

A comparative analysis of senescence in adult damselflies and dragonflies (Odonata)¹

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Abstract

Any population whose members are subject to extrinsic mortality should exhibit an increase in mortality with age. Nevertheless, the prevailing opinion is that populations of adult damselflies and dragonflies do not exhibit such senescence. Here we challenge this contention by fitting a range of demographic models to the data on which these earlier conclusions were based. We show that a model with an exponential increase in age-related mortality (Gompertz) generally provides a more parsimonious fit than alternative models including age-independent mortality, indicating that many odonates do indeed senesce. Controlling for phylogeny, a comparison of the daily mortality of 35 odonate species indicates that while male and female mortality are positively correlated, mortality tends to be higher in males of those species that exhibit territoriality. Hence we show for the first time that territoriality may impose a survivorship cost on males, once the underlying phylogenetic relationships are accounted for.

Keywords: ageing, Odonata, mortality, phylogeny, sex, territoriality.

Introduction

Actuarial senescence (“ageing”) is one of the most universal properties of organisms and is characterized by a population-level increase in rates of mortality and/or decrease in fecundity with chronological age (see Partridge & Gems 2002; Hughes & Reynolds 2005; Bonsall 2006; Williams *et al.* 2006; Sherratt & Wilkinson 2009 for reviews). Age-dependent increases in mortality have now been reported in natural populations of a range of vertebrates (for a review see Brunet-Rossini & Austad 2006), including mammals (e.g. Promislow 1991; Gaillard *et al.* 2003) and birds (Ricklefs 1998; Reed *et al.* 2008). While the detection of senescence is particularly challenging in short-lived species with high overall rates of mortality (Hayflick 2000; Kirkwood & Austad 2000), increases in age-specific mortality have nevertheless been reported recently in a variety of natural populations of short-lived insects (antler flies *Protopiophila litigata* (Bonduriansky), Bonduriansky & Brassil 2002, 2005; neriid flies *Telostylinus angusticollis* (Enderlein), Kawasaki *et al.* 2008; honeybees *Apis mellifera* (L.), Dukas 2008; crickets *Teleogryllus commodus* (Walker), Zajitschek *et al.* 2009a).

Adult odonates (damselflies and dragonflies) are good candidates for investigating actuarial senescence in the field, because they are large enough to be marked individually and they can be re-sighted without the need for recapture (Cordero-Rivera & Stoks 2008). However, until recently, the prevailing opinion was that odonates do not show actuarial senescence (e.g. Banks & Thompson 1985; Fincke 1986; Hamilton & Montgomerie 1989; Bennett & Mill 1995; Cordero-Rivera & Stoks 2008). This conclusion may have been somewhat premature however, since the vast majority of the above studies have based their conclusions simply on a qualitative assessment of the linearity of the logarithmic survivorship plots. Even those studies that have evaluated the fits of a wide range of different demographic models to odonate mark-recapture data using quantitative model selection criteria (e.g. Andres & Cordero-Rivera 2001; Anholt *et al.* 2001), have only rarely attempted to any fit demographic models that allow for age-dependent changes in mortality. Analyzing an intensive mark-recapture study of the damselfly

¹ Version of record can be viewed at the publisher and should be cited as: [SHERRATT, T. N., HASSALL, C., LAIRD, R. A., THOMPSON, D. J. & CORDERO-RIVERA, A. 2011. A comparative analysis of senescence in adult damselflies and dragonflies \(Odonata\). *Journal of Evolutionary Biology*, 24, 810-822.](#)

Coenagrion puella (L.) conducted over two separate years, Sherratt *et al.* (2010) recently fitted such models, and in so doing provided strong evidence of senescence in a damselfly under field conditions. The question remains however, whether many more examples of senescence in adult odonates have gone undetected, or whether this example of senescence in *C. puella* remains the exception rather than the rule. Here, we begin by fitting a range of demographic models to the log-survivorship plots depicted in a range of different mark-recapture studies of adult odonates, testing whether models with age-dependent mortality provide a superior fit to the data than models with age-independent mortality. Elucidating the shape of the senescence curves is not only helpful in documenting the precise nature of the age-dependent changes, but may also play a role in identifying the general proximate and ultimate mechanisms responsible for any observed pattern. For example, evolutionary theory predicts that population level accumulation of deleterious mutations (Medawar 1952), trade-offs between early- and late-life performance (Williams 1957; Kirkwood 1977), and decelerating selection for somatic repair (Gavrilov & Gavrilova 2001; Laird & Sherratt 2009) should all lead to actuarial senescence. While human mortality curves are Gompertzian (exponential) in form (Gompertz 1825), the simplest versions of reliability theory which assume gradual loss of redundant elements (Gavrilov & Gavrilova 2001) predict an initial near-Weibull (power) mortality function with an upper plateau, while evolutionary theories such as antagonistic pleiotropy (Williams 1957) can only explain asymptotic plateaus in mortality rates with some difficulty (Pletcher & Curtsinger 1998; Wachter 1999).

The nature of the mating systems differs dramatically among odonate species, with males of some species exhibiting high territoriality and males of other species exhibiting little or no territoriality, so our comparative approach has also allowed us to evaluate for the first time the implications of territoriality for overall differences in the rates of mortality between the sexes. Previous studies in a range of taxa such as lizards (e.g., Vanhooydonck *et al.* 2005; Lailvaux and Irschick 2007), indicate that male-male interactions in territorial species are more likely to escalate to fighting than in non-territorial species. Likewise, there is ample evidence that territorial male damselflies and dragonflies aggressively interact with one another in an energetically and physically demanding way, to an extent rarely seen in non-territorial males. For example, as Corbet (1999, p.449 and citations within) reports, while territorial male *Calopteryx* rarely fight directly, they frequently physically collide during territorial disputes, and they often can sustain damage to their wings and legs. In territorial libellulids, male territorial disputes can sometimes involve direct attacks including ramming and physical fighting including biting.

Earlier broad cross-species comparisons in other animal taxa have revealed that overall rates of mortality can indeed be shaped by the mating strategies that have evolved. For example, Promislow (1992) found that the degree of male bias in adult mortality in mammals was positively correlated with the degree of sexual size dimorphism. Similarly, Liker & Szekely (2005) conducted a phylogenetically controlled analysis of sex-specific adult mortality over 194 bird species and found that evolutionary increases in male-male competition were associated with male-biased mortalities. Our prior expectation was that territoriality would impose a relative cost on males in terms of reduced survivorship compared to females. This prediction was in part influenced by the anticipated greater energetic and physical demands imposed by maintaining a territory. However, our prediction was also motivated by the observation that many non-territorial damselfly species exhibit female-limited polymorphism, a phenomenon that is believed to have arisen in response to excessive harassment of females by males (Van Gossum *et al.* 2008). Since male harassment may well lead to a decline in female survivorship (Córdoba-Aguilar 2009), then the opportunities for harassment generated by lack of male territoriality may act to lower the survival rates of females compared to males.

Methods

Fitting of demographic models

We used VistaMetrix® (www.skillcrest.com) to extract cumulative survivorship data from the semi-log plots (log numbers alive or log proportion alive vs. time since marking) depicted in a range of different mark-recapture studies (summarized in **Electronic Appendix 1**). In all cases we attempted to take readings to the highest level of precision possible. Studies involving an initial marked sample size of less than 50 mature adult individuals of a given sex were not considered (for example, ruling out Bennett & Mill 1995 with $n = 24$ and 18 males and females, respectively). The semi-log plots were derived indirectly from the data presented by Pajunen (1962) and Tsubaki *et al.* (1997). **Figure 1** shows the semi-log plots we derived (points) as well as the best fitting models (continuous curves) – see below. We have complemented our analyses of extracted data with a quantitative analysis of the original tabular data of recaptures of males of *Pyrrhosoma nymphula* (Sulzer) (Corbet 1952).

We used the demographic analysis software WinModest 1.0.2 (Pletcher 1999) to identify the mortality model that most closely fits the observed mortality patterns, and to estimate the corresponding model parameters (see Min & Tatar 2006; Styer *et al.* 2007 for recent examples of this approach). Demographic models often represent death rates as the age-specific hazard (or instantaneous risk of failure) rather than the discrete-time probability of death (Gavrilov & Gavrilova 1991; Lee 1992). An estimate of this instantaneous rate of mortality μ_x at age x is approximated by:

$$\mu_x = -\ln\left(\frac{N_{x+1}}{N_x}\right) \quad (1)$$

where N_{x+1} / N_x estimates the fraction of the population alive at age x that also survives to age $x + 1$.

Note that if a constant fixed proportion of the marked population is unavailable for re-sighting on any given day, then equation (1) still estimates hazard rate, since the ratio of recaptures is unchanged.

The WinModest 1.0.2 software fits four inter-related models (**Table 1**) that may account for some of the observed changes in the age-specific hazard (see **Figure 2**). Estimates of the parameters of each model are derived by maximum likelihood estimation (MLE), and the most appropriate model chosen on the basis of log-likelihood (the less negative the log-likelihood, the better the fit). 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. Of the four candidate models, the Gompertz equation simply assumes that mortality starts at rate a and increases with age at exponential rate b . Adding a constant c to the Gompertz equation introduces 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. A fifth model, a single parameter “no senescence” model simply assumes that mortality rates are constant throughout an individual’s lifetime. Since 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® v12. Unfortunately in one field study (Koenig & Albano 1985) the fate of the oldest 5% of individuals were not depicted, so in this case the parameter estimates of the Gompertz and no-senescence models were based on fitting the appropriate cumulative survivorship curves by non-linear least squares (Ricklefs & Scheuerlein 2002).

Two features are immediately apparent from the semi-log plots we have collated (**Figure 1**). First, many of the plots exhibit a marked decline in apparent survivorship the day after marking (see Cordero-Rivera & Stoks 2008), which may arise as a consequence of slight damage during the marking process and/or as a consequence of stress-induced dispersal (Cordero 1994; Cordero-Rivera & Stoks 2008). To allow for these effects, we decided at the outset to look for evidence of age-dependent mortality starting the day after the first day of marking.

Second, the semi-log plots at each time step show, as might be expected, an increase in variance as the size of the surviving population diminishes. Although qualitative evidence of senescence is sometimes based on directly regressing age-specific mortality against age (see for example Hughes & Charlesworth 1994; Stearns & Kaiser 1996), the regression method alone is not a reliable test of senescence, because it does not incorporate information on the variances of estimated probabilities of survival (Slade 1995). One potential solution to the problem is to conduct a standard linear regression of hazard rate vs. age, yet weight the hazard rate by the square root of the number alive at age x (Promislow 1991). This weighting is appropriate because the standard error of binomially distributed data is proportional to $1 / \sqrt{n}$ where n is the sample size. Exploratory Monte-Carlo simulations covering population sizes and mortality rates typical of the above odonate examples (**Electronic Appendix 2**) show that while weighted linear regressions can produce slightly higher than the usual permissible type I error rate (rejection of H_0 of no senescence when true), they are considerably more reliable than unweighted regressions on the same data. As a first screening we have therefore cautiously applied weighted linear regression models to the data to test for significant changes of hazard with age. Strictly speaking equation (1) is only valid if the length of the time intervals is large enough to include at least one observed death. Therefore to be conservative, our direct estimates of hazard were not derived once the population ever reached such a small size that there was no change in the numbers alive on consecutive days. Despite all of these precautions, the weighted regression method simply provides a transparent alternative approach to evaluating the strength of evidence for senescence. Our primary method of analysis was that of maximum likelihood estimation coupled with log likelihood ratio tests – see above – since it is generally acknowledged that this approach involves less bias (Mueller *et al.* 1995; Pletcher 1999; Nussey *et al.* 2008).

Differences in overall mortality between species

While odonate populations may potentially show age-related increases in mortality, the overall average mortality (and hence longevity) of cohorts of odonates may differ between sexes of the same species and among species. Here we analyze data collated by Cordero-Rivera and Stoks (2008) detailing the estimated daily survival rate of males and females based on 53 mark-recapture studies of 35 species (**Electronic Appendix 3**). Although territoriality is something of a continuum – for example the coenagrionid *Pyrrhosoma nymphula* is only weakly territorial in adult stage – we simply classified each species as territorial or non-territorial, using Cordero-Rivera and Stoks' (2008) descriptions, which were assigned without regard to mortality rates.

To test for patterns in differential rates of mortality between the sexes we conducted a cross-species comparison of male mortality (= 1-estimated daily survivorship), employing the arithmetic mean mortality when multiple estimates had been made. Since mortality rates may potentially co-vary with mean species body size, we also included mean male abdomen length (in mm), using data compiled from a variety of sources (**Electronic Appendix 3**). Our first analysis involved fitting a General Linear Model (GLM Type III, simultaneous sums of squares) with presence/absence of male territoriality as a fixed factor and male size and female mortality as covariates, as well as a female mortality*territoriality interaction to allow the gradient of the fitted relationship between female and male mortality to differ, dependent on whether the species was territorial or non-territorial.

One key issue of particular concern in the above sets of analysis is the potential lack of independence of species data through shared phylogeny. For example, male *Calopteryx japonica* (Selys) and male *Calopteryx virgo* (L.) are both territorial damselflies and both species appear to exhibit higher male mortality than female mortality, yet the pairing of mortality and territoriality traits may be ancestral, so it is questionable whether they should be treated as providing independent data points (Harvey & Pagel 1991). An additional set of analyses which attempted to control for the phylogenetic effects was therefore performed.

Due to the absence of a well-supported phylogeny for the 35 species, a full phylogenetically controlled analysis was not possible. In its place, we present three complementary analyses. The first two methods account for hierarchical levels of classification but either ignore, or make simplifying assumptions about, the true phylogenetic distances. The third method (based on a reduced data set) incorporates current estimates of phylogenetic differences. Our first two approaches analysed the attributes of all 35 species in Cordero-Rivera & Stoks' (2008) review. The assumed phylogenetic relationships underlying these two analyses were based on O'Grady & May (2003), Rehn (2003) and Ware *et al.* (2007). **Figure 3a** shows how territoriality maps onto this phylogenetic tree, and demonstrates that territoriality is common on some branches of the phylogeny but not others. In our first attempt to control for phylogeny, male mortality, male size, female mortality and territoriality were entered separately as response variables in ANOVAs with genus nested within family, nested within suborder. Using the resulting residuals for each variable, we fitted the model "male mortality = territoriality + male size + female mortality + female mortality *territoriality". While this approach does not account for all phylogenetic autocorrelation, it does ameliorate the problem (Purvis, 2008). Our second approach fitted the same model to the same phylogeny, this time using the comparative generalised estimating equation function "compar.gee" in the APE package (Paradis *et al.* 2004; Freckleton 2009) in R (R Development Core Team, 2010) while making the simplifying assumption that the branch lengths were consistently 1.

Our third analysis was restricted to 16 species (6 territorial and 10 non-territorial) for which comparable genetic sequences were available (18S rRNA+5.8S rRNA+28S rRNA, see **Electronic Appendix 3 Table S3** for GenBank accession numbers). Sequences were aligned using MEGA4 (Tamura *et al.* 2007) and phylogenies constructed using the neighbour-joining method and 1000 bootstrap replicates. The model "male mortality = territoriality + male size + female mortality + female mortality*territoriality" was again fitted to the resulting (reduced) phylogeny (**Figure 3b**) using "compar.gee" in the APE package (Paradis *et al.* 2004).

Results

Both our comparisons of the fits of candidate demographic models, and our weighted linear regression analyses, indicated that a significant majority of odonate species surveyed exhibit significant increases in mortality with time from first marking (**Table 2**). Hazard rates do indeed appear to increase with age in many species (**Figure 2**). The three exceptions to this pattern were the damselflies *Ischnura elegans*, *Argia chelata* and the dragonfly *Plathemis lydia* – the available data on these species do not allow us to unequivocally reject the null hypothesis of no senescence. As might be expected these particular species have the lowest estimated exponential coefficient *b* after fitting the Gompertz – so small that inclusion of the parameter does not improve the fit (**Table 2**). Intriguingly, across all of the cases examined (with the exception of *Plathemis lydia* where parameters were necessarily estimated using NLLS) there was a significant negative correlation between the MLE estimates of *a* and *b* ($r = -0.526$, $df = 14$, $P = 0.036$ after fitting Gompertz to the additional three cases where no senescence represented the most parsimonious

model; $r = -0.367$, $df = 11$, $P = 0.218$ without these three cases), suggesting that populations with high initial mortality exhibited little sign of ageing, while those with low initial mortality show more rapid ageing.

Prior to phylogenetic control, male mortality was significantly positively related to female mortality (see **Figure 4**), but not male abdomen size (see **Table 3** for all significance tests). There was no significant effect of territoriality on male mortality and the female mortality*territoriality interaction was not significant. Using the nested ANOVA as a method for phylogenetic control, male mortality was significantly positively related to female mortality and positively related to territoriality, but abdomen size was not significant and neither was the female mortality*territoriality interaction. Very similar results (highlighting the significance of territoriality as a main effect increasing male mortality when controlling for phylogeny in the nested model) were obtained when the dependent variable was the continuity-corrected estimate of mortality, male hazard ($= -\ln(\text{daily survivorship})$). Moreover, when we fitted a phylogenetically controlled model to the entire phylogeny using the GEE method and assuming fixed branch lengths of 1, territoriality was consistently significant at least as part of the interaction, whether the dependent variable was male mortality or hazard. When the comparative GEE method was used on the restricted data set for which phylogenetic distances could be estimated, there were no significant relationships between male mortality and male size, female mortality, territoriality and the female mortality*territoriality interaction (**Table 3**).

Discussion

We fitted a range of models to the log-survivorship plots of a range of odonate species, and concluded, in contrast to the conclusions drawn in earlier papers, that the majority of these studies exhibit a degree of actuarial senescence (**Table 2**). Thus, adult odonates should no longer be treated as anomalous with respect to senescence. These conclusions were generally robust whatever the methodology we applied to detect senescence – whether it was through weighted regressions of daily hazard rates, or through the fits (and comparisons) of demographic models via maximum likelihood. Indeed, an alternative method of estimating model parameters – this time by non-linear least squares fitted directly to the cumulative survivorship plots – produced qualitatively identical results (**Electronic Appendix 5, Figs S2a,b**). Corbet (1952) had previously tentatively proposed that the results of his mark-recapture analysis of *P. nymphula* were consistent with a survival-rate which decreases with age – and our re-analysis of the data he presented confirms this suspicion. Not only do the estimates of hazard tend to increase with time since marking (**Figure 2**) but the downward curvature of a number of logarithmic survivorship plots is evident (**Figure 1**), which in itself is indicative of an increase in mortality with advancing age. This downward curvature is evident in a number of logarithmic survivorship plots on odonates in addition to the ones analyzed here, including the dragonfly *Sympetrum danae* (Sulzer) under natural and semi-natural conditions (Fig. 4 of Michiels & Dhondt 1989) and a range of damselfly species reared under laboratory conditions (Fig. 1 of Cordero 1994). However, the specific census points in each of these cases were not depicted, so they were not analyzed.

Of course, with the exception of Corbet (1952), all of our data were gleaned from published graphs as opposed to the raw data. Nevertheless our method of data extraction was highly repeatable in that when the same set of data was independently extracted by two different researchers the two data sets were highly correlated ($r > 0.99$ for all tested combinations of species, sex and morph). More importantly, our approach necessarily involved treating the entire population of marked individuals as a single cohort, even though they were marked on a range of days. The “single cohort” approach not only reflects the standard way that odonate survivorship curves have been generated and interpreted, but it has been extensively employed in previous studies on senescence in wild-caught insects (Bonduriansky & Brassil 2002; Kawasaki *et al.* 2008; Dukas 2008) on the basis that the prevailing weather conditions at the time of the study were sufficiently uniform to allow combining data in this way. Reassuringly, our earlier analyses

of the demography of the damselfly *C. puella* (Sherratt *et al.* 2010) yielded quantitatively similar results, whether the data were treated as a single cohort or not.

The papers from which we extracted data generally refer to reproductively active (mature) individuals, but a second factor that may add significant noise is uncertainty over the individual's age on first marking. Although one might argue that: (i) adult age should be measured from the time maturity is reached, and (ii) any new visitors to the water body will tend to be recently mature individuals, the fact remains that the exact adult age on first marking is not known. Uncertainty over the precise age will no doubt add noise, but (as we have seen) it is unlikely to confound our analysis because actual age is likely to correlate well with time since first marking. Crespin *et al.* (2006) describe a simulation model which supports the validity of this approximation, while our own analysis of senescence in *C. puella* of known age (marked as newly emerged teneral) yielded similar conclusions to those in an analysis of a larger cohort of *C. puella* at unknown age at time of marking (Sherratt *et al.* 2010). While innovative methods now exist to evaluate senescence in populations in which subjects are of unknown age at the time of marking (Müller *et al.* 2004; Zajitschek *et al.* 2009b) these approaches necessarily assume a fixed population density and stable age structure, which are unfortunately invalid in odonates with seasonal emergence patterns.

Field studies have a special role to play in understanding senescence, not least to ensure that laboratory results are not just artefacts of laboratory conditions. For example, Linnen *et al.* (2001) showed that wild caught *Drosophila* lived for as long as those in an inbred laboratory *Drosophila* line under selection for longevity for nearly 20 years. Although the overall age-dependent increases in hazard were consistently best explained by a simple exponential rise, the selection of Gompertz model may be as much a function of its simplicity as the goodness of fit it provides. Of the range of recent laboratory studies of insect demography which use Pletcher's (1999) WinModest software to fit and compare a range of mortality curves, there are a number of examples that also find Gompertzian mortality (e.g., Iliadi *et al.* 2009, Maklakov & Fricke 2009, Scannapieco *et al.* 2009), while others have found logistic mortality (e.g., Bilde *et al.* 2009, Gomez *et al.* 2009, Burger *et al.* 2010), so it is clear that our finding of Gompertz is not entirely a consequence of high extrinsic rates of mortality and low sample sizes associated with field conditions. Likewise, it is not known why *Ischnura elegans*, *Argia chelata* and *Plathemis lydia* show no evidence of senescence while other species do, although it is clear that it is not a question of the sample size of marked individuals alone, because populations in several studies employing smaller sample sizes exhibited senescence.

Intriguingly the Gompertzian parameters a and b were negatively correlated among species when the entire data set was considered. Ricklefs & Scheuerlein (2002) suggest that when deaths arise early on in an organism's life then they are likely to arise as a result of "extrinsic" factors such as predation, while those deaths that arise late in an organism's life are much more likely to arise due to "intrinsic" factors, such as wing-wear. The authors used this observation to propose that increases in extrinsic mortality could effectively mask intrinsically driven mortality. One possible mechanism that may enhance the effect is condition-dependent mortality, with populations exhibiting high early mortality effectively purged of members of the population with weak constitution.

As a consequence, Ricklefs & Scheuerlein (2002) suggest that b should decrease to compensate for an increase in a thereby maintaining an approximately constant age-dependent component of mortality ($\sqrt{a/b}$). We have found some evidence for this phenomenon here, although only when species with low age-dependent exponents (b) were included in the analysis.

Given the paucity of data on senescence in odonates, and the lack of analyses for age effects, our comparative analyses of the effects of territoriality were necessarily restricted to analyzing overall daily mortality rather than senescence (a change in daily mortality) *per se*. We found that the mortality rates of

male and female odonate species were strongly positively correlated across species. Part of this relationship may be attributed to shared environment of the two sexes (because mortality is likely to vary even among populations of the same species), but it is likely that it also reflects an underlying robustness of individual species. Controlling for female mortality, there was no significant effect of territoriality on male mortality when phylogenetic relationships were ignored. However, when analyzing the survivorship patterns of the 35 species, we found a significant effect of territoriality on male mortality in the anticipated direction (territoriality increasing male mortality rates after controlling for female mortality), once the underlying phylogenetic relationships were accounted for. Our analysis of a much smaller data set (16 species) using the estimated phylogenetic distances did not detect such a pattern, but the low sample size inevitably reduces the power of this test.

Why should territoriality act to reduce male survivorship relative to female survivorship? As previously noted, territoriality might expose males to increased damage caused by male-male conflict while non-territoriality might expose females to increased damage caused by male harassment. This raises the further question of why natural selection does not make territorial males (and females in non-territorial systems) more robust, to fully deal with their higher damage rates. Classical evolutionary theory suggests that, over generations, direct, extrinsic reductions in male relative survivorship could result in the evolution of males of territorial species also having *intrinsically* reduced survivorship compared to males of non-territorial species (Medawar 1952; Williams 1957 but see Abrams 1993). Recent work in evolutionary reliability theory also suggests that where there is decelerating selection for robustness against damage, natural selection will typically 'under-compensate' for this damage (Laird & Sherratt 2009), again predicting that territorial males should also be intrinsically more likely to have reduced survivorship. Intriguingly, in *Mnais pruinosa costalis* (Selys), territorial male morphs appear to have shorter lives than non-territorial male morphs, even under lab conditions (Tsubaki *et al.* 1997), suggesting that patterns of mortality are not simply a direct reflection of extrinsic mortality.

While this current study has focused on survivorship over the reproductive stage of mature adult odonates, previous work has examined how territoriality might influence differential activity patterns and survivorship of males and females prior to maturation (Anholt *et al.* 1991; Anholt 2008). In particular, while females of a range of odonate species increase in mass between emergence and maturity by an average of 125%, only males of territorial species exhibit a comparable increase (Anholt *et al.* 1991), possibly as a consequence of their relatively high energy demands (see also Anholt 2008). So, while some of the costs of territoriality may well arise before reproductive maturity, here we have some evidence to suggest that territorial males pay at least some of the price for their behavior post reproduction.

Cross-species patterns in mortality as a consequence of sexual selection have previously been reported in other taxonomic groups, although not so far in the context of territoriality. For example, Promislow *et al.* (1992) found that the differences in mortality rates between the sexes of different species of passerine birds increased with male plumage brightness (see also Promislow *et al.* 1994). The findings of this current study not only challenge the view that odonates are too short lived to exhibit senescence, but also indicate that their survivorship patterns are shaped by a combination of intra-sexual and inter-sexual conflict (Svensson & Sheldon 1998).

Acknowledgements

We thank Carlos Esquivel and Enrique González Soriano for providing data on the body sizes of several species in our data set. We are grateful to NSERC (TNS & RAL), the Government of Ontario (CH), NERC – NE/C511205/1 (DJT) and the Spanish Ministry of Science and Innovation (CGL2008-02799) for funding.

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Table 1. 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 in days between marking + 1 (to account for initial marking mortality) and last recapture for the i^{th} individual, and n is the size of the marked population resighted on at least day 1 following marking. 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 the function $\omega(x)$ 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	$\mu_x = ae^{bx}$	$a \exp\left[bx - \frac{a}{b}(e^{bx} - 1)\right]$
Gompertz-Makeham	$\mu_x = ae^{bx} + c$	$(c + ae^{bx}) \exp\left[-\frac{a}{b}(e^{bx} - 1) - cx\right]$
Logistic	$\mu_x = ae^{bx} \omega(x)^{-1}$	$ae^{bx} \omega(x)^{-(s+1)/s}$
Logistic-Makeham	$\mu_x = ae^{bx} \omega(x)^{-1} + c$	$e^{cx} \omega(x)^{-1/s} (ae^{bx} \omega(x)^{-1} + c)$

Table 2. Parameter estimates of the most parsimonious models, obtained using WinModest 1.0.2 software (Pletcher 1999). The models were fitted to explain the decline in the marked population from the day after their first day of marking to overcome any marking effects. The likelihood ratio test shows the final outcome of model comparisons, moving to a higher parameter alternative only if it provides a significantly better fit. In most cases the two parameter Gompertz model provided the best fit, with the simpler (1 parameter) model of no senescence generally rejected. The confidence limits for parameter *a* after fitting the no senescence model involved identifying values of *a* that reduced the log likelihood by ($\chi^2_{1, 0.05} / 2 = 1.92$) units from the maximum log likelihood. The penultimate column gives the significance of weighted (by root surviving population size) regression of mortality hazard vs age for the cohort, excluding any data at and beyond the observation period over which no deaths (or disappearances) were evident.

Species	Sex	a (95% LCI, UCI)	b (95% LCI, UCI)	LogLikelihood, Best model, LR significance probability over non-senescent model	Weighted regression: significance probability	Reference (and figure/table) from which data were extracted
<i>Ceriagrion tenellum</i>	Male	0.086 (0.075, 0.099)	0.045 (0.034, 0.061)	-1751.75 Gompertz P < 0.001	P = 0.004	Cordero-Rivera & Stoks (2008) Fig 2.5 (see Andres & Cordero 1998 for primary data).
<i>Ceriagrion tenellum</i>	Female	0.092 (0.074, 0.115)	0.065 (0.045, 0.095)	-682.06 Gompertz P < 0.001	P = 0.001	
<i>Ischnura elegans</i>	Male	0.214 (0.192, 0.238)		-836.38 Constant P = 0.1054	P = 0.348	Cordero-Rivera & Stoks (2008) Fig 2.5 (see Cordero <i>et al.</i> 1998 for primary data).
<i>Ischnura elegans</i>	Female	0.165 (0.140, 0.195)	0.040 (0.022, 0.074)	-940.44 Gompertz P = 0.002	P = 0.619	
<i>Enallagma hageni</i>	Male	0.036 (0.021, 0.062)	0.143 (0.100, 0.204)	-197.64 Gompertz P < 0.001	P = 0.019	Fincke (1986) Fig 3 (data from 1982 chosen since it also included an adjacent field).
<i>Enallagma hageni</i>	Female	0.065 (0.036, 0.118)	0.153 (0.092, 0.254)	-114.40 Gompertz P < 0.001	P = 0.016	
<i>Coenagrion puella</i>	Male	0.102 (0.076, 0.138)	0.111 (0.075, 0.163)	-395.23 Gompertz P < 0.001	P = 0.044	Banks & Thompson (1985) Fig 2
<i>Coenagrion puella</i>	Female	0.111 (0.084, 0.149)	0.088 (0.055, 0.139)	-368.19 Gompertz P < 0.001	P = 0.054	
<i>Pyrrhosoma nymphula</i>	Male	0.103 (0.082, 0.129)	0.053 (0.033, 0.085)	-566.78 Gompertz P < 0.001	P < 0.001	Corbet (1952) Table 6. All individuals recaptured at least once.
<i>Argia chelata</i>	Male	0.121 (0.105, 0.138)		-657.49 Constant P = 0.1065	P = 0.481	Hamilton & Montgomerie (1989) Fig 4 (first step on y-axis assumed to be 1

<i>Argia chelata</i>	Female	0.150 (0.110, 0.198)		-127.57 Constant P = 0.4843	P = 0.073	not 0).
<i>Plathemis lydia</i>	Male	0.128 (0.118, 0.138)	0.032 (0.016, 0.047)	Gompertz (LCL for parameter b > 0)	P = 0.389	Koenig & Albano (1985) Fig 5. The fate of the oldest ~5% is not depicted, so parameter estimates based on fit of cumulative survivorship by NLLS.
<i>Plathemis lydia</i>	Female	0.103 (0.094, 0.108)		Constant (LCL for parameter b < 0)	P = 0.679	
<i>Mnais pruinosa</i> Age zero at first sighting	Male (orange- winged)	0.099 (0.075, 0.129)	0.187 (0.145, 0.242)	-469.68 Gompertz P < 0.001	P = 0.002	Tsubaki <i>et al.</i> (1997) Fig 3. Time units 5 days. Only individuals recaptured at least once presented, so first day also considered for regression and MLE.
<i>Mnais pruinosa</i> Age zero at first sighting	Male (clear- winged)	0.108 (0.081, 0.142)	0.226 (0.176, 0.290)	-446.94 Gompertz P < 0.001	P = 0.004	
<i>Leucorrhinia dubia</i>	Male	0.035 (0.024, 0.054)	0.078 (0.054, 0.111)	-309.35 Gompertz P < 0.001	P = 0.003	Pajunen (1962) Fig 7 (1959 study, recaptures only).

Table 3. The results of our comparative analyses of male mortality, not controlling for phylogeny and controlling for it in 3 separate ways. In each case a model with male abdomen size, female mortality, male territoriality and a female mortality*territoriality interaction was fitted. The degrees of freedom for the first two methods of analysis were consistently 1 and 30. For the simplified fixed branch length tree (35 species), the "phylogenetic degrees of freedom" were estimated as 13.48. For the reduced tree with estimated branch lengths (16 species), the phylogenetic degrees of freedom were 6.25.

Dependent Variable		Method of analysis			
		GLM (no control)	Nested ANOVA	Fixed branch length tree	Reduced tree
Male daily mortality	Male abdomen size	F=0.6621, p=0.422	F=1.8938, p=0.179	t=1.285, p=0.233	t=-4.629, p=0.098
	Female mortality	F=19.6499, p<0.001	F=33.3371, p<0.001	t=8.439, p<0.001	t=1.634, p=0.311
	Territoriality	F=1.070, p=0.309	F=16.4076, p<0.001	t=-0.918, p=0.013	t=-0.355, p=0.773
	Female mortality* territoriality	F=0.8745, p=0.357	F=0.0657, p=0.799	t=2.730, p=0.024	t=0.906, p=0.506
Male hazard	Male abdomen size	F=0.7314, p=0.399	F=2.1048, p=0.1572	t=1.522, p=0.164	t=-4.729, p=0.095
	Female hazard	F=12.5494, p=0.001	F=31.4971, p<0.001	t=7.219, p<0.001	t=1.540, p=0.329
	Territoriality	F=1.0689, p=0.309	F=31.0213, p<0.001	t=-1.757, p=0.115	t=-0.420, p=0.735
	Female hazard * territoriality	F=3.8019, p=0.061	F=0.010, p=0.921	t=4.339, p=0.002	t=1.030, p=0.462

Figures

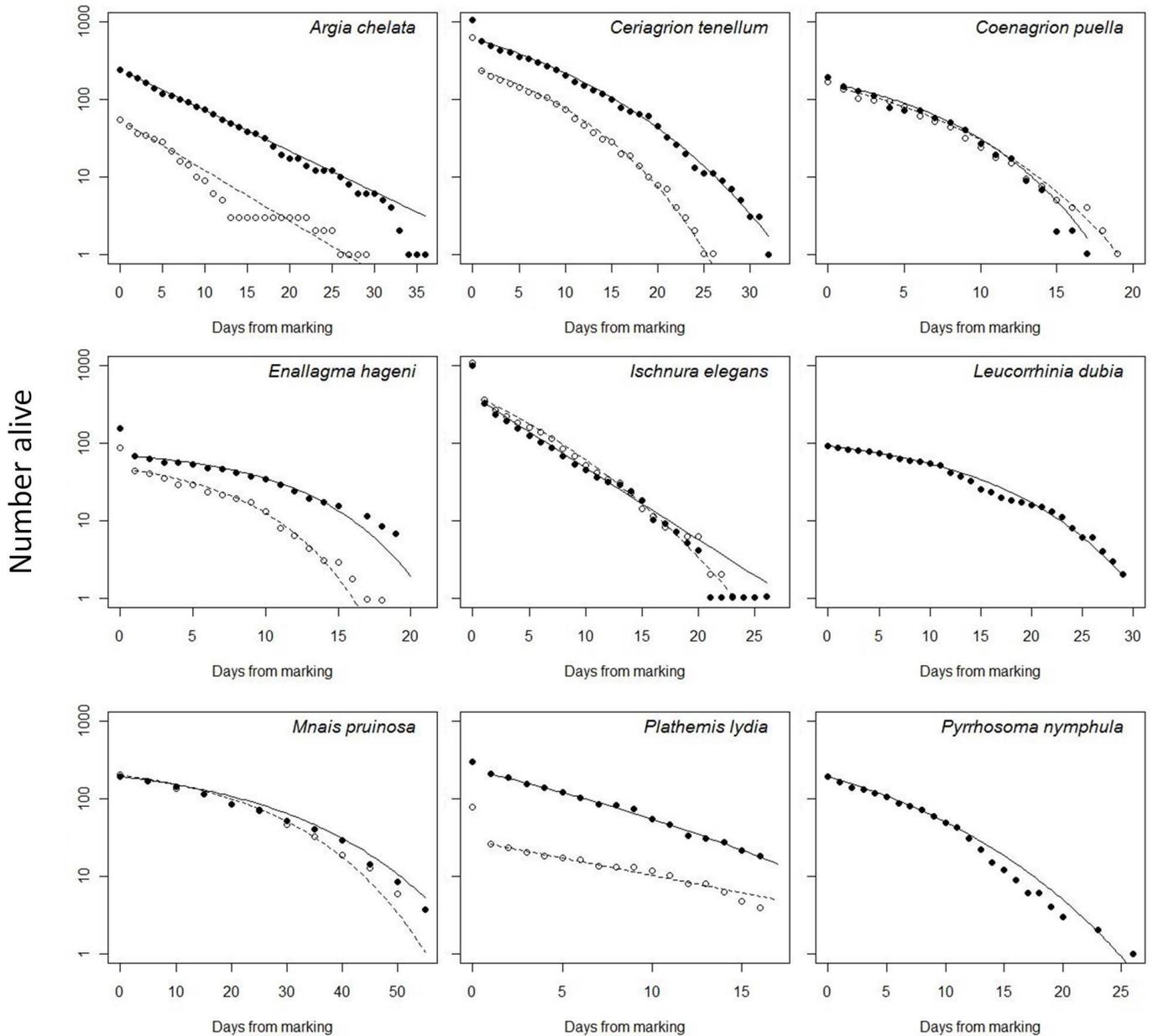


Figure 1 Semi-log plots depicting the cumulative decline in the logarithm of the number of marked individuals alive, as reported in a variety of mark-recapture studies on damselflies and dragonflies. See Table 2 for original data sources. If daily rates of mortality were independent of age then these plots should be strictly linear, reflecting a constant proportion of individuals lost from the population each time step. Dark filled circles represent males, while open circles represent females (with the exception of the data for *Mnais pruinosa* where filled circles represent orange-winged males and open circles represent clear-winged males). Fitted lines (solid, males; dashed, females) show the best fits of the most parsimonious model (Gompertz or no

senescence) as translated to the cumulative survivorship curve (where $l_x = \exp(-\int_0^x \mu_t di)$ so that

$l_x = \exp\left\{-\left(\frac{a}{b}\right)(\exp(bx) - 1)\right\}$ for Gompertz and $l_x = \exp(-ax)$ for no senescence), with best fit parameters given in Table 2.

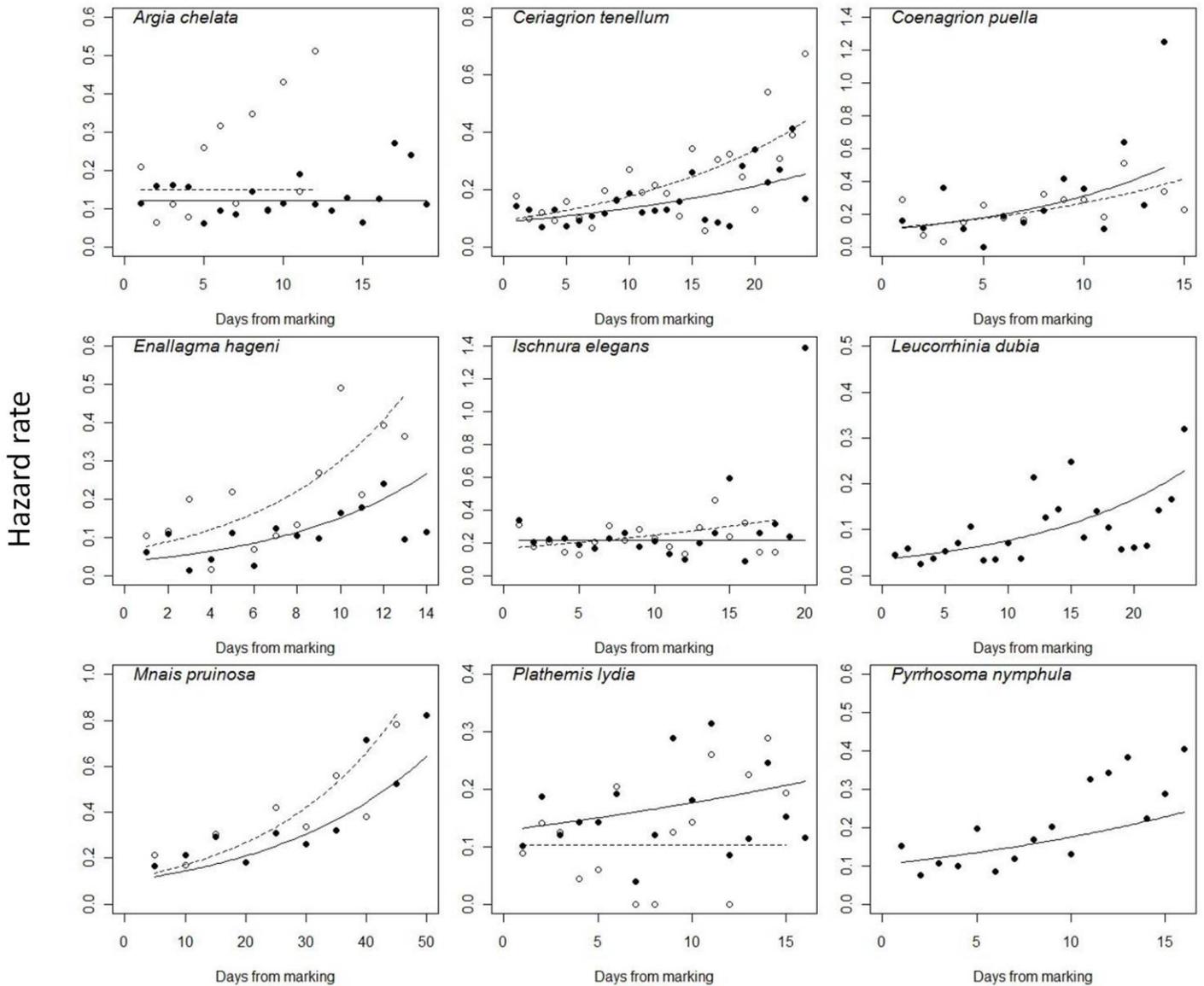


Figure 2 Estimated hazard rate ($-\log$ [proportion of population lost] for each time step), derived from the semi-log plots for each species. Hazard rates were not calculated from marking to day 1, thereby excluding all marked individuals that were never seen again. Moreover, the estimates of hazard depicted do not always extend the full duration of the relevant study because we stopped hazard estimation once the population had reached such a small size that there was no change in the numbers alive on consecutive days. Fitted lines (solid, males; dashed, females) show the best fits of the most parsimonious hazard model (Gompertz or no senescence; see Table 1 for hazard functions), with best fit parameters given in Table 2.

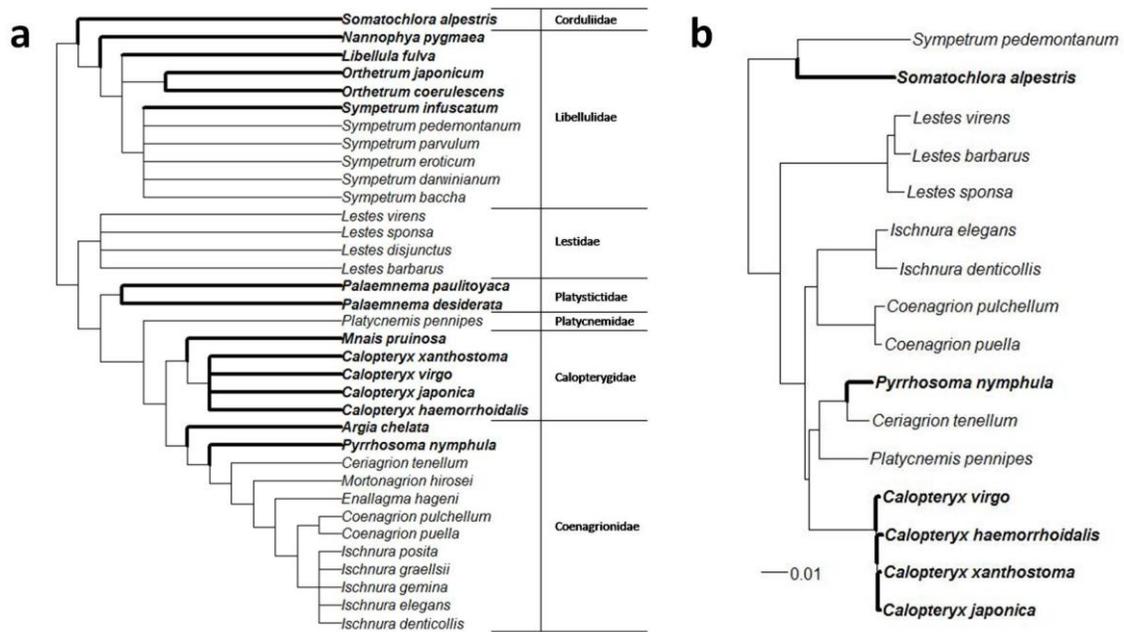


Figure 3 a,b (a) Cladogram showing the presence of territoriality (in bold) in the 35 odonate species for which survivorship data are available; phylogenetic relationships based on O'Grady & May, 2003; Ware *et al.*, 2007; Rehn, 2003 and (b) phylogeny of 16 species for which comparable sequences are available showing territoriality (in bold).

Figure 4

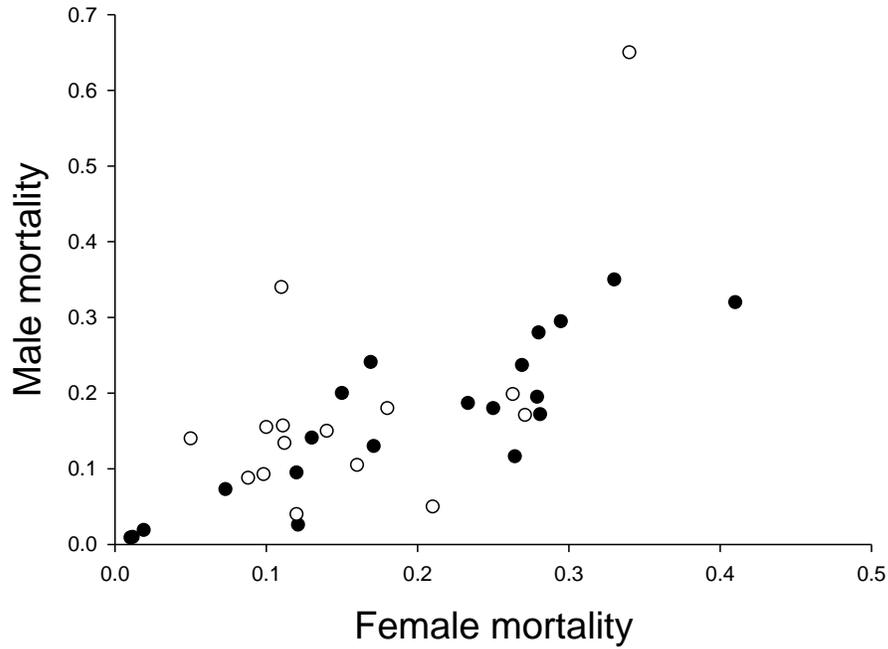


Figure 4 The relationship between male and female daily mortality in 35 species of damselfly and dragonfly (data from Cordero-Rivera and Stoks 2008). Open circles represent species with territorial males, while the closed circles represent species with non-territorial males.