ON THE BIOLOGY OF THE GREATER SPOTTED EAGLE, (*AQUILA CLANGA* PALLAS 1811).

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ABSTRACT. – A study of Greater Spotted Eagles (GSE) (*Aquila clanga*), was carried out by direct observation from 20 April to 19 August 1997 in the Biebrza National Park in north-east Poland. This study provided information on home range, flight behavior, hunting methods, hunting territory, prey composition, and interaction with other other species. Behavior was recorded at 5 min intervals, and was plotted on map quadrants 200 x 200 m in size. Observations were carried out daily from 0800 to 1800 H. Since the first pair (M1 and F1) selected for study did not attempt to breed, attention was shifted to a second pair (M21 and F2), whose young fledged on 16 August. Sexes were determined at copulation and, thereafter, by moulting pattems. Both males (M1 and M2) hunted chiefly on the wing (soaring in search of prey and stooping to the ground) and were regularly observable (40% of the time). Females (F1 and F2) were seldom observed hunting. Flight activity lasted between 0.5 and 7.5 H/day, largely between 0900 and 1700 H, with a peak between 1000 and 1400 H. Accordingly, the major proportion of prey was also recorded between these hours. Between 1400 and 1500 H, there was usually a period of repose. The start of hunting by F2 (on 12 July when the eaglet was about 3–4 weeks old) led to a clear decline in M2's flying activity. The territorial flights of M2 (undulating display flights), however, increased. The breeding and hunting territories marked out were defended against members of the same species, the closely related Lesser Spotted Eagle (LSE) (*Aquila pomarina*) and other large birds of prey. Male GSEs in the Biebrza valley probably have clearly defined territories that they defend. Up to mid-July the male's hunting success was 34%. The success of hunting on the wing declined to below 20% during the day. Since prey continued to be carried to the eyrie, this clearly indicated a strategic change in favor of still-hunting or hunting on foot. For the most part, M2 arrived with mice (65%, likely *Microtus*), and frogs (19%, *Rana* spp.) at the eyrie. F2, so far as it could be observed, showed a preference for frogs. Based on the estimated weight of the observed dietary needs, as compared with the presumed needs of the young eagle based on the literature, an attempt was made to determine the completeness of observations of arrivals with prey at the nest for the total observation period. This led to the conclusion that 2/3 of the arrivals with prey was likely observed. The two pairs (1 and 2) of GSE defended home ranges of 15 km^2 and 19 km^2, respectively. These values correspond to those given in the literature. However, studies of LSEs by conventional telemetry have revealed clearly larger home ranges than those assessed from direct observation. The breeding territories of GSEs in Biebrza valley displayed a variety in landscape structure. There were clearly defined areas for hunting, for conflicts with other large birds of prey, and areas where undulating display flights were performed. The hunting grounds of M2 clearly shifted after 12 July. This could have resulted from avoidance of increased in human activity in the meadows

of the old hunting territory, which had been mown by this date; as well, large numbers of other raptors and White Storks (*Ciconia ciconia*) in search of prey began to appear after this date. In this, GSEs studied clearly differed from the closely related LSE. We recognized a "contact call", a "territorial call" connected with the undulating display flights and a special, quite distinct "warning call" or "alarm call" which was audible when other large birds of prey were around.

The Greater Spotted Eagle (*Aquila clanga*) is one of 24 European bird species regarded as globally vulnerable (Collar et al. 1994). Formerly common in several east European countries, less than 1000 pairs may have survived in these areas, mainly in the European part of Russia; the global breeding population has been estimated at less than 2500 pairs (Tucker and Heath 1994, Meyburg et al. 1997). This unfortunate situation is even more serious since our knowledge of the biology and ecological requirements of this species is quite limited, severely hindering protection activities. In the western part of its range, it occurs with the Lesser Spotted Eagle, (*A. pomarina*), a species considered so similar, that together they were formerly considered as a single species or semi-species (Zhezherin 1969, Meyburg 1974, Meyburg 1994, Bergmanis 1996, Seibold et al. 1996). Up to now, little remains known of the differences between the ecological requirements of both species.

There is no explanation as to why the breeding range of the Greater Spotted Eagle (GSE) is limited westwards by eastern Poland although the similar-looking Lesser Spotted Eagle (LSE) occurs further to the west as far as east Germany. On the other hand, the breeding area of the LSE is restricted in the east by an indistinct (or inadequately known) border situated near Moscow although the area of its sister species stretches far to the east through Siberia extending to the Pacific Ocean (Meyburg 1994).

We tried to contribute to the solution of these questions by direct long-time observation of two pairs of GSE nesting in Biebrza National Park in eastern Poland.

METHODS

This investigation was carried out in Biebrza National Park in northeast Poland, near the city of Bia?ystok. Core to this area is the highly meandering Biebrza River, which floods the surrounding complex of fens each spring until late May. There is also a high diversity of marsh and moorland plants, fish species, and 179 species of breeding birds (Dyrcz et al. 1972, Schäffer 1996).

In 1997, preparatory observations were made from 20 April to 17 May to select suitable pairs of GSE for systematic data sampling; this was followed by daily observations from 0800–1800 H (Central European Summer Time: UTC + 2 hrs) from 1 June to 19 August. Since the pair initially selected for study (Male 1 – M1; Female 1 – F1) made no attempt to breed, attention was shifted between 21 June and 19 August to another pair (Male 2 – M2; Female 2 – F2), whose young eventually fledged on 16 August.

Using a point-sampling method, all observations were documented every 5 minutes while all locations were assigned to map quadrants of 200 x 200 m in area. Spatial patterns were calibrated with the help of geographic data (Biebrza National Park, records of the late 1970s, as well as aerial photographs of 1994) and various landmarks.

Observations were made with 10 x 50 binoculars and a telescope equipped with a 30 X wideangle lens from a fixed point; this allowed for flying eagles to be spotted at a distance of up to 2.5 km in the area surrounding both observation points. Nest observations were made from a fixed position at a safe distance from the eyrie to avoid disturbance of the birds (400 m). At least both males studied could be observed by this relatively simple, direct method during a substantial part of their daily activity (see below).

Birds could be recognized individually by moult pattern. Using size and other individual characteristics, we could differentiale among males and females; copulations that were observed occasionally also confirmed gender.

Calls were recorded on a Sony Cassette-Recorder WM-6C and K6ME67 microphone (Sennheiser Electronic KG, Wedemark, Germany) and later analyzed using the "Avisoft SASLabPro programme" (Raimund Specht, Berlin).

RESULTS

Weather. – For all observations, there was no period of bad weather lasting longer than one day. Temperatures were always above 20° C (up to 35° C) during the day and not lower than 10° C at night. Wind speed rarely increased before 0900 H. No storms were encountered during the whole period. Flights made by M2 were predominantly during weak winds, while on calm days it was significantly reduced (chai square-test, $P < 0.001$), even when in fair weather thermals could be expected. Eagles avoided flying in rain; of 740 data points recording rain, M2 was only observed 6 times, likely because of a lack of updrafts, this in contrast to 1688 observations under alternative weather conditions (chai square-test, $P = 0.0001$). M1 was observed twice providing itself with plenty of food before rainfall commenced.

Flight Activities. – Within 56 days during which, theoretically, about 6000 data points (at 5 min intervals) would have been possible, M2 was observed at 2500 five-minute intervals, i. e., in about 40 % of the entire observation time (Fig. 1). On average, the successfully breeding M2 was observed for 4 H/day with a maximum of over 7 H. The remaining time included activities for the most part not recorded by direct observation, e. g., resting, comfort behavior (preening, etc.), the unobserved part of hunting from perch or on foot, etc. Consequently, the data shown represents the entire flight activity of the eagles.

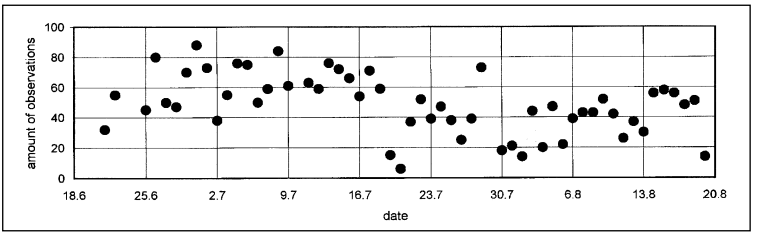


Figure 1. Number of data points (at 5 min intervals) at which Male 2 (M2) was observed during 56 days of observation. At each point, observations of one whole day are summarized.

Over the course of our observations, the frequency of sighting of the birds generally decreased. Furthermore, a more abrupt decline in flight activity was observed after mid-July.

In contrast to the scattering of data during the entire observation period (Fig. 1), the diagram showing the observations of M2 during the day demonstrates a lesser degree of scatter (Fig. 2).

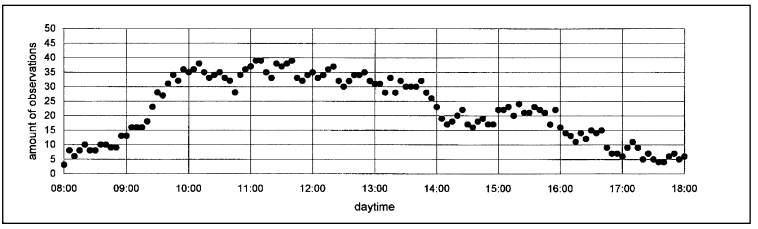


Figure 2. Number of daily observations of flight activity of M2. Each point represents the sum of all observations during the entire observation period at the given time.

Although this in part may be caused by the smoothing effect generated by summarizing all observation points for the whole period at the given time, we believe it represents a rather conservative course of the eagle's day, less dependent on the progress of the breeding period. The main activity period was between 0930 and 1400 H. There was very little flight activity before 0900 and after 1700 H. Between 1400 and 1500 H, a break was noticed. A significant part of M2's daily time budget was spent hunting and carrying prey, in addition to soaring and territorial display flights (Fig. 3). The main hunting period and, accordingly, highest intensity of conveying prey was between 1000 and 1400 H, whereas the display flights seemed to be confined to a shorter

period. The break in activity, mentioned above was more clearly observed in hunting activity (Fig. 3) and was even more marked in calm weather (not shown). The number of attempts at prey capture from searching flight decreased after 1600 H; however, the frequency of conveying food to the eyrie increased after this time, indicating a shift in strategy from searching flights to hunting from perch or on foot, the latter of which was not often observed. This behavior is more clearly demonstrated if these data are applied in relation to flight activity as a whole (Fig. 3a).

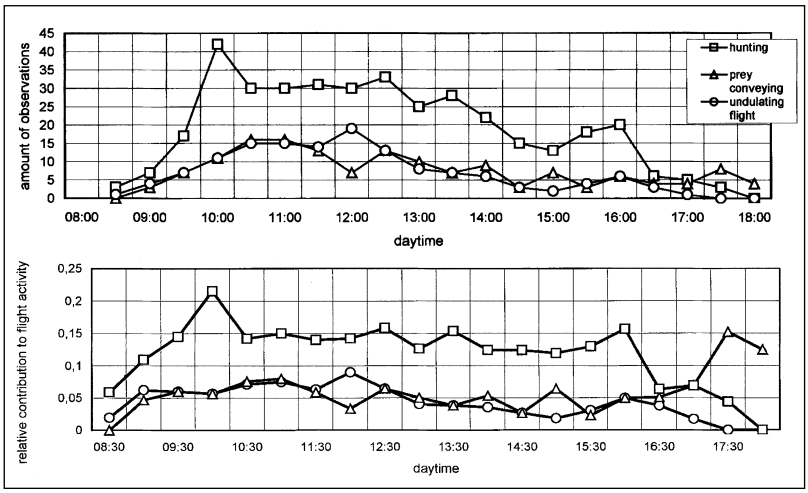


Figure 3. Activity of M2 hunting, conveying prey to the eyrie and performing undulating display flights of all days of the observation period. Data are summarized in half-hour periods to smooth the curve.

Figure 3a. Crepuscular hunting strategy is more clearly demonstrated if the data are applied in relation to flight activity as a whole.

Concerning the activities during the 56 days observation period, the decrease in flight and hunting activity after mid-July (Fig. 1) was more striking when the data were summarized in seven-day periods (Fig. 4). At this time, F2 began to leave the immediate vicinity of the eyrie (on 12 July, when the eaglet was about 3–4 weeks old) and participated in hunting. Previously, it had guarded the young almost continuously. The participation of the female in hunting at least for its own requirements also became noticeable through a marked decrease of prey conveyed by the male.

The frequency of territorial display flights increased from the end of July, representing more conflicts with other large raptors now appearing more often flying above the territory having already concluded their breeding period.

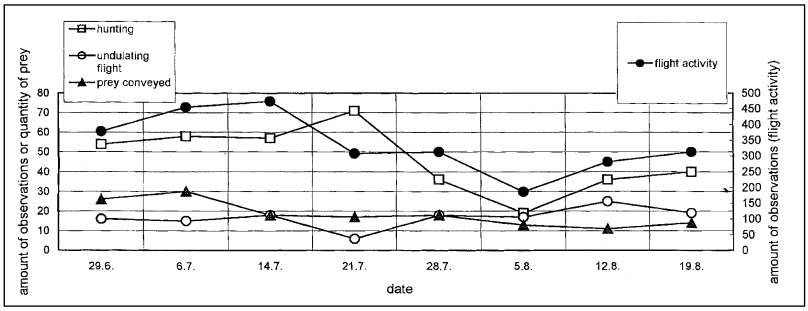


Figure 4. Entire flight, hunting and undulating flight display activity as well as amount of prey conveyed to the eyrie during a period of 8 weeks summarized in sevenday periods. Note the different seale ofentire flight activity in contrast to the other data shown.

Hunting was mostly observed during soaring (search) flights, from which the eagles performed sudden dives to the ground. Alternative hunting strategies, e.g., from perch or on foot, could be only seldom recorded by our method of direct observation from a fixed point. Mean hunting success in the morning from search flight was about 39% (107 attempts were successful out of 375 recorded). Hunting success decreased linearly during the day (Fig. 5) and (not linearly) during the observation period. Hunting success declined abruptly from 33.8% to 23.6% after 12 July (chai square-test, P = 0.0001).

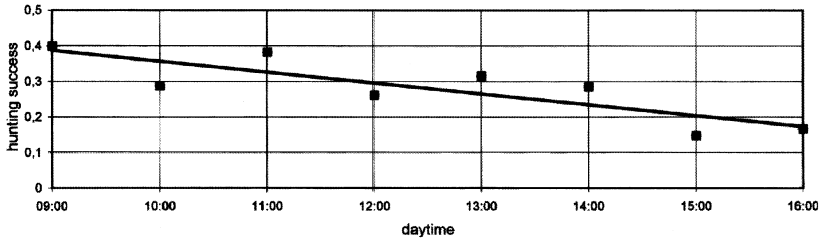


Figure 5. Changes in daily hunting success (by flight) of M2. Success decreased linearly by a factor of 2 (gradient: −0.03; R = 200.96; P = 0.011). The data are summarized in one-hour periods.

The female (F2) was never observed hunting from searching flights; it was altogether much more secretive than M2, even after beginning to hunt on its own in mid-July.

Prey. – The main prey constituents were mice, mostly voles, and frogs (Tab. 1). The masses given in this table are calculated based on data from Meyburg (1970). Parallel to the moment when the female was first seen outside the area of the eyrie and also parallel to the male's change of main hunting area, a shift was to be observed in prey composition to more frogs (Tab. 2). As far as could be distinguished, the female generally preferred frogs.

As known from both Spotted Eagles, most prey was transported individually in the bill. Sometimes a change from bill to talons or vice versa could be observed.

Table 1: Prey conveyed to the eyrie during the whole observation period.

Prey	**M2**	**%**	**Mass (g)[a]**	**F[b]**	**%**	**Mass (g)[a]**
Unknown	12	8.3	300	2	15.4	50
Unknown (small)	2	1.4	20			
Unidentifled (rest of prey)	1	0.7	100			
Frogs (*Rana* spp.)	28	19.4	420	9	69.2	135
Reptiles (*Lacerta* spp.)	1	0.7	15			
Mice	91	63.2	2275	2	15.4	50
(*Microtus* spp.)						
Small rodents (Soricidae)	3	2.1	30			
Marten (*Martes*)	1	0.7	100			
Nestlings	3	2.1	90			
Passerines	1	0.7	30			
Non-passerines	1	0.7	500			
Total	144		3880	13		235
Transported by talons	6	4.2		1	7.7	

[a] Mean mass of prey are based on values from Meyburg (1970): Duck: 500 g; mouse-weasel, rest of prey: 100 g; Passerines, nestlings: 30 g; voles, unknown prey: 25 g; frogs, reptiles: 15 g; small voles, small unknown prey: 10 g.

[b] The female was only seldom observed hunting or returning to the eyrie, since it showed quke secretive behavior. Additionally, the female was never observed hunting from search flights.

Table 2: Contribution of mice and frogs to the total number of prey (%). On 12 July, the female of the successfully breeding pair was observed hunting on its own for the first time.

Prey	Conveyed by M2 (before 11.07.) (%)	conveyed by M2 (after 12.07.) (%)	conveyed by M2 and F2 (after 12.07.) (%)
Mice	71.2	53.8	47.4
Frogs	9.6	24.6	32.1
Total	80.8 *N* = 73	78.4 *N* = 65	79.5 *N* = 78

Habitats. – The area of pair 1 (M1 + F1, not breeding successfully in 1997) was situated at the edge of a large wet deciduous forest dominated by birch trees (*Betula pubescens*). For years this area has been known to harbour two more GSE, several LSE and a White-tailed Eagle (*Haliaeetus albicilla*) as well as Eagle Owls (*Bubo bubo*), Cranes (*Grus* sp.), Black Storks (*Ciconia nigra*), etc. Adjoining this forest extended a wide plain of fens and Carex-meadows with groups of willow bushes and single birches, which were nearly completely flooded in spring by the Biebrza river. Later in the season, only small water-filled ditches remained. Long, highly differentiated lines characterized the region where woodland changed to open fen- or meadowland.

The home range (area in which M1 was observed during the entire investigation) was about 15 km^2, within which a much smaller area was used for hunting. Less than 20 % of the home range was woodland.

Pair 2 (M2 + F2, observed from 21 June to 19 August) also inhabited a wet deciduous wood about 1.5 x 2.5 km in size, also dominated by B. pubescens. The eyrie was situated in a birch at a height of about 8 m, ca. 200 m from the edge of the wood (Fig. 6). Fens and Carex-meadows with willow bushes and single birches, surrounded this forest. Adjacent to this were hay meadows, which were cut in the middle of July. NW of the eyrie was a small river, the banks of which were covered with reeds. To the N, on the far side of this river, was intensively used farmland while in the NW, a large deciduous wood enclosed territory of both the LSE and GSE. In addition Golden Eagles (*A. chrysaetos*), White-tailed and Steppe Eagles (*A. nipalensis*) were frequently observed near Pair 2.

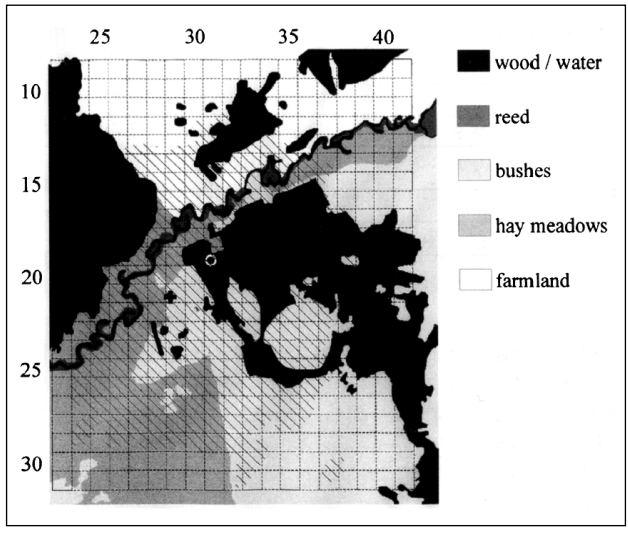
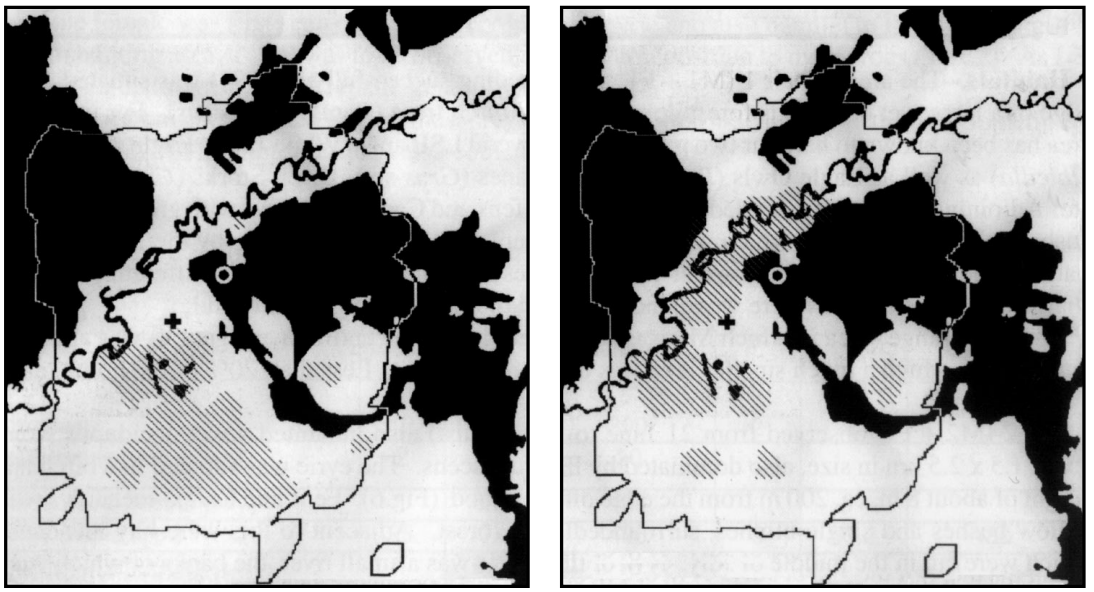


Figure 6. Habitat of the successfully breeding M2 and F2. Habitat structures are indicated by different half-tone representations. (Data: Biebrza National Park, records of the late 1970s, as well as aerial photos of 1994). The grid consists of 200 x 200 m squares. A cross marks the point of the observer; a point, surrounded by a white ring indicates the eyrie. Diagonal hatching indicates the home range. The centre of activity was located near the eyde in square 31/19, half a km from the centre of the home range.

The home range (diagonal hatching) was about 19 km^2, and included a hunting area of about 8.3 km^2 (Fig. 6). The centre of activity was near the eyrie and main hunting sites were 0.5 to 2.5 km from the eyrie. Only 20 % of the home range was woodland. The wood to meadow transition was even more complex than in the case of the home range of Pair 1 since parts of the carex/willow bush area were surrounded by the forest (cf. Fig. 6).

After 12 July, coinciding with F2's start of hunting and the outset of mowing of the meadows, M2 abruptly shifted its hunting area to the border of the nearby small river (Fig. 7), also changing its prey composition to include more frogs (Table 2).

Figure 7. Hunting areas of M2 before and after 12 July (diagonal hatching) within the home range (surrounded by an unbroken line). See also Figure 6.



Conflicts. – Like other eagle species (DelHoyo et al. 1994, Watson 1997) the GSEs observed showed pronounced territorial behavior when larger raptors ventured into their territory. After initiating undulating display flight, the male usually flew towards the intruder, after which in most cases left the territory. Only seldom did the conflicts become more severe to include physical contact. Sometimes, pursuits continued for a long time at high altitude through cloud cover. Conflicts with other large raptors were confined to an area held by M2 of about 8.5 km^2 with centres near the eyrie, at the border to the territory of the neighbouring LSE in the forest to the NW, and in square 27/25 within the hunting area.

Voice. – Calls of the GSE are frequently heard. We distinguished the following calls heard from more than 15 GSES:

1. The most frequent call was a hoarse or "croaky" call like "crych" or "chrych", uttered by the male mostly in the context of territorial behavior during undulating flight, or if the male was attacked by a smaller raptor. This call was not heard from the female during undulating flight that, however, was rarely observed. We name this "territory call".

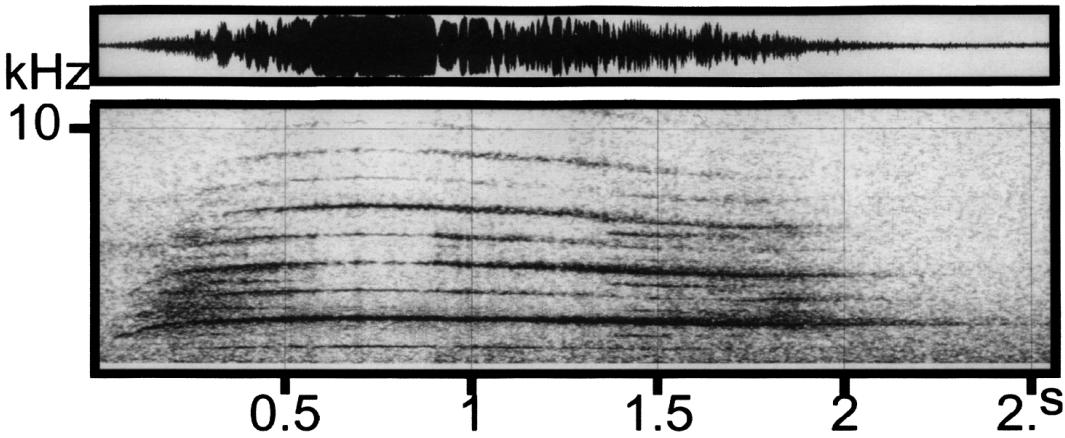
2. A second call, a "kyak-kyak", given in a series of two syllables/s, was the call most often heard before breeding. Used as a begging call, the young eaglet gave this call beginning in the fifth week; from the seventh week with the same volume as the adults, but higher in pitch. It became most

important when the eaglet had left the eyrie and was moving around within the forest.

During this time, the approaching adult used this call to detect the young, which answered immediately. We name this call a "contact call".

3. The third call was quite different from the other two. It was heard when a large raptor such as White-tailed, Golden or Steppe Eagle approached the eyrie, or when an Eagle Owl (*Bubo bubo*) was used near the eyrie as a decoy to capture eagles for attachment of satellite transmitters. This call lasted for several seconds and can be described as a hoarse, expiring "sryeeeeeah". Since we have seen the male approaching rapidly after F2 had used it to signal a White-tailed Eagle close to the eyrie, we call it "warning call" or also "alarm call". Meyburg (1991) described a similar call for the LSE.

Figure 8. Spectrogram of the "alarm call" or "warning call" of a female Aquila clanga.



A spectrogram of this "alarm call" of a female is given in Fig. 8. In the frequency-time sonogram, this call displays complexity in structure, and is composed of "harmonics" (spectral components occurring at integer multipies of a fundamental frequency) and "side bands". The lowest, most prominent track starts at about 1600 Hz, is increased to about 2150 Hz within a short time, and is held most of the time, finally ending with about 2000 Hz. Harmonics can be observed up to 13 100 Hz (sometimes even higher). Between these harmonics, up to 3 "side bands" can be found. This call partially does not represent a clear sound; at the beginning and the end, noisy elements prevail, resulting to the ear in a harsh caw. Its hoarse character is also demonstrated by the irregular amplitude envelope curve shown above (Fig. 8). The impression of lower pitch at start is generated by a lower frequency. At the end, decreased pitch is also well discriminated by the ear, but not so clearly visible in the spectrogram due to the noisy character of this part of the call.

DISCUSSION

The Method Used.–As already indicated, there is an urgent demand for more knowledge of the biology and ecological requirements of this highly endangered species in order to give protection activities a chance. Above all, long-term investigations are needed. These can be accomplished either through observations from a blind close to the eyrie, continuous tracking of transmitter-equipped birds or, as in our case, non-stop, direct observation from a safe distance. Observation from a blind close to the eyrie was in our case impossible for protective reasons, and since this method only provides information about activities in the immediate vicinity of the nest, this would only contribute to a partial knowledge of the bird's biology. Satellite transmitters have been

successfully used to track the migration routes of LSE and GSE (Meyburg et al. 1993, Meyburg et al. 1995, Meyburg and Meyburg 2000, Meyburg et al., in prep.); however, these transmitters are not easily located directly in the field, and satellite data are generally not yet sufficiently precise for accurate short distance locations. We did not use traditional VHF transmitters since exact locations with this method would need more than one person in the field (a requirement not fulfilled during most of the time of this investigation). Yet more adverse is the fact that the batteries of these transmitters generally last for only one season, and there is often no potential for re-capturing birds at the beginning of the breeding season to fit them with a transmitter. Consequently, only the method of direct long-term observation from a safe distance remained.

Since males performed most of their activities while in flight and were consequently more easily detected, we observed males for about 40% of the entire observation time, averaging up to 4 hrs per day with a maximum of more than 7 hrs.

It is well known that resting consumes a large part of the daily time budget of raptors (cf DelHoyo et al. 1994). Consequently, we believe that we have recorded a major part of M2's activity by the method used. In the case of F2, the situation was much less favourable since F2 behaved quite secretively. Sometimes F2 could only be detected when leaving, while in other cases, detection only when approaching the eyrie. Below, when the amount of food conveyed to the young is discussed, it was assessed to what extend, if any, this behavior influenced the conclusions made during this investigation.

Age of the Young. – Considering the date of fledging (16 August), an incubation period of ca. 43 days and a nestling period of ca. 63 days (Wendland 1971, Cramp and Simmons 1980, Meyburg and Pielowski 1991) a hatching date of mid-June and egg laying at the beginning of May can be estimated. When we started our observations of Pair 2, the young would have been almost one week old. On 12 July, the female was observed for the first time hunting; on this date, the young would have been almost 4 weeks old.

Activities. – The preference of males for soaring in updrafts created by thermals or low wind clearly depended on favourable weather conditions. Consequently, observed males were on the wing only in fair weather, and not before 09:00 H. The prevailing hunting method was diving from soaring flight, and was easy to observe by the method used.

Though the growing young should need increasingly more food during the nestling period, there was a conspicuous drop in flight and hunting activity and in the amount of prey transported to the eyrie by M2 in the middle of July. At this time, several events are to be taken into consideration.

On 12 July, the female was first observed leaving the vicinity of the eyrie and participating in hunting by itself. Concurrently, the male was shifting its main hunting area from the hay meadows to the border of the small river situated NE of the home range. As well, mowing of the hay had started, and there was an increase in the amount of frogs taken by the male.

This change in prey composition can perhaps be explained by the physical difference in hunting areas. A shift to the wetter borders of the river would likely cause a change in prey from mice to the more easily caught and more abundant frogs. The decrease in M2's hunting activity and prey amount can be explained by the participation in hunting of the female, at least for its own needs, from this date onwards. Discussed below, we have some arguments supporting the view that the female does not participate substantially in feeding of the young.

More difficult to explain is the shift in the male's main hunting area at this time. There may be a relationship with the start of haymaking, which attracted a huge number of storks, eagles and other birds of prey. Possibly, M2 left these now crowded meadows, to avoid the large number of competitors. This behavior would denote a clear difference to the LSE, which is strongly attracted to recently harvested meadows. On the other hand, we have sometimes observed GSEs on those meadows as well.

Hunting success. – The hunting success of M2 in the moming was near 40%, but decreased

linearly during the day and also, though not linearly, during the observation period (with a step down to about 2/3 after 12 July). The decrease during the day could perhaps be explained by declines in the activity of prey animals. The abrupt change in hunting success in mid-July is not easy to explain; perhaps it had something to do with the concurrent change of hunting area.

Hunting success differs greatly among various birds of prey. Hantge (1980) reports about 5–11% in aerial hunters such as Sparrowhawks (*Accipiter nisus*), Goshawks (*A. gentilis*), Eurasian Hobby (*Falco subbuteo*) and Peregrine Falcon (*F. peregrinus*); for Osprey (*Pandion haliaetus*), 20%. Watson (1997) reports about 29% in the Golden Eagle. Compared with these data, the hunting success of GSE described here is extremely high. This could be due to prey (mice and frogs) or to the favourable prey available in the Biebrza Marshes.

Conflict Handling. – As common in animals, conflict behavior in the eagles was "ritualised" to a rigid pattern whereby severe incidents were avoided, and in most cases, the owner of the territory was respected immediately. Nevertheless, through undulating display and flight towards the intruder, territory was defended, showing that at least the observed males had true defended territories as has been observed in Golden Eagles (cf. Watson 1997). Possibly, this differs from the LSE, for which Meyburg (1991) believes true territories are unlikely. Using transmitters, Scheller et al. (2001) have shown overlapping home ranges in LSE, although this has not been proven with regard to the population density in the Biebrza Marshes. Contrary to M2, F2 was observed hunting undisturbed in parts of the territory of the neighbouring male. However, in this territory there was no female present.

Apart from significance in courtship, another function of this behavior may be to establish territory early in the spring for the later arriving females. Accordingly, in the first territory, one single bird was observed first on 22 April (which later proved to be a male) and persistently performed undulating display flights four days before a second bird appeared (which later proved to be a female). On 2 May, copulation was observed, confirming sex determination.

Food Composition and Consumption. – For both males, small mammals represented the majority of prey items. The proportion of frogs was relatively high (10–30%), while the proportion of birds in the diet was low, this in contrast to the findings of Galushin (1962) who reported 45.6% in the Oka-Valley south-east of Moscow (Russia).

Glotov (1959) collected 323 small mammals, 26 birds and only 3 frogs at an GSE eyrie near Novosibirsk, Russia. Ivanowski (1996a, 1996b, 1999) indicated a proportion of 21% for frogs in territories in Belarus, and stated that the proportion of frogs in the food of GSE would be lower than in LSE (62%). This was not confirmed by our observations since the female, which mostly hunted from perch or on foot, would certainly have obtained more frogs than mice undetected, in addition to the prevalence of frogs (70%; see Table 1). At any rate, for central European LSEs, the predominance of small mammals as the main prey in number and weight is well documented (Sládek 1959, Palá_thy and Meyburg 1973, Meyburg 1991, Gedeon and Stubbe 1991). The contribution of amphibians fluctuated: 0% (Gedeon and Stubbe 1991); 42% in Belarus (Fedjuschin and Dolbik 1967); 15–64%, in the primeval forest of Bialowiecza, Poland (Goloduschko 1958, 1961), depending on weather and ecological conditions, as well as outbreaks of voles (*Microtus* spp.).

It can be assumed that both eagle species opportunistically used all easily obtained prey. This was also shown by the change in prey composition of M2 after mid-July, when the hunting area was shifted to a small river nearby.

Since there are no publications describing continuous long-time observations at an eyrie of GSEs, it was difficult to validate our estimate of food consumption by the eaglet. Accordingly, we were forced to use the well documented data of Meyburg (1970) derived from investigations on LSE, and moreover, conducted under quite different ecological conditions (low, dry mountain range in Slovakia). For simplicity, in this estimate we supposed that the supply of food was regular during the entire time of rearing the eaglet and that the female consumed a similar amount of food as the

young. In fact, the situation may have been different; after the female started hunting on its own, the amount of prey conveyed by the male was not halved, which would be expected, but decreased by only 1/3. Consequently, we have to assume that: a) within the first 3 weeks the female got less food than the young (or provided itself at least in part with food); and, b) that the female after mid-July also did not contribute significantly to feeding the young. Similarly, Meyburg (1970) reported that over 14 days of observation from June to August, the male LSE brought prey to the eyrie 53 times whereas the female only 12.

In this study, 144 prey items were taken by M2 to the eyrie during 8 weeks (Tab. 1); the eaglet consumed these items during 8 weeks and the female during the first 3 weeks before the start of hunting on its own. Accordingly, 144 prey items were consumed during 11 "eagle weeks" i.e., about 2 prey items or 50 g every day. If we postulated that the female would have contributed to the nutrition of the young by an additional 20%, we get less than 60 g/day for the eaglet. Galushin (1962, 1980) reported that a young GSE required approximately 130 prey items between 10 June and 10 August. Considering the prey spectrum given in this case, one would get 8,500 g in total, i.e., about 140 g per day. This would be significantly more than our value. After 14 days full-time observation, Meyburg (1970) estimated the food consumption of a 10-day-old LSE to be 167.5 g/day, the need of an adult to be 150 g, and that of an energy conserving, breeding female to be 80 g. The difference in size between the young of the GSE and the LSE may possibly have been overlooked considering the more rapid development of the latter (56 days in LSE vs. 63 days in GSE)(Wendland 1971, Cramp and Simmons 1980).

These considerations would mean that in our case, more than half of the prey taken to the eyrie was unobserved. This seems unlikely since the male, playing a major part in the feeding of the young, was easily observed during a substantial part of the day. Reasons for our relatively low values may be as follows. Firstly, the female could have already supplied itself before mid-July. However, considering the short time of 3 weeks before starting to hunt on its own, this would not contribute much to solving the problem. Secondly, the part played by the female in supplying prey was generally more substantial than previously thought. This point is not supported by the literature and would influence the values discussed only slightly. A third factor to consider is the weight of prey animals in the Biebrza marshes could have been higher than in the dry low mountains of Meyburg's (1970) observation area. This could indeed have influenced our calculations, but certainly would not have been the decisive factor. Finally, we overlooked some of the male's flight activity considering the rather fractured habitat. Nonetheless, we cannot believe that an error of over 50% would result. On closer examination of the questionable factors influencing our calculations, we would expect to have missed less than 1/3 of the male's approaches to the eyrie.

Habitat and its Use.–Both observed pairs of GSE occupied wet, deciduous, natural woodlands with adjacent wet fens and meadows. Characteristic features of this region are long, highly differentiated lines of woodland edges. This is similar to the LSE habitats studied in detail by Langgemach et al. (2001) in eastern Germany; however, the habitats in the Biebrza Valley were much wetter and less impacted by humans than in the former. Differences in the ecological requirements between LSEs and GSEs in the Biebrza Reserve were not conspicuous, perhaps in part due to our low degree of knowledge. In this context, it has to be mentioned that a pair of LSE had used the eyrie of GSE Pair 2 the previous year (Kowalski, pers. comm.).

Home Range.–The home ranges of the GSE males observed in this study (15 and 19 km^2) were considerably larger than previously reported for LSEs in East Germany (Gedeon and Stubbe 1991: 3.2 to 3.2 km^2). These latter figures may be an underestimation. Accordingly, Scheller et al. (2001) demonstrated by means of VHF telemetry, that 7 LSE males occupied a much larger home range (22 to 35 km^2), and that flights up to more than 10 km from the eyrie may have occurred. The application of the same method in Latvia resulted in home range sizes between 6.7 and 18.4 km^2 (Scheller et al. 2001). After having regularly observed flights up to 4–5 km from the nest,

Meyburg (1991) has already indicated that home ranges calculated by direct observation tend to be underestimated.

We do not believe that the home ranges of GSE males observed in the Biebrza marshes may be considerably larger than stated, since conflicts with neighbouring territorial eagles would have restricted further spreading. Given the favourable prey situation in the Biebrza Marshes, larger home ranges may in fact not be needed.

Outlook. – at first glance, when comparing the GSE and LSE, the similarities are more evident than the differences. In most activities, in prey species and in general behavior, we could not detect any outstanding dissimilarity. Also, the alternate use of eyries by both species points to similarities. If there were differences, they may only be so slight as to be masked by the low number of observed individuals in our study. Perhaps the shift of hunting area following the start of haymaking to the quieter and less disturbed small river represented a tendency to a more clandestine way of life. Certainly the more eastern distribution of the GSE gives this species the opportunity to settle in more undisturbed habitats than the LSE. In addition, in the Biebrza Valley, we had the impression that GSE occurred more in the central, more undisturbed parts of the National Park, whereas LSE were more often found in the peripheral areas. However, this has not yet been confirmed by reliable monitoring. All these suggestions are very speculative and deserve more study.

Based on migration studies of GSEs using satellite telemetry (Meyburg et al. 1995, Meyburg et al. 1998, Meyburg and Meyburg 2000, Meyburg et al., in prep.), a wintering ground was discovered in Zambia further south than a GSE, a middle distance migrant, had previously been observed. In relation to this, we also discussed whether the Biebrza population of this species could, at least in part, include hybrids between GSE and LSE, the latter known as a long distance migrant. Mixed pairs have been repeatedly reported but never confirmed (Meyburg 1996).

In fact, in the Biebrza Valley in 2000, we observed a male eagle, displaying the known field characteristics of a LSE, supplying a young eaglet for about 2–3 weeks in an eyrie that was guarded by a large, dark brown, unambiguously female GSE. Unfortunately, the eaglet was later killed, apparently by a pine marten (Martes martes). We hope that genetic analysis of the remains will provide further verification.

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