

Reproductive ageing and sexual selection on male body size in a wild population of antler flies (*Protopiophila litigata*)

R. BONDURIANSKY*† & C. E. BRASSIL*

*Department of Zoology, University of Toronto, Toronto, ON, Canada

†School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia

Keywords:

body size;
field study;
life history;
Protopiophila litigata;
senescence;
sexual selection;
trade-off;
wild population.

Abstract

Little is known about the importance of trade-offs between ageing and other life history traits, or the effects of ageing on sexual selection, particularly in wild populations suffering high extrinsic mortality rates. Life history theory suggests that trade-offs between reproduction and somatic maintenance may constrain individuals with higher initial reproductive rates to deteriorate more rapidly, resulting in reduced sexual selection strength. However, this trade-off may be masked by increased condition dependence of reproductive effort in older individuals. We tested for this trade-off in males in a wild population of antler flies (*Protopiophila litigata*). High mating rate was associated with reduced longevity, as a result of increased short-term mortality risk or accelerated ageing in traits affecting viability. In contrast, large body size was associated with accelerated ageing in traits affecting mating success, resulting in reduced sexual selection for large body size. Thus, ageing can affect sexual selection and evolution in wild populations.

Introduction

Senescence ('ageing'), the process of somatic deterioration that occurs as individuals age, is typically manifested in declining survival, reproduction and reproductive value (Partridge & Barton, 1996). Although ageing can have considerable implications for individual fitness, even in wild populations (Nesse, 1988; Bonduriansky & Brassil, 2002), studies have typically relied on aggregate statistics from cohorts, while individual variation in ageing rates (which is the raw material for selection on ageing) remains poorly understood (Austad, 1996; Service *et al.*, 1998; Partridge & Mangel, 1999; Zens & Peart, 2003). Consequently, despite considerable theoretical interest in the role of ageing in sexual selection (e.g. Kokko & Lindström,

1996; Kokko, 1998; Brooks & Kemp, 2001), relevant empirical evidence is scarce. In general, we know relatively little about the importance of trade-offs between ageing rate and other life history traits. Given that environmental factors can have a large influence on the expression of ageing (Roach, 2001; Marden *et al.*, 2003), it is particularly useful to address these questions in wild populations, which can illuminate natural patterns of selection on ageing. Yet, for practical reasons, very little is known about patterns of ageing in the wild.

Life history theory suggests that patterns of survival and reproduction are shaped to a substantial degree by trade-offs between fitness components (Roff, 1992). Such trade-offs may account for the evolution of ageing. Because selection strength invariably declines with age (Medawar, 1946), selection will favour traits that increase reproductive rate in early life while also contributing to somatic deterioration through antagonistic pleiotropy (Williams, 1957). For example, resource allocation to reproduction may trade-off directly against resource allocation to somatic maintenance (Kirkwood, 1977; Kirkwood & Holliday, 1979; Kirkwood & Rose,

Correspondence: Russell Bonduriansky, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia.

Tel.: +61-02-9385-3439; fax: +61-2-9385-1558;

e-mail: r.bonduriansky@unsw.edu.au

Present address: Chad E. Brassil, W.K. Kellogg Biological Station, Michigan State University, 3700 E Gull Lake Dr, Hickory Corners, MI 49060, USA

1991). There is compelling evidence of such trade-offs in many organisms. For example, increased reproductive effort is associated with accelerated ageing and reduced lifespan (e.g. Ernesting & Isaaks, 1991; Rose & Charlesworth, 1981a, b; Tucić *et al.*, 1996; Gasser *et al.*, 2000), and sexual activity suppresses immune function (McKean & Nunnery, 2001; Rolff & Siva-Jothy, 2002). Although antagonistic pleiotropy theory assumes that both reproductive rate and somatic maintenance have a genetic basis, trade-offs between these traits may also result from environmental factors (see Discussion).

Ageing could either strengthen or weaken net sexual selection, depending on the relation between ageing rate and other fitness-related traits. Life history theory suggests that trade-offs between reproductive rate and somatic maintenance may constrain individuals with high initial reproductive rates to deteriorate more rapidly (Fig. 1a). In such a case, ageing could play a role in a life history strategy, involving heavy investment in

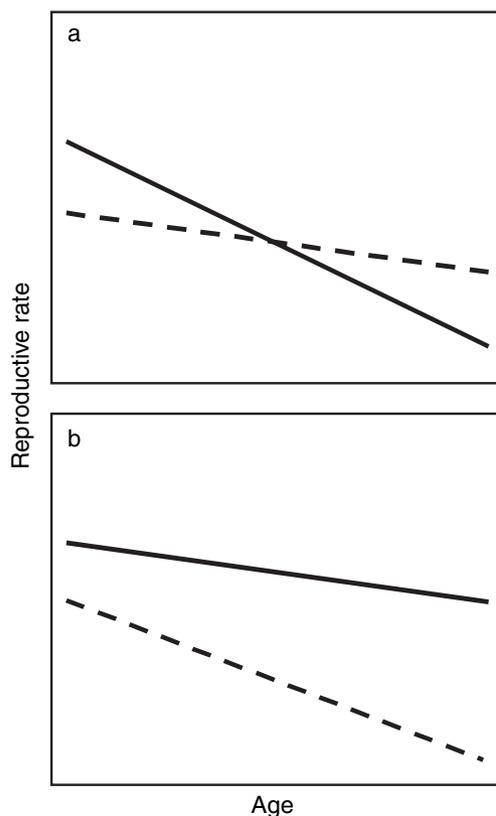


Fig. 1 Contrasting patterns of ageing predicted by life history theory: (a) trade-offs may cause individuals with high initial mating rates (solid line) to age faster than individuals with lower initial mating rates (dashed line); (b) alternatively, large individual variation in condition and increasing reproductive effort with age may enable individuals with high initial mating rates to maintain or increase their relative advantage with age.

reproduction at the cost of rapid deterioration, that only high-condition individuals could afford. Although high-condition individuals would still achieve maximum fitness over their lifetimes, rapid ageing would erode their advantage, thus diminishing the strength of net sexual selection. Such a pattern was observed by Hunt *et al.* (2004) in field crickets. However, it is unclear to what extent the results of their laboratory experiment can be extrapolated to wild populations, which probably experience much higher costs of reproduction and rates of mortality.

However, life history theory also suggests that an alternative scenario is possible. Because reproductive rate typically reflects individual condition (see Clutton-Brock, 1988), variation in condition might mask underlying trade-offs between reproduction and somatic maintenance (see Reznick, 1985; Clutton-Brock, 1988). In particular, if selection favours greater reproductive effort in older individuals (Gadgil & Bossert, 1970; Kokko, 1998; Kemp, 2002; Proulx *et al.*, 2002), reproductive rate may become increasingly condition dependent with age. This may enable individuals with high initial reproductive rates to age less rapidly (Fig. 1b). In this case, ageing would increase the strength of net sexual selection. The effect of ageing on sexual selection is thus an empirical question that needs to be addressed, particularly in wild populations.

The direction of the effect of ageing on net sexual selection is relevant to a host of evolutionary questions. For example, because old age may signal 'good genes' for viability, it has been suggested that females may evolve preferences for old males (Kokko & Lindström, 1996; Kokko, 1998; Brooks & Kemp, 2001; Beck *et al.*, 2002; but see Radwan, 2003). However, if the most successful males lose their intra-sexual competitive advantage with age, then ageing may reduce females' opportunity to exercise preferences for old males. Conversely, if the most successful males can maintain or amplify their competitive advantage with age, then ageing would tend to increase females' opportunity to exercise preferences for old males.

Antler flies (*Protophila litigata*; Diptera: Piophilidae) are small insects (1.5–3.2 mm body length) whose extreme site fidelity and long copulation duration make it possible to obtain longitudinal life history data on marked individuals in the wild (Bonduriansky & Brassil, 2002). Previous research showed that wild males lose at least 20% of their potential fitness from age-related declines in survival and reproduction, although the latter effect (i.e. 'reproductive ageing': age-related deterioration in traits affecting reproductive rate) appeared to have the greater effect (Bonduriansky & Brassil, 2002). In addition, body size is an important determinant of male fitness: large males are more successful at defending territories and more attractive to females (Bonduriansky & Brooks, 1998a, 1999). The importance of ageing rate and body size in this system provided an opportunity to

test for trade-offs between these traits, and to examine the interaction between ageing and sexual selection in a wild insect population.

Materials and methods

Nine discarded moose (*Alces alces*) antlers were set up on 0.8 m high wooden stands in the forest at the Wildlife Research Station in Algonquin Park, Ontario. Male antler flies ($n = 609$) were collected from the antlers, measured and marked individually using the technique of Bonduriansky & Brooks (1997), and released near the antlers. As an index of body size, total body length (abdomen tip to antenna tip) was measured to 0.01 mm using a dissecting microscope and micro-calipers. Mating aggregations on the antlers were surveyed every 2 h during 72 days in June, July and August and the presence and mating status (i.e. single vs. coupled) of each male were recorded. Reproductive ageing analysis was performed using data for males observed for at least 2 days after release ($n = 488$) to eliminate individuals that may have been injured during marking, and excluding data for each male's mark-release day (i.e. incomplete daily records). Body lengths are not available for some males (see Results for actual sample sizes).

Males were assumed to be newly emerged (24–48-hour old) on their mark-release day because, beginning in early May, numerous final-instar larvae were observed leaving the antlers to pupate in the surrounding soil and, from early June (when the first adults were observed on antlers) until early August (i.e. late in the season), teneral adults were frequently observed near the antlers. Moreover, the rate of migration between distant antlers was low, as indicated by the fact that about half of the marked males never moved from the antler where they were first observed to adjacent antlers <5 m away, and <1% of males moved to an antler stationed 100 m away from the cluster of other antlers. Thus, flies newly-emerged from pupae surrounding the antlers very likely constituted a large majority of unmarked adults appearing on the antlers throughout the season. Likewise, marked males disappearing from the population were assumed to have died because the mean daily re-sighting probability for individual males was high (63%) and probability of immigration was low.

Our sample comprised multiple cohorts of males that emerged continually throughout the season. Moreover, mean lifespan, mating success, and mating rate did not change over the season ($P > 0.2$ for all tests). Thus, it is unlikely that our ageing rate estimates are confounded by seasonal variation. However, mean body length of emerging adults declined over the season, perhaps as a result of declining quality of larval food inside antlers. Selection on adults did not contribute to this result, since larger males survived longer on average (see below). Body lengths were adjusted for seasonality using residu-

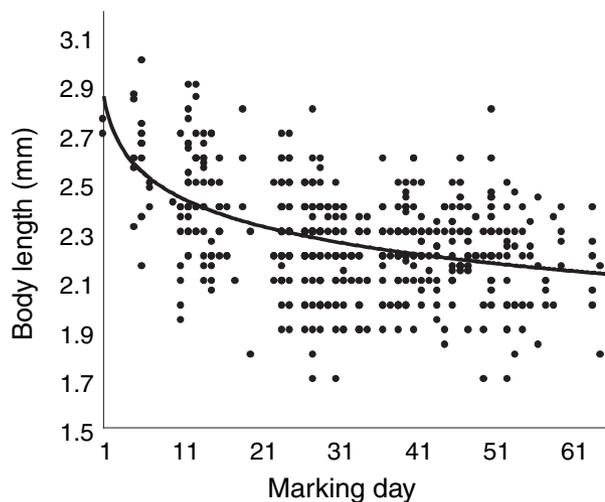


Fig. 2 Change in mean body size over the season, showing fitted regression of log body length on day of marking ($Y = -0.0027X + 0.904$; $n = 526$, $r^2 = 0.16$, $F = 97.9$, $P < 0.0001$).

als from a regression of log body length on the day of marking (Fig. 2), with a constant added to make all residuals positive. We employed residuals instead of including day of marking in the model to simplify our presentation of results, and to maximize power to detect effects of the variables of primary interest (i.e. age, lifespan and body size). Seasonally adjusted body length ('body size') was used as a continuous variable in all analyses. However, for the purpose of illustration only, the sample of males was divided into 'large' and 'small', based on the sign of their body length residual.

The effect of various factors on daily mating success was modelled using maximum likelihood techniques (Hilborn & Mangel, 1997), with likelihood minimization conducted in Mathematica 4.0 (Wolfram, 1999). To determine whether factors affected the rate of ageing, we examined their interactions with age. We added age, lifespan, a lifespan \times age interaction, body size, and a body size \times age interaction incrementally to the model, testing at each step for an improvement in model fit over the previous (simpler) model (Table 1). Note that lifespan and age are not fully independent variables, since only long-lived individuals provide data for advanced ages. Model fit was compared using the Akaike Information Criterion (AIC), a standard method that takes into account both how well a model fits the data (i.e. the log-likelihood) and how simple or parsimonious it is (i.e. the number of parameters estimated in the model), penalizing models that are unnecessarily complex (Sakamoto *et al.*, 1986). Whereas parametric techniques can only be used to compare nested models, the AIC can be used to compare any set of models. A smaller AIC value represents better model fit, with a difference of 1.0 or greater considered significant (Sakamoto *et al.*, 1986).

Table 1 Models describing the number of daily first (μ_1) and second (μ_2) mating for wild antler fly males, showing the sequential addition of parameters and interactions, with tests for improved model fit.

Effect	Model	Maximum likelihood estimates	95% confidence intervals	AIC	Likelihood ratio test <i>P</i> value
Poisson					
Age	$\mu = \lambda$	$\lambda = 0.318$		4721.58	
	$\mu = \lambda \exp(\kappa A)$	$\lambda = 0.392$ $\kappa = -0.0296$		4699.36	<0.001
General Poisson					
Age	$\mu_1 = \lambda_1 \exp(\kappa_1 A)$ $\mu_2 = \lambda_2 \exp(\kappa_2 A)$	$\lambda_1 = 0.418$ $\kappa_1 = -0.0285$ $\lambda_2 = 0.262$ $\kappa_2 = -0.116$		4616.84	
Lifespan	$\mu_1 = \lambda_1 \exp(\kappa_1 A + \phi_1 L)$ $\mu_2 = \lambda_2 \exp(\kappa_2 A + \phi_2 L)$	$\lambda_1 = 0.465$ $\kappa_1 = -0.0117$ $\phi_1 = -0.0184$ $\lambda_2 = 0.172$ $\kappa_2 = -0.180$ $\phi_2 = 0.0661$		4595.60	<0.001
Lifespan \times age	$\mu_1 = \lambda_1 \exp(\kappa_1 A + \phi_1 L + \eta_1 AL)$ $\mu_2 = \lambda_2 \exp(\kappa_2 A + \phi_2 L + \eta_2 AL)$	$\lambda_1 = 0.495$ $\kappa_1 = -0.0270$ $\phi_1 = -0.0222$ $\eta_1 = 0.00082$ $\lambda_2 = 0.156$ $\kappa_2 = -0.149$ $\phi_2 = 0.0725$ $\eta_2 = -0.00183$		4598.56	0.405
Body size	$\mu_1 = \lambda_1 \exp(\kappa_1 A + \phi_1 L + \beta_1 B)$ $\mu_2 = \lambda_2 \exp(\kappa_2 A + \phi_2 L)^*$	$\lambda_1 = 0.312$ $\kappa_1 = -0.0120$ $\phi_1 = -0.0192$ $\beta_1 = 0.662$ $\lambda_2 = 0.171$ $\kappa_2 = -0.179$ $\phi_2 = 0.0661$		4582.34	<0.001
Body size \times age	$\mu_1 = \lambda_1 \exp(\phi_1 L + \beta_1 B + \gamma_1 AB)^\dagger$ $\mu_2 = \lambda_2 \exp(\kappa_2 A + \phi_2 L)$	$\lambda_1 = 0.286$ $\phi_1 = -0.017$ $\beta_1 = 0.80$ $\gamma_1 = -0.025$ $\lambda_2 = 0.171$ $\kappa_2 = -0.179$ $\phi_2 = 0.0660$	(0.216, 0.378) (-0.034, -0.004) (0.410, 1.210) (-0.049, 0.001) (0.106, 0.260) (-0.249, -0.123) (0.026, 0.103)	4580.22	<0.05

* β_2 dropped out as not significant.

† With the addition of γ_1 , κ_1 dropped out as not significant.

P value is based on nested comparison with κ_1 included.

Bold values indicate a significantly improved fit.

A, age; *L*, lifespan; *B*, body size.

Nested models were also compared using the likelihood ratio test. For parameters included in the best-fit model, 95% confidence limits were generated by 1500 bootstraps.

The mean, daily number of mating per fly appeared to conform closely to the assumptions of a Poisson process in that the outcome was discrete (zero, one, or two mating per day), but the underlying rate of attaining mating was a continuous value dependent on factors included in the model. The use of a specific parametric

process in the context of maximum likelihood techniques allowed us to use all the information contained in the observations of individual flies, as opposed to aggregating data in order to meet the normality assumptions of classical statistics. Although a linear model yielded the best fit for net daily mating rate in our previous analysis (Bonduriansky & Brassil, 2002), we used exponential models here because their asymptotic behaviour near zero prevents these models from predicting negative mating rates.

Net daily mating success was first modelled assuming a random Poisson process with a rate constant μ , and then a generalized Poisson process in which the instantaneous rates of attaining daily first mating, μ_1 , and second mating, μ_2 , were specified separately (see Faddy & Bosch, 2001). The rate of attaining daily third mating was set to zero because no third mating were observed, and setting this parameter to zero does not alter the results. Daily first and second mating were modelled as separate parameters because the rate of second mating was $\sim 40\%$ less than that of first mating, probably as a result of long mating duration (2.3 h) and males' need to re-establish territories after each mating (Bonduriansky & Brooks, 1998b, 1999). Use of separate parameters is thus justified biologically, and probably increased our power to detect effects and interactions because the parametric assumptions better match the distribution of the data. However, this analysis is based on the assumption that males gain equal fitness from each copulation, including daily first and second mating. If daily second mating has less fitness value than first mating (e.g. because male fertility declines temporarily after the first mating), then our analysis may over-estimate the actual rate of reproductive ageing. Conversely, if male fertility declines continually with male age, then our analysis may under-estimate the actual rate of reproductive ageing.

Results

We compared models encompassing an increasing range of parameters and interactions to describe the daily probability of mating (Table 1). The overall best-fit model (Table 1, bottom) included differential rates of attaining daily first mating (μ_1) and second mating (μ_2), an age effect for the rate of second mating, a lifespan effect for rates of first and second mating, a body size effect, and a body size \times age interaction in the rate of attaining first mating. The rate of decline in the probability of second mating (κ_2) exceeded that for first mating (κ_1) in every version of the model, and κ_1 was not a significant parameter in the overall best-fit model.

The rate of daily first mating declined with lifespan ($\phi_1 < 0$), whereas the rate of daily second mating increased with lifespan ($\phi_2 > 0$). Overall, this resulted in higher mean mating rates for short-lived flies, suggesting a trade-off between longevity and mating rate. Nonetheless, lifespan did not covary with reproductive ageing (i.e. there was no lifespan \times age interaction). Standardized lifespan (Y) was an increasing function of body size (X) among males observed one or more days after release ($Y = 0.085X - 0.003$; $n = 524$, $r^2 = 0.007$, $F_{1,522} = 3.77$, $P = 0.0527$; Fig. 3). A similar result was obtained if only males observed two or more days after release were included ($Y = 0.085X + 0.079$; $n = 487$, $r^2 = 0.007$, $F_{1,485} = 3.52$, $P = 0.0613$).

Body size was also a significant parameter in the rate of attaining first mating, indicating an advantage for large

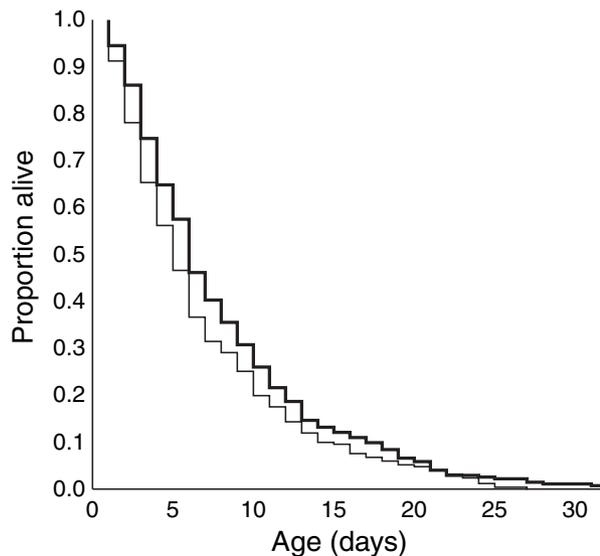


Fig. 3 Survival (l_x) curves for males larger (thick line) and smaller (thin line) than the seasonally adjusted average, plotted for all males observed at least 1 day after release ($n = 534$).

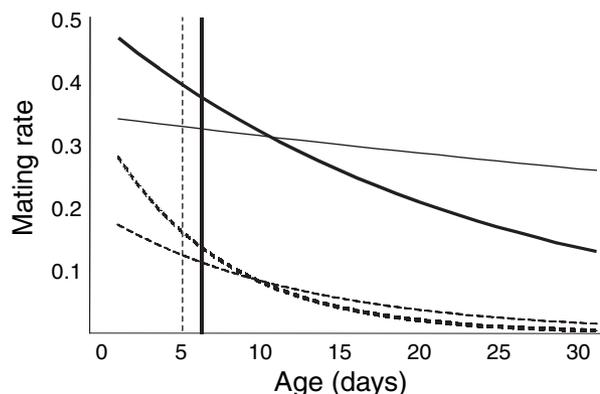


Fig. 4 Reproductive ageing curves: solid and dashed curves show rates of attaining daily first and second mating, respectively, plotted separately for males larger (thick lines) and smaller (thin lines) than the seasonally adjusted average in order to illustrate the body size by age interaction (note that body size was treated as a continuous variable in the analysis). Vertical lines indicate median lifespans for large (solid) and small (dashed) males. The model represented consists of an age effect only.

males ($\beta_1 > 0$). For example, in the best-fit model, a 1-day-old male in the third body size quartile had a 28% greater probability of mating than a similar male in the first body size quartile. The rate of daily first mating also exhibited a body size \times age interaction. Both the AIC and the likelihood ratio test (with γ_1 removed from the model) suggested that γ_1 is significantly less than zero,

although the upper confidence limit for γ_1 slightly exceeded zero. Thus, reproductive ageing rate increased with body size, causing the daily mating rate advantage of large males to decline with age (Fig. 4).

To determine how ageing affects sexual selection on body size in this population, we estimated the effect of the body size \times age interaction on the sexual selection differential (i.e. the regression slope of standardized lifetime mating success on body size). We first calculated lifetime mating success for each individual as the sum of discrete-time (daily) mating success estimates based on the best-fit model (Table 1), and used these (standardized) estimates to calculate the regression of lifetime mating success (Y) on body size (X): $Y = 0.233X + 0.044$ ($n = 488$, $r^2 = 0.054$, $F_{1,486} = 27.8$, $P < 0.0001$). We then removed the body size \times age interaction from the model (i.e. set γ_1 to zero), and recalculated each individual's lifetime mating success. This altered the regression to $Y = 0.244X + 0.044$ ($n = 488$, $r^2 = 0.059$, $F_{1,486} = 30.7$, $P < 0.0001$). Thus, the relation between body size and ageing rate reduces the strength of sexual selection favouring large body size by $0.233/0.244 = 0.95$, or 5% ($P < 0.05$, based on the significance of γ_1 in the best-fit model, Table 1).

Discussion

We found that large males mated more frequently in early life but also suffered more rapid reproductive ageing, manifested primarily as a decline in the occurrence of mating twice in 1 day. The association of large body size with rapid ageing was reflected in weakened net sexual selection for large body size. We also found that males that mated more frequently tended to die sooner. These findings suggest that trade-offs between somatic maintenance and reproduction can affect sexual selection and evolution in wild populations suffering high background mortality rates (~13% per day).

Ageing and sexual selection

Covariation between body size and ageing rate suggests that ageing may affect the mating system and the evolution of body size. Although the advantages of large body size are well documented, the opposing selection vectors that apparently produce net stabilizing selection on this trait are less well understood (Blanckenhorn, 2000). Our results suggest that variation in ageing rate may contribute to stabilizing selection on body size by reducing the strength of net sexual selection. Moreover, our findings support Clutton-Brock's (1988) assertion that cross-sectional mating success assays that ignore the effects of age may yield biased estimates of sexual selection. Because of trade-offs between reproduction and somatic maintenance, laboratory studies that assay the performance of young individuals may tend to overestimate sexual selection

strength, whereas use of old individuals may tend to underestimate it.

Our results also support the findings of an important laboratory experiment. Hunt *et al.* (2004) found that high-condition males invest more heavily in calling but also appear to age more rapidly and tend to die sooner than low-condition males. However, because captive crickets probably experience much lower costs of reproduction and have much longer lifespan than wild ones, it is not clear whether a similar pattern would be apparent in the wild. Our results suggest that the findings of Hunt *et al.* (2004) are indeed relevant to some wild populations.

It has been suggested that females may evolve preferences for old males, because such males are likely to possess 'good genes' for viability (Kokko & Lindström, 1996; Kokko, 1998; Brooks & Kemp, 2001; Beck *et al.*, 2002; Osada *et al.*, 2003). However, sexual selection mechanisms tend to operate in sequence, with male-male interactions often preceding male-female interactions (see Berglund *et al.*, 1996; Bonduriansky, 2003; Bonduriansky & Rowe, 2003). Antler fly females appear to be choosy (Bonduriansky & Brooks, 1998a), although it is not clear whether they can assess male age. Nonetheless, if large males lose their intra-sexual competitive ability with age, then male-male interactions may limit females' opportunity to choose old males (see Bonduriansky & Rowe, 2003). Likewise, if males are able to assess the age of rivals, individual variation in ageing rate may affect the evolution of male-male agonistic interactions (see Kemp, 2002; Hu & Morse, 2004). Thus, individual variation in ageing rate may affect sexual selection, and key aspects of the mating system such as the assessment or potential mates or rivals.

Ageing and body size

Our study provides direct evidence of positive covariation between body size and reproductive ageing rate in a wild population. Body size is associated with competitive ability in many organisms (Blanckenhorn, 2000), including male antler flies (Bonduriansky & Brooks, 1999). However, our findings suggest that large body size (or a correlated trait), which confers high mating rate in early life, trade-offs against the ability to sustain a high mating rate at older ages by avoiding or repairing somatic damage, possibly rendering large body size disadvantageous at older ages (Fig. 4). In contrast, large males tended to survive slightly longer (Fig. 3), although this probably reflects a lower extrinsic mortality rate (e.g. lesser vulnerability to predators) rather than slower ageing in traits affecting viability (i.e. survival).

Inter-specific comparisons suggest that larger organisms tend to age more slowly (Comfort, 1979), perhaps because lower extrinsic mortality rates select for extended reproductive schedules (Kirkwood, 1992). Curiously,

a growing body of evidence points to the opposite pattern within species, consistent with our findings. For example, Hillesheim & Stearns (1992) found that *Drosophila melanogaster* selected for higher body weight exhibited shorter lifespans and more rapid declines in offspring viability. Likewise, mutations that produce dwarf phenotypes in *Drosophila* and mice also tend to prolong life (Coschigano *et al.*, 2000; Bartke *et al.*, 2001; Clancy *et al.*, 2001), and studies on a wide range of organisms show that lifespan can be extended by diet restriction (Medawar, 1946; Bartke *et al.*, 2001; Clancy *et al.*, 2001, 2002; Magwere *et al.*, 2004; Wang *et al.*, 2004). These findings are also consistent with evidence that domestic dogs of larger breeds age more rapidly than dogs of smaller breeds (Patronek *et al.*, 1997).

It is not clear why large individuals tend to exhibit more rapid reproductive ageing. One possibility is a physiological trade-off between the demands of growing rapidly or maintaining a large body, and the demands of avoiding or repairing somatic damage (Metcalf & Monaghan, 2003). Such a trade-off could be mediated by hormones or insulin-like factors (Coschigano *et al.*, 2000; Nijhout, 2003). For example, juvenile hormone regulates the development of primary and secondary sexual traits in insects, but also suppresses immune function (Wedekind & Folstad, 1994; Rolff & Siva-Jothy, 2002; Rantala *et al.*, 2003). In addition, interactions between physiological condition and extrinsic hazards or stresses (see Abrams, 1993; Williams & Day, 2003) may select for relatively greater investment in somatic repair by small males, if a given degree of somatic deterioration results in greater fitness loss for small individuals.

Alternatively, the relation between body size and ageing rate may be an emergent consequence of body size-related behavioural variation. Because large antler fly males tend to defend territories in the densest parts of aggregations (Bonduriansky & Brooks, 1999), they may engage in more frequent or more intense combat, and suffer a greater rate of somatic damage. Such a pattern has been reported in male burrowing bees, where large ('major') males that fight suffer more rapid deterioration than small ('minor') males that employ a searching tactic (Alcock, 1996). Thus, rapid ageing may represent a cost of pursuing a behavioural strategy that yields high lifetime mating success, but is unavailable to small males that fare poorly in agonistic interactions.

If both body size and somatic maintenance have a genetic basis in *P. litigata*, then negative covariation between these traits may reflect antagonistic pleiotropy (Williams, 1957). Body size exhibits additive genetic variance in Diptera (Simmons & Ward, 1991; Bonduriansky & Rowe, 2005). Evolutionary models assume that ageing rate also has a genetic basis, and can be optimized by altering investment in somatic repair (Kirkwood & Rose, 1991). Note, however, that insects cannot repair exoskeletal damage regardless of investment in repair

mechanisms (Wigglesworth, 1972; Chapman, 1998), even though such damage may increase with age (see Otronen, 1996) and reduce fitness (Cartar, 1992; Alcock, 1996).

Longevity and mating rate

Reproduction may entail a combination of immediate and latent (i.e. senescent) costs (see Mair *et al.*, 2003). Male antler flies that achieved a greater lifespan tended to exhibit a lower mean mating rate, suggesting a trade-off between survival and mating. This result contrasts with our previous finding that mating rate in the first 5 days of life did not trade-off against lifespan (Bonduriansky & Brassil, 2002), a difference that may reflect the more complex, nonlinear model fitted in the present study. This result suggests that copulation either increased immediate mortality risk, perhaps by increasing vulnerability to predators (see Rowe, 1994), or accelerated the rate of ageing in traits affecting viability. In *D. melanogaster*, copulation appears to reduce male immunocompetence (McKean & Nunney, 2001), possibly accelerating somatic deterioration.

Ageing in wild populations

There is growing evidence of ageing in wild mammals and birds, although reproductive ageing has thus far received much less attention than age-related declines in survival rate (e.g. Nesse, 1988; Promislow, 1991; Clinton & Le Boeuf, 1993; Loison *et al.*, 1999; Møller & De Lope, 1999; McElligott *et al.*, 2002; Myrsterud *et al.*, 2002; Saino *et al.*, 2002). In contrast, very little is known about ageing in wild insects, and our results may be compared with only a few tentative patterns: Fincke's (1988) study on wild male damselflies provides little evidence of age-related decline in survival rate, but does suggest reproductive ageing. This is consistent with our finding that declines in reproductive rate were more easily detected and more costly than declines in survival rate (Bonduriansky & Brassil, 2002). In another damselfly, the data of Banks & Thompson (1985) suggest age-related declines in both survival and mating. However, reproductive competence initially increased with age in their population (see their Figs 2 and 7), in contrast with the monotonic decline observed in male antler flies (Bonduriansky & Brassil, 2002). Elgar & Pierce (1988) found that male lycaenid butterflies exhibit reduced survival rate at advanced ages (see their Fig. 5.3), but no evidence of reproductive ageing. Clearly, much more research is needed on ageing in wild populations.

Acknowledgments

We thank P.A. Abrams, W.U. Blanckenhorn, L. Rowe, P. Williams and an anonymous reviewer for helpful comments and suggestions. Funding was provided by the

Natural Sciences and Engineering Research Council of Canada through grants to P.A. Abrams and L. Rowe, by the Government of Ontario through Ontario Graduate Scholarships to RB and CEB, by the University of Toronto through a Connaught Scholarship to CEB and by the Natural Sciences and Engineering Research Council (Canada) and Australian Research Council through postdoctoral fellowships to RB.

References

- Abrams, P.A. 1993. Does increased mortality favor the evolution of more rapid senescence? *Evolution* **47**: 877–887.
- Alcock, J. 1996. Male size and survival: the effects of male combat and bird predation in Dawson's burrowing bees, *Amegilla dawsoni*. *Ecol. Entomol.* **21**: 309–316.
- Austad, S.N. 1996. The uses of intraspecific variation in aging research. *Exp. Gerontol.* **31**: 453–463.
- Banks, M.J. & Thompson, D.J. 1985. Lifetime mating success in the damselfly *Coenagrion puella*. *Anim. Behav.* **33**: 1175–1183.
- Bartke, A., Wright, J.C., Mattison, J.A., Ingram, D.K., Miller, R.A. & Roth, G.S. 2001. Expanding the lifespan of long-lived mice. *Nature* **414**: 412.
- Beck, C.W., Shapiro, B., Choksi, S. & Promislow, D.E.L. 2002. A genetic algorithm approach to study the evolution of female preference based on male age. *Evol. Ecol. Res.* **4**: 275–292.
- Berglund, A., Bisazza, A. & Pilastro, A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol. J. Linn. Soc.* **58**: 385–399.
- Blanckenhorn, W.U. 2000. The evolution of body size: what keeps organisms small? *Quart. Rev. Biol.* **75**: 385–407.
- Bonduriansky, R. 2003. Layered sexual selection: a comparative analysis of sexual behaviour within an assemblage of piophilid flies. *Can. J. Zool.* **81**: 479–491.
- Bonduriansky, R. & Brassil, C.E. 2002. Rapid and costly ageing in wild male flies. *Nature* **420**: 377.
- Bonduriansky, R. & Brooks, R.J. 1997. A technique for measuring and marking live flies. *Can. Entomol.* **129**: 827–830.
- Bonduriansky, R. & Brooks, R.J. 1998a. Male antler flies (*Protophihila litigata*; Diptera: Piophilidae) are more selective than females in mate choice. *Can. J. Zool.* **76**: 1277–1285.
- Bonduriansky, R. & Brooks, R.J. 1998b. Copulation and oviposition behaviour of *Protophihila litigata* (Diptera: Piophilidae). *Can. Entomol.* **130**: 399–405.
- Bonduriansky, R. & Brooks, R.J. 1999. Why do male antler flies (*Protophihila litigata*) fight? The role of male combat in the structure of mating aggregations on moose antlers. *Ethol. Ecol. Evol.* **11**: 287–301.
- Bonduriansky, R. & Rowe, L. 2003. Interactions among mechanisms of sexual selection on male body size and head shape in a sexually dimorphic fly. *Evolution* **57**: 2046–2053.
- Bonduriansky, R. & Rowe, L. 2005. Sexual selection, genetic architecture, and the condition dependence of body shape in the sexually dimorphic fly, *Prochyliza xanthostoma* (Diptera: Piophilidae). *Evolution* **59**: 138–151.
- Brooks, R. & Kemp, D.J. 2001. Can older males deliver the good genes? *Trends Ecol. Evol.* **16**: 308–313.
- Cartar, R.V. 1992. Morphological senescence and longevity – an experiment relating wing wear and life-span in foraging wild bumble bees. *J. Anim. Ecol.* **61**: 225–231.
- Chapman, R.F. 1998. *The Insects: Structure and Function*, 4th edn. Cambridge University Press, Cambridge, UK.
- Clancy, D.J., Gems, D., Harshman, L.G., Oldham, S., Stocker, H., Hafen, E., Leevers, S.J. & Partridge, L. 2001. Extension of lifespan by loss of CHICO, a *Drosophila* insulin receptor substrate protein. *Science* **292**: 104–106.
- Clancy, D.J., Gems, D., Hafen, E., Leevers, S.J. & Partridge, L. 2002. Dietary restriction in long-lived dwarf flies. *Science* **296**: 319.
- Clinton, W.L. & Le Boeuf, B.J. 1993. Sexual selection's effects on male life history and the pattern of male mortality. *Ecology* **74**: 1884–1892.
- Clutton-Brock, T.H. 1988. Reproductive success. In: *Reproductive Success, Studies of Individual Variation in Contrasting Breeding Systems* (T. Clutton-Brock, ed.), pp. 472–485. University of Chicago Press, Chicago, USA.
- Comfort, A. 1979. *The Biology of Senescence*, 3rd edn. Elsevier, New York, USA.
- Coschigano, K.T., Clemmons, D., Bellush, L.L. & Kopchick, J.J. 2000. Assessment of growth parameters and life span of GHR/BP gene-disrupted mice. *Endocrinology* **141**: 2608–2613.
- Elgar, M.A. & Pierce, N.E. 1988. Mating success and fecundity in an ant-tended lycaenid butterfly. In: *Reproductive Success, Studies of Individual Variation in Contrasting Breeding Systems* (T. Clutton-Brock, ed.), pp. 59–75. University of Chicago Press, Chicago, USA.
- Ernsting, G. & Isaaks, J.A. 1991. Accelerated ageing: a cost of reproduction in the carabid beetle *Notiophilus biguttatus* F. *Funct. Ecol.* **5**: 299–303.
- Fincke, O.M. 1988. Sources of variation in lifetime reproductive success in a nonterritorial damselfly (Odonata: Coenagrionidae). In: *Reproductive Success, Studies of Individual Variation in Contrasting Breeding Systems* (T. Clutton-Brock, ed.), pp. 24–43. University of Chicago Press, Chicago, USA.
- Faddy, M.J. & Bosch, R.J. 2001. Likelihood-based modeling and analysis of data underdispersed relative to the poisson distribution. *Biometrics* **57**: 620–624.
- Gadgil, M. & Bossert, W.H. 1970. Life historical consequences of natural selection. *Am. Nat.* **104**: 1–24.
- Gasser, M., Kaiser, M., Berrigan, D. & Stearns, S.C. 2000. Life-history correlates of evolution under high and low adult mortality. *Evolution* **54**: 1260–1272.
- Hilborn, R. & Mangel, M. 1997. *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton, NJ, USA.
- Hillesheim, E. & Stearns, S.C. 1992. Correlated responses in life-history traits to artificial selection for body weight in *Drosophila melanogaster*. *Evolution* **46**: 745–752.
- Hu, H.H. & Morse, D.H. 2004. The effect of age on encounters between male crab spiders. *Behav. Ecol.* **15**: 883–888.
- Hunt, J., Brooks, R., Jennions, M.D., Smith, M.J., Bentsen, C.L. & Bussière, L.F. 2004. High-quality male field crickets invest heavily in sexual display but die young. *Nature* **432**: 1024–1027.
- Kemp, D.J. 2002. Sexual selection constrained by life history in a butterfly. *Proc. R. Soc. Lond. B* **269**: 1341–1345.
- Kirkwood, T.B.L. 1977. Evolution of ageing. *Nature* **270**: 301–304.
- Kirkwood, T.B.L. 1992. Comparative life spans of species: why do species have the life spans they do? *Am. J. Clin. Nutr.* **55**: 1191S–1195S.
- Kirkwood, T.B.L. & Holliday, R. 1979. The evolution of ageing and longevity. *Proc. R. Soc. Lond. B* **205**: 531–546.

- Kirkwood, T.B.L. & Rose, M.R. 1991. Evolution of senescence: late survival sacrificed for reproduction. *Phil. Trans. R. Soc. Lond. B* **332**: 15–24.
- Kokko, H. 1998. Good genes, old age and life-history trade-offs. *Evol. Ecol.* **12**: 739–750.
- Kokko, H. & Lindström, J. 1996. Evolution of female preference for old mates. *Proc. R. Soc. Lond. B* **263**: 1533–1538.
- Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T. & Jullien, J.-M. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* **80**: 2539–2554.
- Magwere, T., Chapman, T. & Partridge, L. 2004. Sex differences in the effect of dietary restriction on life span and mortality rates in female and male *Drosophila melanogaster*. *J. Gerontol.* **59A**: 3–9.
- Mair, W., Goymer, P., Pletcher, S.D. & Partridge, L. 2003. Demography of dietary restriction and death in *Drosophila*. *Science* **301**: 1731–1733.
- Marden, J.H., Rogina, B., Montooth, K.L. & Helfand, S.L. 2003. Conditional tradeoffs between aging and organismal performance of *Indy* long-lived mutant flies. *Proc. Natl. Acad. Sci. USA* **100**: 3369–3373.
- McElligott, A.G., Altwegg, R. & Hayden, T.J. 2002. Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*). *Proc. R. Soc. Lond. B* **269**: 1129–1137.
- McKean, K. & Nunnery, L. 2001. Increased sexual activity reduces male immune function in *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. USA* **98**: 7904–7909.
- Medawar, P.B. 1946. Old age and natural death. *Mod. Q.* **1**: 30–56.
- Metcalf, N.B. & Monaghan, P. 2003. Growth versus lifespan: perspectives from evolutionary ecology. *Exp. Gerontol.* **38**: 935–940.
- Møller, A.P. & De Lope, F. 1999. Senescence in a short-lived migratory bird: age-dependent morphology, migration, reproduction and parasitism. *J. Anim. Ecol.* **68**: 163–171.
- Mysterud, A., Steinheim, G., Yoccoz, N.G., Holand, Ø. & Stenseth, N. Chr. 2002. Early onset of reproductive senescence in domestic sheep, *Ovis aries*. *Oikos* **97**: 177–183.
- Nesse, R.M. 1988. Life table tests of evolutionary theories of senescence. *Exp. Gerontol.* **23**: 445–453.
- Nijhout, H.F. 2003. The control of growth. *Development* **130**: 5863–5867.
- Osada, K., Yamazaki, K., Curran, M., Bard, J., Smith, B.P.C. & Beauchamp, G.K. 2003. The scent of age. *Proc. R. Soc. Lond. B* **270**: 929–933.
- Otronen, M. 1996. Effects of seasonal variation in operational sex ratio and population density on the mating success of different sized and aged males in the yellow dung fly, *Scathophaga stercoraria*. *Ethol. Ecol. Evol.* **8**: 399–411.
- Partridge, L. & Barton, N.H. 1996. On measuring the rate of ageing. *Proc. R. Soc. Lond. B* **263**: 1365–1371.
- Partridge, L. & Mangel, M. 1999. Messages from mortality: the evolution of death rates in the old. *Trends Ecol. Evol.* **14**: 438–442.
- Patronek, G.J., Waters, D.J. & Glickman, L.T. 1997. Comparative longevity of pet dogs and humans: implications for gerontology research. *J. Gerontol.* **52A**: B171–B178.
- Promislow, D.E.L. 1991. Senescence in natural populations of mammals: a comparative study. *Evolution* **45**: 1869–1887.
- Proulx, S.R., Day, T. & Rowe, L. 2002. Older males signal more reliably. *Proc. R. Soc. Lond. B* **269**: 2291–2299.
- Radwan, J. 2003. Male age, germline mutations and the benefits of polyandry. *Ecol. Lett.* **6**: 581–586.
- Rantala, M.J., Vainikka, A. & Kortet, R. 2003. The role of juvenile hormone in immune function and pheromone production trade-offs: a test of the immunocompetence handicap principle. *Proc. R. Soc. Lond. B* **270**: 2257–2261.
- Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos* **44**: 257–267.
- Roach, D.A. 2001. Environmental effects on age-dependent mortality: a test with a perennial plant species under natural and protected conditions. *Exp. Gerontol.* **36**: 687–694.
- Roff, D.A. 1992. *The Evolution of Life Histories: Theories and Analysis*. Chapman & Hall, New York, USA.
- Rolff, J. & Siva-Jothy, M.T. 2002. Copulation corrupts immunity: a mechanism for a cost of mating in insects. *Proc. Natl. Acad. Sci. USA* **99**: 9916–9918.
- Rose, M.R. & Charlesworth, B. 1981a. Genetics of life history in *Drosophila melanogaster*. I. Sib analysis of adult females. *Genetics* **97**: 173–186.
- Rose, M.R. & Charlesworth, B. 1981b. Genetics of life history in *Drosophila melanogaster*. II. Exploratory selection experiments. *Genetics* **97**: 173–186.
- Rowe, L. 1994. The costs of mating and mate choice in water striders. *Anim. Behav.* **48**: 1049–1056.
- Saino, N., Ambrosini, R., Martinelli, R. & Møller, A.P. 2002. Mate fidelity, senescence in breeding performance and reproductive trade-offs in the barn swallow. *J. Anim. Ecol.* **71**: 309–319.
- Sakamoto, Y., Ishiguro, M. & Kitagawa, G. 1986. *Akaike Information Criterion Statistics*. D. Reidel, Dordrecht.
- Service, P.M., Michieli, C.A. & McGill, K. 1998. Experimental evolution of senescence: an analysis using a “heterogeneity” mortality model. *Evolution* **52**: 1844–1850.
- Simmons, L.W. & Ward, P.I. 1991. The heritability of sexually dimorphic traits in the yellow dung fly *Scatophaga stercoraria* (L.). *J. Evol. Biol.* **4**: 593–601.
- Tucić, N., Gliksmann, I., Seslija, D., Milanovic, D., Mikuljanac, S. & Stojkovic, O. 1996. Laboratory evolution of longevity in the bean weevil (*Acanthoscelides obtectus*). *J. Evol. Biol.* **9**: 485–503.
- Wang, C., Weindruch, R., Fernández, J.R., Coffey, C.S., Patel, P. & Allison, D.B. 2004. Caloric restriction and body weight independently affect longevity in Wistar rats. *Int. J. Obes.* **28**: 357–362.
- Wedekind, C. & Folstad, I. 1994. Adaptive or nonadaptive immunosuppression by sex hormones? *Am. Nat.* **143**: 936–938.
- Wigglesworth, V.B. 1972. *The Principles of Insect Physiology*, 7th edn. Chapman & Hall, New York, USA.
- Williams, G.C. 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution* **11**: 398–411.
- Williams, P.D. & Day, T. 2003. Antagonistic pleiotropy, mortality source interactions, and the evolutionary theory of senescence. *Evolution* **57**: 1478–1488.
- Wolfram, S. 1999. *The Mathematica Book*, 4th edn. Wolfram Media/Cambridge University Press, Champaign, IL, USA/Cambridge, UK.
- Zens, M.S. & Peart, D.R. 2003. Dealing with death data: individual hazards, mortality and bias. *Trends Ecol. Evol.* **18**: 366–373.

Received 13 December 2004; revised 3 February 2005; accepted 4 February 2005