

Inter-annual and inter-habitat variation in breeding performance of Blue Tits (*Cyanistes caeruleus*) in central Poland

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Studies at various locations in Europe show that nest-box populations of tits in urban areas lay earlier and produce fewer eggs than do birds in rural areas. Long-term data on laying date and clutch size were studied for Blue Tit (*Cyanistes caeruleus*) populations in two, structurally and floristically contrasting sites (an urban parkland and a rich deciduous forest, located only 10 km apart) in central Poland. The peak abundance of caterpillars, the optimal food of breeding tits, was also studied at both breeding areas. We focused on four environmental factors; year, site, insect availability and ambient temperature. Birds initiated breeding earlier in the urban area compared to the forest area and the laying date was highly correlated with air temperature during the period between 15 March and 15 April. At both study areas there was a similar negative temporal trend – birds started breeding earlier with later years. The number of eggs laid per breeding pair tended to be lower in the parkland than in the forest and it is likely that this is due to the habitat-specific pattern of food abundance and patchy environment in the parkland. This study provides new data on the reproductive biology of a model species and also fills up some knowledge gaps concerning inter-habitat and macro-geographic patterns.



1. Introduction

Timing of reproduction and clutch size are considered as the best studied avian breeding traits that are potentially influenced by a cocktail of factors (Murphy & Haukioja 1986, Perrins & McCleery 1989, Belda *et al.* 1998, Williams 2012). Main factors may be external abiotic (weather – ambient temperature, rain, solar activity and resource constraints like nesting sites), external biotic (parasitism, competition) or internal biotic (physiology, genetics). The external environment in which each bird operates is complex, with all the factors being combined in a network of relations. This network is not constant, but changes from year to year (Kluijver 1951).

Patterns in comparative productivity of urban and non-urban populations of tits show that urban birds usually lay earlier and produce lower clutch size than non-urban populations (Perrins 1965, Hōrak 1993, Solonen 2001, Chamberlain *et al.* 2009). Earlier laying dates in urban habitats may be caused by higher urban temperatures (Haggard 1990), tree species composition (Eeva *et al.* 2000) or improved adult condition over winter by human-provided food (Robb *et al.* 2008). Authors also state that lower clutch size in urban areas may be caused at least partially by the poor quality of food before the breeding season, that difference is caused by diversity in arthropod abundance during breeding season or high fragmentation of the urban environment (Riddington & Gosler 1995, Marciniak *et al.* 2007, Harrison *et al.* 2010).

There is a need to study urban and non-urban wildlife populations in order to understand the ecological implications of increasing urbanization and how to reduce its threats to biodiversity (Mörtberg & Wallentius 2000). Chamberlain *et al.* (2009) note that further comparative research between urban and non-urban populations of birds is to be welcomed. Moreover long-term studies (especially from Central and Eastern Europe) that illustrate the operation of a range of external factors in different habitats over a sufficiently long period of time are not very numerous. Many reports refer to usually 2–3 seasons of research and studies often lack any data on the abundance of caterpillars (the most important component of the diet of tits chicks) in the study areas.

This study provides additional data on the ur-

ban and non-urban reproductive biology of the Blue Tit as a model species and also fills up some gaps in the knowledge on inter-habitat and macrogeographic patterns. The main effort of our field study is focused on an analysis of a few environmental factors most often investigated in long-term studies of this model species – habitat type, year, insect availability and ambient temperature. We especially focus on variation in laying dates during 11 breeding seasons in two study sites (urban parkland and forest) and analyze an inter-site difference in clutch sizes in relation to food resources.

The main hypotheses were formulated as follows:

- 1) Urban and forest Blue Tits should differ in the date of initiation of breeding.
- 2) Laying dates should depend on ambient temperature.
- 3) Urban Blue Tits should produce fewer eggs (per breeding pair) than forest because of differences in caterpillar abundance.

2. Material and methods

This study was carried out during the breeding seasons of 1999–2012 as part of a long-term project of research into the breeding biology of hole-nesting birds occupying nestboxes in different habitats around the city of Łódź, central Poland. Study areas are located in two, 10 km apart, structurally and floristically contrasting types of habitats: an urban parkland and a rich deciduous forest. The parkland site (51°45'N; 19°24'E), c. 80 ha (including: the zoological garden of 16 ha and the botanical garden of 64 ha), has a highly fragmented tree cover (formed artificially) and is a major recreation and entertainment area in Łódź. The forest site (51°50'N; 19°29'E) is c. 130 ha area in the center of mature mixed deciduous forest (1,250 ha in total), bordering on the NE suburbia of Łódź. Oaks (*Quercus robur* and *Q. petraea*) are predominant tree species in the forest (Bańbura *et al.* 2013).

The study sites have been supplied with wooden nestboxes – the number of nestboxes as well as the forest study area generally increased over the study period (Table 1). Wooden nestboxes with removable front wall (Lambrechts *et al.* 2010) were used. The nestboxes in both areas

Table 1. The numbers of complete clutches of Blue Tits and available nestboxes (*N*) included in this study.

Year	Parkland	<i>N</i>	Forest	<i>N</i>
1999	25	99	–	0
2000	30	189	–	0
2001	31	189	–	0
2002	25	189	24	110
2003	17	178	35	197
2004	24	178	72	246
2005	30	178	68	246
2006	28	178	41	244
2007	27	178	50	241
2008	28	178	57	244
2009	27	182	28	246
2010	27	184	35	296
2011	33	187	8	296
2012	33	186	17	297
Sum	385	–	435	–

were shared by other species: Great Tits (*Parus major*), Pied Flycatchers (*Ficedula hypoleuca*) and Nuthatches (*Sitta europea*).

The abundance of caterpillars was monitored over the tit breeding seasons 2003–2012, using the frassfall collecting method. Frassfall was collected into tissue collectors, 1 m² on a metal framework, hanged below tree canopies, 5 in the parkland and 9 in the woodland. The collectors were checked and emptied every 5 days. In the laboratory, the samples from frassfall collectors were inspected under the microscope to separate caterpillar frass from other particles, then the frass particles were dried (24 hours in 60°C) and weighted to the nearest 0.1 mg. For each study site, the resulting masses and counts were calculated and are presented in this paper as mean values per trap per day (Marciniak *et al.* 2007).

The temperature data were extracted from TuTiempo.net climate data archive (<http://www.tutiempo.net/en/Climate/LODZ/124650.htm>) – we used the data from meteorological station located in Lodz (51°73'N; 19°04'E). Following Perrins & McCleery (1989), we used a pre-laying-early-laying warmth sum, as measured by the sum of the daily maximum temperatures during the period 15 March–15 April, as an indicator of thermal conditions and examined the influence of this indicator on the timing of breeding (Gładalski 2013, Gładalski *et al.* 2014).

During the breeding season, the nestboxes were visited at least once a week to record the nestbox occupancy, laying date, clutch size. Because second clutches are very rare in Blue Tits, the analysis includes only first clutches. A total of 734 complete first clutches were studied between 2002–2012 and these clutches were included to the between-site comparative analysis (Table 1; 820 first clutches overall between 1999–2012).

Comparative data for the two areas include materials from seasons 2002–2012, except the data used in correlation (mean laying date with warmth sum) that include materials from seasons 1999–2012 in the parkland site. Student's *t*-test for paired samples was used to show differences in caterpillar abundance between the two study sites, while the Mann–Whitney test was used to compare nestbox occupancy. We used linear mixed models (MIXED in SPSS 15.0, SPSS, 2006) assuming normal error structure and applying the identity link to compare mean laying dates and mean clutch sizes in relation to the habitat and year factors. In addition, we also analysed models with year as a quantitative variable rather than a factor to check laying dates and clutch sizes for temporal trends. The nestbox identity was included as a random factor controlling for a potential effect of the repeated use of particular nestboxes. The restricted maximum likelihood method was used to estimate effects and the Satterwaite method was applied to approximate degrees of freedom (West *et al.* 2007). Full models, including all considered factors and covariates, were simplified by removing non-significant interactions of the highest order (West *et al.* 2007). General linear models were used to compare sites with respect to patterns of relationships between per-year mean values of laying dates and warmth sums and between clutch sizes and caterpillar frassfall. Except linear mixed models and general linear models, all other graphical and statistical analyses were conducted applying STATISTICA 6 (StatSoft, Inc. 2003). Results are presented throughout as mean ± SD.

3. Results

Nestbox occupation rate by Blue Tits ranged from 9.6% to 17% in the urban parkland and from 2.7% to 29.3% in the forest during 2002–2012, with no

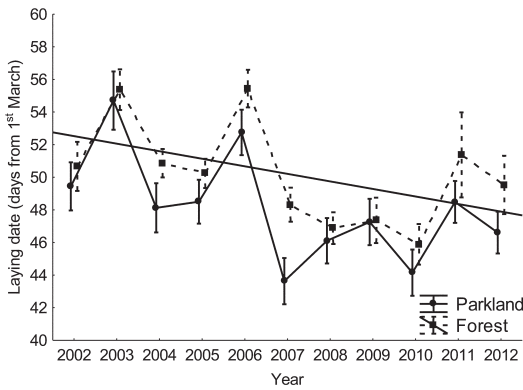


Fig. 1. Mean laying dates (1 = 1 March) in parkland and forest areas with trend line. Mean laying dates are presented as averages \pm 95% confidence intervals.

significant difference having been found (Mann–Whitney test: $U = 62.0$, $n_1 = 14$, $n_2 = 11$, $p = 0.43$) (Table 1). The mean laying date varied inter-annually by 11 days in the parkland, and by 9 days in the forest (Fig. 1). The laying date in the parkland was on average 2 days earlier than in the forest. The year, habitat and habitat–year interaction factors had significant effects on the average laying date (Table 2). When year was treated as a quantitative variable, a negative temporal trend was found over the study period (linear mixed model: $F_{1, 717.2} = 98.9$, $p < 0.001$, trend line is presented in Fig. 1).

Laying dates at both study sites were highly negatively correlated with the spring warmth sums

between 15 March and 15 April ($r = -0.69$, $n = 14$, $p = 0.007$ in the parkland and $r = -0.72$, $n = 11$, $p = 0.012$ in the forest, Fig. 2). A general linear model for per-year mean laying date in relation to the habitat (factor) and warmth sum (covariate) confirms the existence of a strong negative effect of spring thermal conditions on laying dates (warmth sum effect: $F_{1, 21} = 19.42$, $p < 0.001$), with the pattern being similar in both habitats (site effect: $F_{1, 21} = 0.23$, $p = 0.64$, site-warmth sum interaction: $F_{1, 21} = 0.004$, $p = 0.95$).

Controlling for laying date, clutch size tended to differ between the two areas; the overall mean clutch sizes were 10.91 ± 1.45 in the parkland and 11.41 ± 1.97 in the forest (Fig. 3), with other significant effects being year, habitat-year interaction and year-laying date interaction, while the habitat-laying date interaction was nonsignificant (Table 2). When year was input as a quantitative variable, no temporal trend was shown (linear mixed model: $F_{1, 720.1} = 0.69$, $p = 0.41$). The mean clutch size in the parkland showed a significant correlation with the mean clutch size in the forest site ($r = 0.71$, $n = 11$, $p = 0.015$).

The peak caterpillar abundance, as measured by the maximum amount of frassfall, averaged 0.18 ± 0.10 g frass / m² / day in the parkland area and 0.59 ± 0.55 g frass / m² / day in the forest area in 2003–2012. The peak amounts of frassfall differed significantly between the two sites (Student’s *t*-test for paired samples, $t_9 = -2.67$, $p = 0.026$). Caterpillars were more abundant in the fo-

Table 2. Linear mixed model tests for the effects of year and habitat on laying date, and the effects of year, habitat and laying date on clutch size (significant *p*-values in the model are in bold).

Response and effects	Num. df	Den. df	<i>F</i>	<i>p</i>
<i>Laying date</i>				
Intercept	1	324.11	78341.42	< 0.001
Year	10	643.50	44.38	< 0.001
Habitat	1	324.11	32.34	< 0.001
Year \times Habitat	10	643.50	2.28	< 0.05
<i>Clutch size</i>				
Intercept	1	676.41	280.53	< 0.001
Year	10	673.33	2.26	< 0.05
Habitat	1	676.41	3.74	0.054
Laying date	1	677.92	33.36	< 0.001
Year \times Habitat	10	673.33	2.21	< 0.05
Year \times Laying date	10	672.22	1.96	< 0.05
Habitat \times Laying date	1	677.92	2.17	0.141

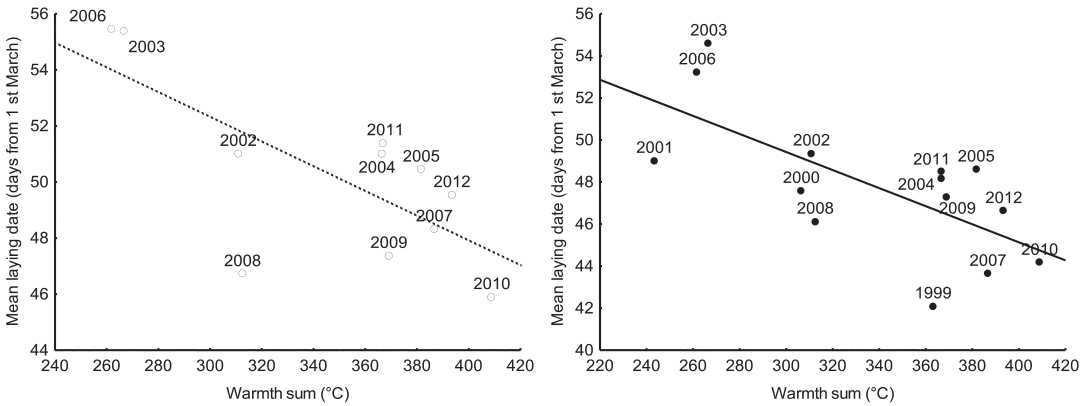


Fig. 2. Relationship between the sum of the daily maximum temperatures from 15 March to 15 April and the yearly mean laying dates for Blue Tits in the parkland area (filled circles, solid line) and in the forest area (open circles, dashed line) (seasons 2002–2012).

rest than in the parkland over the study period. Caterpillars were most abundant in 2003 in both areas (and additionally in 2004 in the forest). Mean annual clutch size showed a significant correlation with the mean caterpillar frassfall in the parkland area $r = 0.65, n = 10, p = 0.040$ and in the forest area $r = 0.73, n = 10, p = 0.017$ (Fig. 4), when 2003 was excluded, the correlation was non-significant ($r = 0.37, n = 9, p = 0.33$). A general linear model for per-year mean clutch size in relation to the habitat (factor) and caterpillar frassfall (covariate) showed a very strong site effect ($F_{1,16} = 491.25, p < 0.001$). There was no significant difference in the effect of frassfall on clutch size between the two sites (general linear model; frassfall and frassfall-

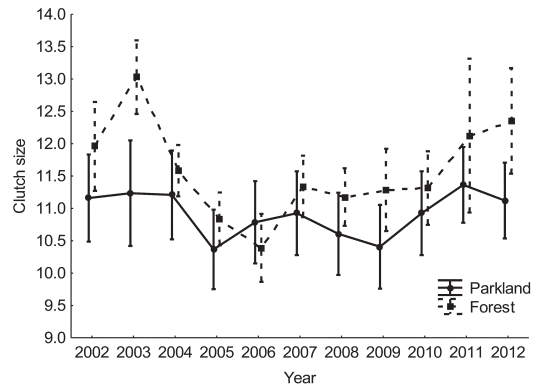


Fig. 3. Year-to-year variation in the mean clutch size in the parkland and in the forest areas. Mean clutch sizes \pm 95% confidence intervals are given.

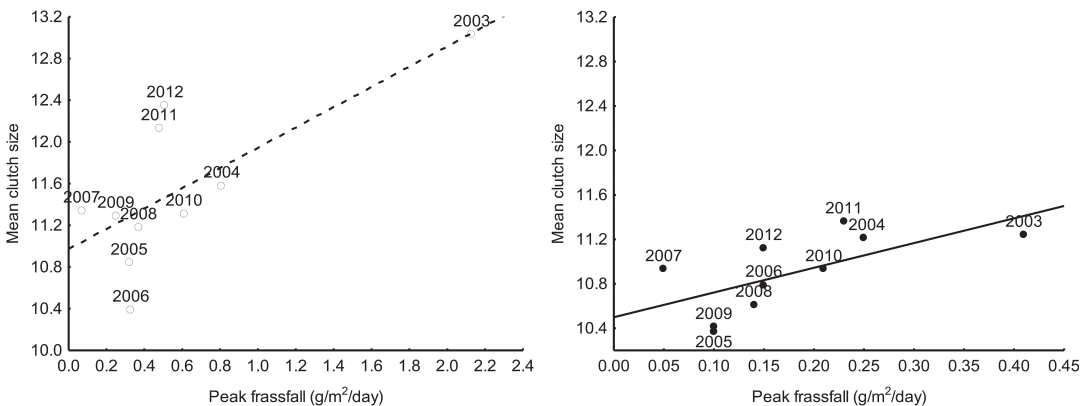


Fig. 4. Relationship between mean clutch size and the caterpillar abundance measured by the per-year peak amount of frassfall in the parkland area (filled circles, solid line) and in the forest area (open circles, dashed line) (seasons 2003–2012).

site interaction $F_{1,16} = 0.58$, $p = 0.46$ and $F_{1,16} = 0.02$, $p = 0.91$, respectively).

4. Discussion

The main hypotheses were confirmed. (1) Urban and forest Blue Tits differed in the date of initiation of breeding and birds in the parkland initiated breeding 2 days earlier than in the forest. (2) Laying dates depended on ambient temperature (crucial period between 15 March and 15 April). Additionally, at both study areas there was a roughly similar negative temporal trend – birds started breeding earlier in subsequent years. (3) Urban tits tended to produce fewer eggs (per breeding pair) than forest birds and mean annual clutch size showed a significant correlation with the mean caterpillar frassfall at both sites.

The earlier initiation of breeding by tits in urban areas compared to nearby forest areas has been found by many authors (Kluyver 1951, Lack 1958, Perrins 1965, Dhondt *et al.* 1984, Cowie & Hinsley 1987). The difference between our study sites is associated with a habitat contrast between an urban parkland (suboptimal habitat) and a rich mature deciduous forest (optimal habitat). Additionally, in urban habitats human-provided food may improve adult condition over winter, leading to earlier lay dates (Robb *et al.* 2008).

The timing of the breeding season is clearly correlated with the ambient temperature before the onset of laying (van Balen 1973, Perrins & McCleery 1989). Periods of time preceding laying taken into consideration vary among different authors and are often associated with latitude of an area where research is conducted (Sanz 1998, 2002, Fargallo 2004). In line with other Tit populations (van Balen 1973, Perrins & McCleery 1989, Bauer *et al.* 2010) in our study sites laying by Blue Tits starts significantly earlier in warmer springs, especially those with a warm spell between 15 March and 15 April and is delayed when cold weather prevails during this period. This supports the idea that local environmental factors trigger fine-tuning of laying date of physiologically activated females (Murton & Westwood 1977, Bañbura 1997, Williams 2012). Spring temperatures also influence the development of vegetation, which stimulates the growth of arthropod

populations, finally bringing about food abundance for insectivores (Fitter *et al.* 1995, Sparks *et al.* 2000, Chmielewski & Rotzer 2002).

Taxonomic composition of tree flora in the parkland results in earlier leafing. Buds and thus larvae on poplars and birches (in the parkland) appear earlier than on oaks (in the forest) (Nowakowska 2007). The leafing phenology of trees directly influences the occurrence of the most important component of the diet of chicks—caterpillars (Blondel *et al.* 1991, Bañbura *et al.* 1999).

There is good evidence from Europe and North America that many avian species nowadays migrate and breed earlier as a result of higher spring temperatures (Bauer *et al.* 2010, Chmielewski *et al.* 2013). Our results are in agreement with other authors in that matter, but only a little more than 10 years of present study should make us restrained. This is too short a period to draw any far-reaching conclusions considering long-term climate change.

We found that Blue Tit clutch size showed inter-annual and inter-habitat variation. The urban tits tended to produce fewer eggs (per breeding pair) than forest birds. Studies in different parts of Europe show that urban tits produce smaller clutches than birds breeding in forest habitats (Perrins 1965, Berressem *et al.* 1983, Cowie & Hinsley 1987, Hůrak 1993, Solonen 2001). In urban habitats paucity of natural food may lead to reduced clutch size and furthermore, over-winter provisioning and access to urban food leftovers may lead to a reduction in fecundity of parents and lower breeding success (Harrison *et al.* 2010).

Probably at least a part of the variation we found could be related to the difference in the observed abundance of food between both study sites. The study sites significantly differ in insect productivity, including caterpillar productivity, with the forest site being characterized by 2–5 times higher abundance of caterpillars than the parkland site, which is typical for similarly contrasted environments in different parts of Europe (Hinsley *et al.* 1999, Solonen 2001). The parkland area is consistently poorer in food than the forest habitat because its structure is less compact, more fragmented and, in addition, the lights surrounding gardens (street and house lights) lure insects out (Marciniak *et al.* 2007). The differences in frassfall in our study was similar to those reported for

urban and rural habitats by Solonen (2001). It is likely that variation in clutch size is the result of the difference in the abundance of caterpillars detected at the inter-annual level. For both our study areas clutches are on average larger in the caterpillar-rich years, in agreement with reports of other authors (Perrins & McCleery 1989, Verboven & Verhulst 1996). Yet the influence of caterpillar frassfall on clutch size at both study areas was present only when correlating mean clutch size with the caterpillar abundance. Additionally, mean annual clutch size showed a significant correlation with the mean caterpillar frassfall in the forest, but when 2003 (which clearly stands out) was excluded, the correlation was non-significant. In 2003 there was an outbreak of caterpillars and this abundance was conspicuous, especially in the forest site. This may suggest that birds may not predict the amount of food with very high accuracy in a given area, but respond well to some unknown correlates of extremely high caterpillar abundance. It may be a case that the number of seasons we included in this analysis is too small and further studies are needed. Thus, another important and underestimated factor influencing the clutch size may be patchy environment, which, among other effects, makes foraging more difficult (Riddington & Gosler 1995, Hinsley *et al.* 2006, Sandström *et al.* 2006). There could be also an additional factor explaining why clutch size shows a less adaptive response to environmental variation compared to lay date in the forest area, but so far it remains undetected.

Although strictly speaking, the analysed differences are between two particular sites, we think that they reflect differences between urban and non-urban habitats and our results are comparable to other similar studies. We found that the inter-annual pattern of variation in the timing of laying by Blue Tits in the deciduous forest and parkland habitats in our study areas is closely linked to air temperature during the pre-laying-early-laying period (between 15 March and 15 April) and the pattern of the influence of temperature on phenology was similar at both study areas. At both study areas there was a similar negative temporal trend – birds started breeding earlier with further years. Variation in caterpillar abundance contributes to inter-annual and inter-habitat differences in clutch size. Additionally patchy environment in the parkland

may affect clutch size. This paper provides additional long-term data on the reproductive biology of the urban and non-urban Blue Tits and complements some gaps in the knowledge on inter-habitat and macro-geographic patterns.

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Sinitiaisen pesimämenestyksen vaihtelu vuosien ja elinympäristöjen välillä Keski-Puolassa

Tutkimukset eri puolilla Eurooppaa osoittavat, että pöntöissä pesivät tiaiset munivat aiemmin ja tuottavat vähemmän munia kaupungeissa kuin maaseudulla. Sinitiaisen (*Cyanistes caeruleus*) muninnan ajoittumista ja munalukua tutkittiin pitkäaikaisaineistosta kahdella, rakenteeltaan ja kasvillisuudeltaan erilaisella alueella (kaupunkimainen puistoalue ja ravinteikas lehtimetsä, 10 km etäisyydellä toisistaan) Keski-Puolassa. Myös pesiville tiaisille tärkeän ravintolähteen, toukkien, huippuesiintymistä tutkittiin molemmilla alueilla.

Keskityimme neljään selittävään tekijään; vuoteen, alueeseen, hyönteisten määrään ja vallitsevaan lämpötilaan. Linnut aloittivat pesinnän aiemmin kaupungissa verrattuna metsään ja muninnan ajoitus oli voimakkaasti yhteydessä ilman lämpötilaan aikavälillä 15. maaliskuuta–15. huhtikuuta. Molemmilla tutkimusalueilla havaittiin samankaltainen ajallinen kehitys – linnut alkoivat pesiä aiemmin. Munaluku oli alhaisempi puistomaisella alueella kuin metsässä, mikä johtuu todennäköisesti elinympäristöjen eroista ravinnon saatavuudessa sekä siitä, että puistoalueella elinympäristö on laikuittaista. Tässä tutkimuksessa esitetään uutta aineistoa mallilajin lisääntymis-

biologiasta sekä uutta tietoa elinympäristöjen välistä ja suopean alueen maantieteellisestä vaihte-
lusta.

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