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The role of caches in the Eurasian Pygmy Owl *Glaucidium passerinum* during the breeding season

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Abstract: Caches, or places where food is scatter hoarded for a short time, play a crucial role in winter for the Eurasian Pygmy Owls *Glaucidium passerinum*. Observations carried out in the Stołowe Mountains (SW Poland) at 25 broods in 1997–2006 indicate that they are important also outside the breeding season. A total of 183 caches, where owls deposited single prey items, were analysed. Food was hoarded near nest holes, almost exclusively by females, at the height of 0–30 m above the ground (mean 13 m) and at the distance of 3–70 m (mean 27.5 m) from the nest hole, mainly on spruce branches and tops of broken tree trunks. Females hoarded and retrieved prey items mostly at sunrise and sunset, which coincided with the timing of food delivery by males. Out of 191 prey items passed by males to females, 40% were stored in caches. Prey items were stored on average for 38 hours. A total of 29 aggressive encounters within a breeding pair were recorded, including 26 (90%) attacks of females against males. The author hypothesises that a strong aggression of a female towards a male near a nest hole is associated with a defence of stored food items.

Key words: Eurasian Pygmy Owl, Strigiformes, Strigidae, food, cache, catching place, female's aggression towards the male

Rola spiżarni u sóweczki *Glaucidium passerinum* w sezonie lęgowym. Abstrakt: Spiżarnie, czyli miejsca czasowego depozytu pożywienia, odgrywają u sóweczki *Glaucidium passerinum* znaczną rolę w okresie zimowym. Obserwacje przy 25 lęgach prowadzone w Górach Stołowych (SW Poland) w latach 1997–2006 wskazują, że również w sezonie lęgowym jest to bardzo ważne dostosowanie gatunku do zmiennej dostępności ofiar. Materiał obejmuje 183 spiżarnie, w których sowy składały pojedyncze ofiary. Były one tworzone wokół dziupli lęgowych niemal wyłącznie przez samicę, na wysokości 0–30 m (średnio 13 m) nad ziemią i w odległości 3–70 m (średnio 27,5 m) od dziupli, głównie na gałęziach świerków oraz na szczytach złamanych pni drzew. Samice składały i pobierały ofiary głównie o wschodzie i o zachodzie słońca, co pokrywało się ze szczytami dostarczania pokarmu przez samce. Spośród 191 ofiar przekazanych przez samce, 40% samice składały w spiżarniach. Ofiary były w nich przechowywane średnio przez 38 godz. Zanotowano 29 agresywnych starć w obrębie par lęgowych, z czego 26 (90%) były to ataki samic na samce. W pracy przedstawiono koncepcję tłumaczącą silną agresję samicy wobec samca w okolicach dziupli lęgowej, jako następstwo obrony zgromadzonych w spiżarniach ofiar.

Słowa kluczowe: sóweczka, Strigiformes, Strigidae, pokarm, spiżarnie, agresja samicy wobec samca

Many animal species, including birds, hoard food for later consumption. A cache, a place where food is hoarded, helps to obtain energy resources when food is scarce, or dose it in periods of food abundance (e.g. Smith & Reichman 1984, Korpimäki 1987a). This

behaviour may be favoured when cycling environmental conditions (e.g. snow cover) result in a low accessibility of the preferred food type (Halonen et al. 2007), when the probability of finding hoarded food is higher than obtaining of a new prey (Moreno et al. 1981), and/or when hunting cost is lower than obtaining of a new food item in the future (np. Smith & Reichman 1984, Källander & Smith 1990). Hoarding behaviour is often observed in harsh climates at high latitudes (e.g. boreal forests) and/or high altitudes, where periods of food abundance and shortage alternate (Smith & Reichman 1984). Such habitat types are occupied by the Eurasian Pygmy Owl *Glaucidium passerinum*. Due to its small body size and the absence of a crop, the species is not able to accumulate much energy reserves in its body (Mebs 1965 cited in Welty 1979, Korpimäki 1987b). At the same time a small body size of the species facilitates manoeuvring during hunting (Village 1998).

Prey hoarding has been recorded in eleven bird families, e.g. falcons Falconidae, shrikes Laniidae and corvids Corvidae. Among owls this behaviour has been found in barn owls Tytonidae and true owls Strigidae (Källander & Smith 1990). Food hoarding by the European Pygmy Owl during winter has been well described by several authors (e.g. Solheim 1984, Ytreberg 1997, Suhonen et al. 2007), however, its scale during the breeding season remains unknown (e.g. Schönn 1980, Mikkola 1983, Mebs & Scherzinger 2000). Such a behaviour may be adaptive: birds hoarding food during pre-breeding period may advance breeding season as they have high-quality territories, and females in a good condition are able to lay more eggs (Sechley et al. 2014).

Owls are characterised by reverse sex dymorphism (RSD – a female larger than a male; e.g. Mikkola 1983) and a clear division of parental duties. In the Eurasian Pygmy Owl only females incubate eggs, and feed and brood nestlings. Food is delivered by a male and transferred to a female. Only a few days after fledging a male starts feeding the young (Schönn 1980, Mikkola 1983, R. Mikusek – unpubl. data).

The aim of this paper was to describe caches of the Eurasian Pygmy Owl and their role during the breeding season. I also present an explanation for a high aggression of a female against a male near a nest hole in relation to food hoarding.

Study area

The study was carried out in the Stołowe Mountains National Park (50°27'N, 16°24'E, the central Sudetes Mts, SW Poland), in the subalpine forest in the area of ca. 63 km^2 and at the altitude of 400–900 m a.s.l. The Stołowe Mountains have the plated structure. Mean annual temperature at the height of 750 m a.s.l. is 6.8°C, and in July 16.8°C on average. Snow cover persists for about 140 days, while vegetation period lasts for 218 days on average. During the study period 90% of the study area was covered by forests, mainly coniferous ones, of a poor condition and anthropogenic origin, transformed by human activities. About 88% of trees constituted the Common Spruce *Picea abies* at a mean age of 75 years, while 7% – the Common Beech *Fagus sylvatica*. Trees older than 80 years constituted 32% of all (Boratyński & Małek 1996, Kabała et al. 2018).

Material and methods

The presented material comes from observations at nest holes of the Eurasian Pygmy Owl collected in 1997–2006. During the study period the area was occupied by about 25 breeding pairs (Mikusek 2001). Data come from observations of 25 broods at 18 nest holes. More than 450 continuous observations were performed, including 14 lasting for

24 hours. The observations were carried out using binoculars and a scope from a distance of at least 25 m from the nest, without using a blind. Despite a short distance I did not record any changes in bird behaviour that could be related to the observer's presence. Sometimes birds left the hole flying towards the observer. Sex was determined based on frequently produced calls, body size and other features helpful in sex identification in the field (the proportion of the head to the rest of the body, plumage, R. Mikusek – unpubl. data). The presented distances and directions refer to the nest tree. The distance between a cache and a nest tree was calculated using a tape measure. The height above the ground (in m) was assessed with the height meter Suunto, and the distance from the tree using the tape, hence the bias in height measurement was not greater than 0.5 m. Apart from this, the species of the cache-tree, the distance between the cache and a tree trunk, age, sex and condition of prey were noted. Caches were photographed and video-recorded for the purpose of future analysis. To estimate how long prey items were stored, cache-trees were marked (a tape with the cache ID attached to the trunk) and regularly visited. Prey hoarding and its retrieval from a cache were not always observed. To estimate the duration of food hoarding I included only the cases where food deposition and retrieval were directly observed, and the cases where the bias associated with these events was not greater than 1–3 hours. I also included the observations of females flying with food in tree canopy over short distances, and after a short time (too short to consume the prey) recorded without the prey item. Prey items were found also in a nest hole. Usually it was difficult to determine whether the prey brought to the hole was supposed to be consumed later, or eaten partly/completely at once, especially during the incubation and nestling periods, when females did not leave the hole afterwards. The breeding season was divided into five parts: mating period (until the beginning of incubation), and four periods of 14 days each: incubation 1 and 2, nestling period 1 and 2.

Results

A total of 183 caches were analysed. Of 520 observations of owls with a prey, 38.3% referred to birds caching and retrieving prey items from a cache. In most cases females hoarded food, and only eight times (4.4%) males deposited or collected prey items from the cache during the absence of their partners. Males approached a nest hole with a prey hunted far away from the nest, or food collected from a cache. I observed only once (during a mating period, on 26 March) a male that hoarded a food item hunted near a nest hole 5 minutes earlier. Of 191 prey items transferred by a male to a female 40.0% were subsequently deposited in a cache. Some prey items brought by males were stiff, presumably due to long storing, which indicates the presence of caches located far from a nest hole. Direct evidence for this hypothesis comes from the observation of a male that collected a mouse (and later consumed it) from a cache located 750 m away from the nest hole. Another source of evidence comes from males appearing with prey items near a nest hole during a very short time. For example, on 25 June in the evening, at the end of diurnal activity, a male brought 4 food items to his mate during only 25 minutes. Females laying prey on branches during the pre-breeding period and just after the breeding season were observed three times: twice in April and once in August.

Cache location

The Eurasian Pygmy Owl cached prey in various, usually non-concealed places, sometimes previous consumption sites. In the latter cases, food was stabilised before consumption,

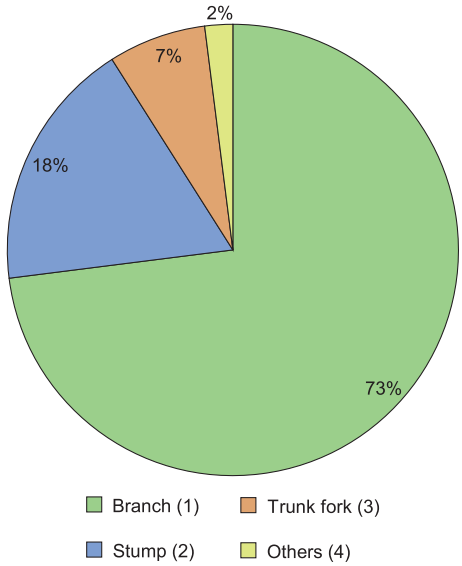

Fig. 1. *Places of prey deposition by female Eurasian Pygmy Owls during the breeding season on the Stołowe Mountains (N=157)*
Rys. 1. Miejsca składania ofiar w sezonie lęgowym przez samice sóweczki w Górach Stołowych (N=157), (1) – gałąź, (2) – pniak, (3) – rozwidlenie pnia, (4) – inne

which facilitated tearing at the prey flesh. Birds consumed their prey usually among dense spruce branches, which provided good shelter from passerines mobbing Pygmy Owls. Mobbing apparently resulted in clear „discomfort" of the owls (R. Mikusek – unpubl. data). Almost all caches were located in open places, exceptionally in nest holes. About 3/4 prey items were situated by females on branches (Fig. 1), mostly of the spruce (Photo 1), which resulted from the spruce dominance in the area. Prey items were located singly on branches, and each time in a different places. Only once did I observe prey deposition exactly at the same place of the spruce branch. Owls cached their prey in dense trees providing a good shelter and stabilisation for prey items. Broken tree tops were also frequently used as caches (18%). Such places seem to be easy to remember and provide proper stabilisation (Photo 2). One broken spruce was used as a cache seven times. Non-typical caches included the ground at the base of a tree trunk and an old nest of the Common Buzzard *Buteo buteo*. Only three times did I observe caching prey in rotten, half-open but sheltered holes. One female collected a prey item from such a cache in the morning after a rainy day (with continuous rain, and the only break between 11 and 16).

Photo 1. Eurasian Pygmy Owl female laying prey on twigs at the base of a branch of the larch tree (Phot. R. Mikusek) – *Samica sóweczki kładąca ofiarę u nasady gałęzi modrzewia*

Photo 2. Eurasian Pygmy Owl female retrieving a bird from a cache on the horizontal spruce branch (Phot. R. Mikusek) – *Samica sóweczki pobierająca ptaka ze spiżarni umieszczonej na poziomej gałęzi świerka*

She hoarded another prey item in the same cache at 10:46. At another locality the female also carried a prey into half-open tree hole during rain. She re-located three prey items brought by a male from dense spruce branches into the hole during a continuous rain.

During the breeding season only single prey items were deposited in caches. Their distribution around three nest trees in the flat area is shown in Fig. 2. Assuming that the entrance to the hole is located at 0°, as many as 85% prey items (N=74) were located within a horizontal radius of 45° around a nest hole. On steep slopes most prey items were deposited at a similar height as the nest hole. With regard to nest trees located at the altitude of 100 m a.s.l., 64% of 47 prey items were hoarded at the height of 90–110 m, only two prey items (4%) below 90 m, and the remaining 32% above 110 m (Fig. 3). In steep areas males arrived with food always from the upper parts of the slope and prey was passed down to the females at the level of the nest or slightly higher (Fig. 4). The mean distance between the place of food transfer and the cache was 20 m (Me=20 m; range 0–80 m; N=25), but at one nest located in a flat area the distance was 30 m (Me=20 m; range 0–150 m; N=20;

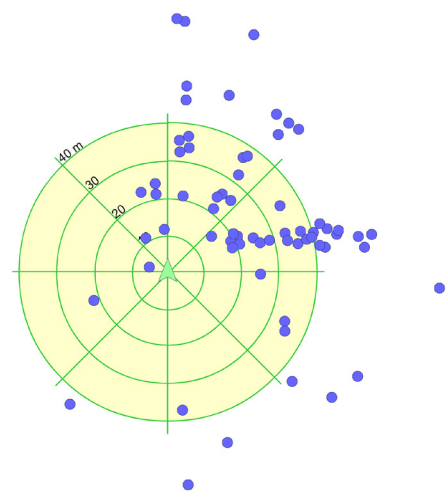

Fig. 2. *Distribution of caches (blue points) around nest holes of the Eurasian Pygmy Owl (central point) in a flat area (data from three nests have been combined, green arrow – nest hole entrance; N=74)*
Rys. 2. Rozmieszczenie spiżarni (niebieskie punkty) wokół dziupli lęgowych sóweczki (punkt centralny) leżących na terenie płaskim (dane zbiorcze dla 3 gniazd, zielona strzałka – ekspozycja dziupli; N=74)

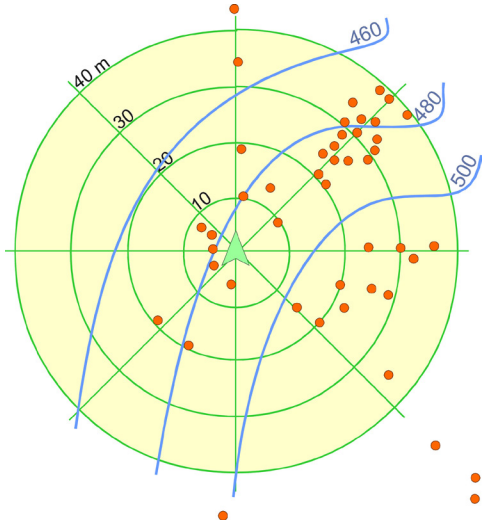

Fig. 3. Distribution of caches (red points) around nest hole of the Eurasian Pygmy Owl (central point) located on a slope (green arrow – nest hole entrance, blue lines – contour lines; N=47)

Rys. 3. Rozmieszczenie spiżarni (czerwone punkty) wokół dziupli lęgowej sóweczki (punkt centralny) położonej na stoku (zielona strzałka – kierunek wylotu otworu; linie niebieskie – poziomice; N=47)

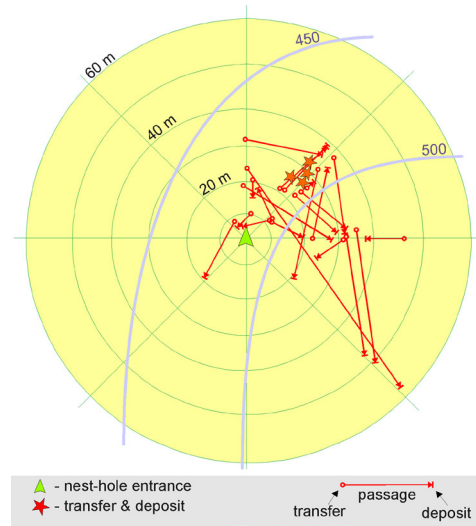

Fig. 4. Places of food transfer and hoarding on a steep slope (green arrow – nest hole entrance; N=25)

Rys. 4. Miejsca przekazania i złożenia pokarmu na stanowisku zlokalizowanym na dużym pochyleniu terenu (strzałka – kierunek wylotu dziupli; N=25)

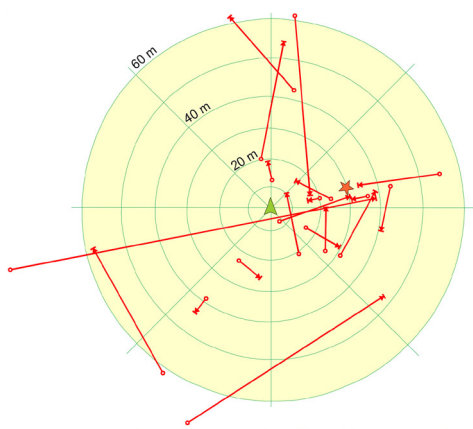

Fig. 5. Places of food transfer and hoarding in the flat area (green arrow – nest hole entrance; N=19)

Rys. 5. Miejsca przekazania i złożenia pokarmu na stanowisku zlokalizowanym na terenie płaskim (strzałka – kierunek wylotu dziupli; N=19)

Fig. 5). The differences between the two sites are not statistically significant (Manna-Whitney test: U=198,5; P=0.240).

Females hoarded food at the distance from 3 to 70 m from the nest tree, on average 27.5 m (Me=25 m; SD=14.7; N=150), and ca. 75% of prey items within a radius of 11–40 m (Fig. 6). I recorded only one case when a female left the prey in a cache situated ca. 200 m from the nest tree, next to the site where a male captured the prey and passed it down to the female. Caches were located at the height of 0–40 m above the ground, on average 12.9 m (Me=12 m; SD=5.6; N=107). The majority of prey items (90%) were cached at the height of 5 to 20 m (Fig. 7). I did not find any significant trends in the caches height (Kruskal-Wallis test: H (3, N=27)= 4.30; P=0.231) and its distance from the nest (Kruskal-Wallis test: H (3, N=50)= 4.92; P=0.177) during the breeding season.

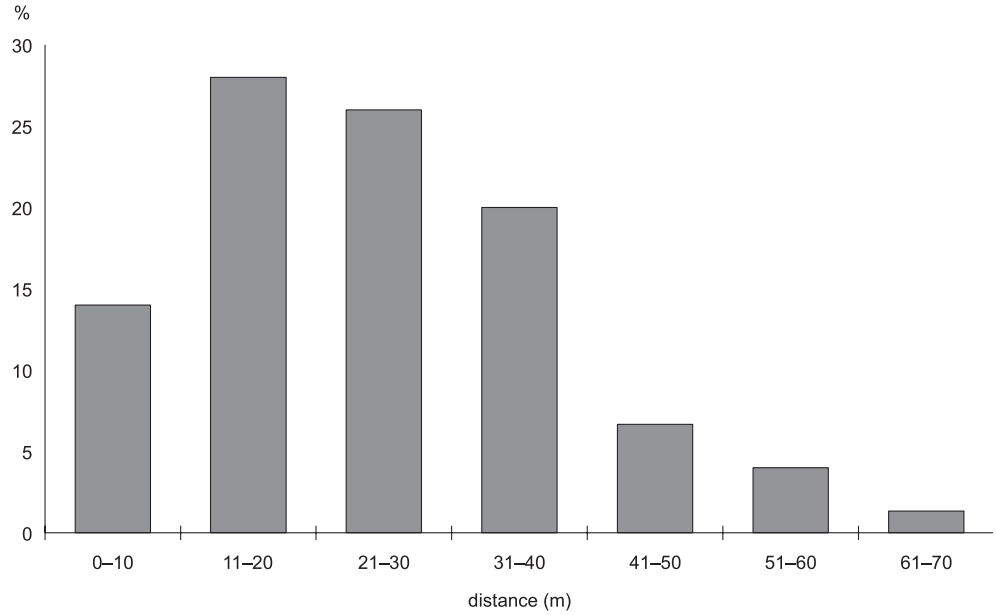

Fig. 6. *The distance between a nest tree and a cache in the Eurasian Pygmy Owl (N=150)*
Rys. 6. Odległość spiżarni sóweczki od drzewa lęgowego (N=150)

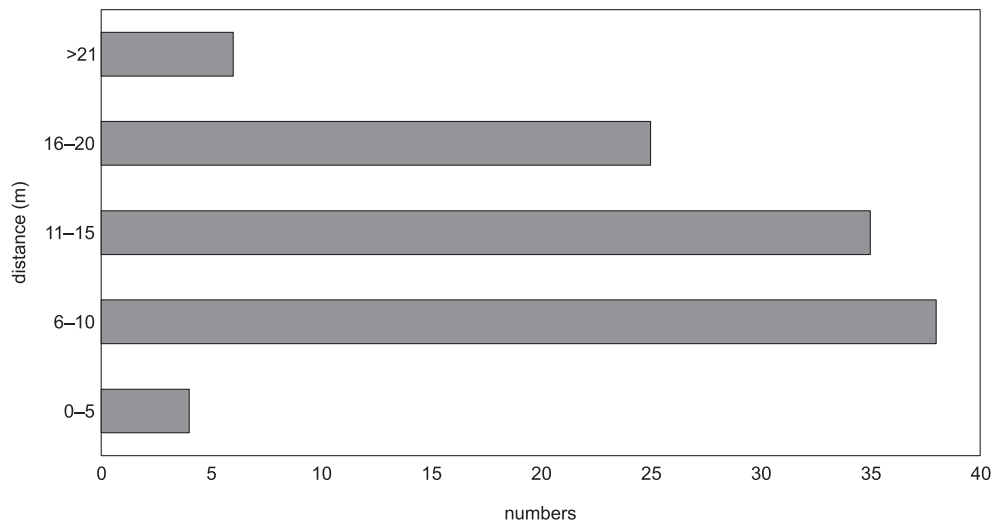

Fig. 7. *The height of caches of the Eurasian Pygmy Owl in the Stołowe Mountains (N=107)*
Rys. 7. Wysokość położenia spiżarni sóweczki w Górach Stołowych (N=107)

Hoarding and retrieving prey items from caches

Observations indicate that each prey item was deposited in a cache and later collected by the same individual. I recorded only one case when a male retrieved the food (probably stored before by his partner) and after a while passed it to the female. A sequence of

Photo 3. A dead Chaffinch *Fringilla coelebs* on the broken trunk of a dead spruce (Phot. R. Mikusek) – *Martwa zięba leżąca w spiżarni na szczycie ułamanego świerka*

behaviours related to food hoarding included: 1) a flight to a suitable place with prey in claws, 2) a transfer of a prey item from claws to the beak, 3) positioning and stabilization of a prey, 4) jump back and observation (probably rest and memorizing), 5) departure.

The mean time interval between the obtaining of food by female from a male and the deposition of prey in a cache was 3 min 43 s (SD=4 min 51 s; range 17 s–29 min 55 s; Me=2 min 05 s; N=121). Birds always used their beaks to stabilize a prey in a cache (Photo 3), sometimes with the help of talons. This activity lasted from 5 to 190 s (mean 53 s; Me=30 s; N=16). Prey retrieval from a cache lasted for a short time: a bird grabbed a prey item with its beak, passed it to talons and flew away (Photo 4).

Most prey items were placed with their back down (Photo 1). The owl stabilized the prey using its beak: it shook the head of a prey and hence pushed it between branches. This behaviour lasted for some time, until the prey was properly stabilised. Only once the prey fell down while being stabilised. After the food had been fixed, the owl made a few steps backwards and waited for a while, probably resting and memorizing details of the place. Observations indicate that caches are well remembered. Food was often retrieved from caches after long flights. Further evidence comes from the following observation. I found a partly feathered, dead nestling of the Song Thrush *Turdus philomelos* on the ground between the roots of a spruce. I assumed that it was a food item that had fallen down from a cache (such cases are pretty frequent), and I moved it to a broken tree trunk nearby. The prey was soon retrieved by a female. Three day later the female sat down on the ground exactly in the place where the nestling had been lying, apparently looking for the prey. Other observations of owls sitting on the ground were always associated with bathing, hunting for mammals and food transfer. Several times I observed owls searching through places used before as caches.

Photo 4. A dead Crested Tit *Lophophanes cristatus* on the horizontal branch of a spruce at the height of 6 m above the ground (Phot. R. Mikusek) – *Martwa czubatka leżąca na poziomej gałęzi świerka na wys. 6 m nad ziemią*

Phenology of cache use

The earliest prey hoarding by a female was noted on 8 April, and the latest on 8 July. For males the respective dates were 26 March and 22 August. It's worth mentioning, however, that each year from late July the data were collected extensively. The earliest record of owlets using caches was observed on the fourth day after fledging (a wing received from the female), while they started catching food regularly two weeks after fledging (a partly eaten bird laid on a branch 25 minutes after its receiving from the parent). Deposition and retrieval of prey from caches was observed between 3.00 and 21.00, with peaks around sunrise and sunset. The number of hoarded prey items was clearly correlated with the activity of a male bringing food to a female (Fig. 8). Therefore more than 80% of observations come from June, when the young are intensively fed in nest holes. **I**n the morning prey was deposited in a cache mostly between 5 and 10 a.m. (29.0% of all observations; 3.7 prey items/h), but some food was hoarded between 4 and 5 a.m. (11.7%; 9 items/h). The evening peak of hoarding was more intense (50.6% cases; 19.5/h). The retrieval of food had two clear peaks, between 4 and 5 (30.8% prey items; 8/h) and between 20 and 21 (23.1%; 6/h). Between 5 and 20 females used caches as a source of food sporadically, on average 0.7/h (Fig. 8).

The duration of storing of a food item in a cache was estimated in 25 cases. On average prey remained in a cache for 38 h (1.5 days). The deposition and retrieval of the same prey was observed directly nine times. The time interval between the two events was estimated at 19.7 h (range 9 min and 115 h). In some cases prey remained intact in a cache.

Among other direct reasons explaining the deposition of prey in the cache I noted: a) difficulties with the transport of a very heavy prey (including medium-sized birds, e.g.

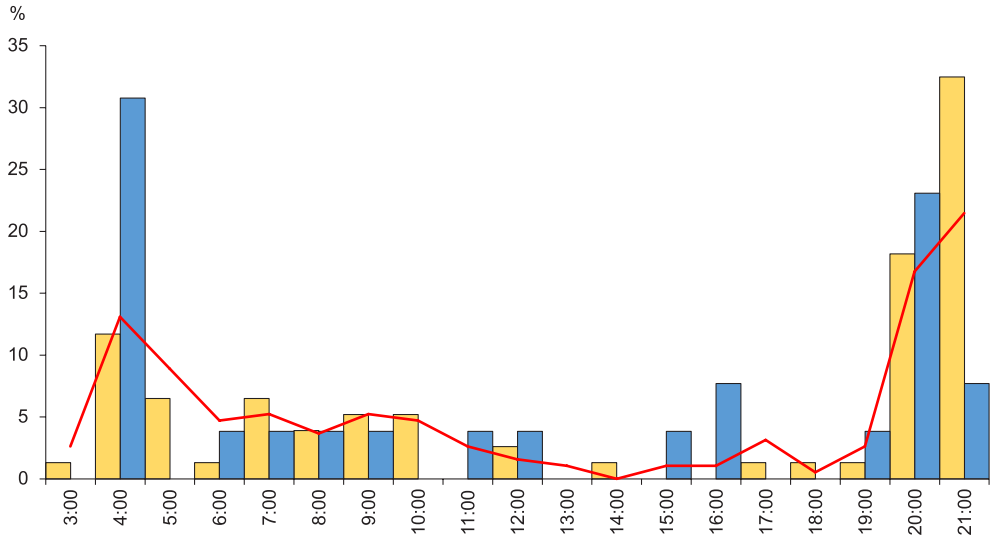

Fig. 8. *Circadian distribution of cache use by female Eurasian Pygmy Owls in relation to food delivery by males. Yellow bars – prey hoarding (N=77), blue bars – prey retrieval (N=26), red line – arrival of males with food (N=191)*

Rys. 8. Rozkład wykorzystania spiżarni przez samice sóweczki w ciągu doby w zestawieniu z aktywnością dostarczania pokarmu przez samce. Żółty słupek – deponowanie ofiary (N=77), Niebieski – słupek pobieranie ofiary (N=26), czerwona linia – przyloty samców z pokarmem (N=191)

Chaffinch *Fringilla coelebs*), especially when the prey was transported up the slope and over a long distance; b) difficulties with carrying a prey into the nest hole, e.g. because of a small entrance diameter, exceptionally large prey size or poor visibility (e.g. on 10 June at 3:40 and illuminance of 1.5 lx a female, after an unsuccessful attempt of carrying an adult Nuthatch *Sitta europaea* into a nest whole, sat down on the ground under a nest tree and after 4 min deposited the prey in the cache, flying into the hole without food; c) the presence of both parents with food near a nest hole (in one case a female retrieved a prey from a cache, but hoarded it again after two minutes when a male appeared near the hole with another food item); d) waiting for a partner (concerns a male with food near the nest, when a female did not leave the hole, or was away); e) hunting (e.g. on 3 July 2001 a male, when a female was absent, left food in a cache to attack a mouse in a while); f) excess food in the nest hole – remains from feeding of the young were taken out of the hole by females and often hoarded (at least 60% cases, N=15). Owls also stored prey items accessible in large numbers for a short time (e.g. altricial nestlings approaching fledging time).

Aggression of a female towards a male

At 10 broods, from April to June, I recorded 29 attacks of a female against a male. These antagonistic interactions occurred at the distance of 8–50 m from the nest. In 90% of cases (N=26) the attacking party was a female. If three series of attacks lasted for fewer than 2 minutes, they were treated as one event (hence N=20; Fig. 9). Half of the attacks (N=10) occurred in the second half of April (the period corresponding with egg laying and early incubation), while 25% (N=5) during first two weeks of nestlings' life. During incubation I recorded this behaviour only once (3 attacks of a female during 30 s), when after the food transfer the male tried to copulate with the female. In one case a male

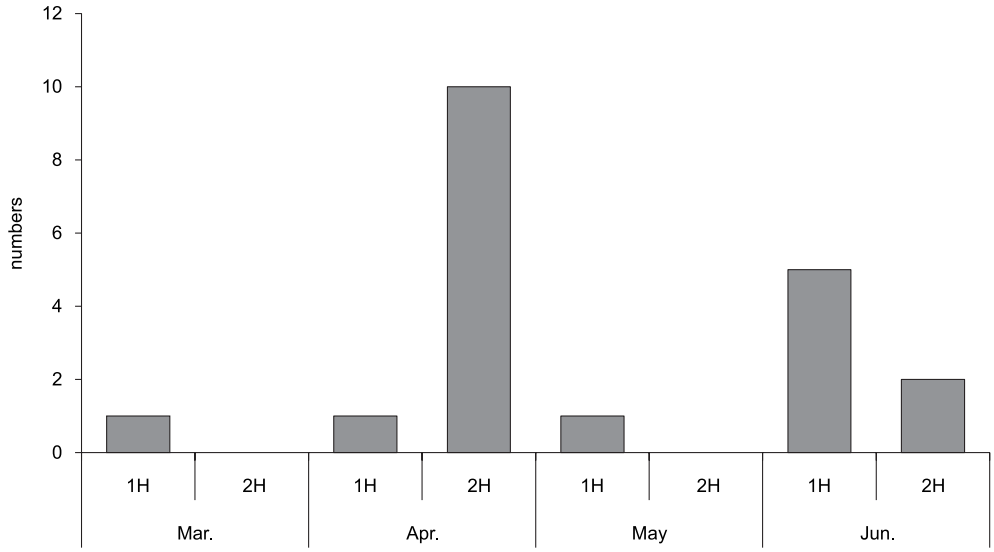

Fig. 9. *Seasonal distribution of aggressive female behaviour against the males of the Eurasian Pygmy Owl in the Stołowe Mountains (N=20)*
Rys. 9. Rozkład czasowy agresywnych zachowań samic sóweczki wobec samców w okresie lęgowym na terenie Gór Stołowych (N=20)

probably mistook his partner for a foreign male who was calling at the territory boundary, and attacked his partner. This attack was very short and birds copulated afterwards. Another attack was associated with the acoustic stimulation near the nest to mist-net and ring the birds. The attracted birds almost immediately attacked each other in the air and then fell down. The birds were clenching for a while on the ground, which helped to catch the female, but the male flew away. In this case it was impossible to establish which bird had started the attack. Another attack was recorded after an unsuccessful food transfer. After food had fallen to the ground, birds locked talons and were falling down with their wings stretched for a while until they let go just before reaching the ground. During three visits I observed repetitive attacks of females against males in series of 2 attacks during 10 s, 3 attacks/30 s and 6 attacks/120 s. The last case was especially interesting: the male appeared at the nest without any prey, while typically at the nestling stage (young were at the age of 8 days) males arrive with some food (Fig. 10). The high number of attacks probably resulted from the fact that the male did not leave the nest tree, despite being attacked. Finally the female entered the nest at the male's presence, and he spent some time near the hole. In most cases after female attacks males left the area with a long straight flight (ca. 72% of 21 cases); other males remained in the area for a while. In 9 cases (31%) a female chased a male just after food transfer, in 5 cases (17%) – after copulation. A very interesting situation was noted on the first day of incubation. A female attacked a male with talons, when he grasped a prey deposited by the female in a cache 14 minutes earlier, close to a place of prey transfer. After this attack the male immediately left.

Mean time of male stay near the nest hole was ca 17 min. (Me=6 min 30 s; N=177). Males remained near the nest hole longer before the start of incubation (ca. 48 min.) than at the nestling stage (ca. 7 min; Kruskal-Wallis test $H_{4,160}$= 60.5; P<0.0001; Fig.

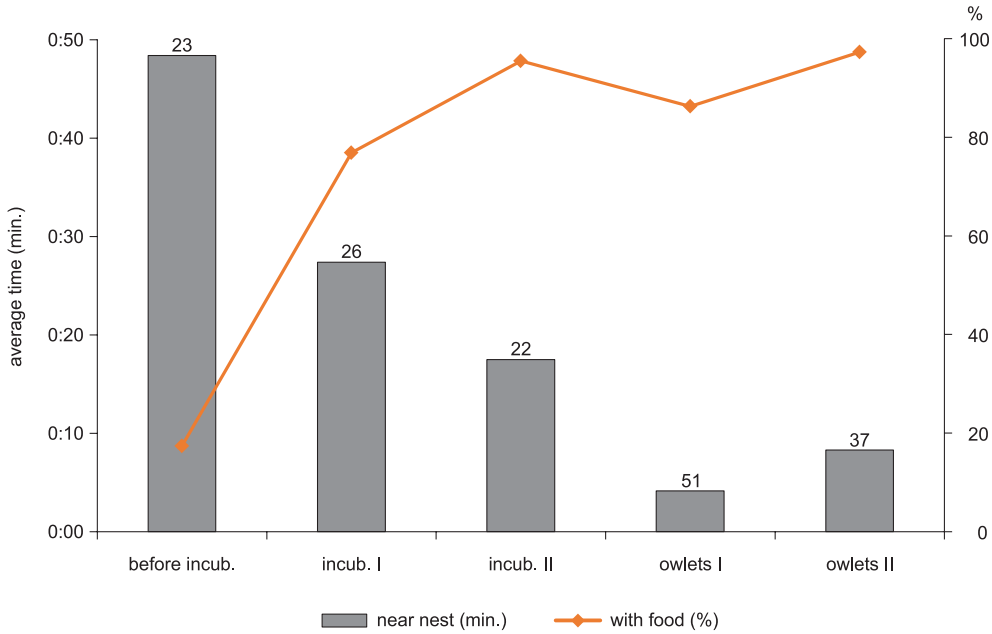

Fig. 10. *Duration (min.) of male stay near a nest hole (left axis) and percent of male visits with food in various parts of the breeding season (right axis). Incubation and owlet periods were divided into two equal sub-stages. Number at bars refer to the number of observations for the focal stage (N=159)*
Rys. 10. Średni czas (min.) przebywania samca sóweczki w okolicach dziupli (oś lewa) oraz procent wizyt samca z pokarmem w różnych okresach sezonu lęgowego (oś prawa). Okres inkubacji i piskląc podzielono na dwie równe części. Cyfry przy kolumnach oznaczają liczbę obserwacji dla danego okresu (N=159)

13). Males approaching the nest hole with food stayed there longer than males without food (with food: 11 min 30 s; Me=4 min 30s; range 10 s–26 min 20 s; N=135; without food: mean 34 min 30 s; Me=16 min 00 s; range 20 s–40 min 00 s; N=42; Mann-Whitney test: U=1015,5; P<0.00001). The proportion of male visits with food at the nest increased as the season advanced, and constituted 17.4%, 76.9% and 95.5% of visits for pre-incubation, early incubation and late incubation, respectively (χ^2=10,79; df=4; P=0.029; Fig. 13). During the nestling stage male visits without food were rare (13.7% and 2.7%, respectively in the first and second half of the nestling stage).

Discussion

Results of this study suggest an important role of caches during the breeding season in the Eurasian Pygmy Owl. Among factors affecting this behaviour are short-lasting availability of some food types (e.g. the young of altricial birds in nests) and the possibility of fast replenishing of energy reserves at dawn (Lack 1954). Almost all prey items brought by males to the nest were transferred to their partners. These observations contradict earlier suggestions that female Pygmy Owls use prey hoarded by males near a nest-hole (np. Voous 1988, König et al. 1999). Males depositing and retrieving food from caches were recorded only eight times, and females using food cached by males were never observed. However, I recorded two times that a male deposited and retrieved the same food item

twice. The act of deposition was not observed by the female who was hunting away or stayed in the hole, and did not react to the male calls.

During the breeding season caches were used only for a short time, probably because of decaying processes. This also explains why nest holes are not used as food deposits: they are damp and food remnants gather at their bottom, despite regular cleaning by females during the nestling period (Schönn 1980, Mikkola 1983, R. Mikusek – unpubl. data). Spatial distribution of caches was associated with places of food transfer and habitat structure. Because caches are scattered in space near the nest, they are difficult to find by food competitors (Smith & Reichman 1984). It has been underlined that the close proximity of caches may facilitate their successful defence (Cade 1967, Hernandez 1997). Eurasian Pygmy Owls well remember their caches, and probably the prolonged stay after prey stabilization helps them to memorize the site. However, it is also possible that birds rest after prey hoarding. Short upward flights of owls may be misinterpreted as „cache searching". Some observations suggest that birds may try to reach high branches to leave or retrieve the prey in this way. In Eurasian Pygmy Owls the hoarding behaviour may be favoured due to the presence of many dispersed places, potentially useful as caches (spruce branches), difficult to find by competitors, such as Jays *Garrulus glandarius* and Squirrels *Sciurus vulgaris*.

A consequence of reverse sexual dymorphism (RSD) in the species is female dominance expressed e.g. by the aggression against her mate (Schönn 1980). This behaviour is often observed in captivity, where some males die as a result of female attacks (Mebs & Scherzinger 2000). High level of aggression in female Eurasian Pygmy Owls may result from the necessity of nest and food defence, and may explain a very low nest predation in the species (Mikusek 2001). Active defence of caches against food competitors has been described in woodpeckers Picidae and shrikes Lanidae (np. Cade 1967, Moskovits 1978). Several hypotheses have been presented in the literature to explain RSD in Eurasian Pygmy Owls: a) female defence of young against males that exhibit cannibalistic behaviour (e.g. Earhart & Johnson 1970); b) selection on males to become efficient foragers (Schönn 1976; Lundberg 1986); c) defence of a female hunting territory against a male (or hypothesis of food relationships, Lundberg 1986). The first hypothesis (male cannibalism) is not supported by my observations, as records of males looking into the hole or visiting it (also with food) during the nestling period, when a female was away, are frequent. I also observed twice male visits in the hole at the presence of watching female, and seven extended male visits with food in the nest hole when the female was absent for a long time. Two further hypotheses are difficult to verify. However, I have never observed both partners hunting close to each other, that might support the third hypothesis. I observed twice male hunting near the nest hole, including the situation when a female was watching a male. A strong aggression of a female near the nest/cache could be explained as a defence against kleptoparasitism. I observed a strong female aggression against the Great Spotted Woodpecker *Dendrocopos major*, Eurasian Jay, Eurasian Nutcracker *Nucifraga caryocatactes* and Eurasian Red Squirrel (R. Mikusek – unpubl. data). A bird silhonette (spreading of slightly lowered wings) during prey hoarding may be associated with kleptoparasitism avoidance. Such a behaviour, called *mantling display,* has been described in birds of prey and some owls, e.g. Snowy Owl *Bubo scandiacus*, and has been explained as a defence of prey against food competitors (Cramp 1985). I observed one attack of a female against the male who tried to retrieve a food item deposited by the female a few minutes earlier. It has been suggested that female aggression may increase during a period of food scarcity and near caches. For example, frequent staying

of Tengmalm's Owls *Aegolius funereus* near their winter caches has been explained as a cache defence (Hayward & Hayward 1993). However, the behaviour of defence of hoarded food in owls has been poorly documented in the literature.

The number of caches in the vicinity of nests has been increasing during the breeding season. At the same time the duration of male stays near the nest hole has declined, which could reflect greater food demands, but also higher female aggression. Female aggression increased in late April (beginning of incubation). During this time also the mean duration of a male stay at the nest rapidly declined, and he started bringing food to the female more often. The duration of stay of a male at the nest hole was six time shorter during the nestling stage compared to the time period preceding incubation, while the number of visits with food increased more than four times (Fig. 10). Ritchie (1975) suggests that the presence of caches may reduce the probability of aggression of larger females. Of 29 within-pair aggressive interactions, 90% were initiated by a female. In two cases attacks seemed very fierce, and in one case the pair fell to the ground. The reason for attacks was the arrival of a male without food at the nest (also after food transfer) and an attempt to steal food from cache. Only once was a male able to retrieve a prey from a cache (deposited before by his partner) to give it back to the female a while later. This is an indirect evidence for the hypothesis that a male may pose a danger to hoarded food.

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