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Live fast, die old: no evidence of reproductive senescence or costs of mating in a damselfly (Odonata: Zygoptera)

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Summary

1. Recent examples of actuarial senescence in wild insect populations have challenged the long-held assumption that the brevity of wild insect lifespans precludes senescence.
2. We investigate age-related patterns in mating behaviour in adults of a short-lived damselfly, *Coenagrion puella*, and the implications of this mating. Using capture histories for 1,033 individuals over two field seasons, we conduct both pooled and stratified analyses of variations in breeding activity.
3. Pooled analyses suggest that there is strong age-related variation in the probability of being present at the mating rendezvous. However, no age-related variation was observed in the probability of mating. Stratified approaches confirmed a general pattern of age-related declines in survival probability, but provided only equivocal evidence of an effect of age on transition between temporary breeding states. Mating males and females showed greater survival than non-mating individuals, possibly as a consequence of higher body condition. Older males that were not currently breeding were less likely to commence breeding on the next day, but showed no patterns in breeding cessation. Overall, transitions between both breeding states declined with age, suggesting that males that breed tend to continue breeding while those that do not breed continue to be unsuccessful. Female mating rates were consistently high across all ages with no age-related decline apparent.
4. While previous research has demonstrated actuarial senescence in this population, as does this study, we find little evidence of either age-related declines in reproductive behaviour or breeding-related declines in survival, which might indicate functional senescence or costs of mating respectively. Indeed, the greater survival in mating individuals of both sexes suggests that variations in individual quality may mediate both reproductive success and longevity.

5. Contrary to recent studies, we found no compelling evidence for reproductive senescence or a cost of mating in an important and well-studied model odonate. The possible link between condition and ageing suggests that individual quality needs to be taken into account when studying senescence. We recommend the use of multistrata models for the future investigation of these phenomena.

Keywords: Ageing, condition, insect, natural population, reproduction, sex, multistrata model.

Introduction

Senescence is considered to be a ubiquitous aspect of an organism's life history, whether it manifests as an age-related increase in mortality ("actuarial senescence") or a decline in performance ("functional senescence"). The putative ubiquity of senescence is believed to be a consequence of reduced selection pressures acting on phenotypic traits later in life (Rose 1991). Nevertheless some studies have failed to uncover evidence of senescence (Promislow 1991), the relationship between age and mortality rates varies markedly between species (Jones *et al.* 2014), and there is evidence that certain clonal taxa may avoid senescence altogether (e.g. *Hydra*, Martínez 1998) while other taxa exhibit "negative senescence" (Vaupel *et al.* 2004). While it has been proposed that senescence would be rare in wild populations due to high natural rates of mortality and thus most individuals die before they deteriorate in condition (Rose 1991; Kirkwood & Austad 2000), there is ample evidence of both actuarial and functional senescence in long-lived wild vertebrates, and several recent studies have demonstrated similar effects in short-lived invertebrates (Nussey *et al.* 2013).

The majority of previous studies of senescence have emphasised actuarial senescence (Ricklefs 2010; Nussey *et al.* 2013), but this focus neglects other important components of individual fitness (Partridge & Barton 1996). Age-related declines in the functioning of the reproductive system ("reproductive senescence") have been demonstrated in several taxa and in both sexes. For example, pup weight, pup survival, litter size, and litter frequency decline with age in female meerkats (Sharp & Clutton-Brock 2010), laying date is delayed and clutch size reduced in female swans (McCleery *et al.* 2008), and lamb production and weaning success decline with age in bighorn ewes (Bérubé, Festa-Bianchet & Jorgenson 1999). Older female cockroaches produce fewer and smaller clutches than younger cockroaches in the laboratory (Moore & Moore 2001) and older male antler flies mate at a lower rate than younger antler flies in the field (the only comprehensive description of reproductive senescence in a wild insect population under natural conditions, and a study which was limited to males, Bonduriansky & Brassil 2002; Bonduriansky & Brassil 2005). A recent study of males of the damselfly *Hetaerina americana* compared "mature" and "young" males (defined loosely according to wing flexibility) and showed that males in the mature age class were more likely to copulate (González-Tokman, González-Santoyo & Córdoba-Aguilar 2013). However, that study did not investigate female reproductive senescence, observed only 63 copulations from 239 males, and provided no quantitative measure of age. Age-related declines in female egg loads (e.g. in female parasitoids, Mangel & Heimpel 1998) and male sperm loads (e.g. in male ferrets, Wolf *et al.* 2000) represent declines in reproductive function which may also cause conflict between the sexes.

While reproductive senescence involves age-related declines in one or more components of reproduction, the "costs of mating" can be defined as reproduction-related declines in survival or function (Daly 1978). The idea that reproduction can reduce longevity has a long history (see Kirkwood 2001 for a review) and it is now clear that the specific aspect of reproduction (if any) that can affect mortality varies from system to system. For example, laboratory selection experiments to enhance longevity in *Drosophila melanogaster* (Meigen) produced long lived individuals with relatively low early fecundity (Zwaan, Bijlsma & Hoekstra 1995); egg laying increases age-related mortality in rose-hip flies, while mating itself has no effect (Roitberg 1989); by contrast, the act of mating has been shown to reduce female survival, for example, via the action of male seminal proteins in *Drosophila* (Chapman *et al.* 1995) or genital damage in *Callosobruchus maculata* (Crudgington & Siva-Jothy 2000).

While there have been a number of studies documenting age-related variations in performance, such studies are complicated by the issue of variation in individual quality (Vaupel & Yashin 1985; McCleery *et al.* 2008). High quality individuals may not only live longer but also exhibit greater reproduction, leading to a positive relationship between age and reproduction as poor-quality individuals are lost from the population (Vaupel & Yashin 1985; Abrams 1993; Williams & Day 2003). Such an outcome can arise even if there is an individual cost of reproduction, with variation in condition masking effects of the cost of reproducing.

Field studies of reproductive senescence in natural populations of insects are rare (Bonduriansky & Brassil 2005), yet essential if we are to obtain a complete picture of senescence in the wild. Here we present a detailed analysis of the relationship between reproduction and ageing in the damselfly *Coenagrion puella* (L) (Odonata: Zygoptera) which has previously been shown to exhibit actuarial senescence in the form of an age-related increase in daily mortality (Sherratt *et al.* 2010). Sherratt *et al.* (2010) analysed capture histories independent of the reproductive status of the individuals in question, i.e. whether they were seen alone or they were engaged in tandem or in copula. Therefore, age-related changes in the rate of reproduction were not investigated in this earlier study, and neither were the effects of reproduction on mortality. Nevertheless, there is good reason to believe that such effects might arise. In other species of odonates for example, a number of age-related changes in physiology have been documented including transitions between colour morphs (Sanchez-Guillen, Van Gossum & Cordero Rivera 2005), increases in muscle mass during adult maturation (Marden, Fitzhugh & Wolf 1998), increases in flight-related thermal sensitivity (Marden 1995), a transition from territorial to sneaker mating strategies (Forsyth & Montgomerie 1987), and increased wing tatter (Banks & Thompson 1985). To date, none of these changes has been linked directly either to age-related patterns in mortality or reproductive function. We therefore tested whether there is an age-related decline in mating behaviour (characterised by a decline in the daily rate of onset of mating and an increase in the daily likelihood of cessation of mating, Figure 1A) and/or an effect of mating status on daily survival (a "cost of mating", characterised by reduced survival when mating compared to non-mating, Figure 1B).

Methods

Data collection

A mark-recapture study of *C. puella* was conducted over two consecutive breeding seasons at an isolated (nearest neighbouring wetland >1 km), small pond (maximum dimensions 32 m long, 14 m wide, and 1.5 m deep; perimeter 75 m) in southern England (50°57′39″N, 0°58′41″W). Full details of the study can be found in Thompson *et al.* (2011), which also contain details of sources for climate (temperature, precipitation and sunshine hours) and ectoparasitic mite data. Fieldwork commenced 11th May 2005 and 17th May 2006 before the major flight period for the species (June-mid July) and continued until the end of July (29th 2005 and 30th July 2006). Three to six people surveyed the site for *C. puella* every day from 09:30 hours local time until 15:30-17:30 hours when no further flight activity was evident. All unmarked individuals were caught and marked on first encounter, ensuring that days since marking was a good approximation of days since reproductive maturity. The actual age since emergence of newly marked adults may vary due to slight variations in the immature period (the time between emergence from the natal water body and the return to the water body as a reproductively mature adult, estimated as 13.2 (SE 0.22) days for males and 16.5 (SE 0.34) days for females; Banks & Thompson 1985), but this is unlikely to have significant impacts on our results (for discussion, see Sherratt *et al.* 2010; Sherratt *et al.* 2011).

The average copulation duration of *C. puella* is 28 minutes, and males subsequently engage in contact mate-guarding during oviposition site selection and egg-laying for an average of 84 minutes (Banks & Thompson 1985), making it likely that individuals engaging in reproductive activity will be seen around the pond. Over the two field seasons, a total of 620 males and 429 females were captured and marked. Of these individuals 1,049 individuals, 841 (80.2%) were resighted at the study site. If an individual was seen repeatedly on a given day but on at least one occasion it was seen mating then that individual would be recorded as a mating individual for that day.

Capture and resighting histories for these 1,049 individuals, as singles and/or mating pairs, were analysed using two methods. First, a pooled analysis was used to visualise the reproduction-related patterns in the data. This approach produces straightforward results based on treating all animals as if they emerged at the same time to look at what proportion of individuals of each age are (i) absent from the mating rendezvous, and (ii) engaged in mating behaviour. However, the pooled approach ignores individual differences (e.g. parasite burden) and temporal effects (e.g. daily fluctuations in weather). Therefore, stratified models were fitted using Program MARK. This "multistrata" approach allows one to control for variables such as resighting probability, parasite burdens, and daily climate, while measuring their effects. In particular, multistrata models allow: (i) the comparison of age-related trends in survival between individuals in different states (here we compare currently breeding individuals to currently non-breeding individuals), and (ii) the investigation of rates of switching between states (for example, how likely is an individual to switch from not breeding on one day to breeding on the next at differing ages). See below for details of multistrata models.

Pooled analysis

Capture histories were pooled for each sex in each year to give a single dataset including both years and both sexes. Death was conservatively assumed to have occurred on the day following the final sighting. This allows the calculation, for demonstrably living individuals, of (i) the proportion of individuals of both sexes at the mating rendezvous ("presence"), and (ii) the proportion of present individuals that are seen mating ("mating") on that day. First, variation in the proportion of individuals present, and the proportion of individuals mating, was analysed using a generalised linear mixed effects model (GLMM) in the nlme package (Pinheiro *et al.* 2013) in R (R Development Core Team 2013) with sex (fixed factor), year (random factor), age (covariate) and sex*age as predictors. A binomial error term was applied with a response variable composed of successes and failures (present vs absent, or mating vs non-mating) in two separate columns. To examine trends in more detail, data were analysed separately for each sex using GLMMs with year as a random effect and age as a covariate. Overdispersion was tested for by calculating the ratio of the residual deviance (Rdev) to the residual degrees of freedom (Rdf) and checking that the sum of the squared residuals were χ^2 distributed (Venables & Ripley 2002). Overdispersion was found in models for presence in the combined dataset (Rdev/Rdf=7.842, $p<0.001$) and for males (Rdev/Rdf=5.757, $p<0.001$) and females (Rdev/Rdf=9.710, $p<0.001$) individually, and the model for mating in the combined dataset (Rdev/Rdf=1.355, $p=0.023$). Models for mating in males (Rdev/Rdf=1.141, $p=0.387$) and females (Rdev/Rdf=1.308, $p=0.257$) were not significantly overdispersed. The four overdispersed models were refitted with quasi-binomial errors using the glmmPQL function in MASS (Venables & Ripley 2002).

Stratified analysis

Multistrata models

The stratified models fitted using MARK (White & Burnham 1999) permit the inclusion of a wide array of extrinsic (e.g. temperature, sunshine) and intrinsic (e.g. sex, mite load, age) parameters to explain variation in φ (daily survival) and p (daily re-sighting probability, see Table 1 for a full list of terms). The relationship between these parameters has been established in a previous analysis (Sherratt *et al.* 2010). Here we extend Sherratt *et al.*'s models to include the role of mating status using multistrata models. Briefly, multistrata models build on standard MARK models by decomposing the φ (survival) parameter into a stratum-specific survival (specifically the probability of surviving to time t_i given the stratum at t_{i-1}, designated "S") and a probability of moving between strata (designated "ψ"). This approach makes use of an individual-based capture history that records not simply the presence of an individual, but the state (or stratum) in which the animal is found. Figure 2 provides a schematic of how a certain capture history might arise from different combinations of events, as well as the parameters that describe those patterns. We use multistrata models to investigate the effects of different breeding states on rates of senescence, and how the likelihood of switching between breeding states changes with age. Overall probabilities of an individual occupying a given state can be calculated as the stationary states of the stochastic matrices describing the transition probabilities at each time step. The results of these models describe the effects of being in a particular breeding state on the response variables, but this does not imply that particular individuals always occupy a given stratum: the states themselves are transient but permit an insight into how particular states influence population parameters as a whole.

Model selection

Multistrata models were constructed in the program MARK through the RMark package (Laake 2010) in R (R Development Core Team 2013). These fitted models were then compared using Akaike's information criterion corrected for small sample sizes (AICc). In these models, capture histories were coded such that an individual that was not sighted on a given day received a "0" for that day, an individual observed to be mating at any stage during that day was given "M" ("mating") and an individual not observed to be mating but present at the pond was given "N" ("non-mating").

In the first stage of modelling, we used a set of models testing for an effect of breeding stratum (mating vs non-mating, designated as “strat” in the models) in each of p, S, and ψ. All eight potential combinations of "dot" (i.e. floating intercept) and strata terms were used. We then built on the models constructed by Sherratt *et al.* (2010), who demonstrated that resighting probability (p) was best explained using climate variables (collectively designated “c”) and mite loads (“m”), and that survival (S) was best explained using age (“x”) and mite loads. To limit the potentially enormous number of models that could be explored, we held constant the resighting and survival portions of the models as: p(c+m+strat) and S(m+x+strat+x*strat) in favour of investigating the factors influencing the transition probabilities between breeding states. In each model due to non-linear effects, age (x) and mites (m) are accompanied by the corresponding quadratic terms (x^2 and m^2), which we omit from the notation to enhance clarity. Removal of the age term from the survival model resulted in a substantial decrease in explanatory power (as indicated by the difference in the Akaike Information Criterion, ΔAICc=16.5 compared with best model) confirming the importance of age even when accounting for the variation due to breeding state. Climate data were added as a unit (i.e. all three variables together) and replaced time in the resighting (p) models, since it has been demonstrated that daily variations in resighting are caused by meteorological variations (Sherratt *et al.* 2010). The inclusion of strata in the survival term enables us to test for a difference in survival between breeding states (a "cost of mating") using the main effect, and a difference in the nature of the age vs. survival relationship between breeding states using the interaction.

Finally, we explore the probability of transition between mating states in more detail to test for the presence of reproductive senescence. In estimating the breeding state and sex-specific transition probability ψ in a given season, the following variables were allowed to vary in all their permutations: (i) mite load (number of ectoparasitic mites counted at first capture, and quadratic, collectively designated as "m") as an individual covariate, (ii) body size (length of the right forewing, and quadratic, collectively designated "s") as an individual covariate, (iii) age (days since first capture, and quadratic, collectively designated "x"), and (iv) climate (the daily temperature, precipitation and sunshine hours, collectively designated "c") as time-varying covariates. Mite numbers are unlikely to increase after emergence and the impacts of mites are fixed after engorgement so the mite count on first capture is representative of parasitic burden (Hassall *et al.* 2010). All variables had some effect on actuarial senescence in a previous study (Sherratt *et al.* 2010) and the inclusion of age specifically allows us to test for age-related variation in mating behaviour transitions (reproductive senescence). The four variables (mites, size, age, and climate) give a total of 15 permutations, leading to 60 models across the two seasons and two sexes. This count excludes the $\psi(.)$ model which was already tested against $\psi(\text{strat})$ above. Model averaging was then performed on the best-fitting models (ΔAICc<4) to produce estimates for each parameter.

To provide a metric of reproductive success that is comparable to previous studies (Banks & Thompson 1985; Banks & Thompson 1987), we calculated inter-mating interval (IMI) which gives the number of days between observed matings. For female *C. puella* IMI strongly correlates with clutch size, and the total number of clutches produced by a female explains 90% of total lifetime egg production while clutch size *per se* explains only 10% (Banks & Thompson 1987). While the interpretation of IMI is more complex for males, as its relationship with fitness will be determined by sperm competition and female egg loads at the time of copulation, IMI still indicates a level of mating frequency that is at least partially correlated with fitness. IMI for each age was calculated as the reciprocal of the equilibrium value (based on the transition (ψ) matrix) of the proportion of individuals mating. Multistrata recapture histories, data for the cohort analysis, individual covariates and climate data are all available to download (Hassall *et al.* 2015a) along with the R code for the analysis (Hassall *et al.* 2015b).

Results

Pooled analysis

Males were significantly more likely to be present at the mating rendezvous, but females were significantly more likely to be seen mating. There was a negative main effect of age in predicting both the presence of individuals at the mating rendezvous and the proportion of individuals mating (Table 2). As the significant sex*age interaction complicates the interpretation of the models, further GLMMs were constructed to analyse the sexes separately. Older males were significantly less likely to be present at the mating rendezvous, but of those males present older males were significantly more likely to mate. Older females were no less likely to be present at the mating rendezvous, but of those animals present there was a slight tendency for older females to mate less (Table 2). However, as can be seen from Figure 3, these patterns are subtle.

Stratified analysis – Costs of mating

The addition of breeding stratum to simple models consistently improved model fit for survival across both sexes and both years, suggesting a difference between breeders and non-breeders in patterns of survival (Table 3, see Table S1 and Table S2 for more extensive model sets). Age-related declines in survival varied more strongly between the two years of the study than between the sexes, with individuals showing lower rates of actuarial senescence in 2005 than in 2006. In both sexes and both years there is evidence that individuals who were observed to be mating exhibited slower declines in survival than individuals that were observed not mating, an effect which is clearest in 2006 (as can be seen from the non-overlapping 95% confidence intervals around the survivorship curves in Figure 4B and D). These results run counter to the range of predictions of the cost of mating hypothesis (shown in Figure 1A-C). However, the situation in 2005 is more complex. The average survival probabilities for females in 2005 were consistently higher in mating individuals than non-mating individuals, although females of intermediate and older ages (5-20 days) showed considerable overlap in confidence intervals (Figure 4A). For males, younger mating individuals have significantly greater survival until day 7 and then the 95% confidence intervals for the survivorship curves begin to overlap, suggesting more rapid late-life senescence in mating males and negligible senescence in non-mating males (Figure 4C). Model-averaged parameters for models with ΔAICc<4 showed that being in the non-breeding stratum had a negative effect in both sexes in both years, and this effect was significant and negative in males in 2006 and females in both years (see Table S4). Age had a significant negative relationship with survival in non-breeding males in 2005, but not breeding males. Age had a non-significant, negative relationship with survival in both non-breeding males and breeding males in 2005. There were no significant relationships between age and survival in females when separated into breeding strata (Table S4).

Stratified analysis – Reproductive senescence

Breeding status (i.e. mating or non-mating) was also found to be important in the probability of transitioning between mating states (ψ), as demonstrated by AICc (Table 3). When individual and time-varying covariates were included in models, clear differences arose between those parameters that were selected to explain transitions ψ in females and those selected for males (Table 4). No model for female transition probability ψ with ΔAICc<2 contained age, suggesting that the reproductive behaviour was independent of the age of the female, as was found in the pooled analysis. Figure 5A and B show that females exhibited a very low probability of transition from mating to non-mating (breeding cessation) and a very high probability of transition from non-mating to mating (breeding commencement). This pattern of transition probabilities results in very little variation in IMIs for females (ranging between 1.05 and 1.15 days, see Figure 6) that appears independent of age. Males, on the other hand, showed a more complex relationship with different patterns in each year: in 2005 males under 10 days since capture showed a high likelihood (40-50% of stopping breeding on any given day, while once they had stopped breeding they were decreasingly likely to start as they aged (as indicated by the gradual decay in the white dotted line and dark shaded area in Figure 5C). In 2006, non mating males were quite likely to start breeding if they were not already, although this tendency decays with age as observed in 2005. However, in 2006 mating males were more likely to continue mating, as shown by the consistently low probability of transition for mating males in Figure 5D.

Male breeding transitions ψ were best explained by models including age. The probabilities of transitions from non-mating to mating (breeding commencement) show monotonic declines with age from 0.319 to 0.100 in 2005 and 0.558 to 0.175 in 2006 (Figure 5). The probabilities of transitions from mating to non-mating (breeding cessation) were complex and varied between years. In 2005, males showed an initial increase in the probability of breeding cessation between the ages of 1 and 6 days since capture. From 6 days, the probability declined monotonically until 21 days after first capture, the maximum longevity of males in 2005. This leads to a unimodal pattern of IMI variation with age (Figure 6). In 2006, males showed relatively little variation in patterns of breeding cessation over ages 1 to 20 days since first capture. Only 6 out of 351 males that were marked in 2006 survived to 20 days after first capture, so the slight increase following that age is based on very few individuals. In 2005, therefore, males follow the predictions of reproductive senescence until age 6 days (Figure 1C). Beyond this age, both transition probabilities decline showing that individuals are more likely to remain in whatever breeding state they occupy. In 2006, most individuals are breeding (as shown by a relatively high commencement rate and a low cessation rate). However, over time the commencement rate declines, as predicted under reproductive senescence, while the cessation rate remains low. Again, this suggests that older individuals are more likely to remain in whatever breeding state they occupy. Details of model-averaged parameters for models with ΔAICc<4 can be seen in Table S4. Absolute probabilities of breeding, calculated from the stationary states of the transition matrices, can be seen in Figure S1 with data in Table S5.

Discussion

There has been a substantial increase in the reporting of senescence from wild populations, spanning a wide range of taxa (Nussey *et al.* 2013; Jones *et al.* 2014). We use a wild population of a model insect, the damselfly *C. puella*, to evaluate age-related patterns in breeding (reproductive senescence) and breeding-related patterns in mortality (costs of mating). Using two complementary forms of analysis (pooled and stratified) we find that while survival declines with age, breeding behaviour occurs at rates that are largely independent of age. Females exhibit high frequencies of breeding irrespective of their age. Males exhibit an age-related decline in the probability of switching from non-breeding to breeding, indicative of reproductive senescence, although patterns of breeding cessation are more complex. In males and females, the breeding state was associated with higher rates of survival in both years, contrary to the simplest interpretation of the cost of mating hypothesis. Body condition may play an important role mediating the effect here (see below). Indeed, breeding state in 2006 was associated with negligible senescence, suggesting that those animals that are capable to find a mate and copulate exhibit mortality rates that are independent of their age. In males in both seasons, both transition probabilities (commencement and cessation of breeding) decline with age, suggesting that males are more likely to remain in whatever breeding state they occupied on the previous day. Taken together, these findings suggest that individuals that breed successfully are of greater individual quality and, as a result, are more likely to survive and breed in the future.

In a previous manuscript, we described age-related declines in survival in the same population of *C. puella* (Sherratt *et al.* 2010) and these effects of age on survival remain when accounting for breeding state. However, it appears that whatever processes are underlying those declines in survival have only a weak effect on an individual's probability of mating and this effect is only present in males. Decoupling of the age-dependent patterns in mortality and reproduction may result from the scramble mating system in this species, which is common to many other invertebrates (Thornhill & Alcock 1983). In scramble mating there is a focus on mate finding ability, with a limited role for physical condition compared to territorial or lekking species. Furthermore, since male odonates tend to surround the water body that acts as a breeding rendezvous, there is as much chance of encountering a female and mating for a low quality male as there is for a high quality male. As such, while poor quality males may be more susceptible to predation and less capable of prey capture, it is likely that the effect of functional senescence on mating success is negligible due to the low correlation between male performance and mating in this system. Similarly for females, which are operationally the rarer sex, mating is almost guaranteed on arrival at a mating rendezvous to the point that a proportion of females in many species of odonates have evolved to mimic males in order to reduce harassment (Van Gossum, Sherratt & Cordero-Rivera 2008).

Reproductive senescence

Reproductive senescence has only previously been documented in natural populations of one species of invertebrate, *Protopiophila litigata* (Bondurianksy) (Diptera: Piophilidae) (Bonduriansky & Brassil 2002; Bonduriansky & Brassil 2005); a second study using the field cricket *Teleogryllus commodus* (Walker) demonstrated reproductive senescence, but was conducted under semi-natural conditions with enclosures (Zajitschek *et al.* 2009). Both studies also demonstrated actuarial senescence. However, having demonstrated the presence of actuarial senescence in *C. puella* (Sherratt *et al.* 2010) and further confirmed it here, we now find no evidence of reproductive senescence in the same population. While Banks and Thompson (1987) demonstrated that reproductive capacity declines with age in female *C. puella* (inter-clutch interval increases as females age), their analysis considered only a subset of females aged >5 days since first capture. Incorporating all females in the population, we demonstrate no evidence for a decline in the proportion of females mating (Figure 3B, Table 2), no evidence for a strong effect of age on transition between breeding states (Figure 5, Table 4), and negligible age-related change in IMI (Figure 6). Elsewhere, Banks and Thompson (1985) provided evidence for a positive relationship between mating rates and age in male *C. puella*. We demonstrate more complex patterns of age-related IMI variation in males, with a unimodal relationship in 2005 and negligible change in IMI in 2006 (Figure 6).

We have found little evidence for reproductive senescence in *C. puella*, a species that is effectively non-territorial. In looking more broadly for evidence of reproductive senescence in odonates, work on territorial species is of relevance, particularly work investigating which factors influence success in territorial disputes. With territorial success comes a thousand-fold increase in mating success associated with territorial over non-territorial behaviour (Plaistow & Siva-Jothy 1996), providing a potential source of age-related variation in breeding. However, the effects of age on the outcome of territorial contests is inconsistent (Suhonen, Rantala & Honkavaara 2008). One mechanism by which age can influence competitive/reproductive success is through the gradual attrition of fat reserves after maturity. Adult males build large reserves of fat prior to entering their territorial state, which are then burnt during territorial contests. The amount of fat remaining determines the outcome of those contests, meaning that older individuals are at a disadvantage (Marden & Waage 1990; Plaistow & Siva-Jothy 1996). Where age does have an effect, it is the younger males who displace older males from territories (Forsyth & Montgomerie 1987).

It is likely that there is no such role for fat in non-territorial species, given the lack of pre-reproductive mass gain in non-territorial species (Anholt, Marden & Jenkins 1991). However, given the fact that males do not invest in energetic reserves, it is surprising that there is no age-related decline in reproductive activity. Harassment experienced by tandem pairs and greater risk of predation make this a very energetically-costly behaviour (Córdoba-Aguilar 2009). Despite this, in a previous study *C. puella* was shown to exhibit an increase in mating rates with age from 1-6 days since first marking (Banks & Thompson 1985). This relationship is absent from our pooled analysis (Figure 3), and evidence from the stratified analysis suggests that, if anything, the probability of breeding cessation increases slightly during this time (Figure 5). Not only do those individuals that are expending energy in these activities exhibit greater mating success but they also survive better.

Costs of mating

In a previous study of *C. puella* mating there was no relationship between longevity and the rate of clutch production in females, which suggests that there is no cost of mating (Banks & Thompson 1987) as found here. Daily mating rate was positively correlated with longevity in younger male *C. puella* (≤6 days since first marking), then negatively correlated with age in older males (>6 days old) (Banks & Thompson 1985). Our results from 2006 suggest a similar nonlinear response where breeding individuals survive better until age 12 days, at which point the survivorship curves of breeding and non-breeding strata cross such that non-breeders survive better beyond 12 days (Figure 4B). However, this is not present in the 2005 data (Figure 4A). Nevertheless, our finding of consistently higher survival in mating males is consistent with the positive association of mating and longevity reported by Banks and Thompson.

Mating produces a number of stressors that could conceivably increase mortality rates in both sexes. Females suffer an energetic cost via harassment during scramble competition among males (Bots *et al.* 2009). There are also costs associated with increased predation during mating and oviposition, especially when the female submerges to oviposit (Zeiss, Martens & Rolff 1999). Males also experience an increase in predation during mating, although this may not be as high as in females (Michiels & Dhondt 1990). In both sexes, age is associated with wing wear (Marden & Waage 1990; Siva-Jothy & Tsubaki 1994), although the effect of insect wing wear on survival and flight is unclear (e.g. Hedenström, Ellington & Wolf 2001). Despite the costs associated with mating, we show that mating individuals of both sexes tend to exhibit greater survival probabilities over the following 24 hours than non-mating individuals.

Selection on individual quality could explain both the greater survivorship in breeding individuals and the absence of clear reproductive senescence in older individuals (Abrams 1993; Williams & Day 2003). Variation in some aspect of underlying quality may result in individuals that persist in populations due to high survivorship and also breed at later ages, since poor quality individuals are lost at early ages (Vaupel & Yashin 1985; Abrams 1993; Williams & Day 2003). However, it is unclear how to quantify independently individual quality in this species. As we discuss above, fat reserves have been identified as an important measure of quality in territorial odonates (Marden & Waage 1990; Plaistow & Siva-Jothy 1996), but this may not play a role in species such as *C. puella* that exhibit scramble competition (Stoks 2000). Arguably size could be a measure of condition, but previous work has demonstrated stabilising selection on mating success with peak mating rates at intermediate body sizes (Banks & Thompson 1985; Stoks 2000). Previous studies have suggested that chance encounters with females, in conjunction with fluctuations in local weather conditions, may form the primary determinants of male mating success (Banks & Thompson 1985) and that weather may be the primary determinant of female reproductive success (Thompson 1990).

In general, it has been observed that individual quality is poorly defined in the majority of studies (Wilson & Nussey 2010) and it is unclear in this system why there appears to be a correlation between success in multiple life history traits. Fluctuating asymmetry (FA) correlates with mating rates in some species (e.g. Harvey & Walsh 1993; Cordoba-Aguilar 1995) but not in others (e.g. Leung & Forbes 1997; Carchini *et al.* 2000). FA is proposed to be an indicator of developmental stability, or the ability of an individual to weather environmental insults during ontogeny. As such, it is considered to be a measure of individual quality. A complicating factor is the role of parasitic mites which have been shown to affect fitness in this species (Thompson *et al.* 2011). Lifetime mating success in *C. puella* has been shown to correlate with FA (Harvey & Walsh 1993), but this may result from parasitism by mites affecting both mating and FA (Bonn *et al.* 1996). In this study, survivorship of both sexes in both field seasons peaked at an intermediate number of mites, indicated by a positive relationship with mites as a main effect, combined with a negative relationship with mites as a quadratic term. Intermediate mite infestations were also related to peak transitions in females in 2005 and 2006, and to peak transitions in males in 2005. In 2006, male peak transitions showed the opposite trend, with a dip in transition rates at intermediate mite numbers. However, while mites were present in the best-fit model for ψ in 2006, the main and quadratic parameters were not significantly different from zero.

It is worth noting the additional benefits afforded by a transition-based approach to studying senescence. To a certain extent this approach simply provides an alternative method of visualizing (and conceptualizing) the relationship between past and future breeding and the effect of age on commencement/cessation of breeding, although we believe this to be an important contribution in itself. However, the ability to decompose breeding probability into those animals who begin to breed and those who stop breeding allows additional insights. It may be, for example, that in a territorial system animals are unable to breed until they displace an existing male from a territory. Such territorial success could be age-dependent and so p(N->B) increases with age. However, once a territory has been established that male will remain in the territory until it expends its resources or senesces, so p(B->N) will start high and decline with age. Such a pattern would manifest as an age-invariant trend in p(breeding) if the two trends averaged one another out. Furthermore, the transitions between breeding states will vary depending upon the reproductive skew of a population. We have examined a damselfly system which operates based on scramble competition and so there is reasonably low reproductive skew compared with territorial mating systems. However, the application of the transition-based analysis to other systems could yield insights into the drivers of skew and the factors predicting individual success in territorial systems (i.e. covariates in the $\psi()$ term in MRR models).

Studies of senescence in natural populations of insects are relatively rare (Bonduriansky & Brassil 2002; Sherratt *et al.* 2010; Sherratt *et al.* 2011). Male antler flies exhibit decreased daily mating rates with increasing age (Bonduriansky & Brassil 2002), as expected from theory (Bonduriansky *et al.* 2008). In contrast, we present an example of a system with male-biased mortality rates (Sherratt *et al.* 2011) but where there is little evidence of a cost of mating or reproductive senescence. This may result from a scramble mating system that does not necessarily reward animals in good condition with more matings. Based on this study, we recommend that future studies of senescence take into account breeding status using stage-structured or multistrata models, since different types of individual may senesce at different rates.

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Data accessibility

- Multistrata capture histories: figshare doi: 10.6084/m9.figshare.1422087
- R scripts: figshare doi: 10.6084/m9.figshare.1422127

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Tables

Table 1 – Abbreviations for terms used in the models.

Abbreviation	Term	Definition
Model components		
p	resighting probability	The probability of an individual being sighted
S	survivorship	The stratum-specific probability of an individual *s*urviving
ψ	transition probability	The probability of an individual moving between strata (in this analysis: (i) breeding, and (ii) non-breeding)
Covariates		
.	"dot"	This indicates a fixed value for a given parameter
t	time	The day of the study.
x	age	The age of an individual on day t
m	mite burden	The number of ectoparasitic mites an individual was carrying on first capture
c	climate	Three climate variables: daily temperature, daily precipitation and daily hours of sunshine.
s	size	Length of the right fore wing
strat	breeding stratum	The breeding status of an individual ("breeding" or "non-breeding")

Table 2 – Generalised linear mixed effects models from the “pooled” analysis showing how the proportion of damselflies present at a mating rendezvous (“presence”), and the proportion of damselflies mating (“mating”) varies with age. In both models year is a random effect. All models for presence and the mating model including both males and females are fitted with quasibinomial errors to take into account overdispersion (see text for details). Parameter estimates for the “Sex” term are for males compared to females as the baseline, such that a positive value indicates that the response is higher in males. Significant terms are highlighted in **bold**.

			Presence				Mating			
		DF	Estimate	SE	t	P	Estimate	SE	Z	p
Females and males	(Intercept)	136	**0.298**	**0.121**	**2.469**	**0.015**	**1.458**	**0.282**	**5.168**	**<0.001**
	Sex	136	**1.346**	**0.191**	**7.029**	**<0.001**	**-2.277**	**0.120**	**-18.959**	**<0.001**
	Age	136	-0.015	0.010	-1.456	0.148	**-0.016**	**0.008**	**-1.994**	**0.049**
	Sex*Age	136	**-0.089**	**0.021**	**-4.298**	**<0.001**	**0.060**	**0.014**	**4.330**	**<0.001**
Females	(Intercept)	71	**0.298**	**0.135**	**2.209**	**0.030**	**1.344**	**0.146**	**9.227**	**<0.001**
	Age	71	-0.015	0.012	-1.303	0.197	**-0.012**	**0.006**	**-2.008**	**0.045**
Males	(Intercept)	64	**1.642**	**0.129**	**12.761**	**<0.001**	**-0.802**	**0.348**	**-2.307**	**0.021**
	Age	64	**-0.105**	**0.015**	**-6.831**	**<0.001**	**0.043**	**0.009**	**4.563**	**<0.001**

Table 3 – Results of MARK models showing that breeding status (strat) is important in determining resighting, survival and breeding status transitions in both sexes in both years. For the full model fits see Table S1.

			Male 2005		Male 2006		Female 2005		Female 2006	
Model			ΔAICc	w_i	ΔAICc	w_i	ΔAICc	w_i	ΔAICc	w_i
p(strat)	S(strat)	ψ(strat)	0.00	0.73	0.00	0.63	0.00	0.85	0.00	0.86
p(strat)	S(.)	ψ(strat)	1.99	0.27	39.77	0.00	7.13	0.02	25.34	0.00
p(strat)	S(strat)	ψ(.)	66.43	0.00	1.05	0.37	4.16	0.11	12.20	0.00
p(.)	S(strat)	ψ(.)	69.03	0.00	152.14	0.00	126.35	0.00	261.29	0.00
p(strat)	S(.)	ψ(.)	69.61	0.00	39.32	0.00	7.33	0.02	30.04	0.00
p(.)	S(strat)	ψ(strat)	71.05	0.00	32.29	0.00	61.11	0.00	3.73	0.13
p(.)	S(.)	ψ(.)	77.52	0.00	220.52	0.00	150.76	0.00	313.61	0.00
p(.)	S(.)	ψ(strat)	79.53	0.00	92.86	0.00	82.36	0.00	24.16	0.00

Table 4 – Results of MARK models incorporating breeding status (strat), climate data (c, comprising mean daily temperature (°C), daily precipitation (mm) and hours of sunshine), individual mite burden (m), size (s, indicated by fore wing length) and age (x). All models containing "x", "s", or "m", also contain the respective quadratic terms that have been omitted from the table for clarity. Only models with ΔAICc<4 are shown – see Table S3 for the total model set. All models contained the terms p(c+m+strat), S(x*strat+m+strat).

Sex	Year	Psi	df	logLik	AICc	delta	weight
Female	2005	strat+m	19	-1218.265	2475.670	0.000	0.511
		strat+m+s	20	-1218.231	2477.723	2.053	0.183
		strat+m+x+x*strat	23	-1215.737	2479.139	3.469	0.090
	2006	strat+c+s	22	-2723.190	5490.998	0.000	0.379
		strat+c	20	-2725.348	5491.209	0.211	0.341
		strat+c+m+s	24	-2722.822	5494.378	3.380	0.070
		strat+c+s+x+x*strat	26	-2720.791	5494.443	3.445	0.068
		strat+c+m	22	-2725.011	5494.639	3.642	0.061
		strat+c+x+x*strat	24	-2722.984	5494.703	3.705	0.059
Male	2005	strat+c+s+x+x*strat	26	-1736.061	3525.473	0.000	0.379
		strat+c+m+s+x+x*strat	27	-1735.157	3525.770	0.297	0.327
		strat+c+x+x*strat	24	-1738.844	3526.840	1.367	0.191
		strat+c+m+x+x*strat	26	-1737.602	3528.554	3.081	0.081
	2006	strat+c+m+s+x+x*strat	27	-2558.061	5170.994	0.000	0.246
		strat+c+m+s	23	-2562.217	5171.069	0.075	0.237
		strat+c+s+x+x*strat	25	-2560.726	5172.201	1.207	0.135
		strat+c+s	21	-2564.922	5172.375	1.381	0.124

	strat+c+m+x+x*strat	26	-2560.343	5173.495	2.501	0.071
	strat+c+m	22	-2564.497	5173.577	2.583	0.068
	strat+c+x+x*strat	24	-2562.658	5174.007	3.013	0.055
	strat+c	20	-2566.900	5174.282	3.288	0.048

Figures

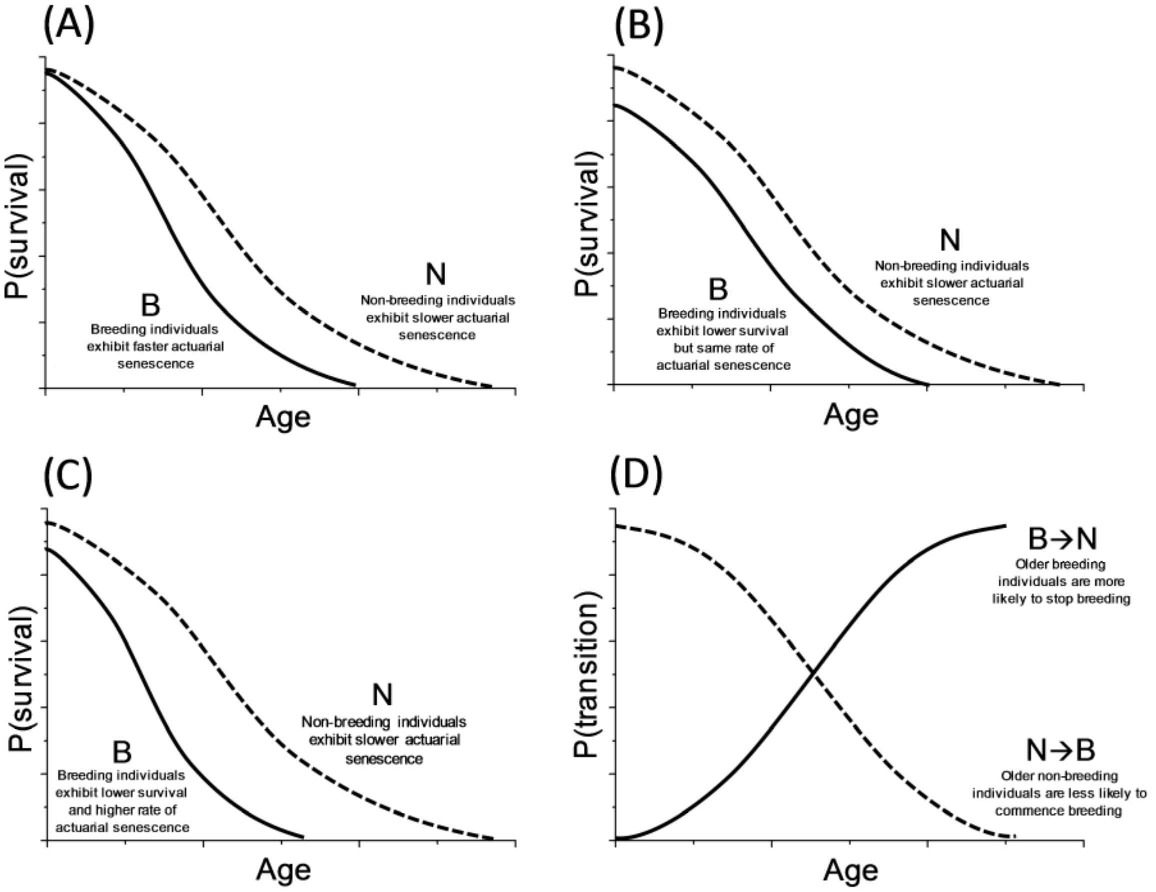

Figure 1 – Predictions of three different models of costs of sex (A-C) and reproductive senescence (D). (A) Breeding animals senesce at a greater rate than non-breeding animals, (B) breeding animals incur a fixed cost of breeding but senesce at the same rate as non-breeding animals, (C) breeding animals pay a fixed cost and senesce at a greater rate than non-breeding animals, and (D) older individuals are less likely to begin breeding (N→B) and more likely to stop breeding (B→N) ("reproductive senescence").

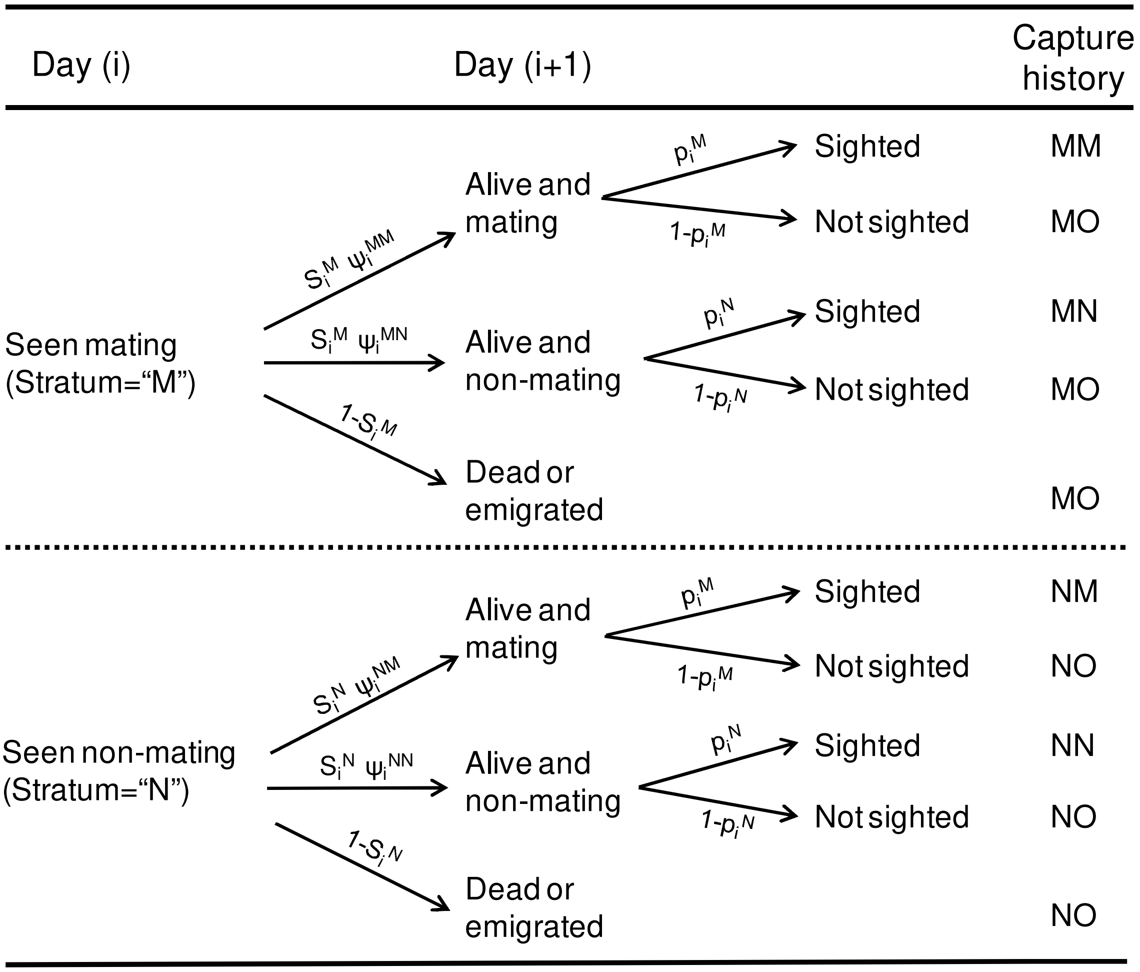

Figure 2 – An illustration of the parameters used in multistrata models (S=survival, p=resighting probability, ψ=transition probability between strata) and the capture histories that they describe (M=mating, N=non-mating, 0=absent). Note the same capture history (the sequence of interactions between the researcher and the individual animal) can arise from multiple sequences of events. Stratified modelling allows us to estimate the probability of events even when we do not directly observe an animal. Illustration based on Figure 1 in Nichols *et al.* (1994).

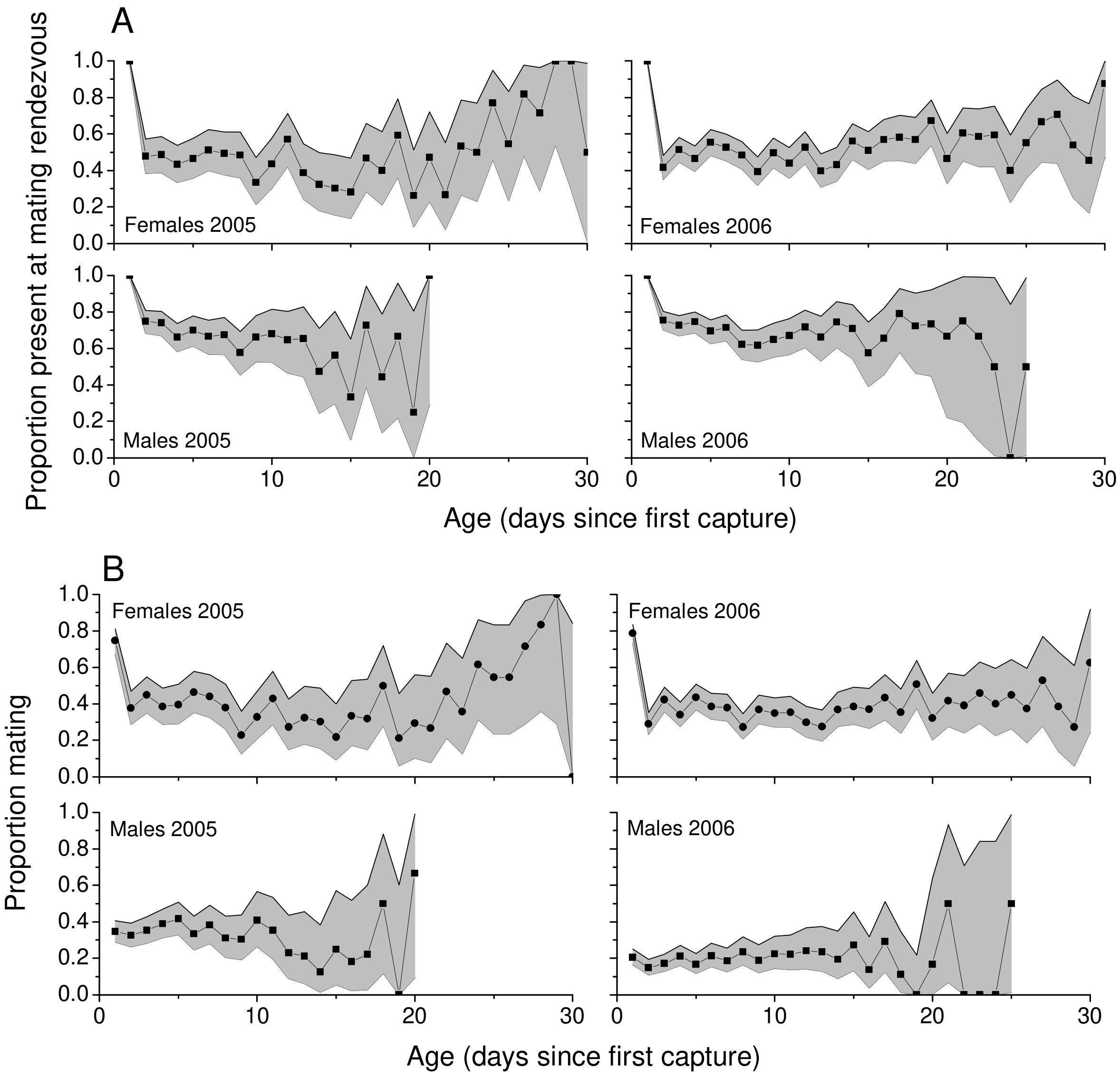

Figure 3 – (A) The proportion of living individuals present at the mating rendezvous, and (B) the proportion of living individuals that were observed mating in the pooled analysis. Shaded areas represent 95% Clopper-Pearson confidence intervals for the proportions.

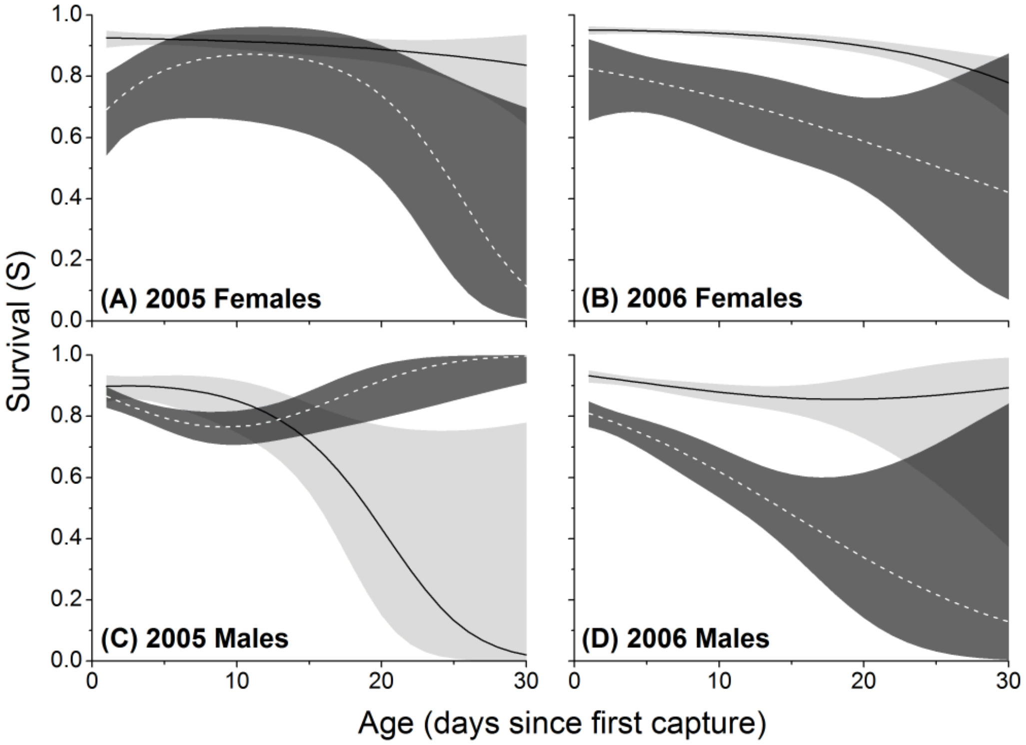

Figure 4 – Variation in age-related changes in daily survival (S) in the damselfly *Coenagrion puella*: (A) females in 2005, (B) females in 2006, (C) males in 2005, and (D) males 2006. Parameter values are taken from best fit models in Table 3. Dotted lines with black 95% confidence regions are non-breeding individuals, and solid lines with grey error regions are breeding individuals.

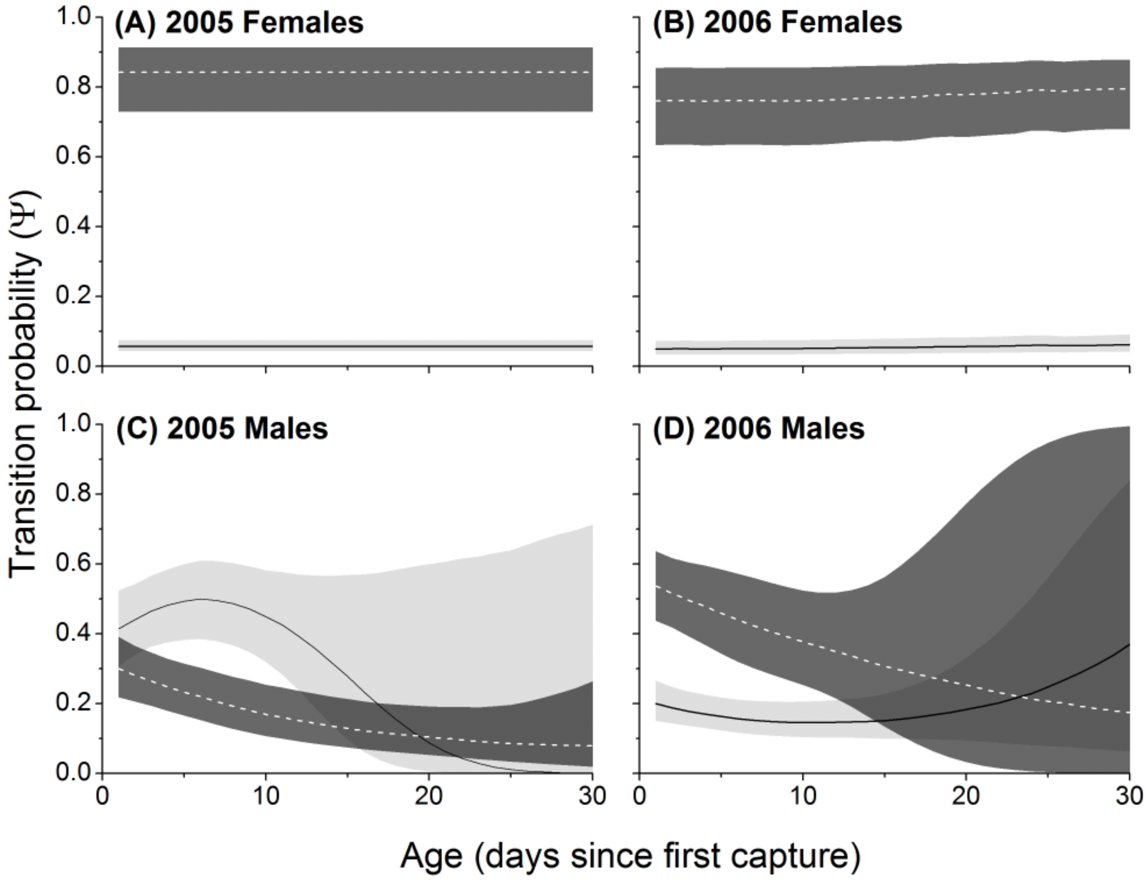

Figure 5 – Variation in age-related probability of transition between breeding states (Ψ) in the damselfly *Coenagrion puella*: (A) females in 2005, (B) females in 2006, (C) males in 2005, and (D) males 2006. Parameter values are taken from best fit models in Table 3. Dotted lines with black 95% confidence regions are non-breeding individuals, and solid lines with grey error regions are breeding individuals. The transition probability represents the daily probability of changing to the other breeding state (e.g. stopping breeding or starting breeding).

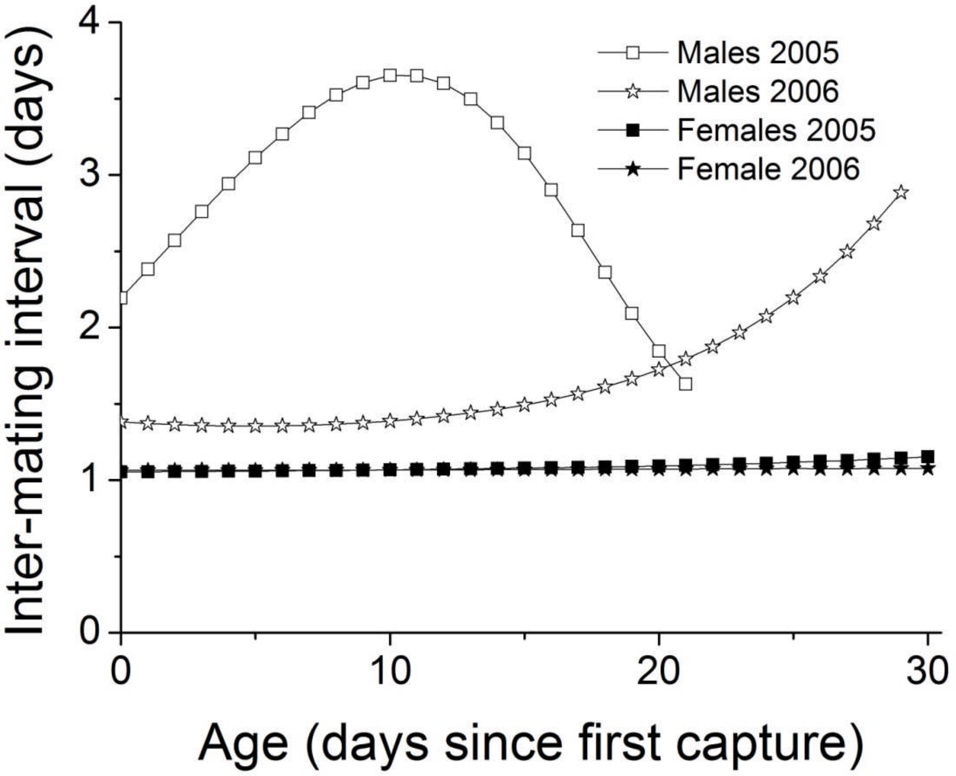

Figure 6 – Age-dependent change in inter-mating interval (time between clutches fertilised or laid) in *Coenagrion puella*.