Effects of fat reserves on annual apparent survival of blackbirds *Turdus merula*

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Summary

1. Fat reserves are stored energy that may help birds survive periods of harsh winter weather. This hypothesis predicts that annual apparent survival is higher for birds with large fat reserves than for birds with few or no fat reserves in winter.

2. Blackbirds (*Turdus merula* Linnaeus) were ringed in central Italy from 16 November to 20 February during 1990–2001. Fat scores were recorded for each bird. We used these capture–mark–recapture data for 1703 blackbirds to estimate the effect of large fat reserves on annual apparent survival, while controlling for transients, using computer programs SURVIV and MARK. Probability of birds retaining large fat reserves, or retaining few fat reserves, over 2 successive years was also estimated.

3. Birds with large fat reserves did not have higher estimated annual apparent survival than birds with few fat reserves (*ϕ*large = *ϕ*few = 0.595, SE = 0.043), inconsistent with our prediction. No effects of age, sex or year were detected on annual apparent survival. Birds with few fat reserves in any given year tended to have few fat reserves the following year (*ψ*few→large = 0.332, SE = 0.052). Birds with large fat reserves in any given year were unlikely to have large fat reserves the next year (*ψ*large→few = 0.585, SE = 0.080).

4. Large fat reserves may not increase annual survival of blackbirds wintering in central Italy. Winter weather in our study area may be too mild to effect survival. Alternatively, increased predation risk associated with large fat reserves may counteract any benefits of reduced starvation risk.

Key-words: blackbird, capture–recapture analysis, fat reserves, survival, wintering.

Introduction

Fat reserves are the most important source of stored energy in passerines (Blem 1990, p. 99).

Birds in general, with high energy reserves in winter, may have higher fitness than birds with low energy reserves. Such an increase in fitness might be achieved through higher survival during periods of harsh weather (Blem & Shelor 1986; Rogers 1987; Blem 1990; Witter & Cuthill 1993), higher survival during spring migration (Blem 1980) or higher reproductive output in the following breeding season (Ankney & MacInnes 1978; McLandress & Raveling 1981; MacInnes & Dunn 1988). In non-breeding passerines, fat reserves generally increase until mid-winter and decline thereafter (Haftorn 1992; Waite 1992; Pravosudov & Grubb 1997; Cresswell 1998). An increase in fat reserves during cold periods may provide energy overnight, or for the duration of a winter storm, thereby reducing risk of starvation (Blem 1976; Blem & Pagels 1984; Blem 1990; Lahti et al. 1998). Low fat reserves may also reduce survival by reducing the ability of passerines to escape predators because flying draws energy from fat (Berger & Hart 1974; Blem 1990, p. 61). Alternatively, extremely high fat reserves may increase risk of predation through reduced manoeuvrability or increased exposure time (Lima 1986; McNamara & Houston 1990; Witter, Cuthill & Bonser 1994; Pravosudov & Grubb 1997).

A positive correlation exists between body condition and annual survival of adult female greater white-fronted geese, *Anser albifrons frontalis* (Schmutz & Ely 1999) and survival of nesting great tits, *Parus major* is correlated positively with body weight (Tinbergen & Boerlijst 1990). However, we are unaware of previous studies reporting a relationship between annual survival...
and body condition or fat reserves of any passerine species. We examined the hypothesis that large fat reserves increase fitness in blackbirds (*Turdus merula* Linnaeus), a common passerine wintering throughout much of Europe. We estimated the effect of large fat reserves on annual apparent survival of blackbirds using long-term ringing data collected in a Wintering Bird Project. The project followed the standardized field protocol agreed upon by the European Union for Bird Ringing (EURING) (see www.euring.org). Our a priori predictions were that birds with high fat reserves have higher annual apparent survival than birds with low fat reserves and that birds with high fat reserves during one year are likely to have high fat reserves the following year.

**Materials and methods**

Blackbirds were ringed in central Italy at the Presidential Estate of Castelporziano, a protected area covering approximately 6000 hectares located 20 km south of Rome (41°44′N–12°24′E). The vegetation in the study area consists mainly of forest of broad-leaved species, including *Quercus ilex*, *Quercus cerri*, *Quercus robur*, *Quercus suber*, *Quercus farnetto*, *Pirus pinea*, Mediterranean scrub, domestic pine, large grazing areas and oats farming (Anzalone, Lattanzi & Lucchese 1991). The roost is located in a patch of wood dominated by *Quercus cerri* Linnaeus and *Quercus robur* Linnaeus, mixed with *Erica arborea* Linnaeus, *Pistacia lentiscus* Linnaeus and *Pyrus piriaster* Burgsd.

Blackbirds were captured weekly using mist-nets and constant trap effort throughout the year during 1990–2001. We restricted our analysis to birds ringed before 0800 h during 16 November–20 February. Start and end dates were the 2 days on which sunrise in Rome was 0700 h in the autumn and winter of 1995–96. All newly captured birds were marked individually with a unique metal leg ring. Sex and age of each bird was determined based on plumage characteristics (Svensson 1992).

Subcutaneous fat reserves were estimated for each bird each time it was captured, except when caught repeatedly on the same day. Field estimates of fat reserves were based on the Kaiser scale (Kaiser 1993), a scale of 0–8, with 0 meaning no fat was present and 8 meaning much fat was present. We classified all birds as having either relatively few fat reserves (Kaiser scale = 0–2) or relatively large fat reserves (Kaiser scale = 3–6). We caught no birds with fat scores of 7 or 8. If an individual bird was captured more than once within a season, we used its mean fat reserve score. Only five birds were classified differently than would have been the case based on their first capture within a given season.

Multi-state multinomial models were created using program MARK (White & Burnham 1999) to estimate mean annual apparent survival ($\phi$), capture probabilities (p), and probability of change in, or movement between, fat reserve classes ($\psi_{\text{large-to-small}}$, $\psi_{\text{small-to-large}}$). For additional descriptions of multi-state models, how they work, their structure and their potential applications see Hestbeck, Nichols & Malecki (1991), Nichols & Kendall (1995) and Hines (1998).

A potentially large proportion of passerines captured in mist-nets may be transients which are unlikely ever to be recaptured (Pradel et al. 1997). The presence of transients may bias survival estimates low. Furthermore, if most transients have large (or few) fat reserves, and transient probability is not estimated, we might conclude erroneously that annual apparent survival differs between fat reserve classes when no difference actually exists. Chi-square tests using program RELEASE (Burnham et al. 1987) suggested transients were present, at least for adult females [test 3.SR, $P_{\text{adult females}} = 0.11$, $P > 0.31$ for other age–sex classes (Lebreton 2001)].

Therefore, we modified the multi-state design of Hines (1998) to include a transient term by combining Brownie & Robson’s (1983) Model 2 with Hines’s (1998) **mSURVIV**. This approach works by allowing annual apparent survival of newly banded birds ($\phi_t$) to differ from annual apparent survival of birds recaptured ($\phi_i$) that same year. Brownie & Robson’s (1983) Model 2 and the transient model in **mSURVIV** (Pradel et al. 1997) are the same model related in any given breeding season by:

$$(1 - \zeta) = [1 - (\phi_1/\phi_2)],$$

where: $(1 - \zeta) =$ transient probability in **mSURVIV**.

For example, if $\phi_t = 0.20$ for adults banded in breeding season $i$ and $\phi_i = 0.80$ for recaptured adults in breeding season $i$, then the estimated transient probability $(1 - \zeta)$ for adults banded in breeding season $i$ is $(1 - 0.25) = 0.75$ and resident probability $\zeta$ is 0.25. A standard error of $\zeta$ was estimated using the delta method (Seber 1982).

A general model was constructed that allowed annual apparent survival the first year after banding to differ between sexes ($s$), between fat reserve classes ($c$) and among years ($t$), $\phi_{i-cst}$, and allowed annual apparent survival in subsequent years to differ between sexes and between fat reserve classes ($\phi_{i-t}$). Transient probability and annual apparent survival are confounded for immature birds (Pradel et al. 1997). Our data set was too small to allow both adult transient probabilities and immature survival probabilities ($\phi_{t}$) to vary among years in the most general model. Instead, our most general model included the same apparent survival probabilities for immatures and adults within each fat reserve class the first year after banding ($\phi_{i-cst}$). Annual apparent survival of adults ($\phi_{t}$) and immatures ($\phi_{i}$) were estimated separately in some models by defining all birds as residents ($\phi_t = \phi_i$ for adults); a transient probability $[1 - (\phi_1/\phi_2)]$ could be estimated in other models by constraining apparent survival equal for adults and immature birds ($\phi_{t} = \phi_{i}$). Annual apparent survival of recaptured birds ($\phi_i$) was not allowed to vary among years due to sparse data.
Movement probabilities in the most general model varied by sex, age and fat reserve class ($\psi_{few-large, sa, \text{fat}}$), but too few data were available to allow movement probabilities to vary among years. In our subscript notation $\psi$, mean $\psi_{\text{large} \rightarrow \text{few, sa}}$. Capture probabilities ($p$) varied by sex, year and fat reserve class ($\rho_{\text{fat}}$) in the most general model.

We programmed our most general model into $\text{surviv}$ (White 1983) and estimated model fit, $\hat{c}$, using 100 bootstrap simulations (Anderson, Burnham & White 1994; Burnham & Anderson 2002).

An a priori set of 17 competing models was constructed (Table 1). Akaike’s Information Criterion, adjusted for small sample size and over-dispersion (QAIC$_c$, Anderson et al. 1994; Burnham & Anderson 2002), was used to select the most parsimonious model. Capture probability was strictly a nuisance variable, so this parameter was modelled first. The primary interest was effect of fat reserve class on survival, so $\phi$ was generally modelled last. Temporal variation in $\phi$ was examined early due to sparse data. Akaike weights were calculated for each model and model-averaged parameter estimates were examined if no single model had an Akaike weight $> 0.95$ (Anderson et al. 2001; Burnham & Anderson 2002).

## Results

We included 1703 blackbirds in this analysis. The encounter history matrix is available from the authors. A mean of 170.3 (SD = 87.5) birds were ringed each field season during 1990–2000. Of these birds, 50.7% were females, and 53.0% were adults when ringed. Most birds (64%) had few fat reserves when ringed. A total of 136 blackbirds (8.0%) were recaptured at least once. Of all captures used in this study, 13.9% were in November, 23.3% in December, 46.9% in January and 15.8% in February.

Little overdispersion was detected with the most general model ($\hat{c} = 1.168$). Test 3.5m and Test 2 in $\text{release}$ were not significant for any age–sex class ($P > 0.30$). The lowest QAIC$_c$ model (QAIC$_c$ = 1302.945, Akaike weight $= 0.40$, Table 1) suggested that fat reserves did not affect mean annual apparent survival ($\hat{\phi}_{\text{large}} = \hat{\phi}_{\text{few}} = 0.595$, SE = 0.043). Nor did apparent survival vary between sexes, between age classes or among years. Apparent survival estimates for resident birds from the lowest QAIC$_c$ model, were virtually identical to model-averaged survival estimates ($\hat{\phi}_{\text{female}} = 0.598$, SE = 0.049; $\hat{\phi}_{\text{male}} = 0.597$, SE = 0.050).

Transients were indicated ($\hat{\phi}_{\text{large}} = \hat{\phi}_{\text{few}} = 0.259$, SE = 0.053) by the lowest QAIC$_c$ model. Indeed, most birds were transients ($1 - \hat{c} = 1 - 0.259/0.595 = 0.565$, SE = 0.098). Transient probability was equal for birds with large fat reserves and birds with few fat reserves. Model-averaged estimates of apparent survival the first year after banding ($\hat{\phi}_{\text{female}} = 0.264$, SE = 0.062; $\hat{\phi}_{\text{male}} = 0.260$, SE = 0.061) were similar to those given above from the lowest QAIC$_c$ model.

### Table 1. Competing models of mean annual apparent survival for blackbirds captured during 16 November–20 February 1990–2000 near Rome, Italy. Each model allows for estimation of a transient term $[1 - (\hat{\phi}_t/\theta_t)]$ unless stated otherwise.

<table>
<thead>
<tr>
<th>Model no.</th>
<th>Model</th>
<th>QAIC$_c$</th>
<th>Delta QAIC$_c$</th>
<th>QAIC$_c$ weights</th>
<th>Parameters</th>
<th>Deviance</th>
<th>Model description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$\phi, \phi_r, \rho, \psi$</td>
<td>1302-94</td>
<td>0</td>
<td>40</td>
<td>14</td>
<td>376-01</td>
<td>Model 10; survival constant, transients present</td>
</tr>
<tr>
<td>2</td>
<td>$\phi_{1-t}, \phi_{2-t}, \phi_r, \rho, \psi$</td>
<td>1303-98</td>
<td>1.04</td>
<td>24</td>
<td>15</td>
<td>375-02</td>
<td>Model 9; transients present</td>
</tr>
<tr>
<td>3</td>
<td>$\phi, \phi_r, \rho, \psi$</td>
<td>1304-55</td>
<td>1.60</td>
<td>18</td>
<td>15</td>
<td>375-58</td>
<td>Model 10; survival probability varies by fat reserve class</td>
</tr>
<tr>
<td>4</td>
<td>$\phi, \phi_r, \rho, \psi$</td>
<td>1306-12</td>
<td>3.18</td>
<td>0.08</td>
<td>16</td>
<td>375-12</td>
<td>Model 10; survival probability varies by sex; transients present</td>
</tr>
<tr>
<td>5</td>
<td>$\phi, \phi_r, \rho, \psi$</td>
<td>1306-47</td>
<td>3.53</td>
<td>0.07</td>
<td>16</td>
<td>375-47</td>
<td>Model 10; survival varies by fat reserves; transients present</td>
</tr>
<tr>
<td>6</td>
<td>$\phi, \rho, \psi$</td>
<td>1310-99</td>
<td>8.04</td>
<td>0.01</td>
<td>13</td>
<td>386-08</td>
<td>Model 1; no transients</td>
</tr>
<tr>
<td>7</td>
<td>$\phi, \rho, \psi$</td>
<td>1312-15</td>
<td>9.20</td>
<td>0.00</td>
<td>14</td>
<td>385-21</td>
<td>Model 4; no transients</td>
</tr>
<tr>
<td>8</td>
<td>$\phi, \rho, \psi$</td>
<td>1312-53</td>
<td>9.59</td>
<td>0.00</td>
<td>14</td>
<td>385-60</td>
<td>Model 5; no transients</td>
</tr>
<tr>
<td>9</td>
<td>$\phi, \rho, \psi$</td>
<td>1313-08</td>
<td>10.13</td>
<td>0.14</td>
<td>14</td>
<td>386-14</td>
<td>Model 6; survival varies between age classes; no transients</td>
</tr>
<tr>
<td>10</td>
<td>$\phi_{1-t}, \phi_{2-t}, \rho, \psi$</td>
<td>1313-28</td>
<td>10.33</td>
<td>0.00</td>
<td>20</td>
<td>374-11</td>
<td>Model 11; movement does not differ between sexes</td>
</tr>
<tr>
<td>11</td>
<td>$\phi_{1-t}, \phi_{2-t}, \rho, \psi_{\text{sa}}$</td>
<td>1316-72</td>
<td>13.78</td>
<td>0.00</td>
<td>22</td>
<td>373-46</td>
<td>Model 12; movement does not differ between age classes</td>
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<tr>
<td>12</td>
<td>$\phi_{1-t}, \phi_{2-t}, \rho, \psi_{\text{sa}}$</td>
<td>1321-66</td>
<td>18.72</td>
<td>0.00</td>
<td>26</td>
<td>370-18</td>
<td>Model 13; transient term does not vary among years</td>
</tr>
<tr>
<td>13</td>
<td>$\phi_{1-t}, \phi_{2-t}, \rho, \psi_{\text{sa}}$</td>
<td>1356-99</td>
<td>54.04</td>
<td>0.00</td>
<td>62</td>
<td>329-89</td>
<td>Model 16; p varies among years</td>
</tr>
<tr>
<td>14</td>
<td>$\phi_{1-t}, \phi_{2-t}, \rho, \psi_{\text{sa}}$</td>
<td>1371-03</td>
<td>68.08</td>
<td>0.00</td>
<td>72</td>
<td>322-38</td>
<td>Model 16; p varies by sex and year</td>
</tr>
<tr>
<td>15</td>
<td>$\phi_{1-t}, \phi_{2-t}, \rho, \psi_{\text{sa}}$</td>
<td>1375-62</td>
<td>72.68</td>
<td>0.00</td>
<td>62</td>
<td>348-53</td>
<td>Model 13; survival varies between ages; no transients</td>
</tr>
<tr>
<td>16</td>
<td>$\phi_{1-t}, \phi_{2-t}, \rho, \psi_{\text{sa}}$</td>
<td>1375-82</td>
<td>72.87</td>
<td>0.00</td>
<td>92</td>
<td>283-32</td>
<td>Most general model</td>
</tr>
<tr>
<td>17</td>
<td>$\phi_{1-t}, \phi_{2-t}, \rho, \psi_{\text{sa}}$</td>
<td>1412-40</td>
<td>109-45</td>
<td>0.00</td>
<td>53</td>
<td>404-49</td>
<td>Model 16; p is constant</td>
</tr>
</tbody>
</table>
Blackbirds with large fat reserves in a given year were unlikely to have large fat reserves the following year \((\psi_{\text{large-large}} = 0.585, \text{SE} = 0.080)\). Birds with few fat reserves in a given year were likely to have few fat reserves the next year \((\psi_{\text{few-few}} = 0.332, \text{SE} = 0.052)\). Model-averaged movement probabilities were identical to those given above from the lowest QAIC\(_2\) model.

In our best model, capture probabilities varied among years, but not between sexes or fat reserve classes. Mean annual capture probability was \(\bar{\psi} = 0.176 (\text{SE} = 0.037)\).

Models 1–3 were the only models with an Akaike weight > 0.10. Model 2 included age-specific survival \((\hat{\psi}_{\text{A1}} = 0.237, \text{SE} = 0.054; \hat{\psi}_{\text{A2}} = 0.595, \text{SE} = 0.043; \hat{\psi}_{\text{A}} = 0.284, \text{SE} = 0.063)\) and a transient term. Model 3 was identical to Model 1 except that resident probability was allowed to differ between birds with large fat reserves \((\hat{\psi}_{\text{large-l}} = 0.241/0.598 = 0.403, \text{SE} = 0.103)\) and birds with few fat reserves \((\hat{\psi}_{\text{few-f}} = 0.273/0.598 = 0.456, \text{SE} = 0.107)\).

Models 1–5 were relatively simple in structure and included a transient effect. Model 5 was the lowest QAIC, model to include an effect of fat reserves on apparent survival of resident birds. However, in this model the point estimate of apparent survival was higher for birds with few fat reserves \((\hat{\psi}_{\text{few-f}} = 0.630, \text{SE} = 0.106)\) than for birds with large fat reserves \((\hat{\psi}_{\text{large-l}} = 0.543, \text{SE} = 0.167)\). Models 6–17 had virtually no support. Generally these models included annual variation in apparent survival, sex-specific survival or movement probabilities, or absence of a transient effect.

### Discussion

We found no evidence that high fat reserves increase annual apparent survival of blackbirds wintering in central Italy, nor did we detect evidence that blackbirds in our study area strive to achieve or maintain high fat reserves. Perhaps in harsh winter climates birds with high fat reserves may realize higher fitness than birds with few fat reserves. However, Rome has a Mediterranean climate with relatively warm wet winters. Perhaps winter climate in our study area is too mild to affect blackbird survival. Furthermore, carrying unnecessary fat reserves could have an adverse effect on survival by increasing susceptibility of birds to predation (Lima 1986; Houston & McNamara 1993; Bednekoff & Houston 1994; Witter, Cutthill & Bonser 1994). As such, perhaps large fat reserves have no advantage for blackbirds wintering in central Italy. We caution, however, that our annual sample size and number of recaptured birds was relatively small, and our resident and movement probabilities, in particular, had large standard errors.

Model 5 suggested weakly that large fat reserves may actually reduce annual apparent survival of blackbirds, one prediction of optimal fat reserve models (Lima 1986; Houston & McNamara 1993; Bednekoff & Houston 1994). Our Model 5, however, had little support (Akaike weight = 0.07). Unfortunately we had too few recaptures to include three fat reserves classes in our study to estimate if apparent survival might be highest with an intermediate level of fat reserves as predicted by optimization models (Bednekoff & Houston 1994).

The lowest QAIC, model with an effect of age on apparent survival (Model 2) suggested that immature birds had much lower apparent survival than adults. However, survival and transient probabilities for young birds were confounded in this model, biasing the survival estimate low. Note that this model, with \(\hat{c} = 1.035\), could not be derived from our general model.

Most mortality of young passerines is thought to occur before their first fall migration (Magrath 1991). Blackbirds are practically fully grown by their first winter (Cramp 1988), and they breed in their second spring (Snow 1958a). This may explain partially why we did not detect a difference in apparent survival of young and adult birds in our lowest QAIC, model.

We detected no difference in apparent survival of male and female blackbirds. Females appear to perform most, but not all, incubation (Snow 1958b; Cramp 1988), and both sexes feed nestlings (Chamberlain, Hatchwell & Perrins 1999). Further, the two sexes are similar in size and males are not brightly coloured (Cramp 1988). As such, neither sex appears significantly more prone to higher predation risk associated potentially with providing parental care or with bright plumage colouration. Hatchwell, Chamberlain & Perrins (1996) also did not detect a difference in annual apparent survival of male and female blackbirds in their study in Britain.

Fat reserves are dynamic, and can change during the day (Cresswell 1998). We controlled for diurnal change in fat reserves by restricting our analysis to birds captured before 08.00 h, \(\leq 1\) h after sunrise during the ringing period. Fat reserves in wintering blackbirds also vary among months, tending to be highest in mid-winter (Cresswell 1998). However, use of mean fat reserves changed the fat reserve classification for only five of 164 birds from that based on their first capture in a given year.

Body condition might be a more quantitative covariate for similar survival modelling efforts in the future. Fat scoring is only a fair index of total body fat, and the ability to assign fat scores varies among ringers (Krementz & Pendleton 1990). We doubt that observer differences in fat scoring influenced our results significantly, however, because we grouped fat scores into only two broad categories. Body condition could not be estimated in this study because we did not have data on tarsus length, beak length or wing chord for all recaptured birds (Merilä & Svensson 1997; Cichoń, Oljniczak & Gustafsson 1998). Muscle may be a better indicator of body condition than fat and could be considered in future studies (Chandler & Mulvihill 1992; Gosler & Carruthers 1999).

When ringed most birds in our study had fat scores of 2 (41.9\%) or 3 (23.7\%) on the Kaiser scale. This
relatively small difference in fat reserves for many birds might be partially responsible for our not detecting an effect of fat reserves on apparent survival. Adding additional years of data to the analysis or increasing field effort in the morning would probably not change the proportion of birds with a score of 4–6 on the Kaiser scale.

We speculate that ringing blackbirds as they fly to their evening roost might provide a more robust estimate of effects of fat reserves on survival if night is a period of high energetic stress.

Future examination of interesting large-scale ecological hypotheses concerning avian energetics should be possible using either fat reserves or body condition in combination with multistate modelling by including a spatial component. Ringing stations within regions could be grouped, and regions could be considered a factor in the modelling process, thereby enabling estimation of differential dispersal, as well as survival, of birds with different levels of fat reserves.

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