No evidence for survival selection on carotenoid-based nestling coloration in great tits (*Parus major*)

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Abstract

In several vertebrate species evidence supports the hypothesis that carotenoid-based coloration of adults has evolved due to sexual selection. However, in some birds already the nestlings display carotenoid-based coloration. Because the nestling's body plumage is typically moulted before the first reproductive event, sexual selection cannot explain the evolution of these carotenoid-based traits. This suggests that natural selection might be the reason for its evolution. Here we test whether the carotenoid-based nestling coloration of great tits (*Parus major*) predicts survival after fledging. Contrary to our expectation, the carotenoid-based plumage coloration was not related to short- nor to long-term survival in the studied population. Additionally, no prefledging selection was detectable in an earlier study. This indicates that the carotenoid-based coloration of nestling great tits is currently not under natural selection and it suggests that past selection pressures or selection acting on correlated traits may have led to its evolution.

Introduction

In many vertebrate species carotenoid-based coloration is considered during female choice and is thus an important trait in sexual selection (e.g. Milinski & Bakker, 1990; Hill, 1991; Faivre et al., 2001). By preferring intensely coloured males (Milinski & Bakker, 1990; Hill, 1991) females select less parasitized (Milinski & Bakker, 1990; Hill & Brawner, 1998; Brawner et al., 2000; Hörák et al., 2001; Hill & Farmer, 2005), more immunocompetent (Bendich & Shapiro, 1986; Bendich, 1991; Blount et al., 2003; Saks et al., 2003) and better caring fathers (Hill, 1991; Senar et al., 2002). Brighter coloured males are therefore able to reproduce at a higher rate and thus females impose directional selection on the male's plumage coloration (Badyaev et al., 2000).

However, in some bird species already the nestlings show an intense carotenoid-based plumage coloration (Brush, 1978). Because juvenile passerines moult their plumage before their first reproduction (Jenni & Winkler, 1994), sexual selection hardly explains the evolution of the nestling's carotenoid-based colour traits. This suggests that intensely yellow-coloured nestling plumes may have evolved due to natural selection. Support for this hypothesis is provided by different studies, which indicate that natural selection acts on nestling coloration (e.g. Lyon et al., 1994; Götmark & Olsson, 1997; Hill, 2002). As predators are important determinants of fledgling survival (Naef-Daenzer et al., 2001), plumage colours which provide camouflage will be selected for (e.g. Butcher & Rohwer, 1989; Götmark & Olsson, 1997). Parents may as well select for brightly coloured nestling traits by allocating food to nestlings in relation to their coloration (Lyon et al., 1994; Hill, 2002). Beside these inter- and intraspecific factors, abiotic factors may favour a specific plumage coloration. For example, the colour determines how much light will be reflected and thus advantageous thermoregulatory properties of a given colour may be selected for (e.g. Ellers & Boggs, 2003). The bird's plumage as well protects against mechanical impact, solar radiation and water (see Jenni & Winkler, 1994, for a review). Because the effectiveness of the protective properties depends on the incorporated pigments and on the feather structure, which as well determines the plumage coloration (Bleiweiss, 2004) selection acting on the protective function of the plumage may select for a specific coloration. Therefore

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parents, predators and abiotic factors may impose directional, stabilizing or disruptive selection (Kingsolver & Smith, 1995), and thus lead to the evolution of carotenoid-based nestling plumage coloration.

We recently showed that in great tits the nestling’s plumage coloration does neither influence the parental feeding behaviour (Tschirren et al., 2005) nor the nestling’s survival before fledging (Tschirren et al., 2003). Thus, selective pressures directly acting on the carotenoid-based coloration during the nestling period may not be present or they may be very weak and thus remained undetected. This suggests that the nestling’s plumage coloration may have evolved because of selective advantages after fledging, e.g. camouflage, parental feeding preferences, thermoregulation or the protective functions of the plumage. In this study, we therefore test whether survival selection is acting after fledging on the carotenoid-based plumage coloration of nestling great tits. To test this hypothesis we link nestling survival with plumage coloration (Gregoire et al., 2004). By applying models including short- (first-year) and long-term survival we further examine when selection is acting.

Methods

Species description

The great tit (Parus major) is a small hole nesting passerine, which inhabits deciduous forests, hedges, parks and urban areas (Gosler, 1993). Nestling great tits display a bright yellow carotenoid-based plumage coloration, which arises due to the incorporation of the carotenoids lutein and zeaxanthin into the feathers (Partali et al., 1987). Because carotenoids cannot be synthesized by animals the amount of incorporated carotenoids depends on the amounts of the ingested carotenoids as well as on the nestling’s condition (Tschirren et al., 2003). Thus the plumage coloration is a reliable signal of early nutritional condition (Tschirren et al., 2003). Carotenoid pigments reflect light only in the human visible range of the spectrum (e.g. Hill, 1998, 2002; O’Neill et al., 2001). Therefore quantifying plumage coloration using a digital camera reliably measures differences in the carotenoid content of the feathers (Tschirren et al., 2003).

Selection on nestling plumage coloration

In 1998 the breast plumage coloration of 191 nestlings originating from 30 nests and in 1999 the colour of 164 nestlings originating from 50 nests were measured. The natural range of the plumage coloration was 40.9–47.1° (43.4° ± 0.06 SE) for hue, 37.9–61.3% (50.5% ± 0.002 SE) for saturation, and 64.6–92.3% (80.7% ± 0.002 SE) for brightness. In the years 1999, 2000 and 2001 all great tits breeding in nest boxes within our study area (consisting of approximately 800 nest boxes within 16 km²) were captured to assess the survival of the birds. The survival estimates (Φ) are based on birds recaptured during the breeding period and within the study area. Survival estimates therefore correspond to the probability of recruiting locally. Adult great tits were captured at the nest when their offspring were 14 days old. For the estimation of the probability of recruiting locally and for the estimation of the recapture probability we used the program MARK (White & Burnham, 1999; White, 2000) using Cormack-Jolly-Seber models (e.g. Jolly, 1965; Lebreton et al., 1992). Before analysis we confirmed, by a goodness of fit test, that the starting model adequately fitted the data using a bootstrap approach (White, 2000). As our starting model was over-dispersed (1000 simulations, P < 0.012) we adjusted the variance inflation factor (c-hat) with the quotient of the observed inflation factor and the mean simulated inflation factor (c-hat = 1.206 ± 0.069) from the bootstraps (Lebreton et al., 1992; Burnham & Anderson, 1998; White, 2000). Survival analyses were started with the full model including year and age. Age was modelled as first year or older than 1 year (Clobert et al., 1988). We first modelled the recapture probability (Table 1A) and subsequently the probability of recruiting locally (Table 1B). Model selection was based on the Akaika Information Criterion (AIC) and differences between two models of ±2 AIC were considered as being significantly different (Burnham & Anderson, 1998). The
Table 1. Models of selection on nestling plumage coloration. The effects of age (a) and year (y) are shown for both (A) the recapture probability (p), and (B) the probability of recruiting locally (q). The best model selected in sections (A) and (B) corresponds to the basic model against which the models incorporating the covariates were tested. The basic model is marked in bold. Models are numbered according to decreasing complexity but ordered according to AIC. (C) Long-term survival models incorporating the first (PC1), second (PC2), and third (PC3) principal components of plumage coloration. (D) Models incorporating plumage coloration as an age-dependent covariate acting on first-year survival only (linear and/or quadratic terms were included). (E) Long-term survival models incorporating the covariates body condition, clutch size, and hatching date. (F) Models incorporating body condition, clutch size, and hatching date as age-dependent covariates acting on first-year survival only. (G) Models incorporating both the plumage coloration and the covariates body condition, clutch size and hatching date. Only models with lower AIC than the basic model are given (sections C-G).

<table>
<thead>
<tr>
<th>Model</th>
<th>QAICc</th>
<th>ΔQAICc</th>
<th>Parameters</th>
<th>Q</th>
<th>ΔQ</th>
<th>QAICc weight (%)</th>
<th>Model explanation</th>
<th>Selection gradient ± SE (on logit scale)</th>
<th>Models compared, likelihood ratio test</th>
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<tbody>
<tr>
<td>(A) Recapture probability</td>
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<tr>
<td>5. $\phi_{ap}$</td>
<td>246.1</td>
<td>4.6</td>
<td>6</td>
<td>233.9</td>
<td>1.5</td>
<td>Intercept</td>
<td>4–5, $P = 0.34$</td>
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<td>4. $\phi_{ap}a$</td>
<td>247.3</td>
<td>5.8</td>
<td>7</td>
<td>233.0</td>
<td>0.8</td>
<td>Age dependent</td>
<td>3–4, $P = 0.66$</td>
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<tr>
<td>3. $\phi_{ap}y$</td>
<td>250.2</td>
<td>8.7</td>
<td>8</td>
<td>233.8</td>
<td>0.2</td>
<td>Year dependent</td>
<td>2–3, $P = 0.24$</td>
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<tr>
<td>2. $\phi_{ap}ay$</td>
<td>250.9</td>
<td>9.4</td>
<td>9</td>
<td>232.4</td>
<td>0.1</td>
<td>Age + year dependent</td>
<td>1–2, $P = 1$</td>
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<tr>
<td>1. $\phi_{ap}ay$</td>
<td>253.0</td>
<td>11.5</td>
<td>10</td>
<td>232.4</td>
<td>0.1</td>
<td>Age x year dependent</td>
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<td>(B) Survival estimates</td>
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<tr>
<td>7. $\phi_{ap}a$</td>
<td>244.1</td>
<td>2.6</td>
<td>5</td>
<td>233.9</td>
<td>4.2</td>
<td>Age + year dependent</td>
<td>6–7, $P = 1$</td>
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<tr>
<td>6. $\phi_{ap}a$</td>
<td>246.1</td>
<td>4.6</td>
<td>6</td>
<td>233.9</td>
<td>1.4</td>
<td>Age x year dependent</td>
<td>7–8, $P &lt; 0.001$</td>
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<td>5. $\phi_{ap}$</td>
<td>251.0</td>
<td>9.5</td>
<td>4</td>
<td>251.0</td>
<td>0.1</td>
<td>Year dependent</td>
<td>7–9, $P &lt; 0.01$</td>
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<td>4. $\phi_{ap}$</td>
<td>251.4</td>
<td>9.9</td>
<td>3</td>
<td>245.4</td>
<td>0.1</td>
<td>Age dependent</td>
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<tr>
<td>(C) Long-term survival models incorporating PC1, PC2, and PC3 of the plumage coloration with lower AIC values than the basic model</td>
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<td>10. $\phi_{ap}PC1 + PC1^2$</td>
<td>244.2</td>
<td>2.7</td>
<td>7</td>
<td>229.9</td>
<td>3.8</td>
<td>Stabilizing or disruptive selection on PC1</td>
<td>PC1: 0.228 ± 0.217; PC1$^2$: −0.365 ± 0.277</td>
<td>7–10, $P = 0.14$</td>
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<tr>
<td>11. $\phi_{ap}PC1 + PC1^2$</td>
<td>247.9</td>
<td>6.4</td>
<td>7</td>
<td>233.6</td>
<td>0.6</td>
<td>Stabilizing or disruptive selection on PC2</td>
<td>PC2: 0.126 ± 0.257; PC2$^2$: 0.028 ± 0.224</td>
<td>7–12, $P = 0.86$</td>
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<td>12. $\phi_{ap}PC2 + PC2^2$</td>
<td>245.8</td>
<td>4.3</td>
<td>6</td>
<td>233.6</td>
<td>1.7</td>
<td>Directional selection on PC2</td>
<td>0.136 ± 0.249</td>
<td>7–13, $P = 0.58$</td>
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<tr>
<td>13. $\phi_{ap}PC3 + PC3^2$</td>
<td>245.8</td>
<td>4.3</td>
<td>7</td>
<td>233.6</td>
<td>1.8</td>
<td>Directional selection on PC3</td>
<td>0.246 ± 0.188</td>
<td>7–14, $P = 0.30$</td>
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<tr>
<td>14. $\phi_{ap}PC3 + PC3^2$</td>
<td>245.7</td>
<td>4.2</td>
<td>6</td>
<td>233.5</td>
<td>1.9</td>
<td>Directional selection on PC3</td>
<td>0.176 ± 0.252</td>
<td>7–15, $P = 0.53$</td>
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<td>15. $\phi_{ap}PC3 + PC3^2$</td>
<td>246.0</td>
<td>4.5</td>
<td>6</td>
<td>233.8</td>
<td>1.6</td>
<td>Directional selection on PC2</td>
<td>0.127 ± 0.189</td>
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<tr>
<td>(D) Models incorporating plumage coloration as age-dependent effect acting on first year survival only, which have lower AIC values than the basic model</td>
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<tr>
<td>16. $\phi_{ap}PC1 + PC1^2$</td>
<td>245.9</td>
<td>4.4</td>
<td>7</td>
<td>231.7</td>
<td>1.6</td>
<td>Stabilizing or disruptive selection on PC1</td>
<td>PC1: 0.176 ± 0.252; PC1$^2$: −0.299 ± 0.291</td>
<td>7–16, $P = 0.33$</td>
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<tr>
<td>17. $\phi_{ap}PC1 + PC1^2$</td>
<td>245.1</td>
<td>3.6</td>
<td>6</td>
<td>233.9</td>
<td>2.4</td>
<td>Directional selection on PC1</td>
<td>0.219 ± 0.222</td>
<td>7–17, $P = 0.32$</td>
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<tr>
<td>18. $\phi_{ap}PC2 + PC2^2$</td>
<td>248.0</td>
<td>6.5</td>
<td>7</td>
<td>233.7</td>
<td>0.6</td>
<td>Stabilizing or disruptive selection on PC2</td>
<td>PC2: −0.073 ± 0.297; PC2$^2$: 0.088 ± 0.237</td>
<td>7–18, $P = 0.91$</td>
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<tr>
<td>19. $\phi_{ap}PC3 + PC3^2$</td>
<td>246.0</td>
<td>4.5</td>
<td>6</td>
<td>233.8</td>
<td>1.6</td>
<td>Directional selection on PC2</td>
<td>−0.059 ± 0.302</td>
<td>7–19, $P = 0.75$</td>
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<td>20. $\phi_{ap}PC3 + PC3^2$</td>
<td>246.9</td>
<td>5.4</td>
<td>7</td>
<td>232.6</td>
<td>1.0</td>
<td>Stabilizing or disruptive selection on PC3</td>
<td>0.216 ± 0.274; PC3$^2$: −0.267 ± 0.283</td>
<td>7–20, $P = 0.52$</td>
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<tr>
<td>21. $\phi_{ap}PC3 + PC3^2$</td>
<td>245.8</td>
<td>4.3</td>
<td>6</td>
<td>233.6</td>
<td>2.1</td>
<td>Directional selection on PC3</td>
<td>0.126 ± 0.225</td>
<td>7–21, $P = 0.40$</td>
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<tr>
<td>(E) Long-term survival models incorporating the covariates body condition (BC), clutch size (CS), and hatching date (HD), with lower AIC values than the basic model</td>
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<tr>
<td>22. $\phi_{ap}BC + BC^2$</td>
<td>248.2</td>
<td>6.7</td>
<td>7</td>
<td>233.9</td>
<td>0.5</td>
<td>Stabilizing or disruptive selection on BC</td>
<td>BC: 0.034 ± 0.201; BC$^2$: 0.036 ± 0.203</td>
<td>7–22, $P = 1$</td>
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<tr>
<td>23. $\phi_{ap}BC$</td>
<td>246.1</td>
<td>4.6</td>
<td>6</td>
<td>233.9</td>
<td>1.5</td>
<td>Directional selection on BC</td>
<td>0.022 ± 0.192</td>
<td>7–23, $P = 1$</td>
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<tr>
<td>24. $\phi_{ap}CS + CS^2$</td>
<td>246.1</td>
<td>4.6</td>
<td>7</td>
<td>233.9</td>
<td>1.6</td>
<td>Directional selection on CS</td>
<td>CS: 2.760 ± 2.266; CS$^2$: −2.852 ± 2.240</td>
<td>7–24, $P = 0.35$</td>
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<td>25. $\phi_{ap}CS$</td>
<td>245.8</td>
<td>4.3</td>
<td>6</td>
<td>233.6</td>
<td>1.7</td>
<td>Directional selection on CS</td>
<td>−0.109 ± 0.194</td>
<td>7–25, $P = 0.58$</td>
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<tr>
<td>26. $\phi_{ap}HD + HD^2$</td>
<td>241.6</td>
<td>0.1</td>
<td>7</td>
<td>227.4</td>
<td>1.1</td>
<td>Stabilizing or disruptive selection on HD</td>
<td>HD: 5.724 ± 4.084; HD$^2$: −6.382 ± 4.295</td>
<td>7–26, $P = 0.04$</td>
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<tr>
<td>27. $\phi_{ap}HD$</td>
<td>242.0</td>
<td>0.5</td>
<td>6</td>
<td>229.8</td>
<td>1.6</td>
<td>Directional selection on HD</td>
<td>−0.360 ± 0.179</td>
<td>7–27, $P = 0.04$</td>
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Table 1: Continued.

<table>
<thead>
<tr>
<th>Model</th>
<th>QAICc</th>
<th>QAICc Parameters</th>
<th>QAICc difference</th>
<th>QAICc weight (%)</th>
<th>Model explanation</th>
<th>SE (on logit scale)</th>
<th>Selection gradient ± SE (on logit scale)</th>
</tr>
</thead>
<tbody>
<tr>
<td>28</td>
<td>241.1</td>
<td>0.9</td>
<td>232.8 ± 0.231</td>
<td>B: 0.227 ± 0.251</td>
<td>Stabilizing or disruptive selection on BC BC: 0.227 ± 0.251; BC 0.092 ± 0.290</td>
<td>7–28, P = 0.58</td>
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<tr>
<td>29</td>
<td>246.5</td>
<td>1.4</td>
<td>232.9 ± 0.224</td>
<td>B: 0.234 ± 0.241</td>
<td>Directional selection on BC 0.234 ± 0.241</td>
<td>7–29, P = 0.58</td>
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<tr>
<td>30</td>
<td>245.8</td>
<td>1.8</td>
<td>233.5 ± 0.222</td>
<td>B: 0.235 ± 0.241</td>
<td>Directional selection on CS 0.235 ± 0.241</td>
<td>7–30, P = 0.58</td>
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<td>31</td>
<td>245.4</td>
<td>1.5</td>
<td>233.3 ± 0.223</td>
<td>B: 0.234 ± 0.241</td>
<td>Directional selection on HD 0.234 ± 0.241</td>
<td>7–31, P = 0.58</td>
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<tr>
<td>32</td>
<td>241.5</td>
<td>1.4</td>
<td>233.5 ± 0.224</td>
<td>B: 0.234 ± 0.241</td>
<td>Directional selection on HD 0.234 ± 0.241</td>
<td>7–32, P = 0.58</td>
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<td>33</td>
<td>241.3</td>
<td>1.4</td>
<td>233.3 ± 0.223</td>
<td>B: 0.234 ± 0.241</td>
<td>Directional selection on HD 0.234 ± 0.241</td>
<td>7–33, P = 0.58</td>
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<td>34</td>
<td>241.2</td>
<td>1.4</td>
<td>233.3 ± 0.223</td>
<td>B: 0.234 ± 0.241</td>
<td>Directional selection on HD 0.234 ± 0.241</td>
<td>7–34, P = 0.58</td>
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</table>

From previous studies it is known that the nestling’s plumage coloration is correlated with parameters that may influence survival: the nestling’s body condition, brood size (Tschirren et al., 2003), and hatching date (Svensson, 1997; Fitze et al., 2004). We therefore included brood size (the number of hatched offspring), hatching date, and nestling body condition as covariates in the analyses to control for confounding effects. Body condition was defined as the residuals of a linear regression of body weight on tarsus length. Like for the colour variables we modelled brood size, nestling body condition, and hatching date as linear and/or quadratic terms that affected first-year or long-term survival (Table 1E,F). We then selected the best fitting model (lowest QAIC) of the models presented in Table 1E,F and added the three colour covariates. We generated all statistical correct models including at least one of the colour covariates. The models with lower QAIC values than the model selected in Table 1E,F are presented in Table 1G. To indicate the strength and the direction of

model with the lowest AIC was selected as the best model using AIC-weight and is referred to as the basic model (Table 1B: $\Phi_{\text{basic}}$). Due to the adjustment of the variance inflation factor the AIC criterion is referred to as QAIC. Likelihood ratio tests were used to confirm the model selection. After selecting the basic model we introduced the parameters describing the nestling’s plumage as covariates (Table 1C) to investigate whether plumage coloration predicts survival. Because H, S and B were inter-correlated (H–S: $R^2 = 0.029$, $\beta = 0.171$; H–B: $R^2 = 0.147$, $\beta = -0.383$; S–B: $R^2 = 0.053$, $\beta = -0.231$) we first conducted a principal component analysis including the three colour variables. The first principal component (PC1) explained 51.1% of the variance and it mainly reflects H and B (factor loadings: H: 0.639, S: 0.47, B: 0.608). The second principal component (PC2) explained 28.5% of the variance and reflects S (factor loadings: H: 0.221, S: 0.870, B: -0.441) and the third principal component (PC3) again reflects H and B (factor loadings: H: 0.737, S: 0.147, B: 0.660). For all three covariates we introduced a linear term to test for directional selection and a quadratic term to test for stabilizing or disruptive selection (Lande & Arnold, 1983; Kingsolver & Smith, 1995) and we run two types of models: models where the covariates affect survival during the entire life (long-term survival, Table 1C,E) and models where the covariates affect survival only during the first year of life (first-year survival, Table 1D,F). We distinguish between these two types of models because juveniles moult their nestling body plumage in autumn after fledging and because the nestling’s plumage coloration is not correlated with the first-year plumage coloration (Fitze et al., 2003a). Thus nestling plumage coloration, if being directly selected for, should predict first-year survival but not necessarily long-term survival.
the selection we give the selection gradients on a logit scale (Kingsolver & Smith, 1995) for all covariates.

Results

The probability of recruiting locally was both age and year dependent (Table 1B) whereas the recapture probability did not depend on age and year (Table 1A). We therefore selected the model with age and year dependent survival as basic starting model ($\Phi_{\text{age+year}}$). This model was subsequently used for the analysis of directional, stabilizing, and disruptive selection on colour PC1, PC2 and PC3. In a first step we tested whether nestling plumage coloration predicts long-term survival (Table 1C). Only the two models including PC1 ($\Phi_{\text{age+year+PC1+PC1}^2}$ and $\Phi_{\text{age+year+PC1}}$) fitted the data similarly well as the basic model, but $\Delta$QAIC ($\Delta$QAIC between the model in focus and the basic model) was 0.1 and 0.3, respectively, indicating that the two models were not significantly better than the basic model. Similarly, the models including plumage coloration as age-dependent effect fitted similarly well or worse than the basic model (Table 1D). Neither brood size nor body condition improved the model (Table 1E,F). However, hatching date was a significantly better predictor of survival than the basic model ($\Delta$QAIC $\geq$ 2.1; Fig. 1) and it predicted long-term survival better than 1-year survival ($\Delta$QAIC = 2.1, Table 1E,F). Models including two of the three or all three covariates fitted less well (bigger QAICc values) than the model including hatching date only (QAICc: 244.1–248.2; $\Delta$QAIC = 2.5–4.1). Including hatching date and plumage coloration simultaneously into the model and generating all possible and statistically meaningful models revealed that only the model including hatching date as a linear and quadratic term, and PC1 as a quadratic term, showed lower QAIC values than the model including hatching date alone (Table 1G). This model was however not significantly different from the model including hatching date only ($\Delta$QAIC = 0.1). All models including hatching date and PC2 or PC3 as a covariate fitted less well than the model including hatching date only.

Discussion

Young birds often die at high rates shortly after fledging. In great tits for example 47% of the fledglings die within the first 20 days after leaving the nest and in 65% of the cases predation was the cause of mortality (Naef-Daenzer et al., 2001). This indicates that predation is one of the most important selective pressures acting on young birds after fledging and contributing importantly to the low first-year survival (e.g. 7.4% in our study population; Fitze et al., 2004). Consequently, the nestling’s plumage coloration may have evolved as to render a fledgling cryptic (e.g. Butler & Rohwer, 1989; Götmark & Olsson, 1997). Because the nestling’s survival is lowest early after fledging (Naef-Daenzer et al., 2001), because fledglings moult their body feathers in autumn (Svensson, 1992; Jenni & Winkler, 1994) and because their new plumage coloration is not correlated with the nestling’s plumage coloration (Fitze et al., 2003a), we might expect that the plumage coloration affects first-year rather than long-term survival. However, our models including the plumage parameters as an age-dependent covariate acting on first-year survival only (Table 1D) did not fit the data better than the basic model and the only model with lower AIC that included the covariates body condition, clutch size and/or hatching date and the colour parameters (Table 1G), was similarly well fitting as the model including the hatching date only. Similarly, models including the original variables hue, saturation and brightness as linear and/or quadratic term were not fitting better than the models including hatching date only (all QAICc $\geq$ 241.7, analysis not shown). Thus our results suggest that predation or parental feeding preferences impose currently no or only weak selective pressure on the carotenoid-based nestling coloration of great tits. In contrast to our results, Götmark & Olsson (1997) show in great tits that red coloured compared with control nestlings died at a higher rate post-fledging because of predation. The different results of the two studies may be explained by the red plumage coloration that is more visible than the naturally occurring yellow coloration or by differences in predation pressures between populations and/or study years. However, only specific experiments may disentangle between the different hypotheses.

The fact that we do not find evidence for selection acting on the yellow nestling’s plumage coloration neither before (Tschirren et al., 2005) nor after fledging (this study) raises the question why nestlings show this
coloration. One explanation might be that the yellow plumage coloration of the adult great tits is selected and that the nestling's plumage coloration developed as a correlated response (Falconer & Mackay, 1996; Lynch & Walsh, 1998), which is selection neutral and thus maintained until now. However, the nestling's yellow plumage coloration may have evolved because of past selection, which may have led to the optimal plumage coloration, that as a consequence is no longer under selection nowadays (Jennions et al., 2001; Candolin, 2003; for a review). For example, early coloration may have provided nonoptimal camouflage (see discussion on Götmark & Olsson's findings) and predators may have preferentially caught the well-visible birds, thus selecting for cryptic coloration. Plumage coloration may then have adapted to a coloration providing optimal camouflage, which got genetically fixed and is no longer under selection nowadays (e.g. Candolin, 2003 for a review).

Although our results provide evidence for these hypothesis we cannot exclude that weak selection may act on the carotenoid-based nestling's plumage coloration after fledging, because detecting weak selection usually requires huge sample sizes ($N \geq 1000$). Further, selection may differ between habitats, geographical regions or it may differ in time. Because the study included two different years and because there were no interactions between the plumage coloration and the study year (all $\Delta QAI C < 2$) the later hypothesis is unlikely, leaving the possibility open that in other study areas selection on the carotenoid-based nestling plumage coloration might be present.

The results further indicate that in our forest stabilizing selection is acting on hatching date with an optimal hatching date on 10 May. This finding is consistent with earlier studies (e.g. Verhulst & Tinbergen, 1991; Brinkhof et al., 1997; Svensson, 1997) and it is as well consistent with studies showing that the benefits of early hatching are limited by food availability (Drent & Daan, 1980; Van Noordwijk et al., 1995) and with studies showing that late hatching broods are negatively selected for due to reduced food availability (Silamakka, 1998) and/or increased predation pressure (Naef-Daenzer et al., 2001).

In conclusion, our study reveals that the carotenoid-based nestling plumage coloration of great tits is currently not or only under weak natural selection, since on none of the three colour parameters detectable short- or long-term survival selection was acting. Our study therefore indicates that nowadays neither predators nor parents are imposing strong selective pressures on the nestling's plumage coloration. This suggests that past selection pressures, or correlated selection may have led to its evolution.

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