J Ornithol (2015) 156:389–396
DOI 10.1007/s10336-014-1136-7

ORIGINAL ARTICLE

Shortening day length as a previously unrecognized selective pressure for early breeding in a bird with long parental care

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Received: 16 April 2014 / Revised: 17 September 2014 / Accepted: 26 October 2014 / Published online: 23 November 2014

Abstract Several different selective pressures have been suggested to explain an intense competition for early return to breeding grounds in birds. In this study we hypothesized that shortening day length during summer months may constitute additional selective force acting towards early breeding in avian species with long parental care. To test this hypothesis, we studied time budget and foraging activities of early-nesting and late-nesting white storks *Ciconia ciconia* from the Central-European population. We found that duration and distance of foraging trips increased significantly over the course of the reproductive season. The relative frequency of foraging trips increased at the expense of other activities, such as resting, plumage maintenance, and nest maintenance. Mean daily foraging duration increased with increasing day length in the early part of the season, with 0.68 h of foraging per individual per 13.16 h of day length in mid-April increasing to 7.42 h of foraging per individual during solstice (16.61 h of day length). Afterwards, mean foraging duration continued increasing in spite of decreasing day length, reaching 11.63 h of foraging per individual per 14.92 h of day length at the end of the season in mid-August, when storks were forced to continue foraging after sunset in order to meet energy requirements of fledglings. The results suggest that shortening day length during summer months may constitute a serious time constraint on food delivery rates to offspring for late-breeding pairs of white stork.

Keywords *Ciconia ciconia* · Foraging · Photoperiod · Timing of breeding · White stork

Zusammenfassung

Kürzere Tage sind ein bisher unbekannter Selektionsdruck für frühen Brutbeginn in einer Vogelart mit langer elterlicher Fürsorge

Verschiedene Selektionsfaktoren wurden bisher herangezogen zu erklären, warum Vögel so intensiv konkurrieren möglichst früh im Brutgebiet anzukommen. In dieser Studie untersuchten wir die Hypothese, dass kürzere Tage während der Sommermonate in Arten mit langer Elternfürsorge einen weiteren Selektionsfaktor darstellen, der frühen Brutbeginn begünstigt. Um diese Hypothese zu testen verglichen wir die Zeiteinteilung und Dauer der Nahrungssuche bei früh und spät nistenden Weißstörchen *Ciconia ciconia* in einer zentraleuropäischen Population. Die Dauer und Entfernung von Nahrungsflügen nahm im Laufe der Brutsaison signifikant zu. Die relative Häufigkeit von Nahrungsflügen stieg ebenfalls an, was auf Kosten anderer Aktivitäten wie Rast, Gefiederpflege und Nestpflege geschah. Die mittlere tägliche Nahrungsflugdauer nahm früh in der Saison mit zunehmender Tageslänge zu, wobei 0,68 Stunden Nahrungssuche pro Individuum pro 13,16 Stunden Tageslänge Mitte April auf 7,42 Stunden Nahrungssuche pro Individuum während der Sommersonnenwende (16,61 Stunden Tageslänge) anstiegen. Danach nahm die Dauer der Nahrungssuche weiterhin zu, obwohl die Tageslänge abnahm, bis schließlich am Ende der Brutsaison Mitte August 11,63 Stunden Nahrungssuche pro

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Communicated by O. Krüger.

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Individuum auf 14,92 Stunden Tageslänge kamen. Nun waren Störche gezwungen die Nahrungssuche nach Sonnenuntergang fortzusetzen, um den Energiebedarf der Flügglinge zu decken. Diese Ergebnisse zeigen, dass kürzere Tageslängen im Laufe des Sommers für spät brütende Weißstörche eine ernstzunehmende Einschränkung in der Nahrungsversorgung von Nachkommen darstellt.

Introduction

In birds, there is an intense competition for early return to breeding grounds, and a multitude of different selective pressures have been identified to explain this pattern (Kokko 1999). Firstly, early-arriving individuals gain better access to high-quality territories (Forstmeier 2002), which may provide fitness benefits in terms of larger food resources, availability of more favourable nest sites, or lower predatory pressure (Aebischer et al. 1996; Lozano et al. 1996; Cooper et al. 2011). Early arrival also increases the likelihood of acquiring a mate of high phenotypic quality (Potti and Montalvo 1991; Møller 1994), or of acquiring any mate at all (Amrhein et al. 2007).

In animal populations, the timing of one event may determine the timing of the forthcoming events throughout the sequence of the life-cycle stages, which is also known as the “domino effect’” (Piersma 1987). Under such circumstances, one may expect that the timing of arrival at breeding grounds will have profound consequences on the tightly regulated reproductive schedules of birds. In fact, early arrival facilitates early initiation of nesting, which allows birds to better match the peak of the offspring food requirements to the peak of resource availability (Durant et al. 2007; Visser et al. 1998). In most avian species breeding at temperate latitudes, food availability initially increases in spring; but at some point the pattern reverses, and the abundance of available food resources starts to decline as the season further progresses (e.g., Safina and Burger 1985). Thus, early nesting facilitates conclusion of reproductive activities before food resources start to decline, as well as it promotes early departure on autumn migration, which brings large fitness benefits for long-distance migrants (Jenni and Kéry 2003), especially those that begin migration synchronically (Kosicki and Indykiewicz 2011). However, it has not been explicitly recognized that in some avian species with long parental care, early nesting also allows rearing chicks under a more favourable photoperiod.

In this study we hypothesized that shortening day length during summer months may constitute additional selective pressure acting towards early breeding in species with long parental care. Most temperate-breeding altricial birds finish reproduction by the time or soon after the summer solstice, which occurs between June 20 and 22 in the northern hemisphere. When offspring fledge before that date, the increasing food requirements of a brood are accompanied with increasing daylight period, which gives parents continuously more time to find adequate quantities of food for growing chicks. However, in large species, the rearing period may well extend into the summer months, when energy demands of nestlings grow along with decreasing day length. Under such conditions, it may be difficult for adults to maintain delivery of food to fledglings at a sufficiently high rate, unless they restrict investment in self-maintenance, which, in turn, may reduce their future survival and chances for reproduction (Williams 1966). Although general benefits of reproduction under favourable photoperiod are widely recognized (e.g., Sanz 1999), empirical studies on how seasonal changes in day length affect reproductive activities of birds are lacking.

The aim of this study was to test whether reproductive activities could be constrained by shortening day length in a large bird with long parental care, the white stork *Ciconia ciconia*. The entire reproductive cycle, from egg laying to fledging of chicks takes about 3 months in this species (Schulz 1998). This implicates that early-arriving individuals, which usually start nesting by mid-April, may conclude their reproductive activities around the end of June (Fulin et al. 2009), which is a period of maximal day lengths at temperate latitudes. However, large numbers of storks arrive at breeding grounds in Central Europe only in the second half of April or even at the beginning of May (Janiszewski et al. 2013). In such cases, fledging of chicks may occur no earlier than in mid-August, when the period of daylight is already much shorter. In order to investigate, whether white storks may be limited by shortening day length at the late stages of reproductive season, we studied time budget and foraging activities of early-nesting and late-nesting stork pairs from the Central-European population of the species.

Methods

The study was conducted in the districts of Koło (52°12′N, 18°38′E) and Łowicz (52°06′N, 19°56′E), central Poland, during 2007–2009. The study area was covered mainly with agricultural landscape crossed by a relatively large (2–3 km wide) river valley of Bzura. The valley was sparsely forested with vast open areas of wet meadows and pastures that comprised favourable foraging grounds for white storks (Nowakowski 2003). In the remaining part of the study area (beyond the borders of Bzura valley), an agricultural landscape with cereals and root crops prevailed, which was considered a suboptimal foraging habitat for storks.

Timing of fledging within the studied stork population was recorded for 377 successful breeding attempts in the Łowicz district during all 3 years of the study (120–131 breeding attempts per year). All the nests were visited in July/August and the timing of fledging was assigned to one of three following periods: (1) before July 20; (2) between July 20 and 31; and (3) after August 01. The distribution of nests within the population was consistent with a random pattern, where the mean nearest neighbour distance was 1.24–1.47 km (Janiszewski et al. 2014a). Dense colony-like aggregations were not recorded in the study area. For the purpose of behavioural observations we selected seven stork pairs breeding in the areas of moderately high nest densities (3–7 nests per 3 km radius). All selected pairs had easy access to potentially favourable foraging habitats, i.e., meadows and pastures, which covered between 16.2 % and 36.8 % of area in the direct vicinity of the nests (within the radius of 1 km). This suggested that selected pairs held territories of relatively good quality, as the mean share of grasslands in stork territories within the studied population was 9.4 % (Janiszewski et al. 2014b). In the selected pairs, brood size varied between two and four offspring at fledging. Each pair was observed throughout one entire breeding season, starting from arrival of adults (usually at the beginning of April) to the moment of fledging (no later than on August 13). The average duration of observation was 16.6 ± 3.1 [SE] days per pair. Each day of observation was consistent with the entire daily period of stork activity, starting from 5 a. m. to 11 p .m.

During short-distance foraging trips birds were observed from under the nest with 10× binoculars and a 20–60× zooming scope, while birds departing on long-distance foraging trips (up to 3 km) were followed in a car. In the late stage of chick rearing when both partners spent much of their time foraging, one observer followed birds to the foraging grounds, while the second one constantly kept the nest under observation. Duration of foraging time was recorded to the nearest 0.5 min. Distance of foraging trips was recorded with a handheld Global Positioning System (GPS) unit (Garmin GpsMap 60Cx, Olathe, KS, USA). If individuals changed the place of foraging during one trip, the maximal distance from the nest was considered as foraging distance. In total, data on 823 foraging trips were collected with, on average, 117.6 ± 34.3 [SE] foraging trips per pair. Other activities such as resting, plumage maintenance, and nest maintenance were also recorded to the nearest 0.5 min. During all 3 years, behavioural data were collected for nearly 3,000 h of stork activity. For the purpose of analysis, the reproductive cycle of storks was divided into three main stages: (1) incubation of eggs (ca. 33–34 days); (2) early stage of chick rearing, defined as a period when nestlings were continuously guarded by at least one adult (up to ca. 20 days of chick age; Moritzi et al. 2001); and (3) late stage of chick rearing, when adults were not continuously present at the nest.

Relative frequencies of foraging trips and other activities were analysed with the *G* test. Duration and distance of foraging trips, as well as the timing of return from the last foraging trip in relation to the time of sunset were analysed with General Linear Models. The effect of reproductive stage and brood size were included as fixed factors in each model and the effect of date was included as a covariate. As multiple observations of the same pair are not statistically independent, we accounted for the random factor of pair identity in all the analyses to avoid pseudoreplication (Hurlbert 1984). All variables were transformed to improve normality prior to analyses. The stepwise procedures of backward removal were implemented to select for significant independent variables, and β coefficients were used to assess the character and strength of significant relationships. Post hoc comparisons were performed with the Tukey HSD procedures. Simple regression was used to investigate seasonal trends in the mean daily duration of foraging of all pairs included in the study (calculated for the successive 10-day periods). All values were presented as mean ± SE. All statistical analyses were performed using Statistica 10.0 (StatSoft, Tulsa, OK, USA).

Results

The relative frequency of foraging trips increased significantly from 24.6 ± 0.53 % during the period of egg incubation to 39.2 ± 0.60 % during the late period of chick rearing ($G = 22.32$, $df = 2$, $P < 0.001$). Simultaneously, the frequency of other activities, such as resting, plumage maintenance, and nest maintenance decreased significantly in the late stage of chick rearing (resting: $G = 52.61$, $df = 2$, $P < 0.001$; plumage maintenance: $G = 223.06$, $df = 2$, $P < 0.001$; nest maintenance: $G = 121.61$, $df = 2$, $P < 0.001$).

Increasing frequency of foraging trips over the reproductive cycle was accompanied with their increasing duration. There were significant differences in the mean duration of foraging trips between the successive reproductive stages ($F_{2,991} = 60.68$, $P < 0.001$; Fig. 1a). Duration of foraging trips was shortest during the incubation period, when storks spent, on average, 1.03 ± 0.05 h per trip. It increased significantly during the early stage of chick development (1.21 ± 0.04 h per trip; Tukey: $P = 0.006$), and the longest duration of foraging trips was recorded at the late stage of chick rearing (1.95 ± 0.06 h per trip; Tukey: all $P < 0.001$). Increasing duration of foraging trips over the reproductive season could be attributed to the necessity of adults to travel longer distances in order to find sufficient quantities of food. We

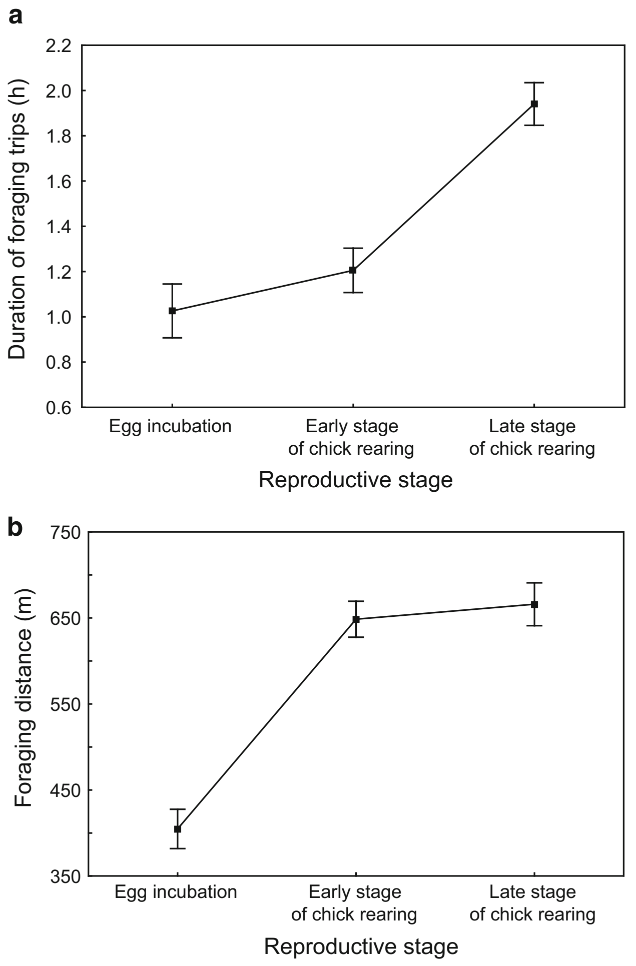

Fig. 1 Mean duration of foraging trips (**a**) and foraging distance (**b**) of white storks during successive reproductive stages. Mean ± SE are presented

found that the mean distance of foraging trips increased from 404.7 ± 22.8 m during the period of egg incubation to 648.5 ± 20.9 m during the early stage of chick rearing ($F_{2,813} = 12.90$, $P < 0.001$; Tukey: $P < 0.001$; Fig. 1b). The difference in the foraging distance between the early and late stage of chick rearing was not significant (Tukey: P = 0.91).

After accounting for the fixed effect of reproductive stage ($F_{2,990} = 13.37$, $P < 0.001$) and for the random effect of pair identity ($F_{6,990} = 6.70$, $P < 0.001$), we found that the duration of foraging trips increased also with date ($F_{1,990} = 9.60$, $P = 0.002$, $\beta = 0.007 \pm 0.002$). We found a similar seasonal increase in the distance of foraging trips ($F_{1,813} = 3.91$, $P = 0.048$, $\beta = 0.040 \pm 0.020$), while controlling for the effects of reproductive stage ($F_{2,813} = 12.90$, $P < 0.001$) and pair identity ($F_{6,813} = 15.84$, $P < 0.001$). Brood size had no influence on the duration and distance of foraging trips ($F_{2,990} = 5.80$, $P = 0.07$; and $F_{2,813} = 0.45$, $P = 0.66$, respectively), and was excluded from the models.

There was a significant relationship between chick fledging date and mean daily duration of adult foraging in the late stage of chick rearing ($F_{1,4} = 10.07$, $P = 0.034$). We found that pairs that fledged chicks later in the season had to spend significantly more time foraging ($\beta = 0.18 \pm 0.06$). The timing of fledgling varied considerably between pairs, ranging from July 02 to August 13, which was associated with day lengths of 16.7 and 14.8 h, respectively. The mean daily duration of foraging increased linearly over the course of the season ($F_{1,12} = 183.02$, $P < 0.001$, $\beta = 0.84 \pm 0.06$; Fig. 2). In consequence, mean daily foraging duration increased with increasing day length in the early part of the season, with 0.68 h of foraging per individual per 13.16 h of day length in mid-April increasing to 7.42 h of foraging per individual during solstice on June 21 (16.8 h of day length). Afterwards, mean foraging duration continued increasing in spite of decreasing day length, reaching 11.63 h of foraging per individual per 14.92 h of day length at the end of the season in mid-August. Consistently, after accounting for the random effect of pair identity, the timing of return from the last foraging trip in relation to the time of sunset was continuously delayed over the course of the season ($F_{1,87} = 13.65$, $P < 0.001$, $\beta = 0.011 \pm 0.003$; Fig. 3), and at the end of the season storks were forced to continue foraging after sunset in order to meet energy requirements of fledglings. At the beginning of the season (mid-April), storks returned from the last foraging trip on average 0.36 h before sunset, while on August 01 the last foraging trip was on average extended for 0.68 h after sunset. Brood size did not affect the timing of return from the last foraging trip and was excluded from the model ($F_{2,87} = 0.18$, $P = 0.85$).

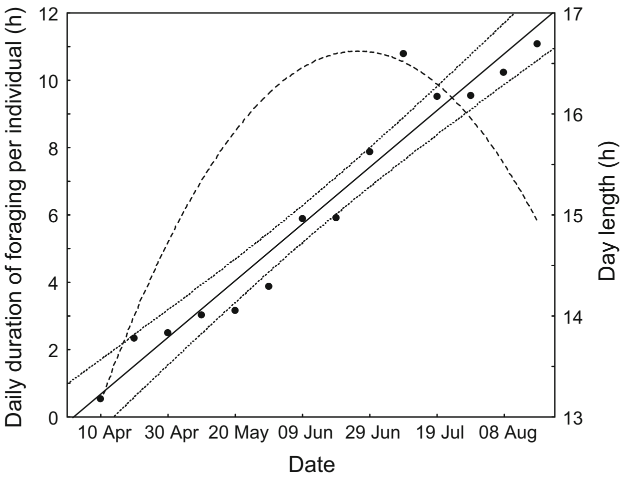

Fig. 2 Seasonal changes in the daily duration of foraging per individual (*solid line*) in relation to day length (*dashed line*). *Dotted lines* indicate 0.95 confidence intervals of the regression line

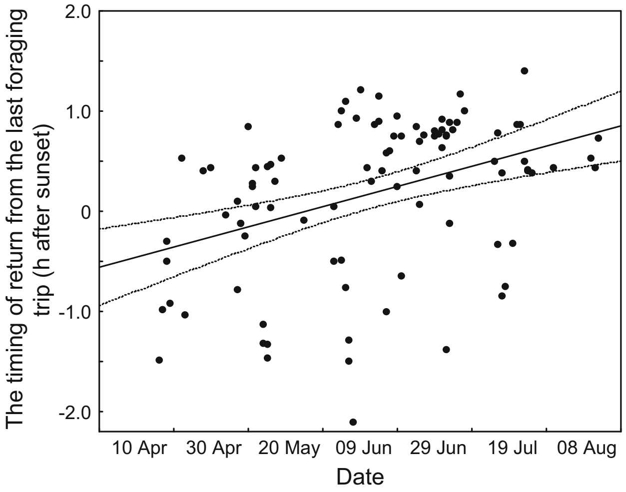

Fig. 3 Seasonal changes in the timing of return from the last foraging trip in relation to the time of sunset. Negative values indicate time before sunset. *Dotted lines* indicate 0.95 confidence intervals of the regression line

There were no between-seasonal differences in the timing of fledging of stork young within the studied population ($G = 4.63$, $df = 4$, $P = 0.33$). In all the years, fledging was tightly synchronized, as, on average, 85.9 % of pairs fledged offspring within a short time window between July 20 and 31 (85.9 %, $N = 377$). Such timing of fledging was associated with moderately favourable day lengths of 15.6–16.1 h. On average, 10.1 % of pairs fledged young under a more favourable photoperiod (before July 20) and only 3.9 % of pairs fledged young under highly unfavourable photoperiod (after August 01).

Discussion

In this study we demonstrated that foraging of white storks may be limited by shortening day length at the end of the reproductive season. As such limitation in the time available for foraging coincides with the peak of the brood energy requirements, we suggest that it may constitute an important selective force acting towards early initiation of breeding in this species. White stork is a species with long parental care, where the entire reproductive success from egg laying to fledging takes up to 3 months (Schulz 1998). In spite of this, individuals that return early at breeding grounds are able to favourably match their timing of reproduction to the seasonally changing photoperiod. The first storks from the Central European population arrive at breeding grounds at the end of March (Tryjanowski and Sparks 2008; Janiszewski et al. 2013), start breeding in the first half of April, and the chicks hatch at the beginning of May (Fulin et al. 2009; Kosicki and Indykiewicz 2011). Under such a reproductive schedule, the increasing food demands of growing offspring are accompanied by increasing day length, and the moment of fledging may coincide with maximum lengths of daylight around the summer solstice. However, in our studied population only 10 % of pairs managed to fledge young under a favourable photoperiod (before mid-July). It must be also borne in mind that the maximum day lengths may not necessarily be associated with the highest foraging possibilities because the length of feeding activities could also depend on local weather conditions, such as temperature and precipitation, as in other avian species (e.g., Sergio 2003).

In the white stork, the timing of departure for spring migration and its duration is highly dependent on the weather conditions (Shamoun-Baranes et al. 2003; Berthold et al. 2004). In consequence, white storks show great within-population variability in the timing of arrival at breeding areas, with the last individuals arriving no earlier than in mid-May to Central Europe (Janiszewski et al. 2013). Consistently, the timing of breeding varies greatly between individuals and the chick rearing period may last even to mid-August, although the proportion of such late breeders is usually very low (3.9 % of pairs fledging young in August within the studied population). Such timing of reproduction implies that offspring are reared under the shortening day length, and fledge during highly unfavourable photoperiod. On the other hand, too early arrival at breeding grounds may also be detrimental for survival and reproductive output of storks (Tryjanowski et al. 2004; Janiszewski et al. 2013), so birds must carefully balance the timing of migration to maximize their fitness. This implies that under stable climatic conditions both the timing of migration and the timing of breeding in birds should be subjected to a strong stabilizing selection (Reed et al. 2009; Dunn et al. 2011).

The evidence that storks may be time-limited at the end of reproductive seasons was inferred from extensive behavioural observations. We found that during the period of shortening day length storks were unable to collect adequate quantities of food during daylight and continued foraging after sunset. We found that at the beginning of the reproductive season (mid-April) storks tended to return to nest from the last foraging trip on average ca. 20 min before sunset, but as the season progressed, storks were forced to extend their foraging after sunset and often returned to the nest after dark. Late-breeding pairs, which still reared chicks in August, tended to return from the last foraging trip on average 40 min after sunset, although foraging in such conditions was likely to be ineffective. The white stork belongs to the obligate diurnal feeders and has potentially inferior nocturnal visual capabilities, as was demonstrated for other wading species, e.g., the White Ibis *Eudocimus ruber* (Rojas et al. 1997). For this reason, nocturnal foraging may also pose a serious threat to birds, as they may not be able to detect and escape predators (McNeil et al. 1993). In spite of this, nocturnal feeding has occasionally been recorded in wading birds which feed primarily during daytime (Whitting and Guinea 1999; Bryan et al. 2001; Kannan and Manakadan 2007), especially when they fail to meet their food requirements during the day (McNeil et al. 1993). Data from nest cameras also confirmed occasional nocturnal foraging in the white stork (Dolata 2006).

We identified two non-exclusive mechanisms that amplified the limiting effect of shortening day length on the time budget of storks at the end of the reproductive season. Firstly, we found that late-breeding birds needed considerably more time to maintain adequate delivery rates to chicks in comparison to early-breeding conspecifics, as the mean time allocated to foraging in pairs nesting late in the season was significantly higher in comparison to those, which fledged offspring earlier. This observation suggests that accessibility to high-quality food of storks may deplete over the course of the season. Storks usually forage on different types of wet grasslands (Carrascal et al. 1993; Nowakowski 2003), where they prey on a wide spectrum of invertebrate and vertebrate animals (Antczak et al. 2002; Tsachalidis and Goutner 2002). Although wet habitats are considered optimal for feeding (Janiszewski et al. 2014b), the availability of food resources is likely to diminish during the summer months, as large areas of floodplains usually dry up. Under such conditions, storks may switch location of foraging patches from grasslands to dry arable lands (Tobolka et al. 2012), where the diet changes from aquatic animals to earthworms, insects, and voles (Tryjanowski and Kuźniak 2002). Even assuming that availability of such prey as insects increases late in the summer, this type of food is associated with low energy intake per time unit, as much time must be invested in food collection. Alternatively, birds may try to locate ephemeral patches of high food availability, such as freshly mowed meadows or harvested fields, but the strategy of optimal patch selection in a dynamic landscape may also be time consuming (Johst et al. 2001).

Secondly, we demonstrated that mean foraging distance increased over the reproductive cycle of storks from ca. 400 m during the period of egg incubation to nearly 700 m during the late stage of chick rearing. This observation indicates that food depletes primarily in the close vicinity of nests, as it may be overexploited by nest owners. Such phenomenon is expected in central-place foragers, which execute foraging trips to remote locations, but consistently return to a central place, the nest, to deliver food to offspring (Orians and Pearson 1979). In such species, travelling long distances to favourable feeding patches is costly in terms of time and energy (Johst et al. 2001), so if food availability allows, they primarily tend to exploit areas in the close neighbourhood of the nest. The evidence that depletion of food availability may increase foraging distances as the season progresses has already been demonstrated for the Spanish population of white storks (Alonso et al. 1997). We also showed that at the late stages of chick rearing birds increased the frequency of foraging trips at expense of other activities, such as resting, plumage maintenance, or nest maintenance, which further indicates that storks are likely to be constrained by time at the end of the reproductive cycle.

It must be acknowledged, that there is also an indirect mechanism that may, at least partially, account for the patterns observed in this study. The timing of spring migration in long-distance migrants is considered a phenotype-dependent process, where only high-quality individuals have capabilities to arrive early at the breeding grounds (Møller 1994). Therefore, it seems safe to assume that storks, which initiated breeding early in April, were of higher phenotypic and/or genetic quality in comparison to late breeding pairs, which could be manifested by the differences in age and physical condition. In such a situation, we might expect that late breeders are likely to forage less efficiently due to their inferior intrinsic characteristics. Likewise, they are likely to occupy territories with poorer accessibility to rich patches of feeding habitat, which can explain longer foraging duration. For these reasons, detrimental effects of shortening day length on the time budget of storks are expected to be mostly pronounced in the pairs of poorest quality.

In conclusion, we suggest that is some avian species seasonal changes in day length may act as a selective pressure for early breeding, allowing matching the peak of brood energy requirements with the most favourable photoperiod. We suggest that this selective force act mainly on temperate-breeding altricial species with long parental care that conclude reproduction after summer solstice, when offspring of late-breeding pairs are fledged under conditions of shortening day length. Under such circumstances, shortened time available for foraging may constitute a serious constraint on food delivery rates to offspring, unless birds decide to reduce investment in self-maintenance. We speculate that a similar mechanism may operate not only in White Stork, but also in other wading birds, seabirds and large raptors, but many more empirical studies are needed to confirm this hypothesis. We are also aware that the small sample size may limit the strength of our conclusions, so behavioural observations on much larger numbers of stork pairs from different populations would be necessary to validate our results.

Acknowledgments The periods of daylight for all nest locations were provided by the Planetarium and Astronomical Observatory of Ary Sternfeld in Łódź. The study was supported by the scholarship of the European Social Fund and the Polish National Budget in the D-RIM project of the Human Capital Programme. PM was financially supported by the Scientific Foundation of the University of Łódź. We thank two anonymous reviewers for helpful comments on the earlier draft of the manuscript.

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