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EFFECTS OF GEOGRAPHIC LOCATION AND HABITAT ON BREEDING PARAMETERS OF GREAT TITS

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ABSTRACT.—I studied variation in laying date, clutch size, and number of fledglings in Great Tits (*Parus major*) in relation to habitat, elevation, and latitude using data from 137 breeding areas. Laying date was not affected by habitat type but increased with elevation and showed a significant quadratic relationship with latitude. Food availability, ambient temperature, and photoperiod together can explain why laying date increases with latitude. However, more information is needed to understand why birds in northern Africa start laying later than in nearby southwestern Europe. Variation in clutch size and number of fledglings was significantly affected by habitat type, with lower values in coniferous forests. Mean clutch size decreased with elevation. Mean clutch size and mean number of fledglings of first and second broods showed a significant quadratic relationship with latitude, with the highest values at about 55 to 60°N. The results suggest that latitudinal variation in life-history parameters is related to variation across marginal and central parts of the species' distribution and is influenced by factors such as daylength, temperature, and/or seasonality of food resources. Birds at southern latitudes are probably under time constraints, whereas birds at northern latitudes are probably under energy constraints. Alternatively, Great Tits at northern latitudes might be less well adapted to these habitats because they invaded northerly latitudes during the last decades. The proportion of pairs laying a second clutch decreased with latitude. The observed pattern of a late start of laying, lower variability in laying date, and lower frequency of second clutches in northern populations likely was due to the late and short growing season for the Great Tit's main prey, caterpillars. *Received 13 January 1997, accepted 22 April 1998.*

THE GEOGRAPHIC TRENDS in reproductive parameters of birds have been well known for decades (Lack 1947, Klomp 1970). The ultimate regulator of the timing of breeding is the requirement that reproduction take place during the season in which birds can raise their young most efficiently (Lack 1950, Drent and Daan 1980, Martin 1987). The availability of food for laying females has been considered to be both an ultimate factor (Lack 1950, Perrins and McCleery 1989, Daan et al. 1990) and a proximate factor (Perrins 1970, Källander 1974, Drent and Daan 1980, Martin 1987) in the timing of the onset of laying. However, factors such as habitat type (Klomp 1970, Blondel et al. 1993), temperature (Svensson and Nilsson 1995), and photoperiod (Meijer 1989; Silverin 1995; Lambrechts et al. 1996, 1997) also may influence the onset of breeding. In areas at high latitudes and elevations, which have progressively cooler climates, the onset of breeding is expected to be delayed owing to low temperatures and slow development of the vegetation (Lack 1950, Slagsvold 1976, Orell and Ojanen 1983a).

The evolution of clutch size is one of the most actively studied of life-history traits in birds (Stearns 1992). Clutch size is constrained by several factors, the most commonly discussed being latitude and habitat (Klomp 1970, Perrins and Birkhead 1983, Murphy and Haukioja 1987). For example, within temperate regions clutches of passerines are larger in deciduous woodlands than in coniferous forests (Klomp 1970, van Balen 1973, Zang 1980, Blondel et al. 1987, Sanz 1995). The trend for clutch size of passerines to increase with latitude is one of the most striking patterns within and among species of birds (Perrins and Birkhead 1983). Clutch size of passerines tends to be two or three eggs in tropical latitudes (Moreau 1944, Skutch 1985), four or five eggs in middle latitudes, and five to seven eggs in arctic latitudes (Ricklefs 1969). This trend occurs in both the Old World (Lack 1968) and the New World

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(Cody 1971) in the Northern Hemisphere, whereas the trend in the Southern Hemisphere is weak (Moreau 1944, Yom-Tov 1987, Yom-Tov et al. 1994, Martin 1996).

Three main hypotheses have been presented to explain the latitudinal trend in clutch size in passerines. First, Lack (1947) suggested that the increase in clutch size with latitude could be attributed to the increase in daylight hours available for parents to collect food for their nestlings. Royama (1969) extended Lack's hypothesis to incorporate the energy requirements of the young relative to ambient temperature and the time available for foraging. Owen (1979) accepted Lack's daylength hypothesis as a partial explanation and introduced the diversity of potential food as an additional factor. Lack's (1947) hypothesis has been reformulated in a life-history context to encompass reproductive costs in terms of adult survival and/or future reproduction involved in raising a certain number of young (Charnov and Krebs 1974), and with a focus on individual differences in quality (Drent and Daan 1980, Pettifor et al. 1988, Slagsvold and Lifjeld 1990).

Second, Ashmole (1961) suggested that bird populations in temperate areas are regulated in the nonbreeding season by food resources. The breeding density thus tends to be low in northern latitudes, and competition for food in spring and summer is relaxed. Reduced competition favors large clutches (Ashmole 1961, Ricklefs 1980, Koenig 1984). Studies typically relate clutch size to differences between winter and summer evapotranspiration (AE), a measure that is tightly correlated with primary productivity (Rosenzweig 1968) and, presumably, with food availability. Correlations between clutch size and seasonality of AE have been found in some studies (Ricklefs 1980; Koenig 1984, 1986) but not in others (Møller 1984, Dunn and MacInnes 1987, Young 1994). It may be questioned whether so crude an estimate of resource levels can justify rejection or acceptance of this hypothesis (Møller 1984).

Third, Skutch (1949) invoked predation as a possible factor in the evolution of clutch size. The classic interpretation has been that reduced nest predation favors larger clutches (Skutch 1949, Cody 1966, Perrins 1977, Slagsvold 1982, Ekman and Askenmo 1986, Lima 1987, Kulesza 1990, Martin 1992) by allowing more young to be fed over a longer nestling period or more energy to be invested in a single nesting attempt rather than in several attempts (Slagsvold 1982). The degree of nest predation seems to decrease with increasing latitude (Ricklefs 1969, Jehl 1971, Pedroli 1978, Kulesza 1990; but see Martin 1996).

The preceding hypotheses predict a positive relationship between clutch size and latitude, but this trend may not be linear. A linear increase in clutch size with latitude has been found in many studies (e.g. Lack 1947, Ashmole 1961, Cody 1966, Slagsvold 1975a, Kulesza 1990, Young 1994), but exceptions are not rare (e.g. Owen 1979, Orell and Ojanen 1983b, Møller 1984, Isenmann 1987, Soler and Soler 1992, Sanz 1997). Ecological factors can influence to a different degree the breeding decisions at different latitudes. At low latitudes, predation or the availability of daylight can be the most important factors (Sanz 1999), whereas at high latitudes, variability or unpredictability of food and weather may be more important (Järvinen 1983). Northern breeding populations of passerines are more unstable, and their environment is more unpredictable, than are southern populations (O. Järvinen 1979, Slagsvold 1981, A. Järvinen 1983). Stability is defined as year-to-year persistence of community structure (i.e. total density, number of species, diversity and frequencies of species; Järvinen 1979). Järvinen (1979) showed that population stability of birds is greatest in the areas of maximum density (usually in the southern or central parts of the range). At high latitudes, birds under severe climatic conditions are probably near their ecological limit in terms of acquiring enough energy for maintenance and reproduction (Järvinen 1983). Moreover, for some passerines clutch size tends to be lower in marginal habitats than in nearby optimal habitats (Klomp 1970, van Balen 1973, Källander 1975, Alatalo et al. 1985, Sanz 1995). Peripheral and central parts of the geographic ranges of species are associated with marginal and optimal habitats, respectively (Slagsvold 1981). The existence of a distributional limit may reflect that the conditions for reproduction are poor and larger clutches cannot be selected for (Slagsvold 1981). Therefore, a nonlinear relationship of clutch size or brood size with latitude may exist, with the maximum values occurring in the central parts of the distribution (Sanz 1997, 1999).

The Great Tit (*Parus major*) is one of the most well-studied bird species. Great Tits breed from about 10°S to 71°N (Gosler 1993), and they are resident even at the northern limit of their breeding distribution (Cramp and Perrins 1993, Silverin 1995). In a pioneering study, Lack (1950) showed that clutch size increases with latitude for different races of Great Tits breeding in Asia. He suggested that clutch size is smaller in the Mediterranean region than farther north, although data from this region were limited at the time. Breeding Great Tits have been studied in many parts of Europe, and the resulting data have been subjected to geographic comparisons (Berndt et al. 1983, Orell and Ojanen 1983b). However, these studies disagreed about clutch-size variation over the geographical range. A tendency for clutch size to increase northward in Europe (Berndt et al. 1983) or an unclear pattern with respect to latitude were claimed (Orell and Ojanen 1983b). These different conclusions possibly resulted from the relatively small number of studies considered in both reviews ($n = 28$ in Berndt et al. 1983; $n = 27$ in Orell and Ojanen 1983b) and from the narrow latitudinal range studied (50 to 55°N in Berndt et al. 1983). Because of the large number of studies published on the Great Tit near the peripheral parts of its range in the Palearctic (Gosler 1993), it is now possible to analyze variation in reproductive parameters using a large data set ($n = 137$ areas) from an extensive geographic range (33 to 70°N).

My review is based on breeding data collected from a variety of studies that were conducted using wooden nest boxes in which rates of predation and partial losses of nestlings often are lower than in natural cavities (Nilsson 1984, 1986). Nest-box studies are designed to reduce levels of predation, and this may have obscured important selective pressures on the life-history strategies of the birds (Lindén and Møller 1989). The presence of nest boxes alleviates the typically severe shortage of nesting sites, and in the absence of this limitation, reproduction may occur at a maximum rate (Lindén and Møller 1989). Rates of predation at nest boxes and the density of predators are rarely reported. Therefore, the effect of predation rate on latitudinal variation in breeding parameters cannot be tested with published data. My review will thus unavoidably give a partial view of the factors affecting the evolution of breeding time and clutch size in Great Tits.

The aims of my study are to: (1) document latitudinal variation in laying date, clutch size, number of fledglings, and proportion of second clutches in the Great Tit using a large data set collected over an extensive geographic range; (2) determine whether a linear or nonlinear relationship exists between clutch size and latitude; (3) determine whether the inclusion of habitat type and elevation affect latitudinal trends; and (4) discuss these results relative to the hypotheses that attempt to explain geographic trends in these breeding parameters.

METHODS

I obtained from the literature the mean, standard deviation, and coefficient of variation of laying date, clutch size, and number of fledglings (in some cases, the number of nestlings in the nest two or three days before fledging) at different breeding sites. These studies included only broods in which at least one young fledged. Therefore, the estimates of reproductive success presented are overestimates and do not correspond exactly to the natural average reproductive success of the populations. Clutches were separated into two categories: first and second broods (clutch laid following a successful one). Data were available for 137 study areas (see Appendices 1 and 2). No effect of nest-box size on mean clutch size or laying date was assumed. If data for several years were available, I included the mean values for each area in the analyses. In addition, I used my own data from two breeding populations in Lauwersmeer, The Netherlands (see Sanz et al. 1998) and Valsaín, Spain (see Sanz 1995).

For all areas, the coordinates (latitude and longitude in decimal degrees) and elevation were determined. In some study areas, I obtained the geographic variables from topographic maps. Additional variables included in the analyses were number of study years, number of nests per study area, and main habitat type. Data from urban habitats were not included in the analyses. The habitat types were coniferous forest ($n = 42$), mixed coniferous/deciduous ($n = 31$), and deciduous forests ($n = 53$). The southernmost study area was in northern Africa (33°30′N; Chabi 1998), and the northernmost was in northern Finland (69°42′N; Veistola et al. 1995). Elevations ranged from 5 to 1,600 m. The mean number of study years was 7.1, with a range of 1 to 25 years (in eight study areas, the number of years was not reported precisely but was always more than one). The mean number of clutches per study area was 178, with a range of 4 to 2,346.

The distributions of mean clutch size, number of

TABLE 1. Laying date (1 = 1 April), clutch size, and number of fledglings of first clutches of Great Tits with respect to habitat type. Values are $\bar{x}$ ± SD, with n in parentheses.

	Habitat type		
Variable	Coniferous	Mixed	Deciduous
Laying date	31.53 ± 10.98 (30)	31.72 ± 8.48 (23)	29.78 ± 9.96 (36)
Clutch size	8.74 ± 0.78 (40)	8.88 ± 0.91 (31)	9.15 ± 0.82 (52)
No. of fledglings	6.00 ± 1.38 (23)	6.37 ± 1.04 (5)	7.09 ± 1.44 (23)

fledglings, and laying date of first and second broods did not differ from normal (Kolmogorov-Smirnov test, $P > 0.05$). Elevation was normalized using logarithmic transformation. I used analysis of covariance (ANCOVA) with habitat as a factor and latitude and elevation as covariates to separate the relative importance of these variables to Great Tit breeding parameters. Latitude and longitude for each breeding population were positively correlated ($r = 0.50$, df = 137, $P < 0.001$), and I included only latitude in the analyses because the distribution of Great Tits shows a southwest to northeast trend. I included latitude squared as a covariate when it significantly increased the explained variance. When one covariate did not show a significant effect on the dependent variable, I excluded it from the analysis. As a post-hoc comparison of means, I used the Tukey test for unequal sample sizes (Spjøtvoll and Stoline 1973). Values are presented as means ± SD.

RESULTS

First clutches.—No relationships were found (multiple linear regression) between either the number of study years or number of clutches used in the analysis and mean laying date ($F = 2.50$, df = 2 and 71, $P = 0.09$), mean clutch size ($F = 2.12$, df = 2 and 101, $P = 0.12$), or mean number of fledglings ($F = 2.34$, df = 2 and 34, $P = 0.06$) per study area.

The mean laying date for all areas was 1 May ± SD of 9.98 days ($n = 97$). Mean laying date did not differ between habitats (Table 1) when the effects of latitude and elevation were controlled (ANCOVA; model, $F = 34.24$, df = 5 and 83, $P < 0.001$; factor habitat, $F = 1.23$, df = 2 and 83, $P = 0.30$; covariate latitude, $F = 16.53$, df = 1 and 83, $P < 0.001$; covariate latitude squared, $F = 30.43$, df = 1 and 83, $P < 0.001$; covariate elevation, $F = 7.90$, df = 1 and 83, $P = 0.006$). The mean laying date showed a significant quadratic relationship with latitude (Fig. 1) and increased significantly with elevation ($\beta = 0.19$, $t = 2.81$, df = 83, $P = 0.006$) after controlling for the other variables. Latitudinal variation in laying date was explained better by a quadratic model (63.2%) than by a linear model (54.6%). Including elevation into the model, 65.1% of the variance in laying date along the latitudinal cline was explained by these variables. The variability in mean laying date (coefficient of variation) declined with latitude ($r = -0.68$, df = 43, $P < 0.001$).

Mean clutch size in all areas was 9.01 ± 0.89 eggs ($n = 130$). The habitat type of the study area had a significant effect on mean clutch size (Table 1) when the effects of latitude and elevation were controlled (ANCOVA; model, $F = 10.76$, df = 5 and 117, $P < 0.001$; factor habitat, $F = 4.16$, df = 2 and 117, $P = 0.018$; covariate latitude, $F = 6.78$, df = 1 and 117, $P = 0.010$; covariate latitude squared, $F = 4.46$, df = 1 and 117, $P = 0.037$; covariate elevation, $F = 5.68$, df = 1 and 117, $P = 0.019$). Clutch sizes were significantly larger in deciduous forests than in coniferous forests (Tukey test, $P = 0.03$; Table 1). Mean clutch size showed a significant quadratic relationship with latitude (Fig. 1) and decreased significantly with elevation ($\beta = -0.21$, $t = 2.38$, df = 117, $P = 0.019$) after controlling for the other variables. Latitudinal variation in clutch size was explained better by a quadratic model (22.7%) than by a linear model (18.5%). Including elevation and habitat into the model, 30.5% of the variance in clutch size along the latitudinal cline was explained by these variables. The variability in clutch size (coefficient of variation) did not show any trend with latitude ($r = 0.04$, df = 50, $P = 0.77$).

The mean number of fledglings in all areas was 6.61 ± 1.57 young ($n = 52$). The habitat type of the study area had a significant effect on the mean number of fledglings (Table 1) when the effect of latitude was controlled (ANCOVA; model, $F = 6.34$, df = 4 and 46, $P < 0.001$; factor habitat, $F = 4.06$, df = 2 and 46, $P = 0.024$; covariate latitude, $F = 6.26$, df = 1 and 46, $P = 0.016$; covariate latitude squared, $F = 4.87$, df = 1 and 46, $P = 0.032$). Significantly more nestlings were fledged in deciduous for-

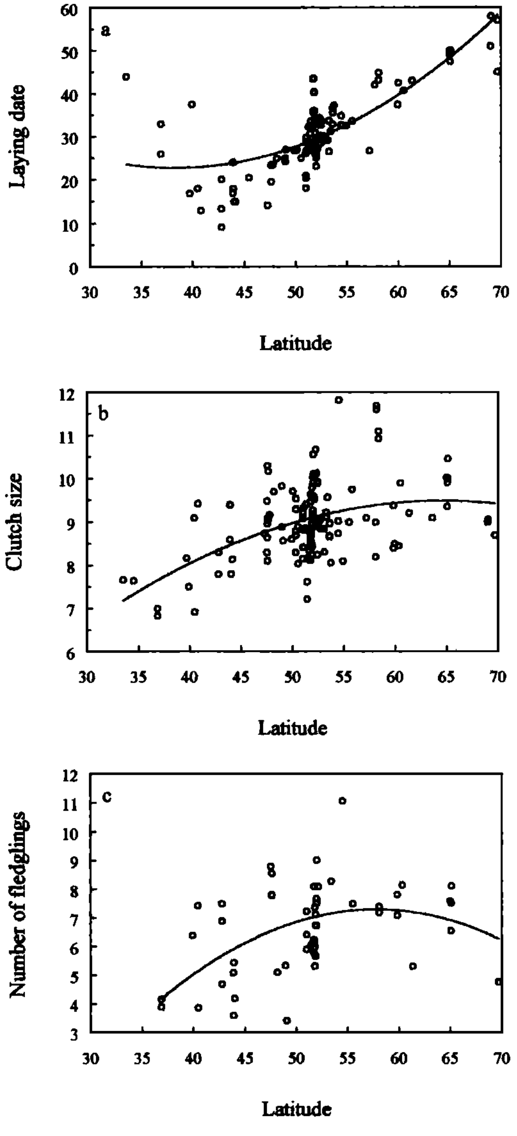

FIG. 1. Relationships between: (upper panel) mean laying date (1 = 1 April); (middle panel) mean clutch size; and (lower panel) mean number of fledglings of first clutches and latitude (°N). Relative to laying date: $Y = 75.69 - 2.76X + 0.04X^2$ ($F = 82.73$, df = 1 and 94, $P < 0.001$). Relative to clutch size: $Y = -0.54 + 0.31X - 0.002X^2$ ($F = 18.60$, df = 2 and 127, $P < 0.001$). Relative to number of fledglings: $Y = -17.00 + 0.84X - 0.007X^2$ ($F = 8.14$, df = 2 and 49, $P < 0.001$).

ests than in coniferous forests (Tukey test, $P = 0.01$; Table 1). The mean number of fledglings showed a significant quadratic relationship with latitude (Fig. 1) but did not show any relationship with elevation ($\beta = 0.02$, $t = 0.13$, df = 45, $P = 0.90$). Latitudinal variation in number of fledglings was explained better by a quadratic model (24.9%) than by a linear model (13.0%). Including habitat in the model, 36.0% of the variance in number of fledglings along the latitudinal cline was explained by these variables. The mean number of fledglings and the mean clutch size of each study population were positively correlated when the effect of latitude was controlled (partial $r = 0.48$, df = 47, $P < 0.001$).

Second clutches.—The mean proportion of second clutches decreased significantly with latitude (Fig. 2). The mean clutch sizes of first and second broods of each study population were positively correlated when the effect of latitude was controlled (partial $r = 0.44$, df = 34, $P = 0.01$). Mean clutch size showed a significant quadratic relationship with latitude (Fig. 2), as did the mean number of fledglings from second clutches (Fig. 2).

DISCUSSION

Laying date.—The mean laying date of Great Tits typically differs among habitats (van Balen 1973, Zang 1980, Blondel et al. 1987, Sanz 1995). In the present study, mean laying date did not differ among habitats after I controlled for elevational and latitudinal variation. Mean laying date was affected by elevation when the effects of habitat and geographic variation were controlled. Great Tits bred earlier at lower elevations, presumably because conditions (food availability, weather) were favorable earlier at lower elevations (Zang 1980, Sanz 1995).

Mean laying date increased significantly with latitude when the effects of habitat and elevation were controlled. The mean laying date occurs in April in southwestern and central Europe and in May in northern Europe. However, in northern Africa birds start to breed later than in nearby southwestern Europe. This quadratic relationship between mean laying date and latitude has also been found in Pied Flycatchers (*Ficedula hypoleuca*; Sanz 1997). Food availability for the young has been suggested as the ultimate factor determining the onset of breeding (Lack 1950, Drent and Daan 1980, Perrins and McCleery 1989, Daan et al. 1990). The timing of the peak date of caterpillars is a major selection pressure on the timing of

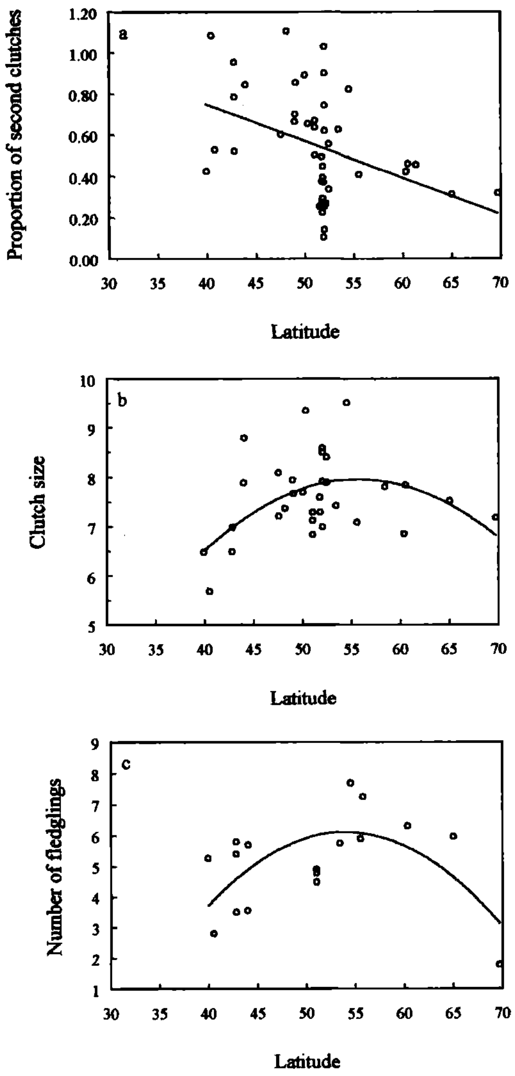

FIG. 2. Relationships between: (upper panel) proportion of second clutches (arcsine transformed); (middle panel) mean clutch size; and (lower panel) number of fledglings of second clutches and latitude (°N). Relative to proportion of second clutches: $Y = 1.46 - 0.02X$ ($F = 8.28$, df $= 1$ and 43, $P = 0.006$). Relative to clutch size: $Y = -10.10 + 0.65X - 0.006X^2$ ($F = 5.52$, df $= 2$ and 31, $P = 0.009$). Relative to number of fledglings: $Y = -29.10 + 1.30X - 0.012X^2$ ($F = 4.67$, df $= 2$ and 14, $P = 0.028$).

breeding in tits (Blondel et al. 1993). Presumably, parents must have mechanisms to anticipate the most favorable period for raising their young (Perrins 1970). The onset of breeding is therefore influenced by a variety of proximate factors. The amount of food available for egg-laying females has been postulated as an important factor (Perrins 1970, von Haartman 1971, Drent and Daan 1980). When experimentally provided with extra food, tits (*Parus* spp.) advance the timing of the egg laying by two to eight days (see Svensson and Nilsson 1995, Nager et al. 1997). Therefore, above a certain critical level of food availability, laying females probably use other cues in their decision to start breeding (Svenson and Nilsson 1995).

Ambient temperature has been suggested to influence laying date along an elevational or latitudinal cline. As pointed out by many authors (e.g. Kluijver 1951; Perrins 1965, 1991; van Balen 1973; van Noordwijk et al. 1995), the onset of laying is correlated with ambient temperature in two ways: first by the sum of the daily mean ambient temperature a few days before laying, and second by some peaks of temperature above 10°C. Ambient temperature decreases with latitude and elevation and might be an ultimate factor causing environmental changes in vegetation phenology that determine the peak of food abundance (Perrins 1970, Perrins and McCleery 1989, Blondel et al. 1993). In tits, caterpillars are the preferred food during the nestling period (Perrins 1965, van Balen 1973, Blondel et al. 1991, Banbura et al. 1994). As has been demonstrated, the timing of breeding by insectivorous birds is adjusted to the emergence of caterpillars, and their young are present in the nest around the peak of food abundance (Perrins 1965, Perrins and McCleery 1989, Blondel et al. 1993, Svensson and Nilsson 1995).

The onset of gonadal development in Great Tits is probably determined by photoperiod (Silverin 1994). In a proximate sense, photoperiod opens and closes a window during which reproduction in birds is possible, but within this window, the actual onset of egg laying is determined by additional fine-tuning and supplementary mechanisms that optimize the timing of breeding (Martin 1987; Perrins 1991; Nager and van Noordwijk 1995; Lambrechts et al. 1996, 1997). The onset of gonadal development is regulated by an increase in the secretion of gonadotrophin that is regulated by the number of hours of daylight (i.e. the photoperiodic threshold; Silverin et al. 1989). Variation in photoperiodic threshold values may account for latitudinal differences in the timing of breeding among birds (Silverin et al. 1993). The photoperiodic threshold increases with increasing latitude (Silverin et al. 1993). Comparing the critical daylength when the photoperiod initiates gonadal development with the time of year daylength reaches this threshold at different latitudes, Silverin (1995) concluded that providing extra food during the prebreeding period can never advance egg laying more than a week, which is in agreement with food-provisioning experiments (see Svensson and Nilsson 1995, Nager et al. 1997). At different latitudes, the onset of breeding cannot occur much earlier than the observed dates for the laying of the first eggs in the population (Silverin et al. 1993). Silverin et al. (1993) showed that although Great Tits normally do not breed at the earliest time possible, the delay in breeding once conditions are favorable becomes shorter the farther north the birds breed. This reflects the fact that the breeding season of northern birds is short (Ricklefs 1966, Orell and Ojanen 1983a). Thus, three related factors—food availability, ambient temperature, and photoperiod—together can explain why laying date increases with latitude. However, why do birds breeding in northern Africa start laying so late? Photoperiod cannot explain this fact, but the peak of food abundance may be later in northern Africa. More information is necessary to understand this difference.

The coefficient of variation in mean laying date decreased significantly with latitude, indicating a shorter breeding season at high latitudes. A similar breeding synchrony occurred in Great Tits during years with "late" springs (Slagsvold 1976). Hence, increased synchrony as laying date increases may be the rule in this species (Slagsvold 1976, Orell and Ojanen 1983a). This pattern might be due to local adjustment to environmental conditions and may be a consequence of later and shorter growing seasons farther north for the Great Tit's main prey, caterpillars (Slagsvold 1975a).

Clutch size.—Mean clutch size and the production of fledglings in Great Tits typically differ among habitats (van Balen 1973, Zang 1980, Blondel et al. 1987). In the present study, these differences remained after controlling for variation in elevation and latitude. In agreement with an earlier study (Zang 1980), I observed a decrease in clutch size with increasing elevation. This is in contrast to the suggestion that clutch size increases with elevation owing to higher instability and unpredictability in climate at higher elevations (Cody 1966, Stearns 1976). Clutch size was smaller in montane habitats, presumably because breeding conditions (food availability, weather) were less favorable for insectivores (Zang 1980, Järvinen 1983, Sanz 1995). Alternatively, predation rate has been proposed to explain this elevational trend (Slagsvold 1982). Nest predation probably increases with increasing elevation because passerines breed early in the year relative to the stage of vegetation development at higher elevations (Slagsvold 1975b, 1977, 1982). Also, because the structure of the vegetation is less complex, nest detection by predators may be easier at higher than at lower elevations (Slagsvold 1982).

Clutch size and number of fledglings of first and second broods showed a quadratic relationship with latitude, with increasing values up to 55 to 60°N. Similar relationships occurred for the Pied Flycatcher among different breeding populations in Europe (Sanz 1997). An increase in clutch size with increasing latitude has been attributed to the increase in daylight hours available for parents to collect food for their nestlings (Lack 1947, Royama 1969, Owen 1979). Daylength increases with latitude, but the length of activity periods during the nestling period (i.e. the time between the first and last feeding visits to the nest) for both Pied Flycatchers (Sanz 1999) and Great Tits (Sanz et al. 1998) is asymptotically related to daylight hours. That is, at southern latitudes, parents use all of the available daylight hours to collect food for their young, which is not the case at northern latitudes (Sanz et al. 1998, Sanz 1999). Lack (1954) suggested that ". . . an increase in daylength from 12 to 18 hours is probably much more effective than an increase from 18 to 24 hours . . ." and that the increase in clutch size should be small from central to northern Europe. However, as in Pied Flycatchers (Sanz 1997), I found that clutch size in Great Tits does not increase from central toward northern Europe. This suggests that the amount of time available for foraging is not the only variable that affects latitudinal variation in clutch size.

The energy requirement of the brood relative to ambient temperature has been proposed as one of the factors that affect latitudinal variation in clutch size in altricial birds (Royama 1969). Because ambient temperature during the nestling period decreases with latitude (Sanz 1999), the energy requirements of the brood should increase. The balance between the energy requirements of the brood relative to the duration of the activity period and ambient temperature might explain latitudinal variation in clutch size. Parents in the southern part of the range have smaller clutches than in the central part because they are probably under time constraints. In contrast, parents in the northern part of the range may be under energy constraints because the energy requirements of the brood in relation to ambient temperature are higher than in the central part of the range (Sanz 1999).

Ashmole's (1961) hypothesis, which is a modification of Lack's (1947) hypothesis, suggests that competition for resources may be more severe at southern latitudes than at northern ones. This may be due to the fact that northern populations apparently are more variable than southern ones and thus are frequently kept below the carrying capacity of the environment. Because seasonality probably increases linearly with latitude, the hypothesis predicts a linear increase in clutch size with latitude (Ashmole 1961, Ricklefs 1980). However, I did not find a linear increase in clutch size or number of fledglings with latitude. Ashmole's hypothesis has been supported in some studies (Ricklefs 1980; Koenig 1984, 1986) but not in others (Møller 1984, Dunn and MacInnes 1987, Young 1994).

An alternative hypothesis (Skutch 1949, Cody 1966, Perrins 1977, Slagsvold 1982, Lima 1987, Kulesza 1990) suggests that a decrease in nest predation with latitude might result in larger clutches. The present data set includes only nest-box studies, and data on predation rates and densities of predators were not available. However, comparative analyses using different methods that consider the phylogenetic relationships among species indicate that predation rate may be an important factor determining clutch size in some studies (Martin 1995) but not in others (Trevelyan and Read 1989, Yanes and Suárez 1997). Factors that directly affect nest predation potentially may exert a strong influence on life-history evolution (Martin and Clobert 1996). For example, Martin (1995) showed that the type of nest site and migratory habit (i.e. resident vs. migrant) affect nest predation and life-history traits. Moreover, large-scale modification of the environment may have reduced evolutionary constraints of nest predation on life-history traits in European populations of birds (Martin and Clobert 1996). Consequently, patterns of nest predation and the importance of food versus nest predation to life-history variation may change such that food may be a more important influence in Europe (Martin and Clobert 1996).

For passerines, clutch size tends to be lower in marginal habitats than in nearby optimal habitats (Klomp 1970, van Balen 1973, Zang 1980, Sanz 1995, Dias 1996). Peripheral and central parts of the geographic ranges of species are associated with marginal and optimal habitats, respectively (Slagsvold 1981). It has been suggested that breeding populations near the margins of the distributional range are more unstable than those in the central parts of the range (Slagsvold 1981). This is partly based on the finding that the degree of annual fluctuation in breeding density is higher in marginal than in nearby optimal habitats (Kluijver and Tinbergen 1953, von Haartman 1971). The existence of distributional limits may reflect that conditions for reproduction are poor such that larger clutches cannot be selected for (Slagsvold 1981, Sanz 1997). A nonlinear relationship between clutch size or the number of fledglings and latitude can be predicted, with maximum values occurring near the center of the distribution (Sanz 1997). My results agree with this prediction; mean clutch size and number of fledglings were highest more or less near the central part of the species' distribution. Maximum values of production will be affected by habitat quality and also by factors such as daylength/activity period (Lack 1947, Sanz 1999), energy requirements of the nestlings relative to temperature (Royama 1969), and seasonality of food resources (Ashmole 1961, Ricklefs 1980). The lack of a geographic trend in clutch-size variation (i.e. coefficient of variation) and the positive correlation between clutch size and number of fledglings reflect that parents lay a clutch size that they can successfully rear given the local environment (Møller 1984, Sanz 1997).

Finally, there might be alternative explanations to local specialization. For example, Great Tits retreated to the southwestern corner of Europe during the last glaciation, rapidly extended their distribution northeastward after the end of the last ice age (Gosler 1993, Silverin 1995), and invaded northern latitudes about 1,000 years ago (Silverin et al. 1993). However, they have also changed their distribution during the last decades. Before 1930, the Great Tit did not breed north of 63°N, but today they are common up to 70°N (Haftorn 1957, Silverin 1995). This spread to the north is probably due to climatic factors and the ability to winter in areas of human settlement (Haftorn 1957, Cramp and Perrins 1993, Silverin 1995). Recently, Merilä et al. (1996, 1997) discovered that the genetic variability of the Greenfinch (*Carduelis chloris*) is extremely low and decreases with increasing latitude across continental Europe. Merilä et al. explained this result in terms of a Pleistocene bottleneck and gradual loss of variation associated with serial bottlenecking during the recolonization of northern Europe. Great Tits expanded after the last glaciation to new habitats in which they might be less well adapted. The decline in clutch size and number of fledglings from central toward northern Europe may be in agreement with this hypothesis.

By producing a second clutch, an individual Great Tit can enlarge its production of fledglings in a breeding season (den Boer-Hazewinkel 1987, Verboven and Verhulst 1996). Verboven and Verhulst (1996) recently showed that the probability of a second clutch is related mainly to the laying date of the first clutch. In agreement with Orell and Ojanen (1983a), the mean proportion of second clutches was negatively correlated with latitude. This likely is due to the short breeding season in the northern part of the species' distribution, there being no time to complete two breeding attempts in one season. The observed pattern of a late start of laying, lower variability in laying date, and low frequency of second clutches in northern populations may be a consequence of a late and short growing season for the Great Tit's main prey, caterpillars (Slagsvold 1975a).

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APPENDIX 1. Breeding data ($\bar{x}$ ± SD, first clutches only) for Great Tits from different study sites in Eurasia and northern Africa. For laying date, 1 = 1 April (rounded to nearest day); for habitat, Decid = deciduous forest, Conif = coniferous forest, Mixed = mixed deciduous/coniferous forest.

Laying date	Clutch size	No. of fledglings	% Second clutches	Habitat type	Years	*n*	Reference
				Latitude 60 to 70°N			
57 ± 11.1	8.7 ± 1.41	4.8 ± 3.58	9.8	Mixed	1983–93	80	Veistola (1997)
45					1988–92		Silverin et al. (1993)
58	9.1 ± 1.03			Decid	1975–87	17	Järvinen (1986, 1991)
51	9.0					12	Cramp and Perrins (1993)
	10.0			Conif	1970–80	45	Orell and Ojanen (1983b)
50 ± 4.1	10.5	8.1		Decid	1971–80	61	Orell and Ojanen (1983a, b, c)
49 ± 3.4	9.9	7.5		Conif	1969–80	98	Orell and Ojanen (1983a, b, c)
47 ± 3.4	9.4	6.6		Mixed	1969–80	226	Orell and Ojanen (1983a, b, c)
50 ± 3.2	10.0			Decid	1970–80	52	Orell and Ojanen (1983a, b, c)
49 ± 3.9	10.0	7.6	9.5	Conif	1970–80	187	Orell and Ojanen (1983a, b, c)
	9.1			Decid	1984	16	Slagsvold and Lifjeld (1990)
43 ± 8.6	9.2 ± 1.61	5.3 ± 3.08	19.4	Conif	1991–96	404	Veistola (1997)
41 ± 4.8	9.9		19.8	Decid	1953–67	225	Haartman (1969, 1973)
	8.4	8.2	16.9	Conif	1952–63	569	Johansson (1972, 1974, 1977)
42 ± 7.2				Conif	1968–74	35	Slagsvold (1976)
				Latitude 55 to 60°N			
	8.5			Conif	1984–85	20	Slagsvold and Lifjeld (1990)
37							Cramp and Perrins (1993)
	9.4 ± 0.92	7.1 ± 2.60		Conif	1984	8	Björklund and Westman (1986)
	8.4 ± 1.72	7.8 ± 1.33		Decid	1984	10	Björklund and Westman (1986)
	8.4 ± 1.20			Decid	1990–94	73	Dufva (1996)
	11.1 ± 1.30			Mixed	1987–91	206	Hõrak et al. (1995)
	10.9				1989–91	248	Glutz von Blotzheim and Bauer (1993)
	11.7 ± 1.78			Mixed	1983	16	Hõrak et al. (1995)
	11.6 ± 1.67			Decid	1983	22	Hõrak et al. (1995)
45	8.2 ± 1.22	7.2 ± 1.43		Conif	1985–86	35	Lemel (1989)
43	9.0 ± 1.56	7.4 ± 2.01		Decid	1985–86	80	Lemel (1989)
42					1983–92		Silverin et al. (1993)
27	9.1			Decid	1990–92	312	Allander and Bennett (1995)
	9.8			Decid		388	Orell and Ojanen (1983b)
34 ± 4.1	9.0 ± 1.70	7.5	15.9	Decid	1963–70	997	Frederiksen et al. (1972), Larsen (1974)

APPENDIX 1. Continued.

Laying date	Clutch size	No. of fledglings	% Second clutches	Habitat type	Years	*n*	Reference
Latitude 50 to 55°N							
32 ± 4.7	8.1 ± 0.16			Mixed	1951–53	69	Lack (1955)
33 ± 4.6	11.8	11.1	53.9		1952–65	430	Likhachev (1953, 1967)
33	9.0			Conif	1970–75	70	Berndt et al. (1983)
35	8.7			Mixed	1970–75	101	Berndt et al. (1983)
37	8.1			Mixed	1970–75	157	Berndt et al. (1983)
37	8.7			Conif	1970–75	117	Berndt et al. (1983)
36	9.0			Mixed	1970–75	137	Berndt et al. (1983)
33	8.7			Mixed	1970–75	293	Berndt et al. (1983)
31 ± 8.1	9.6 ± 2.11	8.3 ± 2.56	34.4	Decid	1995–96	218	Sanz (unpubl.)
34	9.1			Mixed	1970–75	95	Berndt et al. (1983)
26 ± 7.0	9.2 ± 1.35			Conif	1958–79	1,012	Noordwijk et al. (1981a, b)
29	8.3			Conif	1970–75	261	Berndt et al. (1983)
	8.8			Mixed	1970–75	78	Berndt et al. (1983)
29	8.8			Conif	1970–75	113	Berndt et al. (1983)
30	9.1			Mixed	1970–75	65	Berndt et al. (1983)
	9.0			Conif	1970–75	39	Berndt et al. (1983)
	9.9			Conif		1,108	Glutz von Blotzheim and Bauer (1993)
34	9.0			Mixed	1970–75	124	Berndt et al. (1983)
33	8.9			Mixed	1970–75	314	Berndt et al. (1983)
33 ± 6.7	9.1 ± 0.43		11.0	Conif	1949–57	75	Lack (1955, 1958)
28 ± 6.3	9.9 ± 0.58		27.9	Mixed	1948–57	126	Lack (1955, 1958)
30 ± 6.0	8.2 ± 0.50			Mixed	1948–57	227	Lack (1955, 1958)
34	10.1			Decid	1970–75	423	Berndt et al. (1983)
30	10.7				1955–61	122	Busse and Gotzman (1962), Busse (1967)
27	9.5	8.1	7.0	Decid	1969–77		Zang (1980)
	10.0		73.5	Conif	1922–33		Kluijver (1951)
	9.9		61.5	Mixed	1923–34		Kluijver (1951)
	9.1		45.8	Mixed	1922–34		Kluijver (1951)
	10.6		33.7	Decid	1924–34		Kluijver (1951)
23 ± 6.4	10.0	9.0		Decid	1957–66	132	Balen (1973)
25 ± 7.7	9.6 ± 1.75			Mixed	1955–79	2,346	Noordwijk et al. (1981a, b)
26	9.3	6.7	2.0	Decid	1969–77		Zang (1980)
29	9.2	7.5	6.4	Decid	1969–77		Zang (1980)
26	9.1	7.7		Mixed	1969–77		Zang (1980)
27	9.0	7.1	1.1	Decid	1969–77		Zang (1980)
31	8.5	6.8		Decid	1969–77		Zang (1980)
34	8.4	5.7	13.2	Decid	1969–77		Zang (1980)
	8.3			Decid	1970–75	39	Berndt et al. (1983)
33	9.8			Decid	1970–75	62	Berndt et al. (1983)

APPENDIX 1. Continued.

Laying date	Clutch size	No. of fledglings	% Second clutches	Habitat type	Years	*n*	Reference
36	8.6	5.3	18.8	Conif	1969–77		Zang (1980)
40	8.7	6.0	14.8	Conif	1969–77		Zang (1980)
40	8.8	7.4	8.4	Conif	1969–77		Zang (1980)
29 ± 8.2	9.5 ± 0.99			Decid	1948–57	290	Lack (1955, 1958)
26 ± 8.5	9.6 ± 1.01		5.0	Decid	1947–57	286	Lack (1955, 1958)
	8.6			Conif	1970–75	41	Berndt et al. (1983)
36	8.4	6.1	6.2	Conif	1969–77		Zang (1980)
36	8.4	6.2	22.5	Conif	1969–77		Zang (1980)
43	8.8	8.1	7.1	Conif	1969–77		Zang (1980)
44	8.1	5.8	13.4	Conif	1969–77		Zang (1980)
	8.8			Decid	1970–75	32	Berndt et al. (1983)
32	8.4			Decid	1970–75	79	Berndt et al. (1983)
34	8.2	6.1	6.3	Conif	1969–77		Zang (1980)
	7.6			Decid	1970–75	61	Berndt et al. (1983)
31	7.2			Mixed	1970–75	347	Berndt et al. (1983)
27 ± 6.2	9.4 ± 1.31			Decid	1948–57	260	Lack (1955, 1958)
32	8.8			Decid	1970–75	139	Berndt et al. (1983)
27 ± 5.1	9.3 ± 0.75			Decid	1948–57	102	Lack (1955, 1958)
30	8.8			Decid	1970–75	58	Berndt et al. (1983)
29	8.4			Mixed	1970–75	73	Berndt et al. (1983)
21 ± 4.9	9.1	6.4	38.5	Mixed	1961–78	366	Orell and Ojanen (1983a, b, c)
20 ± 5.1	9.2	7.2	23.3	Decid	1960–78	401	Orell and Ojanen (1983a, b, c)
18 ± 5.6	9.1	5.9	35.4	Decid	1959–78	210	Orell and Ojanen (1983a, b, c)
26	8.2			Mixed	1970–75	58	Berndt et al. (1983)
25	8.0			Mixed	1970–75	69	Berndt et al. (1983)
	8.9 ± 1.53			Conif	1970–82	73	Hamann et al. (1989)
	9.5					46	Glutz von Blotzheim and Bauer (1993)
			37.0				Cramp and Perrins (1993)
	8.7 ± 1.57			Decid	1970–82	69	Hamann et al. (1989)
	9.3 ± 1.48			Decid	1970–82	182	Hamann et al. (1989)
	8.8 ± 1.46			Decid	1970–82	183	Hamann et al. (1989)
	8.3 ± 1.54			Mixed	1970–82	280	Hamann et al. (1989)
27				Decid			Schmidt and Steinbach (1983)
	9.7		60.7	Decid	1967–71	344	Delmee et al. (1972)
				Latitude 33 to 50°N			
27	8.6			Mixed	1970–75	194	Berndt et al. (1983)
27 ± 4.7	8.6 ± 1.25	3.4	57.0	Decid	1982–84	36	Muller (1985)
24	8.9		41.5	Conif	1958–68	417	Balat (1970, 1976)
25 ± 5.6	9.8 ± 1.86	5.4	38.0	Decid	1982–84	65	Muller (1985)
25 ± 2.7	9.7 ± 1.27	5.1	80.0	Decid	1983–84	18	Muller (1985)

APPENDIX 1. Continued.

Laying date	Clutch size	No. of fledglings	% Second clutches	Habitat type	Years	*n*	Reference
24 ± 10.8	9.2				1955–59	127	Zink (1959)
23 ± 7.2	9.1	8.6		Decid	1982–84	20	Török and Csörgö (1988)
20 ± 6.7	10.2	7.8		Decid	1983–84	15	Török and Csörgö (1988)
	9.1	7.8		Decid	1982–84	29	Török and Csörgö (1988)
	9.0 ± 1.33			Mixed	1989–92	93	Nager and Zandt (1994)
	8.6 ± 1.31			Mixed	1989–92	187	Nager and Zandt (1994)
	8.1 ± 1.45			Decid	1989–92	137	Nager and Zandt (1994)
	10.3 ± 0.86	8.8 ± 0.73	32.1			663	Orell and Ojanen (1983a), Sasvári and Orell and (1992)
	9.5					39	Warga (1939)
	8.3 ± 1.31			Conif	1970–82	54	Hamann et al. (1989)
14 ± 5.3	8.7 ± 1.42			Decid	1986–90	61	Báldi and Csörgö (1993)
20					1991–92		Silverin et al. (1993)
15	8.1 ± 1.40			Mixed	1976–79		Michelland (1980)
18	9.4	5.4	56.0	Conif	1979–81	33	Cramm (1982)
15 ± 2.0	7.8 ± 0.40	4.2 ± 0.90		Conif	1982	9	Isenmann (1983)
24 ± 7.4	8.6 ± 1.60	3.6 ± 3.40		Conif	1982–85	85	Blondel et al. (1987)
17 ± 5.6	9.4 ± 1.30	5.1 ± 4.20		Decid	1982–85	31	Blondel et al. (1987)
9 ± 8.3	7.8 ± 1.40	7.5 ± 1.60	50.0	Conif	1989–90	10	Bellavita and Sorace (1991)
20 ± 11.1	7.8 ± 1.20	6.9 ± 1.40	66.7	Decid	1989–90	12	Bellavita and Sorace (1991)
13 ± 1.5	8.3 ± 0.50	4.7 ± 2.20	25.0	Conif	1989–90	4	Bellavita and Sorace (1991)
13 ± 7.2	9.4 ± 1.61		25.6	Decid	1995–97	53	Sanz (unpubl.)
18 ± 8.3	6.9 ± 1.10	3.9	78.3	Conif	1987	24	Fidalgo (1990)
	9.1 ± 0.23	7.4 ± 0.69		Decid	1984–85	38	Pascual (1985)
38	7.5 ± 1.52	6.4 ± 0.10	17.1	Mixed	1978–80	193	Kiziroglu (1982)
17	8.2			Conif	1988–90	59	Barba et al. (1994)
33 ± 13.0	6.8 ± 0.37	4.2 ± 2.14		Conif	1991–94	6	Chabi (1998)
26 ± 13.3	7.0 ± 0.90	3.9 ± 2.74		Decid	1991–94	21	Chabi (1998)
	7.6 ± 1.67			Conif		23	Cramp and Perrins (1993)
44	7.7			Decid			Chabi (1998)

APPENDIX 2. Breeding data ($\bar{x}$ ± SD) for second clutches of Great Tits from different study sites in Eurasia. For laying date, 1 = 1 April (rounded to nearest day).

Laying date	Clutch size	No. of fledglings	Reference
		Latitude 60 to 70°N	
	7.2 ± 2.04	1.8 ± 2.29	Veistola et al. (1995)
91 ± 6.3	7.5 ± 1.59	6.0	Orell and Ojanen (1983a, b, c)
	7.8		Haartman (1969)
	6.9	6.3	Johansson (1972, 1974, 1977)
		Latitude 50 to 60°N	
	7.8		Glutz von Blotzheim and Bauer (1993)
		7.3	Orell and Ojanen (1983b)
	7.1	5.9	Larsen (1974)
	9.5	7.8	Likhachev (1953, 1967)
74 ± 9.1	7.4 ± 1.57	5.8 ± 1.71	Sanz (unpubl.)
	8.4		Glutz von Blotzheim and Bauer (1993)
	8.4		Lack (1958)
	7.9		Lack (1958)
	8.6		Kluijver (1951)
	8.5		Kluijver (1951)
	7.9		Kluijver (1951)
	7.0		Kluijver (1951)
	7.6		Lack (1958)
	7.3		Lack (1958)
	7.3	4.9	Orell and Ojanen (1983b, c)
	7.1	4.5	Orell and Ojanen (1983b, c)
	6.8	4.8	Orell and Ojanen (1983b, c)
		Latitude 40 to 50°N	
	9.4		Glutz von Blotzheim and Bauer (1993)
	7.7		Delmee et al. (1972)
	7.7		Muller (1985)
	8.0		Muller (1985)
	7.4		Muller (1985)
	7.2		Glutz von Blotzheim and Bauer (1993)
	8.1		Warga (1939)
61 ± 2.7	8.8 ± 0.60	5.7 ± 0.90	Isenmann (1983)
	7.9	3.6	Cramm (1982)
	7.0 ± 1.80	5.8 ± 2.40	Bellavita and Sorace (1991)
	6.5 ± 2.00	5.4 ± 1.80	Bellavita and Sorace (1991)
	6.5 ± 0.50	3.5 ± 2.50	Bellavita and Sorace (1991)
69 ± 9.1	5.7 ± 0.87	2.8	Fidalgo (1990)
	6.5	5.3	Kiziroglu (1982)