Long Breeding Season and High Frequency of Multiple Brooding in Great Tits in Northern Japan

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Long breeding season and high frequency of multiple brooding in Great Tits in northern Japan

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The Great Tit *Parus major* is one of the most intensively studied birds and such studies have contributed greatly to the current understanding of the evolution and ecology of natural populations. However, despite its wide geographic distribution and high variation in life history traits among regions, most ecological studies are concentrated in Europe, and there are relatively few studies elsewhere. We studied the breeding ecology of a Great Tit population in northern Japan and compared their breeding parameters to those described previously for European populations. This population was characterized by a long breeding season, up to four months from May to as late as the end of August (egg-laying to fledging), and a high frequency of multiple brooding (≥60%) including two occasions of third broods. In addition, clutch size was large with a mean of over ten, compared to less than eight in European populations at the equivalent latitude. The high productivity of the studied population may be a consequence of the high diversity and abundance of prey items in northern Japan associated with past and present climatic characteristics.

Key words: *Parus major minor*, latitudinal cline, clutch size, multiple breeding, breeding season length

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The Great Tit *Parus major* is one of the most intensively studied wild birds. A great number of evolutionary and ecological studies have been conducted on this species, which have contributed greatly to the current understanding of wildlife natural history (Gosler 1993, McCleery *et al.* 2004, Clutton-Brock & Sheldon 2010). The Great Tit is the most widely-distributed species in the Paridae family and ranges throughout Eurasia from northern Europe and northern Africa to Japan and southern Indonesia. Utilization of diverse habitats has resulted in considerable geographic variation in morphology, physiology, behaviour, life history, and genetics (e.g. Silverin *et al.* 1999, Sanz 1998, Kvist *et al.* 2003).

The species has traditionally been classified into four subspecies: *Parus major major*, *P. m. cinereus*, *P. m. minor*, and *P. m. bakharensis*, but the taxonomic status of these groups is still controversial. Although the Great Tit complex used to be considered as a typical ring species, given its continuous distribution (Kvist *et al.* 2003), recent molecular analyses, on the other hand, indicated discontinuous genetic divergence among these groups (Packert *et al.* 2005). Regardless of the taxonomic ambiguity, phylogenic monophyly and the occurrence of hybridization indicate that the Great Tit complex is on the way to, or has just completed, speciation. Therefore, studying inter- and intra-specific variation in biological characteristics might provide significant insights into speciation processes in the wild.

Geographic variation in the Great Tit is well known even within relatively small geographic scales (e.g. within Europe). For example, there is a latitudinal cline in clutch size, reproductive timing, and energy allocation (Sanz 1998, 2002, Sanz *et al.* 2000). Most ecological studies, however, have been concentrated in

Europe, the western end of its distribution, and very few have been done in the eastern end of the distribution (e.g. Far Eastern Asia, but see Seki & Takano 1998). Consequently, comparative studies of the ecologies of Great Tit populations across a broad geographic scale, such as between the east and west ends of the distribution, have not been conducted. Comparing large-scale latitudinal patterns would elucidate the factors, such as daylength, primary productivity, and climate, causing the well-known but not fully understood patterns (Sanz 1999, Fargallo 2004, Cooper *et al.* 2005).

In the present study, we studied the breeding ecology of a Great Tit population in northern Japan (*P. major minor* or *P. minor*) and compared it with that of European populations, to examine large-scale geographic variation in life history traits. Compared to European populations, the breeding seasons were extremely long, and clutch size and frequency of multiple broods were also large. In addition, we found two occasions of third broods, which previously have rarely been reported. We discuss the potential reasons for the high productivity of this northern Japanese Great Tit population.

Methods

We studied a nestbox breeding population in Tomakomai Experimental Forest (TOEF; 42°40' N, 141°36' E, 200~300m a.s.l.) on the island of Hokkaido, Japan. Latitude in the study area is equivalent to Rome, Italy. The mean annual temperature is 6.4°C (similar to Oslo, Norway), and annual precipitation is *c.* 1450 mm (more than twice the annual average of London, UK). This forest belongs to the cool temperate forest zone and is a secondary mixed forest with approximately 100 tree species, dominated by oaks (*Quercus crispula*), maples (*Acer* spp.), and some plantations of conifers such as larches (*Larix kaempferi*) (Hiura 2001). Leaf flush of *Quercus crispula* and most other trees occur in mid-May, and leaves are shed in late October (Kitaoka & Koike 2005).

A total of 300 nestboxes were hung up regularly 50 m apart within TOEF. During the Great Tit breeding season in 2009 and 2010, each nestbox was visited about once per week and the following variables were recorded: date of egg-laying, clutch size, number of young fledged, and the number of breeding attempts. First egg-laying date (laying date) was calculated assuming one egg was laid per day. Clutch size was recorded by checking the nest once during incubation. Fledging success was calculated as the number of fledglings per number of eggs laid for each breeding attempt. Parents were caught and ringed for individual identification during chick rearing to confirm multiple breeding attempts. Second (or third) clutches were defined as clutches where at least one chick fledged from the first (or second) broods (Verboven *et al.* 2001; Husby *et al.* 2009). We compared the breeding parameters of studied Great Tits to European populations using the data described in Sanz (2002).

Results and discussion

Reproductive parameters of the studied Great Tit population differed considerably from those in Europe. First, this population started breeding very late. Mean laying dates of first clutches were May 16th and 20th in 2009 and 2010, respectively (Table 1). These dates corresponded to the leaf flush of the dominant trees such as *Quercus crispula*, *Magnolia obovata*, and *Carpinus cordata* (Kitaoka & Koike 2005). Mean laying date of the population was three weeks later than comparative populations in Europe at the same latitude (Sanz 1998, 2002) (Figure 1). Surprisingly, however, despite the late start of breeding, this population had an exceptionally long breeding season with a high frequency of multiple brooding. The fledging date of the last nest of

Table 1. The laying date and clutch size of 1st, 2nd and 3rd clutches of the studied Great Tit population. Laying date was calculated taking 1 April as day 1.The mean values are given ± SD.

		2009			2010		
	Clutch order	*n*	Mean	Range	*n*	Mean	Range
Laying date	First	25	46.0±6.2	36–59	34	49.8±5.6	39–61
	Second	14	92.4±9.0	80–107	20	91.5±8.0	80–112
	Third	1	120	-	1	120	-
Clutch size	First	25	10.0±1.0	8–12	34	10.4±1.1	7–12
	Second	14	8.6±1.0	7–10	20	8.4±1.0	7–10
	Third	1	8	-	1	6	-

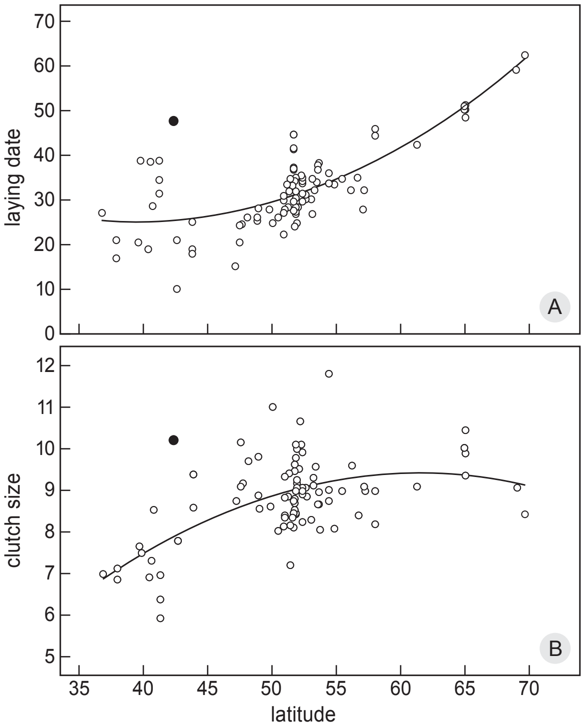

Figure 1. Relationship between mean egg-laying date (A), clutch size (B) and latitude (°N) of the western Palearctic Great Tit populations (open circles: data are extracted from Sanz 2002) and Japanese Great Tits in TOEF (closed circles). Laying date was calculated taking 1 April as day 1.

the season was the end of August or even the beginning of September (Table 1).

The Great Tit is a facultative multiple breeder with great variation in the rate of multiple brooding among populations and seasons (Verboven *et al.* 2001, Husby *et al.* 2009). In the present study, about two thirds of females bred more than once in a season, i.e. 63.2% (12/19) in 2009 and 70.8% (17/24) in 2010. Success or failure of earlier attempts did not affect these rates; including replacement clutches after abandoned and predated attempts, multiple brooding rates were 62.5% (15/24) in 2009 and 69.7% (23/33) in 2010. These rates of multiple brooding may even be underestimated, since after the first brood birds might move out of the study area to breed again, considering that a few breeding pairs each year moved into the study plots and bred during the later breeding period (T. Yuta, unpubl. data). In addition, there were six occasions where pairs attempted third broods, which have previously rarely been reported. One pair successfully fledged all chicks in all three broods, resulting in 25 fledglings in one breeding season (nine, eight, and eight fledglings for each brood). Another pair also fledged offspring in all three attempts, but the number of fledglings was much smaller due to predation (one, two, and four fledglings for each brood). The remaining four of the six pairs attempted the third broods after failure of the earlier two broods during nestling phases (i.e. replacement clutch). The high frequency of multiple brooding is especially interesting considering the late laying date of this population, since the probability of laying a second clutch is strongly dependent on the laying date of the first clutch in European populations (Verboven & Verhulst 1996).

The clutch size of the population was large compared to other Great Tit populations. Mean clutch size of the population for first clutches was 10.0 and 10.4 in 2009 and 2010, respectively (Table 1). The mean clutch size of second broods was smaller (8.6 and 8.4 for 2009 and 2010). These are among the largest clutch sizes for the Great Tit in the western edges of the distribution (i.e. the fifth highest in 92 populations reviewed in Sanz 1998, 2002). Expected clutch size in the European populations at the same latitude is below eight (Figure 1).

The fledging success of the population was relatively high, although a trade-off between offspring number and survival was expected (Smith *et al.* 1989). The rate of fledging success depended almost entirely on predation by Jungle Crow *Corvus macrorhyncus*. Out of 109 nests in the two-year study, 38 nests were predated, and there were eight nests which parents abandoned after laying for unknown reasons. It is difficult to estimate fledging success, since most predations occurred when nestlings were fully grown, and therefore, a few might have successfully fledged as predation occurred (Lima 2009). If we assumed all the fledglings were predated (i.e. the most conservative estimate), overall fledging success (number of fledglings over eggs laid) was 57.9% (589/1018). If we excluded the predation and cases where parents abandoned after laying, fledging success was markedly high (91.1% in two years; average 9.5 fledglings for the 1st broods). There was only one occasion (0.14%) in the two-year study where a growing chick was found dead with the cause presumed to be starvation.

Although we studied only two breeding seasons, we believe that the data represent the population's breeding parameters. The spring temperatures, known to affect the breeding season of the Great Tit (McCleery & Perrins 1998), were within the normal range. Also, there was no special climatic phenomenon or outbreak of potential food resource during the two studied years. The breeding densities of this population may be considered to be a little low (*c.* 0.33–0.45 pairs per ha) compared to other studies of Great Tits (e.g. 0.63–1.29 pairs per ha, Minot & Perrins 1986). Although clutch size is often negatively correlated with density (Both *et al.* 2000), we suppose that a small increase in density would not significantly change the breeding parameters. Nevertheless, long-term monitoring certainly deserves further attention.

In short, breeding season length, multiple brooding rate, clutch size, and fledging success rate all led to exceptionally high productivity of this Great Tit population which is also notable even among the *Parus major* minor group (Yahagi 1996; Seki & Takano 1998). This characteristic may be explained by the great diversity and abundance of food resources for the studied population. Geographic distributions of species and biodiversity are greatly influenced by the fluctuating global climate in the Quaternary period (Hewitt 2000, Taberlet & Cheddadi 2002). Although the studied region belongs to the cool temperate zone, and the current annual temperature is comparable to latitude 60–70° N in Europe, the area was not covered by glaciers during the last ice age as in Europe. This may have led to the current great biodiversity of plants and arthropods in this region (Qian & Ricklefs 2000, Harrison *et al.* 2001).

The great diversity and abundance of food resources might also be caused by the monsoonal climate. The rainy and much overcast weather in summer may extend the plant growth period and consequently the abundance of lepidopteran insects. In fact, a study of macrolepidopteran larvae on oak trees, the dominant trees in the studied forest showed rich food resources for the tits over a long period (Yoshida 1985); the number of individuals and species rapidly increased from May and reached a peak in early June, and after a decrease, it again increased and reached another peak in early August followed by a slow decrease through September. These two peaks of macrolepidopteran abundance corresponded to the peak demand of first and second brood nestlings.

Studies of geographic variation in the Great Tit are numerous but restricted around Europe. The Great Tit is also a common and widely distributed species in Asia. Therefore, close monitoring of populations like the present study would make it possible to study geographic variation within the *Parus major minor* group comparative to the European studies. For example, latitudinal variation in clutch size has been related to differences in daylength (Yom-Tov & Hilborn 1981, Sanz 1999). This study, however, showed much larger clutch sizes than European populations experiencing the same daylength and suggested that food abundance and diversity are important. Currently, an interdisciplinary project has been trying to unravel the genetic bases of life history traits in wild Great Tit populations as a model organism (Santure *et al.* 2011). The key to elucidating genetic components of quantitative traits is interbreeding and common-garden experiments for populations with different life history characteristics (Slate 2005). Therefore, ecological studies of the Great Tit complex across the range would further improve our understanding of the speciation process.

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Samenvatting

De Koolmees *Parus major* is een van de meest onderzochte vogelsoorten ter wereld. De soort heeft een groot verspreidingsgebied (Europa tot ver in Azië), waarbinnen vier ondersoorten worden onderscheiden. Ondanks de variatie in life-history kenmerken binnen dit verspreidingsgebied zijn de meeste studies verricht aan Europese populaties. Dit artikel beschrijft de broedecologie van Koolmezen in een populatie in Noord-Japan. Het broedseizoen van de onderzochte populatie duurde van mei tot eind augustus. De onderzoekers vonden een hoog percentage aan tweede legsels en zelfs twee derde legsels. De gemiddelde legselgrootte was hoog vergeleken met de legselgrootte op dezelfde geografische breedtegraad in Europa. De hoge productiviteit zou kunnen samenhangen met een hoge diversiteit en talrijkheid aan prooidieren in het noorden van Japan, samenhangend met het klimaat in verleden en heden. (KvO)

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