Song Thrushes, and Jays *Garrulus glandarius* comprised 41.5% of the diet.

Changes in the number and mass of delivered prey

The number of prey species and number of individuals caught changed during the breeding season reached a maximum in the 3rd period while the nestlings were in the nest (Table 2). Similarly, the biomass of prey changed during successive periods and reached a maximum in the nestling stage (Table 2).

Body mass of prey ranged from 5.6 (*Regulus* sp.) to 485 g (Wood Pigeon *Columba palumbus*). The mean body mass of caught birds was 40.1 g ($N = 1522$), but species with a body mass of ≤ 35 g prevailed. They predominated during the entire breeding season and in different periods comprised 55.2%-76.7% of the total number of prey (Fig. 1). The number of large birds (> 120

Table 2. Number of species (N_s), number of individuals (Ind.; N_i), and biomass (M) of prey found in the nest area of Sparrowhawks *Accipiter nisus* during successive periods of the breeding season

Period in the breeding season	N_s	N_i			M		
		Ind.	%	ind./d	Weight (g)	%	g/d
Courtship and nest building	38	248	16.3	1.1	14 925.1	24.5	66.3
Incubation and brooding	40	264	17.3	1.8	10 810.9	17.7	72.1
Nestling stage (high food consumption)	53	858	56.4	3.8	29 795.8	48.9	132.4
Post-fledgling stage (self-dependence)	34	152	10.0	1.0	5 457.8	8.9	36.4
Total	-	1522	-	-	60 989.6	-	-

g) decreased from 21.4% to 2.2% as the season progressed. The percentage of medium birds (35-120 g) was constant during the entire breeding season (20.4%-25.8%) (Fig. 1). The number of delivered prey in individual weight classes significantly differed between the 1st period and the 2nd, 3rd, and 4th periods (*G*-test: $G = 35.13$; 98.57; and 33.14, respectively; all $p < 0.001$).

Large birds comprised 54.3% of the total biomass in the 1st period, but this declined to 10.2%-14.9% in the next 3 periods (Fig. 1). The percentage of small and medium birds in the total biomass increased as the season progressed (constituting 35.5%-44.5% and 42.4%-49.7% of the totals in these 3 periods, respectively). These 2 prey groups dominated the Sparrowhawk diet from the incubation and brooding period to the end of the breeding season.

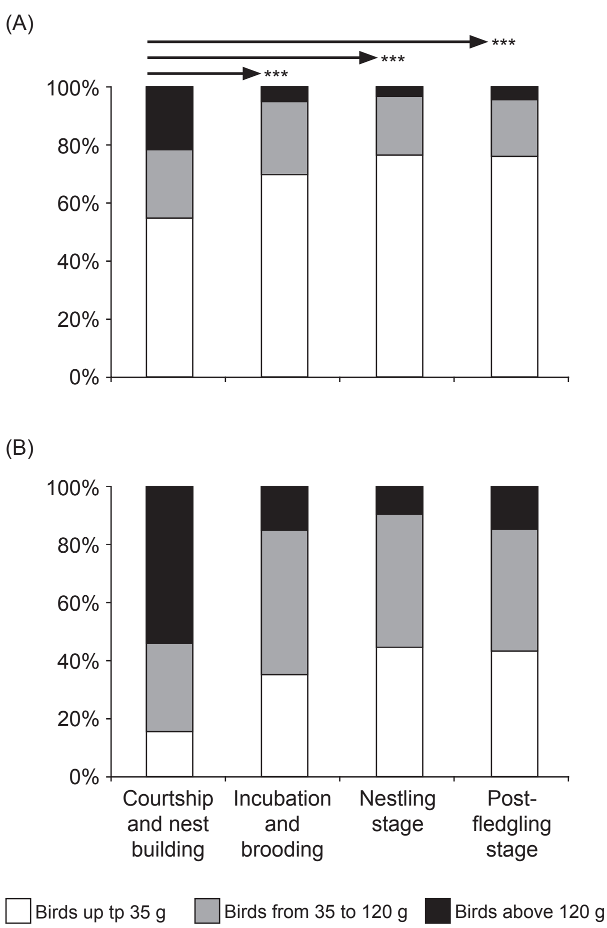

Fig. 1. Percentage of the number (A) and biomass (B) of different prey groups in the diet of Sparrowhawks *Accipiter nisus* during successive periods of the breeding season ($N = 1522$) (arrows indicate differences between periods; *** $p < 0.001$).

Successful attack profit

During successive periods, *K* coefficient values (see "Methods") (seen as the mean body weight of prey caught during a successful attack) significantly increased (Fig. 2). Differences in *K* coefficient values were found between subsequent periods (1-way ANOVA $F_{3,17} = 4.87$, $p = 0.013$). The mean *K* coefficient value in the courtship and nest-building period was significantly lower than those recorded in the nestling and post-fledgling periods (post-hoc LSD test; both $p < 0.01$).

DISCUSSION

Our results on prey species composition of Sparrowhawks agree with those of other studies (Tinbergen 1946, Kramer 1972, Newton 1973, Opdam 1975, Newton 1986, Ortlieb 1987, Selås 1993, Jędrzejewska and Jędrzejewski 1998). Among avian prey families caught by males, the Fringillidae, Passeridae, Emberizidae, and Paridae prevailed, while among female prey, the Turdidae and Sturnidae dominated (Cramp and Simmons 1980). However, prey species compositions may differ between habitats along with availability

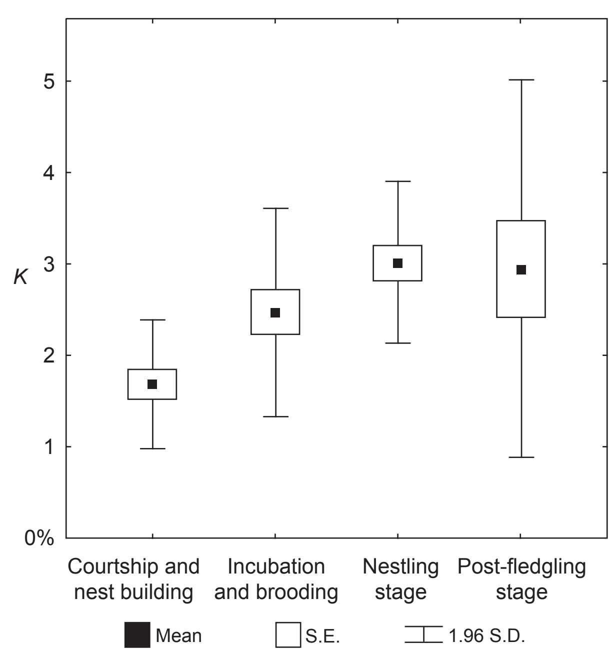

Fig. 2. Changes in the successful attack profit of Sparrowhawks *Accipiter nisus* in the breeding season as reflected in the ratio of the number of prey caught to their body weight (*K* coefficient) ($N = 1522$).

(Newton 1986). The body mass of birds caught by Sparrowhawks ranged from 5 (*Regulus* sp.) to 500 g (Wood Pigeon *Columba palumbus*, Tawny Owl *Strix aluco*, and Carrion Crow *Corvus corone*), but the most frequent prey species weighed ≤ 45 g (Tinbergen 1946, Uttendörfer 1952, Glutz v. Blotzheim et al. 1971, Kramer 1972, Opdam 1975).

During the breeding season, the parents divide responsibilities. The female incubates and feeds the young, while the male hunts. The female may resume hunting when incubation is complete (Newton 1978, Ortlieb 1987). Newton (1978) showed that from the moment incubation is complete, the total biomass of the prey increases, presumably because females are able to catch larger prey. In our study, the total biomass increased as the breeding season progressed. However, this was a result of an increase in the number of prey, not in mean prey weights. Similarly, Opdam (1975) found that the mean body weight of prey caught by both males and females during successive months of the breeding season systematically decreased. This trend was thought to result from an increased proportion of young (not fully grown) birds found in the diet (Opdam 1975). In the present study, the percentage of fledglings in the diet (excluding fully grown juvenile birds) was 13.2% of all prey (unpubl. data). However, during our analyses, the different body masses of fledglings and juvenile birds were not taken into consideration. Hence, the decrease in body mass of prey delivered to the nests did not result from the increased capture of juvenile birds, but from the parents' choice of smaller prey-species. It can be concluded that with the high food demands of rapidly growing Sparrowhawk nestlings, it is more efficient to more-frequently catch smaller birds than to less-frequently catch larger birds. This strategy probably decreases the parents' time and/or energy expenditures for feeding nestlings (Slagsvold and Sonerud 2007).

For forest-dwelling birds of prey, knowledge about roles of the sexes as food providers is incomplete. In southern Scotland, females are more important than males as food providers in the post-fledgling period, and they prefer larger prey (Newton 1978 1986). However, in Scandinavia, 80% of the prey items brought to the nest were caught by the male (Eldegard et al. 2003). A lower female hunting contribution may save or help restore her energy for the next breeding season. In extreme cases, a female's poor physical condition and a small food base may lead to brood desertion (Kelly and Kennedy 1993). Catching small prey by a female may have a similar meaning and might be a consequence of energy-saving needs.

The net energy gain of a prey item should increase with the size of the prey caught (see Ekman 1986). However, Götmark and Post (1996) found that the relative predation risk for potential prey species increased with prey body weight up to a mass of ca. 40 g and then declined with increasing body size. They concluded that larger preys are more difficult to catch.

Changes in the frequency of prey-species delivered might result from their availability (Solonen 2000). Reproductive success of individual prey-species is uneven, leading to differences in their abundances and a possible seasonal skewing of the availability of prey in different weight classes. However, there is some evidence that Sparrowhawk predation declines with an increasing density of potential prey (Götmark and Andersson 2005). Moreover, prey choice among particular species may be sex- and behavior-dependent (Götmark and Post 1996, Götmark et al. 1997, Post and Götmark 2006a-c). The results of our study indicate that the important factor in prey choice is its size, which is related to the energetic expenses of hunting or feeding fledglings.

The Sparrowhawk's strategy of hunting small birds applied by both parents in some habitats or by some populations may be profitable. The basis of that strategy is still not fully understood. However, in the population studied, it might be related to the habitat type, where natural forests dominate, or to fledgling success, when offspring force their parents to fulfill their high food demands.

Acknowledgments: We wish to express our gratitude to A. Bylicka and J. Bylicki for their help with fieldwork. We want to sincerely thank B. Olech, M. Keller, R.G. Bijlsma, J. van Diermen, and anonymous reviewers for critical comments on this paper. We are indebted to I. Newton for critical comments on the manuscript.

REFERENCES

Bylicka M. 2004. Diversity of forest communities on Pogórze Przemyskie. Master's thesis, Agricultural Univ., Kraków, Poland. (in Polish)

Cramp S, KEL Simmons. 1980. The birds of the western Palearctic. Vol. 2. Oxford, UK: Oxford Univ. Press.

Ekman J. 1986. Tree use and predator vulnerability of wintering passerines. Ornis Scand. **17:** 261-267.

Eldegard K, V Selås, GA Sonerud, C Steel, T Rafoss. 2003.

The effect of parent sex on prey deliveries to fledgling Eurasian sparrowhawks *Accipiter nisus*. Ibis **145:** 667-672.
Geer TA. 1978. Effects of nesting sparrowhawks on nesting tits. Condor **80:** 419-422.
Glutz v. Blotzheim UN, KM Bauer, E Bezzel. 1971. Handbuch der Vögel Mitteleuropas. **4.** Frankfurt, Main, Germany: Akademische Verlagsgesellschaft.
Götmark F, M Andersson. 2005. Predation by sparrowhawks decreases with increased breeding density in territorial Great Tits. Oecologia **142:** 177-183.
Götmark F, P Post. 1996. Prey selection by sparrowhawks *Accipiter nisus*: relative predation risk for breeding passerine birds in relation to their size, ecology, and behaviour. Phil. Trans. R. Soc. Lond. **351:** 1559-1577.
Götmark F, P Post, J Olsson, D Himmelmann. 1997. Natural selection and sexual dimorphism: sex-biased sparrowhawk predation favours crypsis in female chaffinches. Oikos **80:** 540-548.
Huang KY, YS Lin, LL Severinghaus. 2006. Comparison of three common methods for studying the diet of nestlings in two *Accipiter* species. Zool. Stud. **45:** 234-243.
Jędrzejewska B, W Jędrzejewski. 1998. Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. Berlin: Springer-Verlag.
Kelly EJ, PL Kennedy. 1993. A dynamic state variable model of mate desertion in Cooper's hawks. Ecology **74:** 351-366.
Kramer V. 1972. Habicht und Sperber. N. B. B. Heft 158, Wittenberg Lutherstand: Ziemsen Verlag, 103 pp.
Marquiss M, I Newton. 1982. Habitat preference in male and female sparrowhawks *Accipiter nisus*. Ibis **124:** 324-328.
Mueller HC, DD Berger. 1970. Prey preferences in the Sharp-shinned hawk: the roles of sex, experience and motivation. Auk **87:** 452-457.
Newton I. 1973. Studies of sparrowhawks. Br. Birds **66:** 271-278.
Newton I. 1978. Feeding and development of sparrowhawk nestlings. J. Zool. **184:** 465-487.
Newton I. 1986. The Sparrowhawk. London: T. & A. D. Poyser.
Newton I, M Marquiss. 1982. Food, predation and breeding season in sparrowhawks (*Accipiter nisus*). J. Zool. **197:** 221-240.
Opdam P. 1975. Inter- and intraspecific differentiation with respect to feeding ecology in two sympatric species of the genus *Accipiter*. Ardea **63:** 30-54.
Opdam P. 1979. Feeding ecology of a sparrowhawk population (*Accipiter nisus*). Ardea **66:** 137-154.
Ortlieb R. 1987. Die sperber. Wittenberg Lutherstadt: Die Neue Brehm-Bücherei.
Post P, F Götmark. 2006a. Seasonal changes in sparrowhawk *Accipiter nisus* predation: prey vulnerability in relation to visibility in hunting habitats and prey behaviour. Ardea **94:** 77-86.
Post P, F Götmark. 2006b. Foraging behavior and predation risk in male and female blackbirds (*Turdus merula*) during the breeding season. Auk **123:** 162-170.
Post P, F Götmark. 2006c. Predation by sparrowhawks on male and female pied flycatchers *Ficedula hypoleuca* in relation to their breeding behaviour and foraging. J. Avian Biol. **37:** 158-169.
Quin JL, W Cresswell. 2004. Predator hunting behaviour and prey vulnerability. J. Anim. Ecol. **73:** 143-154.
Reynolds RT. 1972. Sexual dimorphism in *Accipiter* hawks: a new hypothesis. Condor **74:** 191-197.
Rutz C. 2003. Assessing the breeding season diet of goshawks *Accipiter gentilis*: biases of plucking analysis quantified by means of continuous radio-monitoring. J. Zool. **259:** 209-217.
Sarasola JH, JJ Negro. 2005. Hunting success of wintering Swainson's hawks: environmental effects on timing and choice of foraging method. Can. J. Zool. **83:** 1353-1359.
Schnurre O. 1956. Ernährungsbiologische Studien an Raubvögeln und Eulen der Darßhalbinsel (Mecklenburg). Beiträge Vogelkunde **4:** 211-245.
Schnurre O. 1957. Sperber und Vogelschutz. Gefiederte Welt **81:** 41-42.
Selås V. 1993. Selection of avian prey by breeding sparrowhawks *Accipiter nisus* in southern Norway: the importance of size and foraging behaviour of prey. Ornis Fenn. **70:** 144-154.
Slagsvold T, GA Sonerud. 2007. Prey size and ingestion rate in raptors: importance for sex roles and reversed sexual size dimorphism. J. Avian. Biol. **38:** 650-661.
Solonen T. 2000. Predation by sparrowhawks *Accipiter nisus* and vulnerability of prey. Ornis Fenn. **77:** 27-37.
Temeles EJ. 1986. Reversed sexual size dimorphism: effect on resource defense and foraging behaviors of nonbreeding Northern Harriers. Auk **103:** 70-78.
Tinbergen L. 1946. De Sperber als roofvijand van zangvogels. Ardea **34:** 1-213.
Tolonen P, E Korpimäki. 1994. Determinants of parental effort: a behavioural study in the Eurasian kestrel, *Falco tinnunculus*. Behav. Ecol. Sociobiol. **35:** 355-362.
Uttendörfer O. 1952. Neue Ergebnisse über die Ernährung der Greifvögel und Eulen. Stuttgart, Germany: Ulmer.
Wakeley JS. 1974. Activity periods, hunting methods, and efficiency of the ferruginous hawk. J. Raptor Res. **8:** 67-72.
Zar JH. 1999. Biostatistical analysis. 4th Edition. NJ: Prentice Hall.

APPENDIX. Numbers of bird prey of Sparrowhawk *Accipiter nisus* in 4 periods of the breeding season

Genus or species	Period				
	Courtship and nest building	Incubation and brooding	Nestling stage	Post-fledgling stage	*n*
Acrocephalus scirpaceus	-	2	2	-	4
Aegithalos caudatus	1	-	2	-	3
Alauda arvensis	1	5	15	4	25
Anthus sp.	3	6	27	3	39
Bombycilla garrulus	2	-	-	-	2
Carduelis cannabina	1	3	8	2	14
Carduelis carduelis	-	3	8	-	11
Carduelis chloris	-	-	5	-	5
Carduelis spinus	5	-	2	2	9
Certhia sp.	3	2	5	1	11
Coccothraustes coccothraustes	10	1	12	2	25
Columba livia domestica	4	-	-	-	4
Columba palumbus	-	1	-	-	1
Delichon urbica	-	2	24	1	27
Dendrocopos major	1	-	12	3	16
Dendrocopos minor	-	-	2	-	2
Dryocopos martius	1	-	-	-	1
Emberiza citrinella	1	9	54	10	74
Erithacus rubecula	18	16	49	9	92
Ficedula albicollis	-	1	9	1	11
Fringilla coelebs	10	21	57	15	103
Garrulus glandarius	12	7	16	5	40
Hippolais icterina	1	-	1	-	2
Hirundo rustica	-	1	25	8	34
Jynx torquilla	-	-	1	-	1
Lanius collurio	-	10	32	2	44
Locustela fluviatilis	-	-	1	-	1
Loxia curvirostra	-	1	-	1	2
Luscinia luscinia	-	3	-	-	3
Motacilla alba	-	2	15	3	20
Motacilla cinerea	-	-	2	-	2
Motacilla flava	-	-	1	-	1
Parus ater	16		7	2	25
Parus caeruleus	2	7	14	1	24
Parus major	24	12	45	8	89
Parus montanus	4	1	11	2	18
Parus palustris	2	1	14	-	17
Passer domesticus	2	15	19	7	43
Passer montanus	-	6	39	6	51
Phoenicurus ochruros	2	-	8	-	10
Phoenicurus phoenicurus	-	1	-	-	1
Phylloscopus sp.	3	10	14	3	30
Picus viridis	-	-	1	-	1
Prunella modularis	5	2	5	3	15
Pyrhulla pyrhulla	12	2	9	6	29
Regulus sp.	4	2	3	-	9
Saxicola rubetra	-	6	8	3	17
Serinus serinus	1	-	1	-	2
Sitta europaea	6	2	21	3	32
Streptopelia decaocto	1	-	-	-	1
Strix aluco	1	-	-	-	1
Sturnus vulgaris	9	4	14	2	29
Sylvia atricapilla	9	24	70	9	112
Sylvia borin	-	-	1	-	1
Sylvia communis	2	11	33	6	52
Sylvia nisoria	-	-	2	-	2
Troglodytes troglodytes	-	1	3	-	4
Turdus merula	19	23	57	10	109
Turdus philomelos	14	33	66	9	122
Turdus pilaris	2	1	4	-	7
Turdus viscivorus	34	4	2	-	40
Total	248	264	858	152	1522