

Timing of breeding in rural and urban Tawny Owls *Strix aluco* in southern Finland: effects of vole abundance and winter weather

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Abstract The onset of breeding in boreal owls might be linked to food supply, weather conditions or both, but the relative importance of each is poorly understood. The primary goal of this study was to discuss the impact that fluctuating food supply and various climatic factors have on the timing of breeding in northern Tawny Owls *Strix aluco* in rural and urban environments. The timing of breeding was significantly earlier in urban territories than in rural ones. In accordance with earlier findings, very early clutches occurred mainly in urban habitats. In association with being significantly earlier in urban than in rural habitats, the breeding of Tawny Owls began earlier the higher the (autumn) vole levels and the milder the preceding winter. Owls bred earlier the more there were voles and snow simultaneously. It seems that the state of readiness to start egg laying in urban habitats is in general higher than elsewhere and therefore favourable large-scale environmental conditions may also activate breeding earlier there than in rural areas.

Keywords Capital breeders · Climate warming · Habitat · Prey availability · Repeat and second clutches · Urbanization

Zusammenfassung

Der Einfluss von Wühlmausvorkommen und Winterwetter auf den Brutbeginn ländlicher und städtischer Waldkäuze *Strix aluco* im Süden Finnlands

Der Beginn des Brutgeschäfts bei borealen Eulen könnte von Futter, Wetter oder von beidem abhängig sein. Der relative Einfluss dieser beiden Faktoren ist bisher jedoch noch ungenügend erforscht. Das Ziel dieser Studie war es, den Einfluss eines schwankenden Nahrungsvorkommens und verschiedener Klimafaktoren auf den Zeitpunkt des Brutbeginns bei Waldkäuzen in städtischer und ländlicher Umgebung zu untersuchen. In städtischen Territorien begann das Brutgeschäft signifikant früher, als in ländlichen. Wie bereits in früheren Studien gezeigt, waren die frühesten Gelege hauptsächlich in städtischem Gebiet zu finden. Darüber hinaus war der Brutbeginn bei Waldkäuzen umso früher, je größer die Wühlmausvorkommen im Herbst und je milder der vorangegangene Winter waren. Waldkäuze brüteten umso früher, je mehr hohe Wühlmausbestände und Schnee gemeinsam auftraten. Die Legebereitschaft scheint in städtischen Gebieten generell höher zu sein und daher scheinen zuträgliche Umweltbedingungen hier einen früheren Legebeginn zu bedingen, als in ländlichen Gebieten.

Introduction

The onset of breeding in birds is determined largely by the food availability and prevailing weather conditions (Perrins 1970; Drent and Daan 1980; Korpimäki 1987; Daan et al. 1990; Newton 1998; Dunn 2004; see also Tökölyi et al.

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2012). In particular, the rise in the ambient temperature after winter appears to be a common key factor (von Haartman 1963; Lofts and Murton 1968; Crick et al. 1997; Sokolov and Payevsky 1998; Dunn and Winkler 1999; Svensson 2004; Both et al. 2005a). This implies that the recent rise in spring temperatures in northern latitudes, which indicates global warming, had led to the concurrent earlier onset of breeding, particularly in certain income breeders (e.g. Coppack and Both 2002; Both et al. 2004, 2005b; Dunn 2004; Svensson 2004; Schaefer et al. 2006). The timing of breeding in income breeders such as insectivorous passerines is governed by the food supply in a particular environment during the potential breeding season. The advancement of breeding is not as apparent in capital breeders, such as birds of prey, in which timing of breeding is governed largely by food supply and energy stores accumulated before the breeding season (Daan et al. 1989; Jönsson 1997; see also Houston et al. 2007; Stephens et al. 2009). Nevertheless, their food supply may also be affected by habitat (e.g. Aparicio and Bonal 2002; Chace and Walsh 2006) and variable climatic conditions (e.g. Newton 1998; Both 2010).

The early onset of breeding has been suggested as a favourable trait that evolved to ensure the best feeding conditions for the forthcoming young (e.g. Lack 1968; Perrins 1970; Drent and Daan 1980; Daan et al. 1989, 1990; Verboven and Visser 1998; Blüms et al. 2005) or, typically in various long-lived species of northern latitudes, to ensure that the time-consuming reproduction process can be conducted within the strict limits of tolerable environmental conditions (e.g. Lepage et al. 1996). The latter is particularly important for young birds to successfully reach independence (Newton 1979; Pietiäinen 1989; Grandäns et al. 2009). Early breeding may also offer the opportunity to produce more clutches and young within a season (Fredrickson and Hansen 1983; Korpimäki 1987; Dowding et al. 1999; Blomqvist et al. 2001; Kloskowski 2001; Halupka et al. 2008). Together, these factors mean that the ability to respond quickly to climatic conditions can be considered profitable (e.g. Berthold 1990; Prop and Deerenberg 1991; Sergio 2003). However, sudden shifts to earlier breeding may be detrimental if the critical periods for successful reproduction are changed to less suitable ones (Visser et al. 1998, 2004; Sanz 2003; Both et al. 2005a, 2009; Both and Visser 2005). For instance, it may be possible to advance laying dates to the extent that most or all individuals in a population breed too early (e.g. Cresswell and McCleery 2003).

The Tawny Owl *Strix aluco* is a widespread bird of prey of rural and urban habitats in Europe (Mikkola 1983; Cramp 1985). It commonly occupies habitats in the vicinity of human settlements including near the northern limit of its range in Finland, which was only colonized

approximately 100 years ago (Saurola 1995; Solonen 2005). A suitable nesting cavity is an essential prerequisite for the Tawny Owl's breeding, which is otherwise strictly governed by an adequate availability of food, usually arvicoline voles (Linkola and Myllymäki 1969; Solonen and Karhunen 2002; Kekkonen et al. 2008). The availability of food for breeding Tawny Owls is particularly affected by the pronounced and more or less cyclic fluctuations of vole populations (Solonen 2004, 2010; Sundell et al. 2004), and is modified by habitat (Petty 1989; Solonen and af Ursin 2008) and various climatic factors such as winter temperature and snow cover (Southern 1970; Solonen and Karhunen 2002; Solonen 2004, 2005; Lehikoinen et al. 2011). Generally speaking, the food supply for some species (such as some tits and birds of prey) seemed to be higher in urban habitats than in rural ones, particularly during winter and before the breeding season (Marzluff et al. 2001; Chace and Walsh 2006; Chamberlain et al. 2009). For Tawny Owls, urban habitats seem to be particularly favourable owing to the abundant and relatively stable availability of prey that commonly accompany human settlements (such as various small mammals and birds) as well as the prevailing benign microclimate (Solonen and af Ursin 2008). Mild winters also seem to be favourable, but they may also have negative effects in terms of their variable impact on small mammals (Solonen 2004, 2006). In the heavily fluctuating environmental conditions of the north, breeding of Tawny Owls seem to be most frequent and most successful in territories that provide the most stable year-round food supply (Solonen and af Ursin 2008). In such territories, breeding might also begin earlier than elsewhere. Due to relatively stable environmental conditions, Tawny Owls may even breed throughout the year in some areas of southern Europe (Zuberogoitia et al. 2004).

I examined the timing of breeding in rural and urban Tawny Owls of the capital (Helsinki) district and its surroundings in southern Finland between 1986 and 2011. My primary goal was to assess the role of fluctuating vole abundance and climatic conditions of the preceding winter in the timing of breeding, as well as to highlight the differences between the main habitat types of the study area (rural vs. urban). I expected that (1) Tawny Owls bred earlier in urban habitats than in rural ones, due to more stable and benign environmental conditions, (2) high abundance of voles and mild and less snowy winters advanced the onset of breeding, and (3) the effects of fluctuating vole abundance and winter weather between rural and urban habitats differ, probably due to the additional availability of less variable prey populations and to less frost and snow in urban areas. An alternative explanation could be that urban habitats locally dampen the general vole fluctuations. In particular, I expected that the availability of other prey than small voles was higher in

urban areas than in rural ones, and therefore the level of fluctuating abundance of voles needed to activate breeding in owls was lower in urban than in rural habitats.

Methods

Study on Tawny Owls

The present study was conducted in Uusimaa (60°N, 25°E), near the southern coast of Finland (Solonen and Karhunen 2002) between 1986 and 2011. The study area of more than 500 km² consisted of low-lying rural habitats of mixed fields and forests, as well as the capital district (Helsinki and its surroundings), the most urban area of the country. Tawny Owls occupied the study area in a relatively even manner, following the availability of suitable nest-sites, mainly nestboxes erected throughout the study area. The hatching success of birds was recorded for each year of the study. Only the successfully hatched clutches were included in the present data. Possible biases caused by variable hatching success should be minor because unhatched eggs were rare in successful nests (in nests from which at least one young fledged).

In order to estimate the hatching dates, I measured the wing length of nestlings or recently fledged young from 554 broods using the maximum method (e.g. Svensson 1984), from the carpal joint to the tip of the wing. I estimated the age of the oldest young using Jokinen's (1975) wing-growth curve. The hatching dates were estimated backwards from the age of the young. According to Jokinen (1975), the growth of the wing length in Tawny Owls is rather even and independent on the variations in the food supply. During the first week after hatching, the age of nestlings can be estimated on an accuracy of 1–2 days based on the wing length. Later, the variation somewhat increases but the accuracy is still 3–4 days even during the last half (2 weeks) of the nestling period. For the timing of egg laying, I used an incubation time of 28 days (Cramp 1985; Saurola 1995). Calendar days were converted to Julian days, starting from the first of January.

Habitat, food and weather variables

In order to demonstrate the effect of two main habitat types, the 179 locations of nesting territories were classified into rural (146) and (sub)urban (33). The rural territories were situated in agricultural and silvicultural environments, while the suburban and urban territories were located in recreational forests and parks of built-up areas (Solonen 2008b; Solonen and af Ursin 2008). This rough categorisation seems suitable for the present purpose because the actual hunting areas of the owls were unknown

(cf. Solonen 2008b). In order to demonstrate the effects of local habitats, I gave each nesting territory an individual identity number (ID).

In order to characterise the general level of food supply for owls before the breeding season, I used the regional small vole indices of the preceding autumn ("Appendix"). They seemed to be associated with the occurrence and nesting of Tawny Owls better than the respective spring indices that instead reflect the vole abundance during the nestling period of owls (Solonen 2010). Each index was based on a total of 384 trap-nights of trappings conducted during 2-day periods in early October at two localities near the present study area and included both forest and old field habitats, 192 trap-nights each (Kimpari Bird Projects; Solonen and Ahola 2010; Solonen 2010). Thus, they reflected only general levels of fluctuations in numbers of voles in the district, not particularly in the present rural and urban habitats. These indices seemed to characterise fluctuations in the abundance of voles over a larger area in southern Finland relatively well (Solonen 2004, 2010). The vole species concerned were the Bank Vole *Myodes glareolus* and the Field Vole *Microtus agrestis*. The Field Vole is the most common prey species of breeding Tawny Owls in the study area (Solonen and Karhunen 2002).

I also examined the effects of local mean winter temperatures, including January, February and March, as well as the depth of the snow cover in the middle of March ("Appendix") measured at the Helsinki-Vantaa airport (Finnish Meteorological Institute), roughly in the middle of the present study area. These variables seemed to reasonably characterise the strength of winter before the Tawny Owls' breeding season. Preliminary examination of the data showed that there was a significant negative correlation between the variables ($r = -0.693$, $P < 0.001$, $df = 24$).

Statistics

Trends and other relationships between pairs of variables were examined by least-squares linear regression and the non-parametric Mann–Whitney U test was used for assessing whether hatching dates tend to be earlier in urban than in rural habitats, using VassarStats statistical software (<http://www.vassarstats.net/>). In order to obtain a model, which combined the effects of various explanatory variables, I used mixed effects models (lme) (Pinheiro and Bates 2000) from nlme in the R statistical package (R Development Core Team 2008; Venables et al. 2008). In the analyses, I used the Julian hatching date of the largest (i.e. oldest) young in the brood as the response variable. The explanatory variables (fixed effects) included the general habitat (rural vs. urban), the regional vole abundance index of the preceding autumn, and the weather

variables of the current/preceding winter (mean winter temperature and snow cover in March) (“Appendix”). Separate and joint effects of variables were both considered. The territory ID, indicating impacts of the local habitat and individual birds, and year, indicating annually varying unknown factors, characterised random effects. The general structure of the model was as follows: hatching date \sim habitat + voles + weather + habitat \times voles + habitat \times weather + voles \times weather, random = \sim hatching date/territory \times hatching date/year.

Results

The hatching dates of Tawny Owls varied between Julian dates 21 and 151 (median 119, $n = 554$). The hatching dates of the earliest broods of the season varied annually

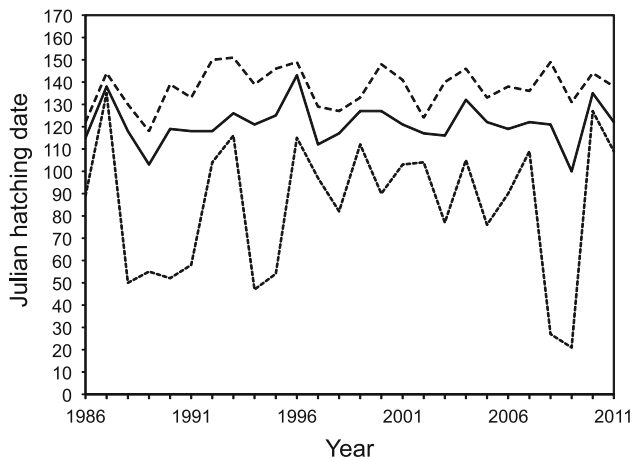
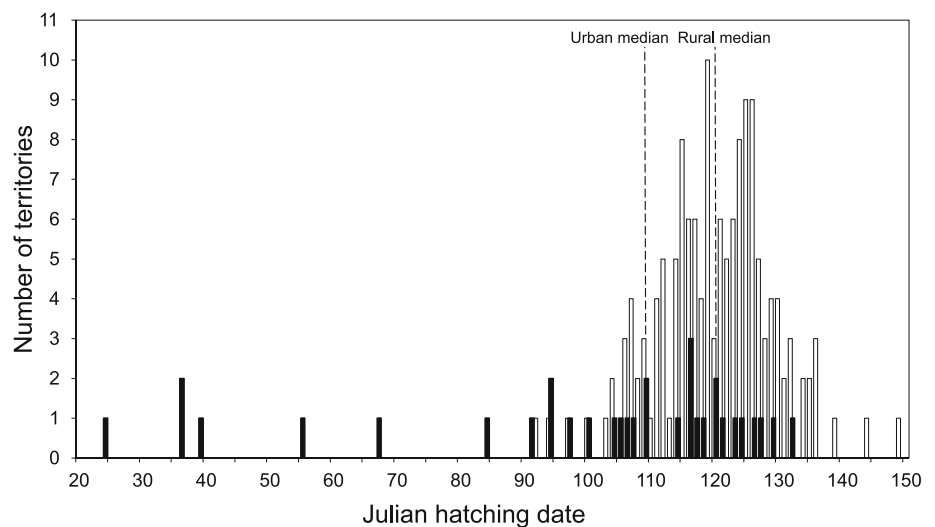


Fig. 1 Fluctuations of the earliest (lowest graph), median and latest hatching dates of the season in a Tawny Owl *Strix aluco* population in southern Finland between 1986 and 2011

Fig. 2 Distribution of median Julian hatching dates in rural (open bars, $n = 146$) and urban (closed bars, $n = 33$) territories of Tawny Owls in a population in southern Finland between 1986 and 2011



between Julian dates 21 (2009) and 135 (1987) and the respective variation in the annual median dates ranged from 100 (2009) to 143 (1996) (Fig. 1). The length of the laying period (days between the earliest and latest hatching date of season) varied between 9 and 122 days, with a median of 45 days. There was no significant trend (based on least-squares linear regression) either in the earliest or the median hatching dates of the population during the study period (Fig. 1; the earliest clutches: $t_{24} = 0.296$, $P = 0.770$; medians: $t_{24} = 0.135$, $P = 0.894$). This also applied to the annual explanatory variables (vole indices, weather variables) studied ($t_{24} < |2|$, $P > 0.05$).

The range in hatching dates was 28–151 (median 120, $n = 453$) in rural habitats and 21–149 (median 109, $n = 101$) in urban ones. The median hatching dates of urban territories were significantly earlier than those of rural ones (median Julian dates 109 and 121, respectively; Mann–Whitney U test, $U_{146,33} = 1239.5$, $z = 4.35$, $P < 0.001$) (Fig. 2). The earliest hatching dates showed a similar pattern (median Julian dates 96 and 112, in urban and rural territories, respectively; Mann–Whitney U test, $U_{146,33} = 978.5$, $z = 5.32$, $P < 0.001$). There were no trends in the earliest or median hatching dates either in rural or in urban environments ($t_{24} < |2|$, $P > 0.05$). The exceptionally early clutches were laid within two periods (1988–1995 and 2008–2009) (Fig. 1) in two urban territories. The two earliest clutches found in the present data were laid in the same urban territory in the 2008 and 2009 breeding seasons. The first eggs of the clutches were laid on 30 December, 2007 and 24 December, 2008, respectively.

In association with the effect of habitat, the breeding of Tawny Owls began earlier the higher the (autumn) vole levels and the milder the preceding winter (Table 1). There also emerged a significant joint effect between the vole abundance and snow cover: owls bred earlier the more there were voles and snow simultaneously. The main

Table 1 The mixed-effects model characterising the roles of the fixed effects, the general habitat (habitat = increasing urbanization), vole abundance (voles), mean winter temperature (temperature) and depth

of the snow cover (snow) in determining (Julian) hatching dates for the clutches of rural and urban Tawny Owls *Strix aluco* in southern Finland between 1986 and 2011

Models and variables	Estimate	±SE	<i>t</i>	<i>df</i>	<i>P</i>
Hatching date ~ habitat + voles + temperature + snow + habitat × voles + habitat × temperature + habitat × snow + voles × temperature + Voles × snow + temperature × snow, random = ~ hatching date territory × hatching datelyear					
Fixed effects (intercept)	139.243	6.346	21.942	524	<0.001
Habitat	−16.070	3.339	−4.813	524	<0.001
Voles	0.035	0.538	0.064	19	0.949
Temperature	4.904	2.016	2.433	19	0.025
Snow	0.871	0.376	2.317	19	0.032
Habitat × voles	−0.506	0.208	−2.438	524	0.015
Habitat × temperature	−2.605	0.894	−2.915	524	0.004
Habitat × snow	−0.189	0.142	−1.328	524	0.185
Voles × temperature	−0.223	0.130	−1.716	19	0.102
Voles × snow	−0.067	0.023	−2.869	19	0.010
Temperature × snow	−0.026	0.039	−0.668	19	0.512
Random effects					

The fixed effects (estimate ± SE), test statistics (*t*), degrees of freedom (*df*), and *P* values are given. The random effects included individual random effects such as the characteristics of nesting territory and individual birds characterised by territory ID and annual random effects characterised by year

effects of the increasing winter temperature and depth of the snow cover on the timing of breeding in Tawny Owls were, however, delaying.

Discussion

Effects of habitat

Tawny Owls bred earlier in urban territories than in rural ones. High general abundance of voles and mild winters advanced the breeding of owls particularly in urban habitats. This suggests that the threshold to start egg laying was lower in urban territories, i.e. urban birds were, on average, better prepared for the onset of breeding, and a smaller improvement in environmental conditions might trigger their breeding.

Early breeding in urban habitats seems to be a widespread phenomenon (see Chamberlain et al. 2009). Exceptionally early clutches of Tawny Owls have been laid in urban habitats, both in the present northern study area (Solonen 2000; this study) and elsewhere at more southern latitudes (e.g. Petriņš 1986; Godovanets et al. 1992; Grandāns et al. 2009). Such clutches have occurred particularly in good vole years. Otherwise, the factors determining the early onset of breeding in urban environments are somewhat unclear. Possible explanations include the better general availability of food, since rodents and small passerines accumulate in urban and suburban areas in

winter due to feeding and other human-provided resources (e.g. Petriņš 1986; Grandāns et al. 2009). In addition, a higher mean ambient temperature (e.g. Marzluff et al. 2001) and anthropogenic light sources in towns and cities might physiologically activate birds earlier in spring than in more natural conditions (Partecke et al. 2004; Grandāns et al. 2009).

Effects of regional vole abundance and winter weather conditions

Besides being significantly earlier in urban than in rural habitats, in association with the effect of habitat the breeding of Tawny Owls began earlier the higher the vole levels and the milder the preceding winter. These findings were in accordance with expectations. However, the main effects of both increasing mean winter temperatures and depth of the snow cover seemed to be the delayed breeding of owls. Instead, owls bred earlier the more there were voles and snow simultaneously. This suggests that deep snow cover was favourable for over-wintering voles (Solonen 2004, 2006).

Winter temperature and snow cover characterise different kinds of constraints set by winter on the breeding of Tawny Owls, namely the effects on the energy requirements of the birds themselves and the impact on the actual availability of their prey, respectively. The direct effects of the present weather variables indicating mildness of winter cover somewhat different periods of time. They may also

have various indirect effects, particularly on the availability of owls' food (Solonen 2004, 2010).

The significant contribution of benign winter weather in advancing the onset of breeding was probably partly associated with reduced energy requirements and better hunting success on small voles in less snowy winters (Solonen 2004, 2005; Grandāns et al. 2009). In particular, under snow hiding Water Voles *Arvicola amphibius* are earlier available after mild winters. In southern Finland, the Water Vole is, in general, the most important prey species of Tawny Owls during breeding (Solonen and Karhunen 2002; Kekkonen et al. 2008). After a mild winter, this may also be the case before breeding, which contributes to the timing of egg laying of owls. It has been suggested that when the importance of small voles is not evident, the abundance of larger Water Voles might play the most important role in the timing of breeding in Tawny Owls (Kekkonen et al. 2008). Also, the advancing effect of the interaction between the abundance of small voles and the depth of the snow cover seems reasonable. When there are voles in abundance in autumn and the snow cover is deep in winter, more voles will survive until spring and to the laying period of owls.

Has the onset of owls' breeding advanced between years?

The Tawny Owl breeding season usually starts in about mid-March across Europe (Mikkola 1983; Petty et al. 1994; Saurola 1995; Grandāns et al. 2009). Recently, however, increasing numbers of early (winter) breeding attempts have been recorded (e.g. Petriņš 1986; Godovanets et al. 1992; Solonen 2000; this study; Owen 2003; Grandāns et al. 2009). These observations might suggest that the onset of breeding in Tawny Owls has advanced not only within the season but also within a longer term between breeding seasons. However, the present data showed no trends in the laying dates of owls nor in the explanatory variables during the study period of 26 years.

Heavily fluctuating food supply and weather conditions seem to cause occasional short-term shifts to advanced breeding among individuals of a population within a season, or in some individuals between consecutive breeding seasons. Long-term advancement of breeding may be possible if there are favourable trends in certain factors governing the timing of breeding. Recent long-term advancements in timing of breeding in birds seemed to be largely human-induced and have appeared either as spatial gradients or temporal trends. The former are largely due to urbanization (e.g. Marzluff et al. 2001; Partecke et al. 2004; Chamberlain et al. 2009), and the latter particularly due to climate warming (e.g. Møller et al. 2010). Global climate warming has also been the

most commonly advocated factor behind advanced breeding in birds (Both et al. 2004; Crick 2004; Dunn 2004). However, even during relatively long periods, such as that of the present study, various climatic factors indicating temperature have not shown any trend to suggest global warming (see also Svensson 2004; Solonen 2008a). In fact, the winter index of the North Atlantic oscillation (e.g. Hurrell et al. 2001), one of the most commonly used indicators of global warming, has actually declined during the 26 years of the present study (<http://www.cru.uea.ac.uk/cru/data/nao.htm>; accessed 6 February 2012). In the present case, the high fluctuations of vole populations may also have blurred any potential trend in the hatching date. Elsewhere, and for longer time scales, however, increasing global or local spring temperatures (suggesting climate warming) as well as advanced breeding in birds have been documented in several cases (e.g. Walther et al. 2002; Crick 2004; Watkinson et al. 2004; Both et al. 2009; Møller et al. 2010; Schroeder et al. 2012). Therefore, the significant relationships between the hatching date and weather factors related to ambient temperature show that the timing of breeding in Tawny Owls may become earlier with warming climate.

Advanced breeding does not necessarily concern total populations, but rather single high-quality individuals, pairs or territories. This is suggested by single and repeated records from various nesting territories. Most early breeders are probably experienced, elderly birds (Blüms et al. 2002; Verhulst and Nilsson 2008; cf., however, Grandāns et al. 2009). In the present study population, an especially long-lived female frequently laid her clutches in January and advanced her breeding significantly during her reproductive career (Solonen 2000). The timing of egg laying fluctuated in accordance with local winter temperatures.

Consequences of advanced breeding

The present results suggest that favourable combinations of environmental conditions may occasionally or repeatedly advance the onset of breeding in Tawny Owls. Advanced breeding may, however, cause chicks to hatch or fledge in hostile weather conditions of early spring, when the general food availability is traditionally at its worst (Solonen 2000). So, this kind of 'mismatching' may reduce the benefit gained from the early breeding if the food supply does not improve with the advancement of breeding (cf. Visser et al. 2004; Schroeder et al. 2012). In most of the species studied to date, the advancement in the beginning of breeding coincided with the advancement in the end of breeding; this resulted in a shift in the entire breeding season, with its length remaining unchanged or slightly shortened (e.g.

Both and Visser 2001; Sanz 2003; Schaefer et al. 2006). Only a few authors have reported lengthening of the breeding season, with similar consequences as in Tawny Owls in some years of the present study (Halupka et al. 2008; Najmanová and Adamík 2009).

After leaving the nest-hole, the mortality of young Tawny Owls may be considerable due to both mammalian predators (such as the Pine Marten *Martes martes* and the Red Fox *Vulpes vulpes*) and avian predators (such as the Northern Goshawk *Accipiter gentilis* and the Eagle Owl *Bubo bubo*) (Sunde 2005; Solonen 2011). The mortality risk may increase with the fledging date from 14 % in April to more than 58 % in June (Sunde 2005). Therefore, the increasing predation of late broods may be an important selective agent for early breeding in the Tawny Owl. However, poor food supply, adverse weather conditions and deficient cover against predators provided by vegetation very early in the spring may have a contrary effect. In timing of breeding, laying females should compromise between optimal food availability for and minimal predation pressure against their young. From a parental perspective, the optimal laying date is a trade-off between self-maintenance costs and fitness benefits for offspring (Daan and Tinbergen 1997). If females lay when the food availability for themselves is low, their reproductive investment and survival will be affected (Drent 2006).

The occasional or regular lengthening of breeding seasons might increase the occurrence of replacement nestings and might even lead to genuine second clutches in Tawny Owls. The breeding schedule of northern owls is, in general, so tight that such replacement nestings or second clutches are not possible (e.g. Mikkola 1983; Forsman et al. 1995). Southern (1970) noted that re-nesting in Tawny Owls occurred only in years when prey levels were high. However, re-nesting appears to be a usual response of diurnal raptors and owls to clutch loss during early incubation (Newton 1979; Mikkola 1983; Forsman et al. 1995). Otherwise, replacement and real second clutches in birds of prey are only known to be common in Barn Owls *Tyto alba* (Taylor 1994; Martínez and López 1999; Roulin 2002). In the Tawny Owl, only one probable case of a second brood after successful breeding has been reported, from Spain (Zuberogoitia et al. 2004). In the two present cases of exceptionally early breeding, in both years (2008, 2009) a new brood appeared in the territory in July (J. Laine, personal communication). Based on the developmental stage of the young, they obviously originated from nests in some of the numerous natural holes of the nesting territory, although the nests were not found. In 2008, at least two cases of re-nesting after the loss of eggs or nestlings were

recorded in two territories in the neighbourhood (E. Haapanen, personal communication).

Concluding remarks

One may ask why the recent early clutches are so prominent in the Tawny Owl even in the present study area where the species is a relatively new inhabitant from more southern areas. The success of colonisation and breeding of the Tawny Owl in Finland is clearly largely due to the association of the species with environments that are strongly influenced by mankind. Of the northern owls, only the Long-eared Owl *Asio otus* resembles to some extent the Tawny Owl in this respect (e.g. Nilsson 1984). Recently, other species of northern birds of prey, particularly the Northern Goshawk and the Eagle Owl, have shown a similar attitude to man-made environments in the present study area (Solonen 2007, 2008b; Solonen et al. 2010). However, the relationship of the Tawny Owl with rural and urban habitats is much stronger than that of the other species of northern birds of prey. Rural and urban habitats, particularly the latter, provide various advantages extensively and effectively used by Tawny Owls (e.g. Solonen and af Ursin 2008). Increasingly favourable wintering conditions due to climate change and urbanization provide advantages that can make advanced breeding and repeat or even genuine second clutches possible for an increasing proportion of the population.

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Appendix

Variables (fixed effects) used to explain variation in the hatching date in the present study population of the Tawny Owl *Strix aluco* in Southern Finland between 1986 and 2011. The regional small vole indices of the preceding autumn are based on a total of 384 trap-nights of trappings conducted during 2 day periods in early October in two localities near the present study area and included both forest and old field habitats, 192 trap-nights each (Kimpri Bird Projects). Local mean winter temperatures (°C), including January, February and March, as well as the depth of snow cover (cm) in the middle of March were measured at the Helsinki-Vantaa airport (Finnish Meteorological Institute), roughly in the middle of the present study area.

Years	Vole index	Temperature (°C)	Snow cover (cm)
1986	13.52	−6.8	47
1987	2.86	−9.6	37
1988	12.22	−3.4	38
1989	11.70	−1.1	0
1990	0.26	−1.5	1
1991	6.24	−2.8	12
1992	9.55	−1.0	3
1993	2.39	−1.1	8
1994	1.35	−5.8	17
1995	13.54	−0.9	9
1996	2.86	−7.3	29
1997	5.73	−3.4	0
1998	8.59	−3.4	3
1999	10.94	−4.2	39
2000	16.97	−2.2	7
2001	3.38	−3.0	12
2002	18.73	−3.0	2
2003	15.88	−6.4	1
2004	3.90	−3.6	33
2005	7.03	−3.4	32
2006	24.74	−6.1	20
2007	0.26	−1.5	0
2008	4.45	0.3	1
2009	22.10	−3.6	26
2010	5.70	−8.2	61
2011	11.8	−7.0	47

References

- Aparicio JM, Bonal R (2002) Effects of food supplementation and habitat selection on timing of Lesser Kestrel breeding. *Ecology* 83:873–877
- Berthold P (1990) Patterns of avian migration in light of current global “greenhouse” effects: a central European perspective. *Proc Int Ornithol Congr* 20:780–786
- Blomqvist D, Wallander J, Andersson M (2001) Successive clutches and parental roles in waders: the importance of timing in multiple clutch systems. *Biol J Linn Soc* 74:549–555
- Blüms P, Clark RG, Mednis A (2002) Patterns of reproductive effort and success in birds: path analyses of long-term data from European ducks. *J Anim Ecol* 71:280–295
- Blüms P, Nichols JD, Hines JE, Lindberg MS, Mednis A (2005) Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. *Oecologia* 143:365–376
- Both C (2010) Food availability, mistiming, and climatic change. In: Møller AP, Fiedler W, Berthold P (eds) *Effects of climate change on birds*. Oxford University Press, Oxford, pp 129–147
- Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411:296–298
- Both C, Visser ME (2005) The effect of climate change on the correlation between avian life-history traits. *Glob Change Biol* 11:1606–1613
- Both C, Artemyev AV, Blaauw B, Cowie RJ, Dekhuijzen AJ, Eeva T, Enemar A, Gustafsson L, Ivankina EV, Järvinen A, Metcalfe NB, Nyholm NEI, Potti J, Ravussin P-A, Sanz JJ, Silverin B, Slater FM, Sokolov LV, Török J, Winkel W, Wright J, Zang H, Visser ME (2004) Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proc R Soc Lond B* 271:1657–1662
- Both C, Bijlsma RG, Visser ME (2005a) Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. *J Avian Biol* 36:368–373
- Both C, Piersma T, Roodbergen SP (2005b) Climate change explains much of the 20th century advance in laying date of Northern Lapwing *Vanellus vanellus* in The Netherlands. *Ardea* 93:79–88
- Both C, van Asch M, Bijlsma RG, van den Burg AB, Visser ME (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J Anim Ecol* 78:73–83
- Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. *Landsc Urban Plan* 74:46–69
- Chamberlain DE, Cannon AR, Toms MP, Leech DI, Hatchwell BJ, Gaston KJ (2009) Avian productivity in urban landscapes: a review and meta-analysis. *Ibis* 151:1–18
- Coppack T, Both C (2002) Predicting life-cycle adaptation of migratory birds to global climate change. *Ardea* 90:369–378
- Cramp S (ed) (1985) *The birds of the Western Palearctic*, vol 4. Oxford University Press, Oxford
- Cresswell W, McCleery R (2003) How great tits maintain synchronisation of their hatch date with food supply in response to long-term variability in temperature. *J Anim Ecol* 72:356–366
- Crick HQP (2004) The impact of climate change on birds. *Ibis Suppl* 1(146):48–56
- Crick HQP, Dudley C, Glue DE, Thomson DL (1997) UK birds are laying eggs earlier. *Nature* 388:526
- Daan S, Tinbergen JM (1997) Adaptation in life histories. In: Krebs JR, Davies NB (eds) *Behavioural ecology: an evolutionary approach*. Blackwell, Oxford, pp 311–333
- Daan S, Dijkstra C, Drent R, Meijer T (1989) Food supply and the annual timing of avian reproduction. *Proc Int Ornithol Congr* 19:392–407
- Daan S, Dijkstra C, Tinbergen JM (1990) Family planning in the kestrel (*Falco tinnunculus*): the ultimate control in covariation of laying date and clutch size. *Behaviour* 114:83–116
- Dowding JE, Wills DE, Booth AM (1999) Double-brooding and brood overlap by Northern New Zealand Dotterels (*Charadrius obscurus aquilonius*). *Notornis* 46:181–185
- Drent R (2006) The timing of birds’ breeding seasons: the Perrins hypothesis revised especially for migrants. *Ardea* 94:305–322
- Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252
- Dunn P (2004) Breeding dates and reproductive performance. In: Møller AP, Fiedler W, Berthold P (eds) *Birds and climate change. Advances in ecological research*, vol 35. Elsevier, London, pp 69–87
- Dunn PO, Winkler DW (1999) Climate change has affected the breeding date of tree swallows throughout North America. *Proc R Soc Lond B* 266:2487–2490
- Forsman ED, Giese A, Manson D, Sovern S, Herter DR (1995) Renesting by Spotted Owls. *Condor* 97:1078–1080
- Fredrickson H, Hansen JL (1983) Second broods in Wood Ducks. *J Wildl Manag* 47:320–326
- Godovanets BI, Bundzyak PV, Skilsky IV (1992) Early breeding of the Tawny Owl in the Bukovina. *Berkut* 1:74–75
- Grandāns G, Keišs O, Avotiņš A (2009) Onset of breeding in Tawny Owl *Strix aluco* in eastern Latvia. *Acta Universitatis Latviensis*, vol 753, Biology, pp 81–87
- Halupka L, Dyrzyc A, Borowiec M (2008) Climate change affects breeding of reed warblers *Acrocephalus scirpaceus*. *J Avian Biol* 39:95–100

- Houston AI, Stephens PA, Boyd IL, Harding KC, McNamara JM (2007) Capital or income breeding? A theoretical model of female reproductive strategies. *Behav Ecol* 18:241–250
- Hurrell JW, Kushnir Y, Visbeck M (2001) The North Atlantic oscillation. *Science* 291:603–605
- Jokinen M (1975) Lehtopöllön poikasten kasvu ja energiankäyttö ja niiden vaikutus pesimätuloksen määräytymiseen. MSc thesis, University of Turku, Finland
- Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78:57–66
- Kekkonen J, Kolunen H, Pietiäinen H, Karell P, Brommer JE (2008) Tawny owl reproduction and offspring sex ratio in variable food conditions. *J Ornithol* 149:59–66
- Kloskowski J (2001) Double-brooding in Red-necked Grebes. *Waterbirds* 24(1):121–124
- Korpimäki E (1987) Timing of breeding of Tengmalm's Owl *Aegolius funereus* in relation to vole dynamics in western Finland. *Ibis* 129:58–68
- Lack D (1968) Ecological adaptations for breeding in birds. Methuen, London
- Lehikoinen A, Ranta E, Pietiäinen H, Byholm P, Sauro P, Valkama J, Huitu O, Henttonen H, Korpimäki E (2011) The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. *Oecologia* 165:349–355
- Lepage D, Gauthier G, Reed A (1996) Breeding-site infidelity in greater snow geese: a consequence of constraints on laying date? *Can J Zool* 74:1866–1875
- Linkola P, Myllymäki A (1969) Der Einfluss der Kleinsäugerfluktuationen auf das Brüten einiger kleinsäugerfressender Vögel im südlichen Häme, Mittelfinnland 1952–1966. *Ornis Fenn* 46:45–78
- Lofts B, Murton RK (1968) Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. *J Zool* 155:327–394
- Martínez JA, López G (1999) Breeding ecology of the Barn Owl (*Tyto alba*) in Valencia (SE of Spain). *J Ornithol* 140:93–99
- Marzluff JM, Bowman R, Donnelly R (eds) (2001) Avian ecology and conservation in an urbanizing world. Kluwer, Boston
- Mikkola H (1983) Owls of Europe. Poyser, Calton
- Møller AP, Fiedler W, Berthold P (eds) (2010) Effects of climate change on birds. Oxford University Press, Oxford
- Najmanová L, Adamík P (2009) Effect of climatic change on the duration of the breeding season in three European thrushes. *Bird Study* 56:349–356
- Newton I (1979) Population ecology of raptors. Poyser, Berkhamsted
- Newton I (1998) Population limitation in birds. Academic, London
- Nilsson IN (1984) Prey weight, food overlap, and reproductive output of potentially competing Long-eared and Tawny Owls. *Ornis Scand* 15:176–182
- Owen J (2003) Early birds: is warming changing UK breeding season? *Natl Geogr News*, June 3, 2003
- Partecke J, Van't Hof T, Gwinner E (2004) Differences in the timing of reproduction between urban and forest European blackbirds (*Turdus merula*): result of phenotypic flexibility or genetic differences? *Proc R Soc Lond B* 271:1995–2001
- Perrins CM (1970) The timing of birds' breeding seasons. *Ibis* 112:242–255
- Petriņš A (1986) Winter breeding of Tawny Owl in towns in Latvia. *Ornithologia* 21:167
- Petty SJ (1989) Productivity and density of tawny owls *Strix aluco* in relation to the structure of a spruce forest in Britain. *Ann Zool Fenn* 26:227–233
- Petty SJ, Shaw G, Anderson DIK (1994) Value of nest-boxes for population studies and conservation of owls in coniferous forest in Britain. *J Raptor Res* 28:134–142
- Pietiäinen H (1989) Seasonal and individual variation in the production of offspring in the Ural owl *Strix uralensis*. *J Anim Ecol* 58:905–920
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-Plus. Springer, New York
- Prop J, Deerenberg C (1991) Spring staging in brent geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87:19–28
- R Development Core Team (2008) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. Available at: <http://www.R-project.org>
- Roulin A (2002) Offspring desertion by double-brooded female barn owls (*Tyto alba*). *Auk* 119:515–519
- Sanz JJ (2003) Large-scale effect of climate change on breeding parameters of pied flycatchers in Western Europe. *Ecography* 26:45–50
- Sauro P (ed) (1995) Owls of Finland. Kirjayhtymä, Helsinki
- Schaefer T, Ledebur G, Beier J, Leisler B (2006) Reproductive responses of two related coexisting songbird species to environmental changes: global warming, competition, and population sizes. *J Ornithol* 147:47–56
- Schroeder J, Piersma T, Groen NM, Hooijmeijer JCEW, Kentie R, Lourenco PM, Schekkerman H, Both C (2012) Reproductive timing and investment in relation to spring warming and advancing agricultural schedules. *J Ornithol* 153:327–336
- Sergio F (2003) Relationship between laying dates of black kites *Milvus migrans* and spring temperatures in Italy: rapid response to climate change? *J Avian Biol* 34:144–149
- Sokolov LV, Payevsky VA (1998) Spring temperature influences year-to-year variations in the breeding phenology of passerines on the Courish Spit, eastern Baltic. *Avian Ecol Behav* 1:22–36
- Solonen T (2000) The story of a Tawny Owl *Strix aluco* female called Lyyli. *Linnut* 35(1):21–23
- Solonen T (2004) Are vole-eating owls affected by mild winters in southern Finland? *Ornis Fenn* 81:65–74
- Solonen T (2005) Breeding of the Tawny Owl *Strix aluco* in Finland: responses of a southern colonist to the highly variable environment of the North. *Ornis Fenn* 82:97–106
- Solonen T (2006) Overwinter population change of small mammals in southern Finland. *Ann Zool Fenn* 43:295–302
- Solonen T (2007) Urban birds of the Helsinki district: winners or losers? *Tringa* 34:94–101
- Solonen T (2008a) Large-scale climatic phenomena and timing of breeding in a local population of the Osprey *Pandion haliaetus* in southern Finland. *J Ornithol* 149:229–235
- Solonen T (2008b) Larger broods in the Northern Goshawk *Accipiter gentilis* near urban areas in southern Finland. *Ornis Fenn* 85:118–125
- Solonen T (2010) Reflections of winter season large-scale climatic phenomena and local weather conditions in abundance and breeding frequency of vole-eating birds of prey. In: Ulrich PK, Willett JH (eds) Trends in ornithology research. Nova, New York, pp 95–119
- Solonen T (2011) Impact of dominant predators on territory occupancy and reproduction of subdominant ones within a guild of birds of prey. *Open Ornithol J* 4:23–29
- Solonen T, Ahola P (2010) Intrinsic and extrinsic factors in the dynamics of local small-mammal populations. *Can J Zool* 88:178–185
- Solonen T, Karhunen J (2002) Effects of variable feeding conditions on the Tawny Owl *Strix aluco* near the northern limit of its range. *Ornis Fenn* 79:121–131
- Solonen T, af Ursin K (2008) Breeding of Tawny Owls *Strix aluco* in rural and urban habitats in Southern Finland. *Bird Study* 55:216–221
- Solonen T, Lehikoinen A, Lammi E (eds) (2010) The bird fauna of the region of Uusimaa, Southern Finland. Helsingin Seudun Lintutieteellinen Yhdistys Tringa, Helsinki

- Southern HN (1970) The natural control of a population of Tawny Owls (*Strix aluco*). *J Zool* 62:197–285
- Stephens PA, Boyd IL, McNamara JM, Houston AI (2009) Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology* 90:2057–2067
- Sunde P (2005) Predators control post-fledging mortality in tawny owls, *Strix aluco*. *Oikos* 110:461–472
- Sundell J, Huitu O, Henttonen H, Kaikusalo A, Korpimäki E, Pietiäinen H, Saurola P, Hanski I (2004) Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. *J Anim Ecol* 73:167–178
- Svensson L (1984) Identification guide to European passerines, 3rd edn. Svensson, Stockholm
- Svensson S (2004) Onset of breeding among Swedish starlings *Sturnus vulgaris* in relation to spring temperature in 1981–2003. *Ornis Svec* 14:117–128
- Taylor IR (1994) Barn Owls: predator–prey relationships and conservation. Cambridge University Press, Cambridge
- Tökölyi J, McNamara JM, Houston AI, Barta Z (2012) Timing of avian reproduction in unpredictable environments. *Evol Ecol* 26:25–42
- Venables WN, Smith DM, the R Development Core Team (2008) An introduction to R. Version 2.8.0. The R Project for Statistical Computing. Available at: <http://www.r-project.org>
- Verboven N, Visser ME (1998) Seasonal variation in local recruitment of great tits: the importance of being early. *Oikos* 81:511–524
- Verhulst S, Nilsson J-Å (2008) The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Phil Trans R Soc Lond B* 363:399–410
- Visser ME, van Noordwijk AJ, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc R Soc Lond B* 265:1867–1870
- Visser ME, Both C, Lambrechts MM (2004) Global climate change leads to mistimed avian reproduction. In: Møller AP, Fiedler W, Berthold P (eds) Birds and climate change. Advances in ecological research, vol 35. Elsevier, London, pp 87–108
- von Haartman L (1963) The nesting times of Finnish birds. *Proc Int Ornithol Congr* 13:611–619
- Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416(6879): 389–395
- Watkinson AR, Gill JA, Hulme M (2004) Flying in the face of climate change: a review of climate change, past, present and future. *Ibis Suppl* 1(146):4–10
- Zuberogoitia I, Martínez JA, Iraeta A, Azkona A, Castillo I (2004) Possible first record of double brooding in the tawny owl *Strix aluco*. *Ardeola* 51:437–439