Empirical evidence of senescence in adult damselflies (Odonata: Zygoptera)

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Summary

1. Age-dependent increases in mortality have been documented in a variety of species of insect under laboratory conditions. However, while strong statistical evidence has been presented for senescence in vertebrate populations in the wild, we know little about the rate and shape of senescence in wild populations of insects.

2. Odonates (damselflies and dragonflies) provide excellent candidate species for evaluating demographic senescence as they are large enough to be marked individually and they are easily re-sighted without recapture. The prevailing opinion – based entirely on qualitative examination of the declines in log numbers alive with time since marking – is that odonates exhibit age-independent daily survivorship.

3. Here, we examine mark–recapture data on the Azure Damselfly *Coenagrion puella* over two consecutive seasons. For the first time, we evaluate and compare the fit of quantitative models that not only account for weather-dependent daily variation in daily re-sighting rates, but also age-dependent variation in daily survivorship.

4. Models with age-dependent declines in daily survivorship provide a more parsimonious explanation for the data than similar models without these age-dependent effects. In general, models in which mortality increases in an exponential (Gompertz) fashion explain the mark–recapture sequences more efficiently than a range of alternative models, including those in which mortality increases as a power function (Weibull) or reaches a plateau (logistic). These results are indicative of a general senescent decline in physiological functioning, which is particularly marked after 15 days as a mature adult.

5. Weather (temperature, sun and precipitation) and initial mite load influenced the probability of daily re-sighting. Weather and mite load also influenced daily survivorship, but their effects differed between seasons.

6. Overall, fitting models with age as an explicit covariate demonstrates that odonates do indeed senesce. This contradicts previously held assumptions that Odonata do not exhibit age-dependent survivorship in the wild.

Key-words: ageing, Akaike Information Criterion, field study, hazard, Makeham, MARK, Odonata, WINMODEST, Zygoptera

Introduction

Senescence is the progressive deterioration in the physiological state of an organism, marked by an increase in mortality and/or decrease in fecundity over time (see Partridge & Gems

2002; Hughes & Reynolds 2005; Rose 2005; Bonsall 2006; Williams *et al*. 2006; Sherratt & Wilkinson 2009 for recent reviews). While several authors have proposed that wild animals seldom live long enough in the field to exhibit senescence (Hayflick 2000; Kirkwood & Austad 2000), increases in age-specific mortality have been reported in natural populations of a variety of vertebrates (for a review see

Brunet-Rossinni & Austad 2006), including mammals (e.g. Promislow 1991; Gaillard *et al.* 2003) and birds (Ricklefs 1998; Reed *et al.* 2008). A similar body of research exists for laboratory-reared insects (see for example Rose 1984; Stearns *et al.* 2000; Carey 2001). These laboratory studies have generated a range of insights, including inspiring strategies to avoid the evolution of pesticide resistance in malarial mosquitoes (Read, Lynch & Thomas 2009). Yet while laboratory studies on insect senescence have been conducted for decades, the only detailed studies of senescence in wild insects have all been published within the past 8 years. Without such field studies it is not possible to evaluate the nature of selection acting on ageing under natural conditions, and the ecological validity of results from laboratory studies cannot be ascertained (Linnen, Tartar & Promislow 2001; Kawasaki *et al.* 2008).

Bonduriansky & Brassil (2002, 2005) investigated the lifetime reproductive success of antler flies, *Protopiophila litigata* (Bonduriansky). After monitoring individually marked adult males on a collection of antlers in the field, the authors found that both the survival rate and rate of mating of these flies declined over consecutive days. Kawasaki *et al.* (2008) likewise found field evidence of age-dependent increases in mortality males of *Telostylinus angusticollis* (Enderlein), a large neriid fly that forms mating aggregations on damaged tree trunks, but found no compelling evidence of senescence in females (possibly as a consequence of sample size). Dukas (2008) investigated senescence in a cohort of marked honeybee (*Apis mellifera* (L.)) foragers, and found that their daily mortality increased approximately exponentially with age, with an additional fixed age-independent mortality rate. Zajitschek *et al.* (2009a) have demonstrated in a near-natural enclosure experiment that female crickets of the species *Teleogryllus commodus* (Walker) exhibit greater rates of senescence than males, but that the change in female mortality arises at a more advanced age.

Odonata (damselflies and dragonflies) are widely regarded as excellent model species for investigating patterns of insect demography in the field, because they are large enough to be marked individually in their adult stages and they can be re-sighted without the need for physical recapture (Cordero-Rivera & Stoks 2008). Somewhat surprisingly, early mark–recapture studies of damselflies that surveyed for individuals throughout their entire adult life span showed little apparent evidence of a change in daily survivorship with age, at least when qualitatively examined (e.g. Fincke 1982; Banks & Thompson 1985, 1987) and the logarithmic survivorship curves have been described qualitatively as straight lines (e.g. Banks & Thompson 1985; Fincke 1986; Hamilton & Montgomerie 1989; Bennett & Mill 1995). Indeed, following at least 23 separate studies quantifying the lifetime reproductive success of cohorts of 20 species of odonates in the field (see Koenig 2008 for review), the current prevailing opinion (Cordero-Rivera & Stoks 2008) is that 'Survival curves for adult odonates are typically type II (age-independent mortality..)'.

Nevertheless, there remains some uncertainty in the literature. Bonduriansky & Brassil (2005) noted that the semilogarithmic plots shown by Banks & Thompson (1985) were suggestive of age-related declines in daily survival, while Cordero (1994) depicted survivorship plots with similar downward curvature for a range of damselfly species reared in the laboratory. In fact, analyses of mark–recapture data of the adults of some damselfly species have occasionally indicated age-dependent mortality. For example, Uéda & Iwasaki (1982) found that the daily mortality rate of *Lestes temporalis* (Selys) from days 6 to 60 (encompassing their protracted prereproductive period) was 0·004, yet this rate increased considerably after reproductive maturity was achieved (males 0·064, females 0·075 over days 81–100). Similarly, Corbet (1952) analysed mark–recapture data of *Pyrrhosoma nymphula* (Sulzer) (cf. Bennett & Mill 1995 above) and argued (page 212) that the 'results are consistent with a survival rate which decreases with age'. Collectively, observations such as these raise doubts over the strict linearity of the semi-log survivorship plots, and warrant a more quantitative examination of the age dependence of survivorship in odonates.

Here, we examine mark–recapture data on adults of the Azure Damselfly *Coenagrion puella* (L.) over two consecutive years, fitting a range of quantitative demographic models to the survivorship data and thereby directly evaluating age dependency of the daily mortality rate. Age dependent declines in the rate of egg-laying by female damselflies have already been established (e.g. Banks & Thompson 1987; Fincke 1988), so here we focus on evaluating the nature of any age-dependent changes in daily mortality. Damselflies have been the subject of a number of detailed mark–recapture analyses in the past (e.g. Andres & Cordero-Rivera 2001; Anholt, Vorburger & Knaus 2001). However, we believe that the present study represents the first quantitative evaluation of the extent and form of age-dependent changes in daily mortality rates in this taxon. We develop this analysis further to investigate the effects of interactions between age and environmental factors on survival.

Materials and methods

STUDY SPECIES AND FIELD EXPERIMENTS

Extensive mark–recapture surveys of adult male and female *C. puella* were conducted at a small pond in Queen Elizabeth Country Park, southern England (50°57′39″N, 0°58′41″W, 104 m above sea level) from 11 May 2005 to 30 July 2005 and from 17 May 2006 to 29 July 2006 (see Lowe *et al.* 2009 for further details). The pond (maximum dimensions 32 m long, 14 m wide, and 1·5 m deep; perimeter 75 m) is *c.* 1 km from any other permanent water body, significantly limiting the rate of population exchange with other ponds (Banks & Thompson 1985; Conrad *et al.* 1999). Three to six people were present at the study site every day from 09:30 hours local time until the last individual of *C. puella* was active (typically between 15:30 and 17:00 hours local time).

Unmarked individual adult *C. puella* were caught using a kite net, marked with a small dot of paint on the dorsum on the thorax (making them easier to see from a distance), sexed, and given a unique number on their left hind wing, which was also measured. Adult females of *C. puella* occur in two different colour morphs (androchrome and gynochrome, Van Gossum, Sherratt & Cordero-Rivera

Table 1. Demographic details of the mark–recapture study conducted on a population of *Coenagrion puella* over two breeding seasons

	2005 season		2006 season	
	Males	Females	Males	Females
Total number of individuals marked	263	159	352	259
Mean time between first and last recapture (days ± SE)	5·42 (±0·27)	8·18 (±0·64)	6·75 (±0·28)	11·61 (±0·53)
Maximum time between first and last recapture (days)	21	36	30	38

2008), so female morph type was noted. In addition, the number of mites (all belonging to the generalist ectoparasitic mite genus *Arrenurus* (Arrenuridae: Hydrachnida)) was counted on first capture. No attempt was made to capture immature individuals as they are easily damaged. Data on daily precipitation (mm), hours of sunshine (hrs) and minimum and maximum daily temperature (°C) were obtained for both the 2005 and 2006 field seasons, from a UK Meteorological Office weather station situated 37 km away from the study pond (Leckford, station identification code 852). Sample size information and basic demographic data are presented in Table 1.

Although days since marking represents the minimum age of an individual as a mature adult, the variability in age on first marking in the above studies may well add noise to any potential age-dependent relationship. To address this concern, we have analysed an additional mark–recapture experiment carried out on 'teneral' (newly emerged, reproductively immature adult) *C. puella* in May, June and July 1983 at Bungalow Pond in north-west England (National Grid reference SJ 234857) – see Banks & Thompson (1987) for full details. Teneral Zygoptera are relatively easy to recognize on the basis of their 'glassy' wings (Corbet 1999) but they are rarely used in field studies due to their fragility. In this study, teneral females were found by searching all vegetation around the pond twice daily from the first date of emergence (15 May). Individuals were taken to the laboratory where they were anaesthetized with carbon dioxide and marked with 'Humbrol' enamel paint on the thorax and a waterproof felt-tip pen ('Edding 404') on the wing. Two hundred and thirteen females were individually marked in this way within 1 day of emergence and subsequently released. The population was repeatedly surveyed throughout the flying season for the presence of these marked individuals.

ANALYSIS

Two complementary quantitative methods were employed to test for the presence of age-dependent daily mortality rates in *C. puella*. Note that while we use methods designed to assess variations in survivorship, it is the converse measure, changes in daily mortality rates that is generally taken to indicate senescence. Due to the nature of the analysis, we will likewise make reference to survivorship.

Method 1: multi-cohort analysis (mark software)

We fitted models for a combination of sex, age- and time-dependent changes in both daily survivorship and daily re-sighting probability using MARK v5.01 software (White & Burnham 1999). Age- and/or time dependency in parameter values was implemented in the first instance by modifying the appropriate parameter index matrix within MARK. Any constraints in the relationships among estimable parameters were then further imposed by modifying the underlying design matrix (DM). A sine link function was used when fitting all unconstrained, non-additive models (see below). However whenever covariates are entered into the model, the DM loses its simple identity format, and a logit link was generally assumed in these cases. The one exception arose when we sought to directly estimate parameters of Gompertz and Weibull functions (see below), where the LogLog link provided the most appropriate transformation (Gaillard *et al.* 2004, see below).

We use the standard MARK terminology when describing the fitted models (Lebreton *et al.* 1992), letting Φ represent daily (by time in season or age) survival probability, and p represent the daily re-sighting probability. We let t = time in season in days (with $t = 1$ as the start date of the study), x = time in days from an individual's first capture (a surrogate of age) and s = sex. The simplest model that could be fitted to the data treats daily survivorship and recapture rates as constant, represented by $\Phi(.) \, p(.)$. Full interactive models (e.g. $\Phi(t*s)$, $p(t*s)$) were fitted, as well as simple additive models comprising only main effects (e.g. $\Phi(t + s)$, $p(t + s)$) – in each case, the levels of the predictor variables were treated as categorical. The model(s) that most parsimoniously explained the observed capture histories were identified using Akaike's Information Criterion (AICc), modified by estimates of over-dispersion (QAICc) obtained through bootstrapping. With so many predictor variables, and ways of combining predictor variables, the total number of models that could be fitted to the data is enormous. Therefore, we screened the fit of a number of radically different models to identify the characteristics of the most parsimonious models, before exploring biologically motivated variants of these candidate models. At this juncture, individual size (wing length) and individual mite load (including squared terms to allow for nonlinearity) and daily weather variables were added to the model to investigate whether these covariates explained any additional variation.

To characterize the nature of age-dependent changes, we directly estimated the parameters of both exponential (Gompertz) and power (Weibull) demographic models within MARK, and evaluated whether they could parsimoniously explain variance above and beyond the equivalent model with no senescence. This was achieved by introducing age x (Gompertz) and log x (Weibull) as linear covariates, identifying the best fit model using the LogLog link function, and modifying the parameter estimates accordingly (see Gaillard *et al.* 2004). To verify that age-dependent mortality rates remained when other factors affecting mortality were accounted for, further models were constructed with the following individual variables included in the selection process: mite number (and mites squared) and size (and size squared), as well as daily weather covariates (sunshine, precipitation and mean temperature, i.e. the average of the minimum and maximum daily temperature).

Method 2: single cohort analysis (winmodest software)

While Gaillard *et al.* (2004) showed how the parameters of some simple demographic models could be estimated through MARK, we cannot fit more complicated demographic models using this approach. Moreover our analyses of senescence in tenerals could not utilize these methods because we lack the detailed recapture data. To address these challenges, we temporarily overlooked the time in the season at which individuals were marked and simply identified the

minimum length of time that each individual lived for from time of first marking (i.e. time of last capture – time of first capture). We then fitted several demographic models with known time-to-death distributions to these data, with the aim of estimating the underlying parameters and comparing the likelihood of the different fitted models. The analysis assumes that any seasonal variation in daily recapture rates and daily survivorship do not confound any age-dependent effects. Nevertheless, since the instantaneous measure of mortality is based on the ratio of numbers seen or inferred (due to subsequent re-sighting) alive on consecutive days, then the estimated mortality parameters derived from models fitted to disappearance times will be representative so long as the re-sighting rates are approximately constant. The 'collated cohort' approach reflects the standard way that odonate survivorship curves have been generated, and it has also been employed in previous studies testing for senescence in wild-caught insects (Bonduriansky & Brassil 2002; Dukas 2008; Kawasaki *et al.* 2008).

Five candidate models were fitted to each data set (Table 2), with the two sexes considered separately. The 'no senescence' model simply assumes that mortality rates are constant throughout an individual's lifetime. The Gompertz model assumes that mortality starts at rate *a* and increases exponentially with age at exponential rate *b*. Adding a constant *c* to the Gompertz equation introduces an additional term that represents a fixed rate of age-independent death – this model is known as the Gompertz-Makeham model. Some demographic studies have found that at very late ages, mortality rates decelerate and may even reach an upper plateau (Carey *et al.* 1992; Vaupel *et al.* 1998). The logistic model allows for such a sigmoidal change in mortality rate with age, yet setting the rate of mortality deceleration *s* to zero recovers the Gompertz. Likewise, adding a constant *c* to the logistic model introduces a source of age-independent 'extrinsic' mortality to this sigmoidal relationship: this model is known as the logistic-Makeham model.

The demographic analysis software WINMODEST 1.0.2 (Pletcher 1999) was used to identify the mortality model that most parsimoniously explained the observed mortality patterns, and to estimate the corresponding model parameters by maximum likelihood. As WINMODEST does not fit the null model of no senescence, we fitted the no senescence model based on our own MLE routines, developed in MATHCAD® *v*12 (cross-checked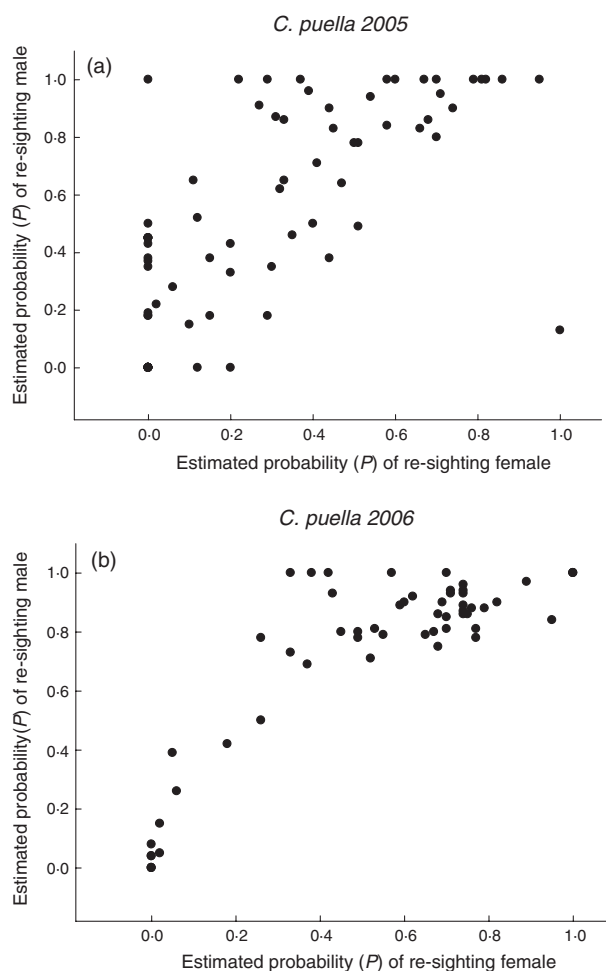 against WINMODEST by estimating the ML parameters of the Gompertz). Moreover, since the fitted models are partially nested, we used likelihood ratio tests (Hilborn & Mangel 1997) to evaluate the effectiveness of models of gradually increasing complexity in parsimoniously explaining the demographic patterns.

Results

MULTI-COHORT ANALYSIS – MARK

Re-sighting probabilities

To begin with we fitted one of the most general possible models $\Phi(s*t)$, $p(s*t)$ to both 2005 and 2006 data. The estimates of male and female re-sighting probabilities (p) over each day within the season were highly correlated in both years (2005 season: $r = 0.703$, d.f. = 75, $P < 0.001$; 2006 season: $r = 0.853$, d.f. = 54, $P < 0.001$; Fig. 1a,b), with male re-sighting rates significantly higher than that of females (paired t-test 2005: $t_{76} = 7.710$, $P < 0.001$; 2006: $t_{55} = 8.820$, $P < 0.001$). Forwards stepwise linear regression (signifi-

Table 2. Five inter-related hazard functions (age-specific hazard rate) and their associated probability density of time to death ($f(x)$). The corresponding likelihood of observing a given distribution pattern of time to death is $\prod_{i=1}^{n} f(x_i)$ where x_i is the time interval between first capture and last recapture for the ith individual, and n is the size of the marked population. Symbols: x, age; μ_x, age-specific hazard rate; a, initial mortality rate; b, exponential rate of increase with age; c, age-independent mortality; s, rate of mortality deceleration. For ease of presentation, we define $\omega(x)$ where $\omega(x) = 1 + \left(\frac{as}{b}\right)(e^{bx} - 1)$

Model	Hazard function	Probability density of time to death $f(x)$
No senescence	$\mu_x = a$	ae^{-ax}
Gompertz	$\mu_x = ae^{bx}$	$a\exp[bx - \frac{a}{b}(e^{bx} - 1)]$
Gompertz-Makeham	$\mu_x = ae^{bx} + c$	$(c + ae^{bx})\exp[-\frac{a}{b}(e^{bx} - 1) - cx]$
Logistic	$\mu_x = ae^{bx}\omega(x)^{-1}$	$ae^{bx}\omega(x)^{-(s+1)/s}$
Logistic-Makeham	$\mu_x = ae^{bx}\omega(x)^{-1} + c$	$e^{cx}\omega(x)^{-1/s}(ae^{bx}\omega(x)^{-1} + c)$

Fig. 1. The estimated probabilities of re-sighting marked male *Coenagrion puella* on a given day compared to the estimated probability of re-sighting marked females on the same day, in (a) the 2005 and (b) the 2006 summer field seasons. These estimates were derived from fitting the general time-dependent model $\Phi(s*t)$ $p(s*t)$ to the mark–recapture data.

cance probability < 0.05 required for entry, Type III sums of squares) indicated that the estimated daily re-sighting rates were also highly weather dependent, with the strongest relationships consistently being with hours of sunshine, and mean temperature controlling for sunshine (the weather variables themselves were partially co-linear). Thus, in 2005 female daily re-sighting probabilities increased significantly with both the amount of sunshine ($\beta = 0.037$, $P < 0.001$) and mean temperature ($\beta = 0.028$, $P < 0.001$) on that day, while male re-sighting probabilities also increased significantly with both the amount of sunshine ($\beta = 0.056$, $P < 0.001$) and mean temperature ($\beta = 0.018$, $P = 0.043$). Likewise, in 2006 female and male daily re-sighting probabilities increased with the amount of sunshine (female $\beta = 0.041$, $P < 0.001$; male $\beta = 0.045$, $P < 0.001$). The correlations with extrinsic weather variables are not only re-assuring, but suggest that a surrogate predictor based on sunshine and minimum temperature might satisfactorily explain variation in these re-sighting parameters (see below).

Survivorship estimates

Separate daily survivorship estimates (Φ) of males and females from the fitted model $\Phi(s*t)$, $p(s*t)$ were not significantly correlated over time in the season in 2005 ($r = 0.131$, d.f. $= 75$, $P = 0.257$) with a weak correlation in 2006 ($r = 0.264$, d.f. $= 54$, $P = 0.049$), although the daily estimates of female survivorship were on average higher than the daily male survivorship in both years (paired *t*-test 2005: $t_{76} = 5.052$, $P < 0.001$; 2006: $t_{55} = 3.854$, $P < 0.001$). The daily estimates of female daily survivorship in 2005 were uncorrelated with any of the five inter-related daily weather variables (precipitation, hours of sunshine, minimum temperature, maximum temperature, mean temperature), and no predictor was entered in the forwards stepwise regression. However, the estimate of male daily survivorship was positively related to the minimum temperature for that day ($\beta = 0.022$, $P = 0.009$). Analyzing the 2006 data, the forward stepwise regression stopped at models in which estimated female and male daily survivorship were both negatively related to the amount of sunshine (female $\beta = -0.005$, $P = 0.043$; male $\beta = -0.006$, $P = 0.045$).

Fitting another general model in which daily survivorship was age rather than time dependent $\Phi(s*x)$, $p(s*t)$ was similarly revealing. Not all parameters of the $\Phi(s*x)$ fitted model were estimable with any degree of confidence (extremely high standard errors) due to low sample sizes at advanced ages. However, in both 2005 and 2006 the estimable survival rates declined significantly with individual age (2005 males $r = -0.404$, d.f. $= 17$, $P = 0.086$; females $r = -0.658$, d.f. $= 17$, $P = 0.002$; 2006 males $r = -0.672$, d.f. $= 23$, $P < 0.001$; females $r = -0.730$, d.f. $= 30$, $P < 0.001$). Overall, the estimated male and female daily survivorship stayed relatively constant for approximately 15 days post-capture before falling (Fig. 2a,b).

Table 3 shows the key results from fitting models of every permutation of time dependent daily survivorship and re-
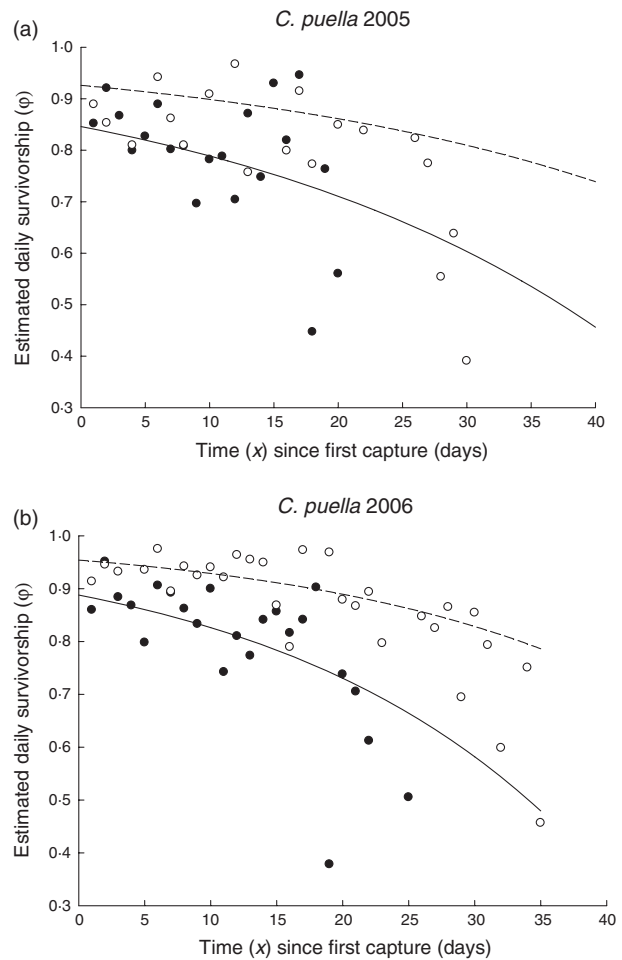
Fig. 2. The estimated daily probabilities of survival of male (filled circles) and female (open circles) *Coenagrion puella* as a function of the time since marking (first capture) in (a) the 2005 and (b) the 2006 summer field seasons. These estimates were derived from fitting the most general age-dependent survival model $\Phi(s*x)$ $p(s*t)$ to the mark–recapture data. Only parameters with standard errors less than 1 are shown. The lines show the best fit of the Gompertz model (solid, males; dashed, females) as estimated from fitting an additive sex and linear age-dependent model with LogLog link function (see Gaillard *et al.* 2004). Parameter estimates 2005: $a = 0.154$ (males), 0.074 (females), $b = 0.03154$; 2006: $a = 0.112$ (male), 0.046 (female), $b = 0.0439$.

sighting rates $\Phi(.|s|t|s*t)$ $p(.|s|t|s*t)$ and age-dependent daily survivorship and re-sighting rates $\Phi(.|s|x|s*x)$ $p(.s|x|s*x)$, as well as a selected number of combined age- and time-dependent models to both the 2005 and 2006 data. See Tables S2 and S3 (Supporting Information) for the full listing. Several key findings apply to both years. First, while $\Phi(s*t)$ $p(s*t)$ provides a better fit than $\Phi(s*x)$ $p(s*x)$, it is $\Phi(s*x)$ $p(s*t)$ that performs best of all the full models, and $\Phi(s*t)$ $p(s*x)$ performs worst of all. Along with the above relationships, this raises the possibility that daily survivorship may be predominantly age dependent, while re-sighting rates are predominantly time dependent. Secondly, we note that most parsimonious of all the full models in both years was $\Phi(s)$ $p(s*t)$. The high explanatory power of the multi-

Table 3. Some of the key models fitted to the 2005 and 2006 mark–recapture data. See Tables S1 and S2 (Supporting Information) for the entire suite of candidate models (66 in total). The table lists the quasi-likelihood Akaike information criterion (QAICc), the quasi-likelihood Akaike information criterion differences (ΔQAICc), the normalized quasi-likelihood Akaike information criterion weighted by number of parameters, and deviance values for each of the tested models. The estimated quasi-likelihood parameters $\hat{c} = 1.062$ and $\hat{c} = 1.034$ – each based on 100 simulated runs fitting $\Phi(s*t)\, p(s*t)$ – were used to adjust the QAICc values for the (slight) overdispersion in the original data in 2005 and 2006 respectively. Symbols: s, sex; x, age; x_3, three-parameter age term; t, time; β, rate parameter representing the use of age (or log age) as a covariate (as opposed to a multi-level categorical predictor)

Year	Model	QAICc	ΔQAICc	QAICc weights	Number of parameters	Deviance
2005	$\Phi(s + \beta x)\, p(s*t)$	3890·89	0·00	0·58	155	2203·03
2005	$\Phi(s + \beta \ln x)\, p(s*t)$	3891·81	0·91	0·36	155	2203·94
2005	$\Phi(s*x_3)\, p(s*t)$	3896·02	5·13	0·04	158	2200·92
2005	$\Phi(s)\, p(s*t)$	3898·10	7·21	0·02	154	2212·64
2005	$\Phi(.)\, p(s*t)$	3926·09	35·20	0·00	153	2243·04
2005	$\Phi(s + x)\, p(s*t)$	3947·36	56·47	0·00	189	2175·79
2005	$\Phi(s*x)\, p(s*t)$	3969·22	78·33	0·00	209	2146·68
2005	$\Phi(s + t)\, p(s*t)$	4008·38	117·48	0·00	219	2159·85
2005	$\Phi(s*t)\, p(s*t)$	4079·66	188·76	0·00	259	2123·70
2005	$\Phi(s*x)\, p(s*x)$	4766·12	875·23	0·00	111	3181·43
2005	$\Phi(s*t)\, p(s*x)$	4907·91	1017·01	0·00	240	3003·69
2006	$\Phi(s + \beta x)\, p(s*t)$	7177·00	0·00	0·97	115	4495·18
2006	$\Phi(s*x_3)\, p(s*t)$	7184·10	7·10	0·03	118	4495·85
2006	$\Phi(s + \beta \ln x)\, p(s*t)$	7190·24	13·24	0·00	115	4508·42
2006	$\Phi(s)\, p(s*t)$	7212·90	35·90	0·00	114	4533·22
2006	$\Phi(s + x)\, p(s*t)$	7217·65	40·65	0·00	151	4457·95
2006	$\Phi(s*x)\, p(s*t)$	7240·70	63·70	0·00	180	4417·00
2006	$\Phi(s + t)\, p(s*t)$	7246·04	69·04	0·00	167	4451·17
2006	$\Phi(.)\, p(s*t)$	7279·61	102·61	0·00	113	4602·07
2006	$\Phi(s*t)\, p(s*t)$	7315·83	138·83	0·00	215	4413·39
2006	$\Phi(s*x)\, p(s*x)$	9260·88	2083·88	0·00	129	6548·97
2006	$\Phi(s*t)\, p(s*x)$	9268·06	2091·05	0·00	204	6390·55

parameter $p(s*t)$ (compared to s or t alone) indicates that re-sighting rates vary considerably from day to day and between sexes. In 2005, the estimated daily survival rates of males and females were 0·833 (95% CI 0·813–0·852) and 0·904 (95% CI 0·887–0·919) respectively, while in 2006 the estimated survival rates of males and females were 0·862 (95% CI 0·847–0·875) and 0·930 (95% CI 0·920–0·939) respectively. These estimates are comparable to daily estimates of 0·86/0·83 (males) and 0·87/0·82 (females) for *C. puella* from two earlier studies in Switzerland (Anholt, Vorburger & Knaus 2001) and the UK (Banks & Thompson 1985) respectively.

Given the relative success of the model $\Phi(s*x)\, p(s*t)$ compared to other full interaction models, one might wonder why the age-independent model $\Phi(s)\, p(s*t)$, provided an even more parsimonious model in both years. Clearly the addition of a large number of parameters required to represent daily age-dependent changes in survivorship are not justified in terms of the additional explanatory power they bring, particularly when daily survivorship stays approximately constant for the first two weeks since capture. We therefore fitted three alternative models, incorporating age effects using reduced parameter models. First, we considered age classes via a three-parameter interactive model $\Phi(s*x_3)\, p(s*t)$ in which age was classified into three discrete classes of 1–10 days (young), 11–20 days (middle-aged) and 21+ days (old). In both the 2005 and 2006, the model $\Phi(s*x_3)\, p(s*t)$ was a marked improvement over the model $\Phi(s)\, p(s*t)$. We then

considered the fits of two constrained linear additive models: $\Phi(s + \beta x)\, p(s*t)$ – reflecting the Gompertz, and $\Phi(s + \beta \ln(x))\, p(s*t)$ – reflecting the Weibull, using the LogLog link function. In both 2005 and 2006 the Gompertz model provided the most parsimonious fit of all to the data, although the Weibull gave an almost as satisfactory fit in 2005. For 2005 the estimated Gompertz rate parameter (b, in the additive model assumed identical for the sexes) was 0·0315 (95% CI 0·0123–0·0508), while in 2006 the Gompertz rate parameter was 0·0439 (95% CI 0·0305–0·0573). Taken together it is clear that models with sex and age-dependent daily survivorship explain the variability better than comparable models without these age-dependent effects.

When further individual-based variables were included in the analysis, models with linear age-dependent daily survivorship were consistently superior to equivalent models without age-dependent daily survivorship, yet models with an individual age-squared component did not provide demonstrably better fits. The most parsimonious model in 2005 involved sex, age and mite-dependent daily survivorship (of quadratic form) and sex, sun, mean temperature, precipitation and mite-dependent (of quadratic form) re-sighting rates (see Table 4 for a summary and Tables S4 and S5, Supporting Information for the full listing). The most parsimonious model for the 2006 data was slightly simpler: survivorship was dependent on sex and age with no effect of initial mite load (linear or otherwise) and, while weather

Table 4. The fit of a range of models in 2005 and 2006 with survival and re-sighting rates constrained by linear combinations of weather (sun, mean temperature, precipitation), age (x), time in season (t), sex (s), mite load (m), wing size (size) and the square of these individual covariates (to encompass any nonlinearities). See Tables S3 and S4 (Supporting Information) for the entire suite of candidate models (43 in total). The bootstrap goodness of fit procedure for estimating $\hat{c}$ within MARK can only be applied to those models without individual covariates. Given that earlier estimates of $\hat{c}$ based on general models were c. 1 (see Table 3), we have not adjusted AICc values in this instance

Year	Model	AICc	ΔAICc	AICc weights	Number of parameters	Deviance
2005	$\Phi\,(s\,x\,m\,m^2)\,p(s\text{ sun temp prec }m\,m^2)$	4387·83	0·00	0·47	12	4363·65
2005	$\Phi\,(s\,x\,m\,m^2)\,p(s\text{ sun temp prec size }m\,m^2)$	4388·41	0·59	0·35	13	4362·20
2005	$\Phi\,(s\,x\,m\,m^2)\,p(s\text{ sun temp prec size size}^2\,m\,m^2)$	4390·44	2·61	0·13	14	4362·19
2005	$\Phi\,(s\,t\,t^2\,m\,m^2)\,p(s\text{ sun temp prec }m\,m^2)$	4392·21	4·39	0·05	13	4366·00
2005	$\Phi\,(s\,m\,m^2)\,p(s\text{ sun temp prec }m\,m^2)$	4399·01	11·18	0·00	11	4376·86
2005	$\varphi\,(s\,t\,m\,m^2)\,p(s\text{ sun temp prec }m\,m^2)$	4400·45	12·62	0·00	12	4376·27
2006	$\Phi\,(s\,x)\,p(s\text{ sun temp prec }m)$	8427·66	0·00	0·46	9	8409·60
2006	$\Phi\,(s\,x\,x^2)\,p(s\text{ sun temp prec }m)$	8428·97	1·31	0·24	10	8408·90
2006	$\Phi\,(s\,x)\,p(s\text{ sun temp prec }m\,m^2)$	8429·65	1·99	0·17	10	8409·58
2006	$\Phi\,(s\,x)\,p(s\text{ sun temp prec})$	8431·85	4·19	0·06	8	8415·81
2006	$\Phi\,(s\,x\,m)\,p(s\text{ sun temp prec})$	8433·55	5·89	0·02	9	8415·50
2006	$\Phi\,(s\,t\,t^2)\,p(s\text{ sun temp prec }m)$	8447·26	19·60	0·00	10	8227·19
2006	$\Phi\,(s\,t)\,p(s\text{ sun temp prec }m)$	8566·05	38·40	0·00	9	8488·00
2006	$\Phi\,(s)\,p(s\text{ sun temp prec }m)$	8474·42	46·77	0·00	8	8458·38

variables had a strong and demonstrable influence on re-sighting rates, the mites-squared term was unsupported. Parameter estimates for the gradients of the age term in linear models that included age were consistently negative. The best-fitting models in both 2005 and 2006 had re-sighting rates positively related to the number of hours of sunshine and mean temperature, yet negatively related to the amount of precipitation. The best supported models in both years involved initial mite burden as covariates (2005 – nonlinear effects on both survivorship and re-sighting probability, 2006 – linear effects on re-sighting only). Specifically, the parameterized quadratic model in 2005 indicates a maximum estimated survival with 30·9 mites on first capture and a maximum re-sighting probability with 30·5 mites on first capture (the mean mite load per individual on capture was 34·41, SE 1·82). In 2006, the re-sighting probability fell at an estimated rate of −0·00376 for each mite an individual initially carried.

### SINGLE COHORT ANALYSIS – WINMODEST

Figure 3a and b show the (log) decline in the numbers known (observed or inferred) alive with time from marking in the 2005 and 2006 field seasons. In both years, a slight downward curvature was evident, indicating accelerating mortality with increasing age. After fitting the five candidate models to the time-to-disappearance distributions, the Gompertz model provided the best fit in all cases except for the females in 2005 (Table 5). For males marked in 2005, the estimated Gompertz parameter of $b = 0·054$ (95% CI 0·032–0·091) was similar to that estimated through MARK (0·032, see above). Likewise, the estimated rates of male (0·053, 95% CI 0·037–0·077) and female (0·046, 95% CI 0·033–0·064) age-related increases in mortality in 2006 were similar to those estimated using MARK (0·044). Overall therefore, this method provides

further confirmation that *C. puella* tend to exhibit age-related declines in daily survivorship. Cursory examination of the semi-log plots for tenerals suggests a convex relationship (Fig. 4a), and the estimated instantaneous hazard rate likewise increases with time since first marking (Fig. 4b). After fitting the five candidate models to these teneral data, the Logistic-Makeham model provided the best fit overall (Table 5).

Discussion

In contrast to the results emerging from intensive studies on laboratory model insects, such as *Drosophila* sp., we know very little about patterns of natural mortality in wild insect populations (Bonduriansky & Brassil 2002). Longitudinal studies of marked or recognizable individuals provide one of the best ways of detecting senescence in the wild (Nussey *et al.* 2008), although large sample sizes are typically needed to detect senescence of mature adults when a high proportion of individuals die before they experience old age. Here we have analysed intensively three data sets on the demography of a damselfly species and find – contrary to previous assertions drawn from qualitative assessments of semi-log mortality plots – direct evidence of an increase in rates of mortality with chronological age. This pattern of age-dependent mortality remains evident even after controlling for other variables affecting mortality, such as weather and ectoparasites.

Many different candidate models are available to describe the rate and shape of senescence in free-living populations. Although the overall age-dependent increases in hazard were generally best explained by a simple exponential rise, there remains a high degree of variability, so the selection of a Gompertz model may be as much a function of its simplicity as the goodness of fit it provides. Although our sample sizes were reasonable for a field-based study over two consecutive
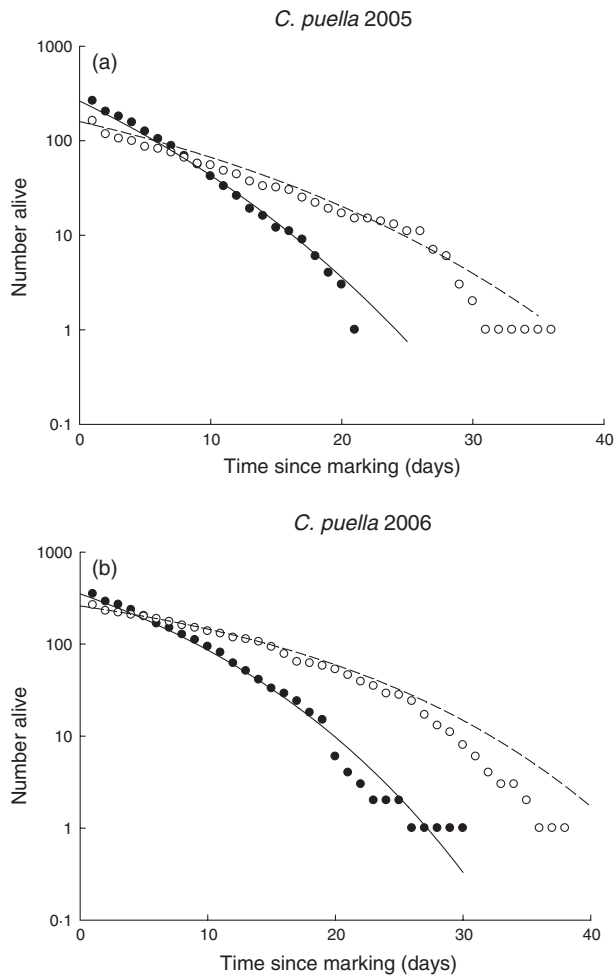
Fig. 3. Semi-log plots showing the decline in the number of marked male (filled circles) and female (open circles) *Coenagrion puella* seen or inferred alive over time since marking, in (a) the 2005 and (b) the 2006 summer field seasons. Fitted lines (solid, males; dashed, females) show the best fits of the Gompertz hazard model as translated to the cumulative survivorship curve (where $l_x = \exp((-a/b)* (\exp(b*x)-1))$, with parameters as given in Fig. 2 legend.

years, one source of this variability may be unavoidable binomial variance which increases as the available sample size of living individuals decreases. Bonduriansky & Brassil (2002) likewise found a high degree of scatter around their fitted Gompertz, with variance increasing with increasing age. The fit of the Gompertz-Makeham model by Dukas (2008) was

much more impressive ($r^2 = 0.93$), but here individual honeybees reside in hives which may provide more stable conditions than those experienced by non-social organisms.

Like many studies of senescence, we have limited our study to quantifying age-dependent mortality in adults. Moreover, we have used 'days since marking' as a surrogate of adult age (see Crespin *et al*. 2006 for simulation models which support the validity of this approximation).

While innovative methods now exist to control for unknown age (Müller *et al*. 2004; Zajitschek *et al*. 2009b) these methods necessarily assume a fixed population density and stable age structure, which are demonstrably invalid in our seasonal *C. puella* populations. Reassuringly however, our analysis of Banks & Thompson's 1983 data restricted to newly emerged tenerals (where age since emergence is known with certainty) yielded qualitatively similar results. While unmarked adults in our surveys are likely to be young when they first turn up to breed, maturation times can vary among individuals and the precise age of an individual on first marking will not be known. In *C. puella*, the mean lengths of the immature period for males and females have been estimated to be 13·2 (SE 0·22) and 16·5 (SE 0·34) days respectively (Banks & Thompson 1985), which coincides remarkably well with the step-wise increase in mortality observed in our teneral data set (Fig. 4b). Variability in the time to reproductive maturity may potentially add noise to the data, but it is clear that it has not been sufficient to obscure age-dependent effects – indeed, one could argue that age should be measured from the time maturity is reached, rather than time of emergence.

We distinguish daily re-sighting probability from daily survivorship probability, which is not always done in mark–recapture studies of odonates (Cordero-Rivera & Stoks 2008). The sex differences in estimated daily re-sighting rates may well arise as a result of a greater tendency of males to remain around ponds, in order to intercept females returning to the water. Zygopterans (damselflies) do not tend to fly in wet and/or cold weather, and re-sighting rates were correspondingly sensitive (in the anticipated directions) to the prevailing weather conditions. Intriguingly, the survival rates of *C. puella* were far less weather dependent, possibly because daily survivorship is more dependent on abiotic conditions summed over a number of days, rather than just 1 day. Nevertheless, in 2005 daily survivorship in males increased with minimum temperature, whereas in 2006 daily survivorship in males and females decreased with hours of sunshine.

Table 5. The maximum log likelihood of the best fitting models after fitting five candidate demographic models to the observed time-to-final disappearance distributions of *C. puella* (*C.p.*), along with the most parsimonious model (based on likelihood ratio tests)

Data	Fixed	Gompertz	GompMake	Logistic	LogMake	Recommended model (log-likelihood ratio test)
Male *C.p.* 2005	−709·47	−702·54	−702·54	−702·45	−702·45	Gompertz
Female *C.p.* 2005	−501·10	−501·08	−498·94	−501·08	−501·08	Fixed
Male *C.p.* 2006	−1022·25	−1009·10	−1009·10	−1008·97	−1008·97	Gompertz
Female *C.p.* 2006	−917·57	−900·74	−899·20	−900·74	−899·21	Gompertz
Female *C.p.* teneral 1983	−829·87	−748·45	−748·45	−730·63	−724·69	Logistic-Makeham

C. puella teneral females

C. puella teneral females
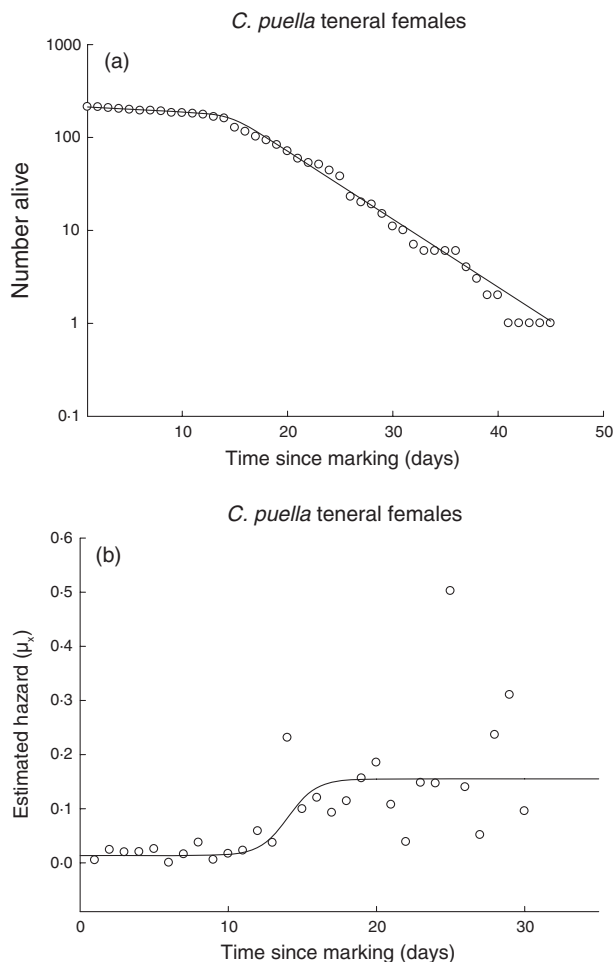
Fig. 4. Semi-log plots showing (a) the changes in the number of marked female *Coenagrion puella* seen or inferred alive over time since their emergence as tenerals and (b) estimated instantaneous hazard rate from the above data. The solid line shows the best fit of the Logistic-Makeham model to the data assuming a single cohort (see Tables 1 and 5) with parameters $a = 6.01 \times 10^{-8}$, $b = 1.04556$, $s = 7.38906$, $c = 0.01355$.

It was significantly cooler in the field season of 2005 compared to 2006 (average mean temperature 15·3 °C vs. 17·8 °C respectively, $t_{133} = 4.259$, $P < 0.001$; average minimum temperature 10·6 °C vs. 12·3 °C, $t_{133} = 3.169$, $P = 0.002$). One possibility therefore is that daily survivorship was reduced in the 2005 season on days with particularly low temperatures, while the high mating activity facilitated by warm sunny weather also reduced daily survivorship. Bonduriansky & Brassil (2005) found that male antler flies that lived longest tended to exhibit a lower average daily rate of mating, although the interval between mating also increased with age, so the relationship may not be causal. The idea that mating can reduce longevity has a long history in biology (see Kirkwood 2001 for a review), and on-going work is attempting to further tease apart the link between individual mating activity and survivorship in *C. puella*.

Differences in survival rates of males and females within the same species are widespread throughout the animal kingdom. In mammals for instance, females tend to live longer than males, while in birds the opposite is generally true (Promislow 2003). Here we found that the daily rates of mortality in female *C. puella* were lower than in males in both years (Fig. 3). Even males of non-territorial damselfly species like *C. puella* spend a large portion of their life span at the pond awaiting mating opportunities, while females tend to spend time foraging and maturing clutches of eggs, and it is possible that the differential mortality arises as a consequence of these different reproductive strategies. There is already evidence that the variation between odonate species in the relative mortality rates of males and females prior to reproductive maturity may be based on mating tactics (Anholt, Marden & Jenkins 1991; Anholt 2008). In vertebrates, intense male–male competition for mates can limit the number of breeding opportunities, which may in turn reduce selection pressure for longevity (Clutton-Brock & Isvaran 2007). In this way, the patterns of survivorship appear to be shaped by a combination of intra-sexual and inter-sexual conflict (Promislow 1992; Svensson & Sheldon 1998).

In addition to investigating demographic senescence, we were also able to analyse the effects of extrinsic variables on survivorship. A number of studies have concluded that ectoparasitic mites can affect longevity of odonates (see Forbes & Robb 2008 for review). However, the vast majority of these studies have not distinguished survival rates from recapture rates, and the reported relationships range from negative to neutral to positive. Our study found that there was a relationship between daily survivorship and the number of mites on first capture in 2005 but not in 2006. The intensity (counts of mites per infected individual) was significantly higher in 2005 than 2006, possibly as a result of the lower temperatures experienced in 2005 (Hassall *et al*. in press) and it may be that the effects of parasitism on survivorship are only evident under very high mite burdens. In addition, adult damselflies caught with high numbers of mites tended to be re-sighted less frequently in both 2005 and 2006. A high mite burden may conceivably create nutritional stress, causing such individuals to forage more, thereby making them less available for re-sighting at the pond. Body size has been shown to be weakly, positively correlated with longevity in male antler flies in the wild (Bonduriansky & Brassil 2005) and negatively correlated with longevity in laboratory populations of *Drosophila melanogaster* (Hillesheim & Stearns 1992). However, it is clear from our field data that adding size as a covariate is not justified in terms of the additional explanatory power it brings. A separate analysis of the mark–recapture data of females in our 2005 and 2006 studies (not shown) indicated no effect of morph type on survivorship or re-sighting rates (see also Andres & Cordero-Rivera 2001).

Taken together our results provide substantial evidence for the existence of age-dependent mortality rates in Odonata, contrary to previous suggestions. This senescence occurs both over the entire adult life span (as evidenced by the study on teneral female *C. puella*) and over only the reproductive adult life span post-maturity. Previous studies which have visually assessed semi-log survivorship plots should be re-evaluated quantitatively in the light of these results.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Fits of 33 models to the 2005 *C. puella* data.

Table S2. Fits of 33 models to the 2006 *C. puella* data.

Table S3. Fits of 22 models involving individual covariates to the 2005 *C. puella* data.

Table S4. Fits of 21 models involving individual covariates to the 2006 *C. puella* data.

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