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The daily activity pattern in males and females of the Mute Swan (*Cygnus olor*, Anseriformes) during different parts of the breeding season

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Abstract. The majority of activities in wild animals show a regular daily pattern with regard to their behaviour, which might be modified by external factors such as weather, food availability, predation level or demands of the body. Additionally, the activity of animals can be shaped by certain periods of their annual life cycle, like migration or breeding seasons. In the majority of bird species' -especially those with prolonged bi-parental care – it is possible to observe modifications in their daily behaviour during the breeding season. Birds involved in parental duties are forced to change their own activities according to the requirements of their offspring. As a consequence, the daily rhythm of their behaviours can vary between different phases of the breeding period. Moreover, each sex may respond individually to demands caused by parental duties. The degree of change in daily behaviour can help to explain the role of each sex in brood care. A time-budget analysis of different 11 breeding pairs of Mute Swan was performed in central Poland in the years of 2005-2007. Here, the daily patterns of the following behaviours of both sexes were the subjects to analysis: incubation; nest (or sleeping platform) building/maintenance; movement; foraging; preening/comfort; resting/sleeping; alert/guarding and aggression. The study revealed a regular daily pattern of five activities (resting, comfort, movement, foraging and nest maintenance). Incubation was performed by females only and showed a defined daily pattern. Two behaviours –resting and nest maintenance – showed sex-related differences in daily rhythm. What is more, females modified their daily pattern of resting and nest maintenance during different phases of the breeding season (incubation vs. fledging phase). Males, on the other hand, did not change their pattern of daily activity during the entire breeding season. Alertness and aggression – behaviours primarily connected with territory-guarding –appeared without any regularity during the day. The study proved that parental duties can influence the daily rhythm of breeding birds, and confirmed the dominant role of the female in direct care for the offspring and the division of parental duties between Mute Swan mates.

Key words: behaviour, Mute Swan, breeding period, sex-related differences.

Introduction

The daily activity of birds tends to be very flexible due to the fact that they adjust their behaviour to their current body demands or external factors such as weather conditions, food accessibility or the activity of predators (Weathers & Sullivan 1993). However, the majority of behaviours show a specific daily rhythm that is generated mostly by a regularity in lighting conditions or internal processes within the body (eg. Hamilton et al. 2002, Houhamdi & Samraoui 2008, Chudzinska et al. 2013). After the night hours, when many species do not forage, individuals have to replenish their body reserves. All birds have to maintain their feathers in the proper conditions necessary for sufficient insulation and flight ability. In addition, some activities (aggression, territory guarding and courtship) appear as a reaction to the behaviour of other individuals, which results in their daily rhythm being shaped by the activity of the conspecifics. Finally, the daily activity pattern can be modified by the life cycle of the species. Reproduction takes up a significant part of the species' annual cycle and significantly influences the daily activity of breeding individuals (Emlen &Wrege 2004, Öst et al. 2002).

Breeders have different requirements from non-breeders stemming from the necessity of territory-guarding or brood care (Henson & Cooper 1992, Earnst 2002). As a consequence they can show a different pattern of daily activity, which is dissimilar to that of non-breeding individuals. Nevertheless, either sex can allocate a variable amount of time to parental duties, modifying its own daily time budget, even in a species characterised by a bi-parental care system (Cockburn 2006). Sex-related differences in parental effort can result in a sex-specific diurnal rhythm of various behaviours. Field studies that analyse variations between behavioural patterns of individuals are usually based on time-activity budgets (eg. Paulus

1988, Schnase et al. 1991, Yang et al. 2007).

Swans and geese are examples of wildfowl species with bi-parental, prolonged brood care (Afton & Paulus 1992). In these groups, both parents are involved in rearing their young (Owen 1980). Moreover, the presence of both parents is essential in order to obtain a high rate of breeding success (Black et al. 1996, Włodarczyk & Minias 2015). This is a unique feature in *Anseriformes*, where uni-parental care predominates (Kear 2005). In addition, both groups are active mainly during the day due to the fact that they locate food through the use of visual cues. Such behavioural traits lead to swans and geese becoming the focal point of studies pertaining to individual variations in daily activity patterns during the breeding period. When observing each sex separately, it is possible to detect modifications of daily activities caused by differences in parental duties between mates.

When studying swans' behaviour, one would expect a modification in the daily activity of each sex, according to the corresponding phase of the breeding season. One could predict that the amount of possible differences would depend on discrepancies between mates in their parental efforts. Daily behaviour ought to be shaped by the direct demands of individuals, which are similar in both males and females. Moreover, activities connected with self-maintenance (i.e. foraging, resting and preening) should exhibit regular patterns throughout the day, whereas activities triggered by external factors/needs (e.g. aggression, alert or nest building) ought to appear randomly during the day in both pair members. A time-budget analysis will help to assess which factors are more powerful when shaping an individual's daily activity pattern, self-maintenance or parental duties. The purpose of this study was to analyse the daily activity pattern in males and females of the Mute Swan during different phases of the breeding season. The research addressed the question of whether both sexes respond to their parental duties when modifying their daily rhythm of performed behaviours.

Materials and methods

Behavioral observations of Mute Swan pairs were carried out between the years of 2005-2007 at 11 different breeding territories situated in the Łódź region of central Poland (51°21′ N, 18°38′ E- 52°07′ N, 20°02′ E). All pairs occupied the territories located at the habitat type which is typical for the species: fish farms (8 pairs) or small ponds in villages used for recreation (3 pairs) (Włodarczyk & Wojciechowski 2001). Pairs differed in the number of eggs laid and cygnets hatched/fledged (Table 1). The activity of each individual was recorded during two-hour units from 3 a.m. till 11 p.m. (10 units per day). Each unit was represented by two randomly selected 30-minute bouts of observation. The order in which the following unit of day was chosen for observations was also chosen randomly as to reduce any possible impact of external factors (weather conditions, accidental situations) on the birds' behaviour. In every pair the male and female were observed separately. The sex of swans was recognized using darvic leg rings (9 individuals), as well as differences in body size and bill knob size – both of these latter features are sex-dependent in the Mute Swan, with males being larger than females (Wieloch et al. 2004, Horrock et al. 2009).

Table 1. Breeding data of pairs used for observations.

Pair	Laying date	Clutch size	Number of cygnets hatched	Number of cygnets fledged
1	14.04.	7	5	4
2	27.03.	8	6	6
3	30.04.	6	5	5
4	26.03.	9	9	8
5	05.04.	9	7	4
6	22.04.	6	5	5
7	30.04.	6	6	4
8	13.04.	8	8	7
9	04.05.	4	4	4
10	02.05.	7	6	3
11	20.04.	4	4	3
Mean (SD)	20.04. (median)	6.73 (1.66)	5.91 (1.50)	4.73 (1.66)

The observations were carried out during three distinct phases of the breeding season: (1) egg incubation; (2) early phase of chick fledging (from hatching to one month of cygnets' age); (3) late phase of chick fledging (cygnets older than two months). In total, 660 hours of data was gathered – 220 hours for each phase of the breeding season. The behaviour was assessed with the accuracy of one minute, and the following categories were taken into account: (1) incubation; (2) nest (or sleeping platform) building/maintenance; (3) movement; (4) foraging; (5) preening and comfort; (6) resting and sleeping; (7) alert/guarding and (8) aggression. Two of these behaviours could appear simultaneously with other activities: incubation and aggression. Here, a bird's activity was identified using two categories: for example, incubation and rest, or feeding with aggressive posture. In all other cases, the activities of swans were recorded using only one behavioural category.

A percentage of time devoted to each activity within each 30-minute trail was used in the analysis of birds' behaviour. The variable was arcsin (square root (x)) transformed in order to improve normality. The daily pattern of each behaviour was analysed using the general linear

mixed model (GLMM) with the period of a day, sex of a bird, and the phase of breeding season being entered as fixed factors. The interaction between these factors was also included in the model. As the repeated observations of the same breeding pairs were non-dependent, pair identity was also entered as a random effect, in order to avoid the pseudoreplication of data (Hurlbert 1984). The results of full models are presented. The differences in mean values of time allocated to each activity during different parts of the day were analysed using Newman-Keulus test (N-K test). All values are presented as means ± SE. Statistical analyses were performed using Statistica ver. 10.0 software (StatSoft 2011).

Results

Resting and comfort behaviour

The daily activity of resting behaviour showed a regular daily pattern that was different in both sexes (interaction term: $F_{9,1270}$=1.86; p=0.05).The mean percentage of time allocated to resting behaviour in females decreased constantly from sunrise to midday, when it reached minimum at the level of 16.3 %, and then again slowly increased till sunset (Fig. 1a). The swans' daily rhythm of resting activity changed during three parts of the breeding season (interaction term: $F_{18,620}$=1.78; p=0.02) (Fig. 1a), and was clearly expressed only during the incubation phase. During both fledging phases from 5 a.m. till 7 p.m., the mean percentage of time spent on resting behaviour did not change significantly (N-K test; all p>0.05). Males' pattern of resting activity also changed during the day (Fig. 1b), but the observed rhythm was independent from the breeding phase (interaction term: $F_{18,620}$=1.58; p=0.06). Males spent significantly more time resting during early morning hours (3-5 a.m.) than during rest of the day (N-K test; all p<0.001). Comfort behaviour showed regular daily pattern ($F_{9,1270}$=8.24; p<0.001) that was similar in both sexes (interaction term: $F_{9,1270}$=0.42; p=0.92), and each phase of the breeding season (interaction term $F_{9,1270}$=1.59; p=0.06). The mean percentage of time allocated to comfort behaviour increased after early morning hours (3-5 a.m.) and stayed at a consistent level till late evening – when it decreased again (N-K test; all p<0.01, Fig. 2a).

Movement

Movement displayed a regular daily pattern ($F_{9,1270}$=2.67; p<0.01) that was not associated with the sex of the bird (interaction term: $F_{9,1270}$=0.87; p=0.55) or phase of the breeding season (interaction term: $F_{18,1270}$=0.68; p=0.81). Breeding swans spent considerably less time on moving activity at 3 a.m. than during early morning hours (5-7 a.m., 9-11 a.m.) and evening (1-5 p.m., 7-9 p.m. ; N-K test; all p<0.05, Fig. 2b).

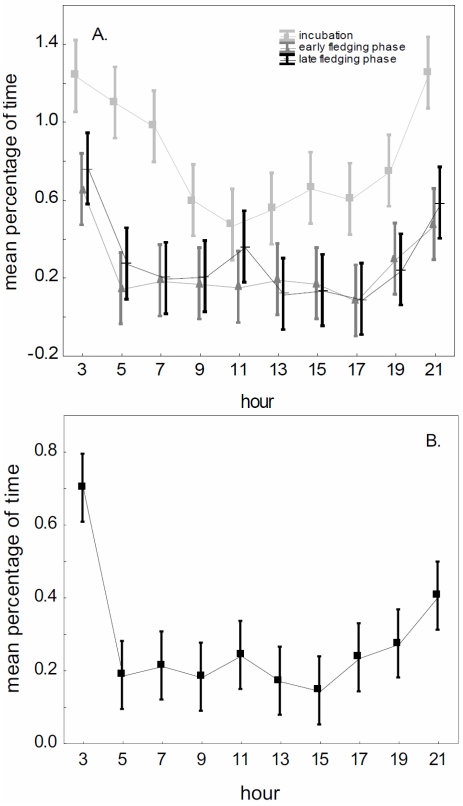

Figure 1. Daily activity pattern of resting behaviour in breeding Mute Swans in females (A) and males (B) during the three parts of breeding season (mean percentage of time transformed [arc sin (sqrt)]).

Foraging

An analysis of foraging activity revealed significant differences in the mean percentage of time allocated to feeding behaviour during the day ($F_{9,1270}$=5.51; p<0.001). However, the occurrence of observable differences did not depend on the reproductive phase (interaction term: $F_{18,1270}$ =0.77; p=0.73) or sex of a bird ($F_{9,1270}$ =0.47; p=0.89). There was a constant increase of foraging activity from 3 a.m. till 3-5 p.m. (N-K test; all p<0.05) (Fig. 3a), when the analysed behaviour reached its maximum – at the level of 19.7 %. From 5 p.m. onwards, the birds reduced foraging behaviour till late evening (N-K test; all p<0.05).

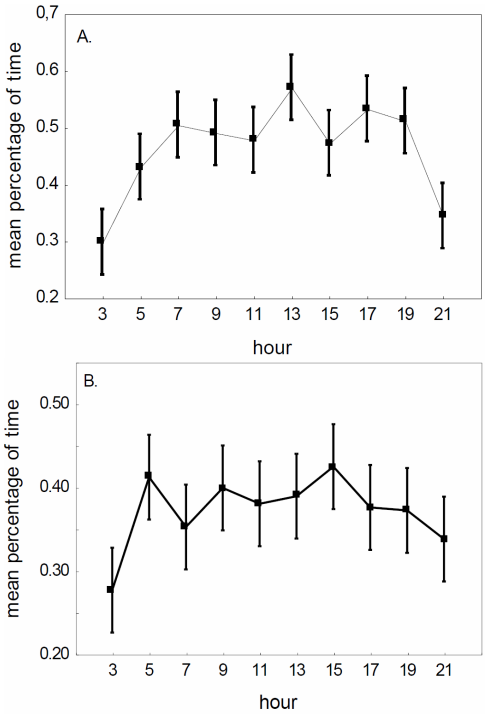

Figure 2. Daily activity pattern of comfort (A) and movement (B) behaviour in breeding Mute Swans during the three parts of breeding season (mean percentage of time transformed [arc sin (sqrt)]).

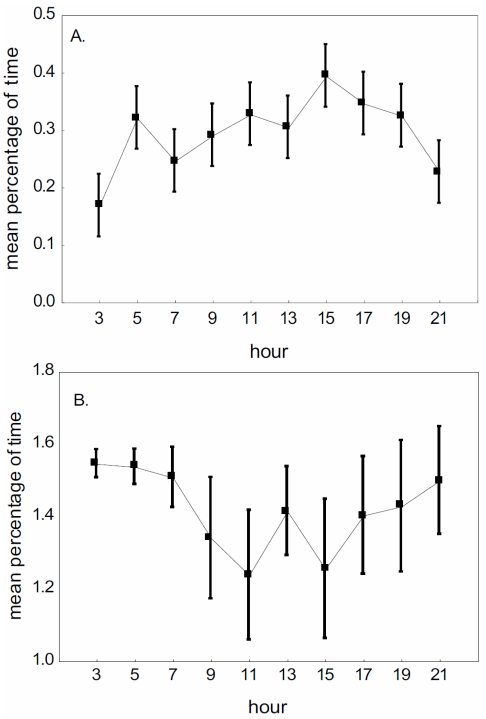

Figure 3. Daily activity pattern of foraging (A) and incubation (B) behaviour in breeding Mute Swans during the three parts of breeding season (mean percentage of time transformed [arc sin (sqrt)]).

Alert behaviour and aggression

There was no regular daily change in time allocated to alert behaviour in the breeding pairs ($F_{9,1270}$=0.96; p=0.47). The absence of daily pattern in alert behaviour was still present when the incubation phase was excluded from the analysis ($F_{9,840}$=0.44; p=0.91). The mean percentage of time spent for aggressive interactions was not time-dependent ($F_{9,1270}$=1.30; p=0.22). Aggression appeared with similar intensity throughout the whole day (range 7.4-11.3 %, N-K test; all p>0.05).

Incubation

Incubation was only performed by females, and covered from 81 to 99 % of their daily activity. This behaviour showed a regular daily pattern ($F_{9,200}$=2.77; p=0.004). Females spent significantly less time on incubation at 11 a.m. and 3 p.m., than during other parts of the day (N-K test; all p<0.05) (Fig. 3b). Incubation breaks were short (median value 8.0 min.; n=53) and associated mainly with feeding activity (correlation coefficient: r=-0.64; p<0.05).

Nest maintenance

The time allocated to nest maintenance activity varied during the day and the observed pattern was sex-dependent (interaction term: $F_{9,1270}$=1.95; p=0.04). Females adjusted their daily rhythm of analysed behaviour to the phase of the breeding season (interaction term: $F_{18,620}$=5.19; p<0.001). Incubating females constantly increased the amount of time spent on nest-building activity along the day till 11 a.m. when it reached the highest value (21.2 %, Fig.4a) (N-K test; all p<0.001). During midday, the analysed behaviour appeared with similar intensity till 5 p.m. In the evening, from 5 p.m. onwards, incubating females reduced the amount of time allocated to the nest maintenance behaviour (N-K test; all p<0.001) (Fig. 4a). However, during both phases of the fledging period, females spent a comparable amount of time on nest maintenance during different parts of the day (N-K test; all p>0.05) (Fig. 4a). The mean percentage of time allocated to nest maintenance by males was time-dependent ($F_{9,620}$=2.26; p=0.017), but there was no clear daily pattern of the analysed

behaviour (N-K test; all $p>0.05$) (Fig. 4b). Moreover, the daily rhythm of nest maintenance was not influenced by the phase of the breeding season in males (interaction term: $F_{18,620}=0.65$; $p=0.85$). There were also no significant differences in nest maintenance intensity during the whole day along three parts of the breeding season (N-K test; all $p>0.05$).

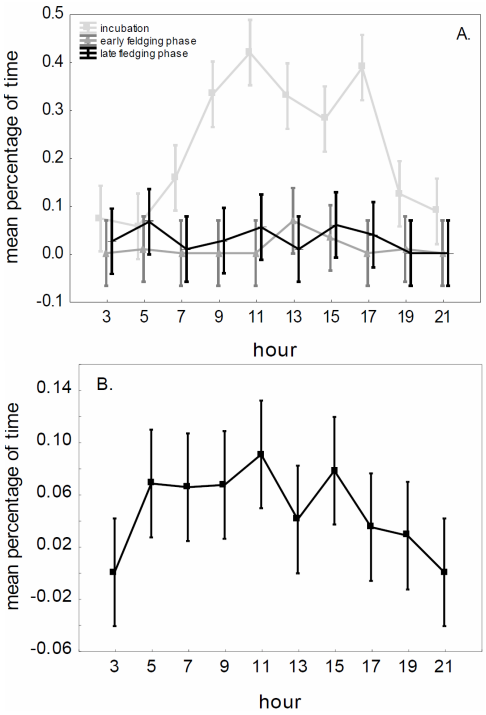

Figure 4. Daily activity pattern of nest maintenance behaviour in breeding Mute Swans in females (A) and males (B) during the three parts of breeding season (mean percentage of time transformed [arc sin (sqrt)]).

Discussion

Time-budgetobservations in breeding pairs of the Mute Swan revealed a regular daily pattern in five activities: resting, preening, movement, foraging and nest maintenance. Body requirements during the day and intercorrelations between the analysed behaviours can explain the obtained results (Vezina & Salvante 2010). In general, foraging allows birds to replenish their body reserves whereas resting and comfort behaviours are related to self-maintenance activities (Ogilvie & Pearson 1994, Randler 2005). As a consequence, these behaviours should appear interchangeably during the day (Dwyer 1975, Dopfiner et al.2009).

The Mute Swan breeding pairs displayed a reduction in the mean percentage of time spent on resting activity soon after sunrise and a renewed increase before sunset, confirming the diurnal nature of the species. Breeding swans were active mainly during the day, devoting the majority of their time to resting behaviour in periods of poor light conditions (i.e. dawn and dusk). On the contrary, wintering swans showed a significant increase in the mean percentage of time spent on resting behaviour in the middle of the day (Józkowicz & Górska-Kłęk 1996). However, wintering birds used bread as a main food type and adjusted their behaviour to human presence and the peaks of artificial feeding. Breeding Mute Swans occupied territories in rural areas with a low degree of human activity and fed on submerged vegetation. Interestingly, females modified their daily pattern of resting behaviour in the course of the breeding season. The incubation phase was characterised by different patterns of resting activity than during both fledging phases. Incubating females gradually reduced their resting activity until the middle of the day, when they became conspicuously active. In order to slow down the process of egg-cooling, the incubating birds should leave the nest during the warmest parts of the day (Mallory & Weatherhead 1993). In consequence, as the study proved, they tend to become active at the midday or in the early afternoon. During the fledging phase, resting activity in females was influenced by the cygnets' demands and became similar to the typical daily pattern observed in diurnal species. Mute Swan males are not involved in incubation and thus they exhibited a constant daily rhythm of resting activity during the whole breeding season.

The breeding pairs of the Mute Swan showed an increase in feeding activity soon after dawn. Birds devoted increasingly more time to foraging until the afternoon hours, when the analysed behaviour reached the highest intensity. The increase of feeding activity during early morning hours was observed in many breeding wildfowl species, eg. Barnacle Geese (*Branta bernicla*), White-fronted Geese (*Anser albifrons*) and Whooper Swans (*Cygnus cygnus*) (Brazil 1981, Stroud 1982, Black et al. 1996). Wintering swans also increased the amount of time allocated to foraging activity soon after sunrise (Józkowicz & Górska-Kłęk 1996, Tatu et al. 2007). The Mute Swans studied in southern Ireland during winter that were analogous to breed-

ing pairs from central Poland showed a stable increase of feeding activity until the hours of late evening (Keane & O'Halloran 1992). However, similar behaviour in this case must have had a different basis due to different environmental conditions in winter and summer. The short duration of sunlight during the day, or a shortage of food - typical for winter time - cannot be a limitation that shapes daily behaviour during the breeding season. In the spring and summer seasons with more favourable weather conditions, birds are not forced to replenish their body reserves in such haste following the night hours. Accordingly, the study revealed that the peak of foraging activity in the early morning hours was not clearly pronounced in breeding swans. However, intensive feeding in the afternoon was still observed. As diurnal birds the swans had to accumulate food reserves before nightfall. On the other hand, many studies have proven that foraging behaviour displays a bi-modal distribution of the daily pattern, with the highest magnitude being in the early morning and late afternoon hours. Two peaks of foraging intensity in birds were explained using different environmental factors: the duration of daylight, diurnal rhythm of food accessibility (e.g. insects) or regular changes in air temperature (Verbeck 1972, Owen & Cadbury 1975, Haftorn 1989, Dall & Witter 1998). This tendency was not observed in breeding Mute Swans. However, the bimodal rhythm of foraging activity is not a fixed rule and can be influenced by food type, body condition or period of the year (Paulus 1988). Wildfowl usually feed on food of low quality or low availability. This forces them to forage with comparable intensity throughout the day, especially in harsh winter conditions (Owen &Black 1990). Moreover, during late winter geese and swans start to accumulate reserves before the exhausting spring migration and allocate similar amounts of time to feeding activity during all parts of the day (Brazil 1981). The daily pattern of foraging behaviour was not sex-dependent in breeding pairs, although field observation showed that incubating females considerably reduced their feeding activity (Włodarczyk & Minias 2015). Females tried to reduce the nest recess to a minimum and their feeding bouts were very short and intensive (Bollinger & King 2002, Włodarczyk & Minias 2015). Nevertheless, they left the nest for feeding primarily at midday or early evening. These periods overlap with the increase of feeding activity observed in both sexes during the entire breeding season. In consequence, there were no significant differences in the daily pattern of analysed behaviour between sexes or between different parts of the breeding season.

The study revealed an increase in the mean percentage of time allocated to comfort behaviour at midday, confirming the assumption about the correlation between different activities observed in wild organisms. Clean feathers are not only necessary to ensure proper flying abilities but also allow birds to sustain constant body temperature due to appropriate insulation in the water (Bech 1980, Stephenson 1997). Following the feeding period in the early morning, birds tend to devote their time to self-maintenance behaviours, especially comfort. This sequence of activities was observed in the wintering flock of the Mute Swan (Józkowicz & Górska-Kłęk 1996). Wintering birds increased the level of preening activity at midday, when they finished a period of intense foraging begun during the early hours of morning. Surprisingly, field observations did not reveal any variations in the daily pattern of comfort behaviour between sexes and different parts of the breeding season even though one would expect that the regular rhythm of the analysed behaviour would be modified by processes such as incubation or moult. Incubating females reduce their level of mobility and – unlike birds with a normal level of mobility – they do not have to spend a significant amount of time on comfort behaviour. What is more, moulting birds tend to devote more time to comfort activity to ensure the proper condition of growing feathers. The moulting period in Mute Swan breeding pairs is sex-dependent – females start moulting soon after hatching, whereas males do not change their feathers until the end of the fledging phase (Wieloch et al. 2004, Czapulak 2002). Therefore, each sex should show a behavioural response to the moulting process by intensifying is comfort activity in different parts of the breeding season. However, as mentioned above, this scenario was not confirmed during field observations. Various time-budget studies have proven that wildfowl during moult usually reduce their daily activity and become inactive (Adam et al. 2000, Portugal et al. 2010). For breeding swans, such modifications in behaviour are not possible as both sexes are involved in parental care and must show a high level of activity (Włodarczyk & Minias 2015).

The study proved that both sexes allocated a similar amount of time to nest maintenance

throughout the day, except for incubating females, which showed two peaks of the described activity. It must be stressed that the data collection covered the period when the nest was already built and the birds were only adding material to the existing construction. In this situation, the maintenance of the nest is not overly time or energy-consuming in comparison to typical nest-building during the pre-laying phase. The birds devoted a negligible amount of time to this behaviour (1-7 % of the observation unit) and did not focus their behaviour on nest-building in any part of the day. It was only incubating females that spent a prominent percentage of time on nest maintenance. Both peaks of nest building behaviour coincided with the period of high feeding activity in incubating females when they left the nest. This correlation is in agreement with behavioural observations of wildfowl –incubating birds often rearrange the construction of their nests before sitting on eggs(Afton & Paulus 1992).

Breeding pairs displayed a time-dependent pattern of movement activity. The Mute Swan, a representative of diurnal wildfowl species, starts its activity soon after sunrise and increases its mobility until midday (Keane & O'Halloran 1992, Józkowicz & Górska-Kłęk 1996). Not long before nightfall, the moving behaviour is reduced (Keane & O'Halloran 1992). During the breeding period, swimming behaviour is usually associated with movements between the nest and feeding areas within the territory. Moreover, males guard territory borders by swimming around the occupied water body (Birkhead & Perrins 1986). Field observations did not find any sex-related differences in the daily rhythm of movement activity despite a significant reduction in swimming behaviour in incubating females (range 0-13% of the observation unit). Again, only females reduced the amount of time devoted to movement but the period of the day when the analysed behaviour was observed did not differ significantly from the pattern observed in males. During the fledging phase, the whole family, both adult swans and cygnets, stays in close visual contact and moves around the breeding territory as a single group (de Jong & Bacon 1979). Daily patterns of movements during this time should be similar in both sexes – as observed in breeding swans from central Poland.

As females of the Mute Swan devoted up to 99 % of daily time to incubation, the results proved an extremely low level of nest recess. This pattern is typical for the species with a female-only type of incubation (Afton & Paulus 1992). In the study, nest-recesses appeared mainly at midday and during the afternoon hours. In wildfowl species, where only one sex incubates the eggs, nest-recess bouts appear during the warmest parts of the day as birds try to minimise the reduction of egg temperature (Owen & Black 1990). Observations of incubating females of the Emperor Goose (*Anser canagicus*) and Blue-winged Teal (*Anas discors*) revealed that the highest intensity of nest-recesses occurred in the afternoon hours (Miller 1976, Thompson & Raveling 1987). Females of the Mute Swan showed a similar pattern of incubation activity as one peak of nest-recesses was observed between 3 and 5 p.m. This part of the day usually corresponds with the highest daily air temperature in areas with a temperate climate (Kożuchowski & Degirmendźić 2005). However, there was also a second peak of nest recesses observed between 11 a.m. and 1p.m. The study area was located in a mild climate with rare periods of unfavourable low air temperatures during spring (Kożuchowski & Degirmendźić 2005). On sunny days, air temperature in the middle of the day is probably sufficient to avoid a rapid cooling of the eggs and lets the females leave the nest earlier than in cold weather conditions. As a result, females are able to start foraging before the peak of daily air temperature, which can be crucial during the energy-consuming incubation phase.

Two activities were not dependent on the time of the day in both sexes: aggression and alert behaviour. All kinds of territory/family guarding are elicited by external factors such as predators, conspecifics or humans. Intruders can appear with random intensity, causing a lack of regularity in aggressive or alert behaviour (Dwyer 1975).

The analysis of behaviour in breeding swans showed that the daily rhythm of birds can be modified according to the particular phase of the breeding season. Females were able to adjust their own daily activity to requirements caused by current parental duties. In contrast, males showed a regular daily pattern of behaviour throughout the whole breeding season. They did not change their daily activity after hatching or during the end of the fledging phase, and did not respond to changing conditions during the breeding season (nest guarding vs small cygnet defence). The observed differences suggest a division of parental duties between sexes in the Mute Swan. Namely, females devote their time to direct parental duties and have to modify the daily rhythm of some activities

(resting, nest maintenance), whereas males are responsible for the most part for territory/family guarding and their behaviour is not shaped by the phase of the breeding season.

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