Survival of suburban blackbirds *Turdus merula* varies seasonally but not by sex

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Survival is a key demographic parameter in bird populations yet remarkably little is known about the seasonal pattern of survival. Mortality may increase as a result of breeding behaviour, harsh environmental conditions, resource limitation or any combination of these; knowing which is important for understanding the ecology of population change. We analyse an intensive ten-year colour marking programme of European blackbirds *Turdus merula* to estimate seasonal and sex-specific survival rates. The annual survival rate (0.67) was similar to that produced from analyses of dead recoveries across Britain, but within year variation was significant. Survival rates were lowest during the early part of the breeding period and highest in the autumn, but there was little difference between the sexes. Understanding this pattern of variation is important in interpreting both life-history variation and the mechanisms of population change.

Benjamin Franklin noted that "in the world nothing can be said to be certain except death and taxes"; birds don't face taxes, but they do face death from a remarkable array of factors. Such factors may relate to the bird's activities, for example, breeding is likely to be a costly exercise (e.g. Williams 1966, Reznick 1985), or simply because of the environment they are in, for instance temperate winters are often harsh with limiting resources leading to increased mortality (e.g. van Balen 1980, Robinson et al. 2007). However, although much has been published on annual survival rates in birds, there is a dearth of information on the timing of mortality. As a consequence, those interested in life-history variation have tended to assume mortality occurs during the breeding period (e.g. Owens and Bennett 1994, Liker and Székely 2005), while those concerned with population ecology have more often assumed greatest mortality in the non-breeding period (e.g. Kanyamibwa et al. 1990, Peach et al. 1999, Robinson et al. 2004). The actual timing of this mortality, though, is critical in understanding both ecological and the evolutionary processes affecting populations as very different drivers may operate in each season (e.g. Newton 1998). Furthermore, the timing of mortality may vary by sex: females bear more of the cost in relation to parental care and are often subdominant in foraging hierarchies so suffer from higher mortality in many species (e.g. Promislow et al. 1992).

Despite the importance of the timing of mortality for population dynamics, there are remarkably few studies explicitly quantifying differences in mortality at different periods (Nilsson 1982, Sillett and Holmes 2002). This is likely to be due, in large part, to the practical difficulties of measuring survival seasonally. Firstly, an intensive programme of trapping and monitoring is required throughout all seasons; secondly, separating emigration from mortality is difficult unless the scale of the study is greater than the scale over which individuals disperse; and thirdly, a general assumption of survival models is that the period of marking is short relative to the period over which survival is measured. Thus, Nilsson (1982) was only able to estimate survival rates in his population of the nuthatch *Sitta europaea* by making the reasonable, but possibly incorrect, assumption that his study birds were entirely sedentary, while Sillett and Holmes (2002) measured survival over the breeding and wintering periods, when birds were resident, for (probably different) populations of migratory black-throated blue warbler *Dendroica caerulescens*, but derived migration mortality by difference from annual estimates.

In this paper, we present seasonally specific survival rates for European blackbirds *Turdus merula* from a ten-year study of colour marked individuals using mark-recapture methodologies to account for variation in detectability and the presence of dispersing individuals. In particular, we test whether survival rates are lower during the breeding (when behaviour may predispose individuals to mortality) or non-breeding (when environmental conditions may be harsher) seasons. We also test whether, as predicted by life-history theory, females have lower survival rates than males.

Methods

The study site was a suburban garden on the outskirts of Thetford (52° 24′N, 0° 43′E), a small town in south-eastern England. The garden is approximately 20 m by 20 m and consists of areas of grass lawn bordered by planted shrubs and trees and is surrounded by other, similar, gardens. Windfall apples were provided freely in the garden and visiting Blackbirds were caught in a 'whoosh' net (Bub 1996) throughout the year between March 1998 and Feb 2008. This colour-ringed population of blackbirds was established between 1996 and 1998 and subsequent catching occurred on an ad hoc basis when un-ringed birds were observed. Birds were observed from a point in the house from where most of the garden could be seen in a single view.

On capture, each bird was fitted with a numbered metal ring and three colour rings in a unique combination allowing the bird to be identified visually without subsequent captures. Each bird was aged (as either in its first-year or as a second-year and older) and sexed according to plumage characteristics (Svensson 1992). Breeding birds were determined by observed nesting behaviour or the presence of a cloacal protuberance (males), or brood patch (females). Because there is likely to be significant natal dispersal, we consider survival in adult birds only (i.e. those in their second calendar summer or older, Snow 1958); birds ringed as juveniles entered the study when they were first observed after March 1 in the calendar year following hatching. Sightings of colour-ringed individuals in the study garden were noted on an ad hoc basis throughout the year, mostly in the early mornings; sightings away from the garden were excluded in order to minimise variation in resighting probability.

For most blackbirds in this population egg-laying begins in late March (although males start singing and setting up territories in February and a few do start laying earlier) and pairs generally raise 2 or 3 clutches. Each successful nesting attempt lasts about thirty days (incubation + fledging), with young remaining dependent for up to three weeks after fledging (Snow 1958). Thus, the breeding season runs through into July, after which adults commence a post-breeding moult, which is completed during September (Ginn and Melville 1983). We divided the year into six two-month periods (1 Jan.–28 Feb., 1 Mar.–30 Apr., ..., 1 Nov.–31 Dec.), and assumed birds survived from the mid-point of one interval to the mid-point of the next. Thus survival was estimated separately for the early and late parts of the breeding (1 Apr.–31 May, 1 Jun.–31 Jul.), post-breeding (1 Aug.–30 Sept., 1 Oct.–30 Nov.), and non-breeding (1 Dec.–31 Jan., 1 Feb.–31 Mar.) periods.

Although British breeding birds are largely sedentary, birds from northern and central Europe are partial migrants and many spend the winter in the eastern counties of Britain (Chamberlain and Main 2002). To exclude these winter immigrant birds, we consider only individuals which were recorded in breeding condition on any capture occasion (not just the first). Initial testing (using U-Care, Choquet et al. 2005) suggested that a simple Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992) fitted the data poorly (sum of tests: $\chi^2_{290} = 681.9$, P < 0.001). Much of this lack of fit appeared to stem from the presence of temporary emigration (transience) amongst marked birds. To account for this finding we split the sample into two groups, those birds recorded in at least one non-breeding (Nov.–Feb.) period (resident birds) and those never recorded during this time (emigrant birds, i.e. birds breeding near the study site but which disperse away from it in winter); note immigrant blackbirds from elsewhere (those never recorded in breeding condition) have been excluded above. This successfully accounted for the transience in the population (test for transience: z = 0.37, P = 0.35) and the fit of this model was better ($\chi^2_{352} = 459.9$, P < 0.001), although there remained evidence of trap-dependence amongst resident birds (z = −10.98, P < 0.001).

One of the general assumptions of mark-recapture modelling is that the period of marking (and re-sighting) should be short relative to the period over which survival is measured (Williams et al. 2002), however, simulation studies have shown that, provided there is no systematic change over the study, biases introduced by violating this assumption are relatively small (Smith and Anderson 1987, O'Brien et al. 2005). As there was no change in recording effort over time, and individual blackbirds were frequently observed several times in a given time period, we assume birds survived from the mid-point of one time interval to the mid-point of the next two months later.

Survival rates were estimated separately for the two groups (residents and emigrants) and were modelled as a function of two-month time period, calendar year and sex. We considered models in which temporal variation in survival was either additive (seasonal variation was parallel between years) or independent (pattern of seasonal variation differed between years). We follow Lebreton et al. (1992) in using subscripts to denote model terms, those that vary additively (in parallel) are joined with a '+' and those that vary independently by a '.'. Similarly, recapture probability, separately for the two groups, was modelled as function of these three variables and also as a linear function of the number of days on which any marked birds were observed as a measure of sampling effort. Survival probability during the first time period following capture was modelled separately and was effectively a measure of transience (Hines et al. 2003). For models in which survival and/or reporting rates were related to two month periods some parameters for emigrant individuals were not estimable as they were not observed in the non-breeding period, so the number of model parameters was calculated accordingly. All models were fitted and the most parsimonious models selected on the basis of AICc. All models (n = 54) were fitted using the R (R Development Core Team 2008) package RMark (Laake and Rexstad 2008) as an interface to Mark (White and Burnham 1999).

Results

Of 2 131 adult birds colour-ringed in the study site, 630 (30%) were recorded in breeding condition, but of these birds, 65 (10%) were never observed in any winter period (Nov. through Feb.) despite often being recorded in more than one breeding period. There were relatively few sightings of colour-ringed birds away from the ringing

site, with most (85%) sightings from distances of 3 km or less, though one individual was reported in three consecutive winters in a garden 365 km to the south-west (in Newton Abbott, Devon). The average re-sighting rate per period of resident birds was 0.51 ± 0.01, but the most parsimonious model (for all forms of survival model) was one in which re-sighting rate differed in each two-month time period, but did not differ between sex (comparing models with lowest AIC for $p_{group.period.year}$ with any other form of p, $\Delta AIC > 68$), so all models referred to include re-sighting probability characterised in this way.

There was clear support for a model with consistent seasonal variation in survival, but with average survival differing between years (Table 1). The average annual survival rate for resident birds was 0.687 ± 0.026 (from φ_{group}, equivalent daily survival rate [dsr] = 0.9990). Survival rates varied within the year (Fig. 1a), with survival rates being lowest during the early breeding season (Apr./May: two month survival rate 0.883 ± 0.018, dsr = 0.9980), and highest in the period immediately following breeding (Aug./Sep.: 0.990 ± 0.025, dsr = 0.9998, estimates from model $\varphi_{group.period}$). This pattern of seasonal variation was consistent between years (comparing model $\varphi_{group.(period + year)}$ with $\varphi_{group.period.year}$ $\Delta AIC = 111.6$), but there was some variation between years, particularly during the breeding period, survival rates in the post-breeding period appeared to vary less. Apparent survival rates of emigrant birds were, unsurprisingly, much lower (0.469 ± 0.084 from ϕ_{group}) as they will also include a component of dispersal.

There was only limited support for differences in survival between the sexes (Table 1) and annual survival rates for females (0.690 ± 0.038, dsr = 0.9990, from model $\varphi_{group.sex}$) and males (0.685 ± 0.036, dsr = 0.9990) did not differ. Survival of females (0.881 ± 0.032, dsr = 0.9979, from model $\varphi_{group.month.sex}$) did appear to be lower than that of males (0.929 ± 0.025, dsr = 0.9988) during the late breeding period, when most birds would have been caring for fledged young (Fig. 1b), but again this difference was not significant (t = 1.18, P > 0.05).

Discussion

The annual survival rate (0.687 ± 0.026) observed here is similar to that obtained from recoveries of dead birds ringed in Britain and Ireland (0.650 ± 0.003, Siriwardena et al. 1998). This suggests that dispersal between breeding attempts of more than a few hundred metres (and so outwith the ambit of the focal garden) is low in the study population, and equally that the survival rates presented

Table 1. Most parsimonious models of survival rates of adult blackbirds. In all models, survival (φ) was modelled separately for resident and emigrant birds (group) as a function of two-month period (see text), calendar year and sex, the three models with lowest AICc are given. Resighting probability (p) varied between time periods but not by sex ($p_{group.period.year}$) in each of these models.

Model	Parameters	Delta AICc	AICc wt	Deviance
$\varphi_{Group.(period + year)}$	116	0	0.966	4065.8
$\varphi_{Group.(period.sex + year)}$	124	6.7	0.033	4052.7
$\varphi_{Group.period}$	100	16.7	<0.001	4118.0
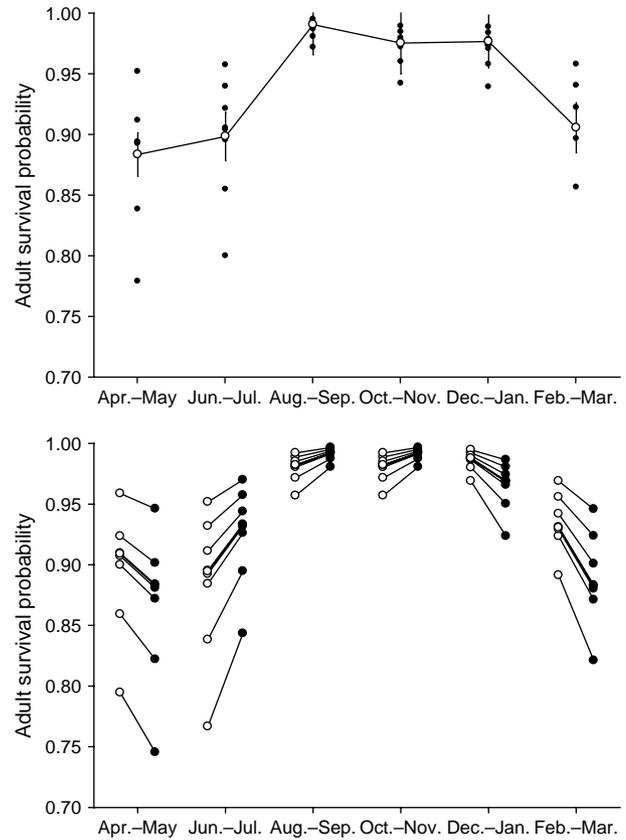
Figure 1. Temporal variation in survival of adult blackbirds. (a) Survival for each two-month time period from the most parsimonious model ($\varphi_{period + year}$), open symbols connected by lines indicate average survival by period (bars indicate ± 1 SE), closed symbols the year-specific estimates. (b) Survival for each period for males (closed) and females (open) symbols (from model $\varphi_{period.sex + year}$). Points for each sex are offset for clarity, lines connect estimates from the same year.

here are likely to be representative of 'true' survival rates. If anything, the survival rates of birds in this study may be higher due to the presence of 'artificial' feed, however, an estimated 30% of British blackbirds occur in similar human habitats (Gregory and Baillie 1998), so this situation is likely to be representative for a significant proportion of the population. Indeed it is perhaps surprising that survival rates are not increased more by the presence of relatively abundant food. Studies have shown that supplemental feeding has greatest effect only when resources are otherwise limiting (e.g. Brittingham and Temple 1988). There is much still to be understood about how survival, and other demographic parameters, vary between habitats and locations.

In this study, most mortality (58%) of blackbirds occurred during the breeding season (combined survival rate Apr.–Jul.: 0.79 ± 0.04). Mortality during the winter (survival Dec.–Mar.: 0.88 ± 0.04, 33%) was much lower and mortality during the autumn (survival Aug.–Nov.: 0.97 ± 0.05, 9%) very low. This confirms the work of Batten (1978) who simply tabulated recoveries of dead blackbirds and found a remarkably similar seasonal pattern of mortality (for the period 1961–70, survival Apr.–Jul.: 0.82; Aug.–Nov.: 0.96; Dec.–Mar.: 0.88). There were no

particularly severe winters during our study, which may have lead to a relatively high over-winter survival rate although blackbird survival is not apparently particularly sensitive to winter conditions (Robinson et al. 2007). Interestingly, mortality was lowest during the period when most birds would have been moulting, which is often considered a costly exercise (e.g. Hemborg and Lundberg 1998), however resources are unlikely to be limiting at this time, so birds may be able to remain in habitats where the risk of predation is lower, so the demographic cost (in terms of reduced survival) of moulting may actually be small even though it is energetically expensive. High mortality during the summer may reflect increased predation pressure from sparrowhawks *Accipiter nisus* and other predators, which are also trying to raise young; females are likely to be particularly vulnerable as they provide most parental care, though this hypothesis only received limited support from our results.

Life-history theory suggests that reproduction is likely to be costly, both in terms of parental-care provision and intra-sexual competition (Clutton-Brock 1991, Andersson 1994), although co-variation with individual quality may mean such costs can be hard to detect from demographic data (Reznick 1985, Cam et al. 1998). In general, mortality appears to be higher in female birds (Promislow et al. 1992). While we found no difference, Siriwardena et al. (1998) modelling national ring-recovery data, did find small, but significant, differences in survival rates between male and female blackbirds. Moreover, female survival was lower only during periods when the population was stable or declining, so it may be that differences in survival are only manifested when resources are scarce or limiting (possibly not the case in this study, although predation pressure was unknown). Understanding such variation in patterns of individual survival will be necessary if we are to accurately predict the effects of environmental drivers on population change.

Siriwardena et al. (1998) found that annual adult survival rates of blackbirds were 5% lower during the period of decline (0.630 compared 0.667 during a period of stable population trend), and similarly 3% higher (0.686) during a period of population increase. It is remarkable that the survival rates presented here are so similar to those quoted by Batten (1978), suggesting there has been little long-term change in survival rates, despite an essentially linear reduction of 30% in the index of breeding numbers between the mid 1960s and mid 1990s (Baillie et al. 2007). However, long-term declines can be precipitated by reductions in vital rates over relatively short periods of time when those rates are density-dependent (Green 1999). Understanding such interactions between seasonal resource availability and demographic traits throughout the year across the urban-rural gradient is a key area of research in determining how avian populations adapt to increasingly human-dominated land-scapes (e.g. McGowan 2001).

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