LETTER

Predatory senescence in ageing wolves

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Abstract

It is well established that ageing handicaps the ability of prey to escape predators, yet surprisingly little is known about how ageing affects the ability of predators to catch prey. Research into long-lived predators has assumed that adults have uniform impacts on prey regardless of age. Here we use longitudinal data from repeated observations of individually-known wolves (*Canis lupus*) hunting elk (*Cervus elaphus*) in Yellowstone National Park to demonstrate that adult predatory performance declines with age and that an increasing ratio of senescent individuals in the wolf population depresses the rate of prey offtake. Because this ratio fluctuates independently of population size, predatory senescence may cause wolf populations of equal size but different age structure to have different impacts on prey populations. These findings suggest that predatory senescence is an important, though overlooked, factor affecting predator-prey dynamics.

INTRODUCTION

Ageing impairs athletic performance. Human athletes provide a clear example (Tanaka & Seals 2008), but athletic senescence has also been documented in horses (Mota *et al.* 2005), dogs (Taubert *et al.* 2007), rodents (Punzo & Chavez 2003), birds (Costantini *et al.* 2008), fish (Reznick *et al.* 2004), and insects (Schumacher *et al.* 1997). In natural systems, athletic senescence pre-disposes older animals to predation (Slobodkin 1968) and thus generates a gradient in prey vulnerability that can promote predator-prey coexistence (Murdoch *et al.* 2003). Age-specific variation in predator ability can also enhance dynamic stability (Maynard Smith & Slatkin 1973). Yet, knowledge of such variation is limited to the difference between juvenile and adult predators; little is known about how adult predatory ability changes with age. Predator-prey studies typically assume that adult predatory success is constant (e.g. Festa-Bianchet *et al.* 2006; Fryxell *et al.* 2007; Nilsen *et al.* 2007) and therefore unaffected by ageing.

Evolutionary theories of ageing predict that the onset and rate of senescence is linked to life history; a faster life history drives an earlier and faster senescent decline (Hamilton 1966; Charlesworth 1980). This has been tested, and largely confirmed, with respect to survival and reproduction (Jones *et al.* 2008) but not to other aspects of animal performance such as predation or to the effect of predation on prey populations. We therefore evaluated how within-individual variation in age affected the ability of wolves (*Canis lupus*) hunting elk (*Cervus elaphus*) in Yellowstone National Park (YNP), USA, to perform each of three predatory tasks (attacking, selecting, and killing) corresponding to the transitions between four behaviours (approach, attack-group, attack-individual, capture) that comprise the typical predatory sequence of cursorial carnivores hunting ungulate prey (MacNulty *et al.* 2007). The physical requirements of each task vary; selecting requires burst acceleration to target an ungulate from a herd, whereas killing requires strength to grab and overpower prey. By contrast, neither exceptional speed nor great strength is crucial to initiating an attack.

The life history of wild wolves includes a short generation time (4 years), early first reproduction (2–4 years-old), high fecundity (5–6 pups·litter⁻¹), and rapid development (80% of adult size acquired by 1 year) (Peterson *et al.* 1998; Fuller *et al.* 2003; MacNulty *et al.* 2009). Thus, we expected wolf predatory performance to decline soon after the age of

2–4 years. And if this change was due to physiological deterioration, we also expected that (1) the rate of decline would be fastest for the most difficult predatory task because the most strenuous activities are typically the most sensitive to ageing (e.g. Walker *et al.* 2002; Gurven *et al.* 2006); (2) the age at onset of the decline would coincide with a drop in physical condition, which we assayed using serum albumin because lower concentrations of this serum constituent have been associated with inflammation, malnutrition, and/or muscle loss in ageing mammals, including dogs (*Canis lupus familiaris*) and humans (Strasser *et al.* 1993; Rall *et al.* 1995; Batamuzi *et al.* 1996; Baumgartner *et al.* 1996); and (3) the risk of mortality would increase with age because loss of physical function generally increases the risk of death. Finally, we evaluated the ecological consequences of predatory senescence by testing whether the quantity of prey killed by wolves was related to fluctuation in the ratio of senescent hunters in the YNP wolf population.

MATERIALS AND METHODS

Age determination

The age of 277 wolves was recorded during handling by management pre- and post-release (1995–1997) and annually thereafter (1998–2008) as part of long-term monitoring that involved capturing and radio-marking 30–50% of pups each winter (Smith *et al.* 2004). Marking of pups provided the only exact measure of age. Tooth wear and cementum annuli were used to estimate the age of live and dead adults, respectively (Gipson *et al.* 2000). Pups that escaped capture were sometimes caught as adults and considered known-aged only if individually recognized from birth via distinct morphological features (e.g. pelage markings, colour, body shape and size). We assigned ages to non-captured wolves ($n = 8$) only if first observed as pups and individually identifiable as adults. We calculated age as an annual fraction according to the number of days since birth, assuming an April-15 birth date (D.W. Smith, unpublished data). Known-aged wolves comprised most of the sample.

Predatory performance

Various assistants and three of the authors (DRM, DWS, and DRS) observed wolves hunting elk during biannual 30-day follows of 3–16 packs from the ground and fixed-wing aircraft in early (mid-November to mid-December) and late (March) winter and during opportunistic surveys throughout the rest of the year (1995–2003). Wolves hunted mainly elk (MacNulty *et al.* 2007) and 97% of 469 wolf-elk encounters were directly observed from the ground in the open grasslands of the Northern Range (NR) of YNP (See

MacNulty *et al.* 2007, 2009 for details). Most encounters (84%) involved groups of elk.

When wolves encountered elk – defined as ≥ 1 wolf orienting and travelling toward elk – we followed the progress of the encounter by noting the foraging state (approach, watch, attack-group, attack-individual, capture; see Table 2 in MacNulty *et al.* 2007 for definitions) of the individual(s) closest to making a kill. We thus recorded the sequential occurrence of the most escalated state of the encounter and the identity of wolves participating in that state. Task performance was equivalent to consecutive participation in a pair of sequential foraging states that comprised a particular task. That is, if an encounter escalated and a wolf continued participating, it was scored as performing the corresponding predatory task (e.g. attack-group → attack-individual = selecting). Conversely, if the encounter did not escalate, or the wolf stopped participating, then the wolf's performance was scored as a failure (e.g. attack-group → approach). Hence, the performance of each individual participating in each sequential foraging state was scored as a binary outcome.

The performance of 94 identifiable individuals, hereafter called focal wolves, was scored repeatedly (1–8 years), and analyzed using generalized linear mixed models (GLMMs) with a binomial error distribution and with individual identity fitted as a random effect. We inferred the effects of age on the probability that an individual performed a given predatory task by evaluating a set of competing marginal GLMMs for each task. Models fit performance as a linear or nonlinear function of age, with the latter fit as a quadratic function or piecewise linear spline with 1–2 breakpoints. Variables containing a linear spline for age were created with the MKSPLINE command in STATA 10.1, with candidate breakpoints selected by inspecting Lowess plots of the raw data and included in GLMMs in lieu of the linear or quadratic age terms. Each model set also included an intercept-only model.

Because ageing patterns can differ between the sexes (Clutton-Brock & Isvaran 2007) and are potentially confounded by selective disappearance of poorer quality individuals from the population at young ages (Nussey *et al.* 2008), we checked if sex-by-age interactions and individual age at last measurement improved model fit, respectively. All candidate models included terms for body mass because it has been shown that mass affects wolf predatory performance independently of age and accounts for the main effect of sex on performance (MacNulty *et al.* 2009). Mass was estimated from an individually based sex-specific growth model derived from measurements of 304 wolves, including 86 focal wolves (See MacNulty *et al.* 2009 for details).

To evaluate task difficulty and between-task differences in the risk of injury, we combined the three task-specific

datasets and tested how task type affected the probability of failure and injury, respectively. We conducted the injury analysis to test the hypothesis that age-related predatory decline stemmed from heightened caution with age rather than from physical deterioration. If so, we expected differences in the rate of decline between different tasks to mirror differences in injury risk. These data were insufficient for a repeated measures analysis, so we used simple logistic regression to evaluate the effect of task type on the probability that ≥ 1 wolf was struck (kicked, trampled, or stabbed with antlers) by an elk. Task difficulty was analyzed with a GLMM that controlled for individual age and mass. In both analyses, we used odds ratios to estimate the relative difficulty and danger of each task.

Serum albumin

Blood serum was collected from 149 (44 focal, 105 non-focal) wolves during post-release management and monitoring (1997–2008). Wolves were darted ($n = 139$) or netted ($n = 10$) at close range from a helicopter, chemically immobilized within 5–10 min of commencing pursuit, and induced within 5–10 min. Blood (*c.* 12 cc) was drawn from the cephalic vein and placed on ice within 10–20 min of induction time. Serum was separated within 6 h and stored at −80 °C. Frozen samples were sent on dry ice to a commercial veterinary laboratory (Wolff Labs, Minneapolis, MN, USA), where they were thawed and analyzed. Serum albumin concentrations were determined on a Cobas Mira S automatic analyzer (Roche Diagnostics, Indianapolis, IN, USA) using the bromcresol green method (Doumas *et al.* 1971).

Serum was not usually collected from the same wolf on multiple occasions, so we performed a cross-sectional analysis of the effects of age on serum albumin concentration using simple linear regression after checking that the data approximated a normal distribution.

We tested for nonlinear trends following the approach described above and checked if sex or a sex-by-age interaction improved model fit.

Mortality risk

We monitored the survival of 226 (70 focal, 156 non-focal) radio-marked wolves within YNP from 15 April 1998 to 15 April 2007. Radio-transmitters contained a mortality sensor and were checked at least once a week from aircraft. NR wolves were checked daily from the ground during each 30-day follow. We excluded observations prior to 1998 to ensure that survival estimates were unaffected by wolf management activities that were restricted to this period. We modelled survival as a function of age using a generalized Kaplan–Meier survival model with staggered entry (Pollock *et al.* 1989). We used a continuous-time methodology whereby time-to-death was measured across uninterrupted timelines with survival time defined as wolf age (number of days alive since 15 April of the birth-year). Survival estimates were conditional on wolves surviving to 0.75 years because pups were not marked until they were *c.* 9-months old. Only natural mortalities ($n = 61$) were considered; we classified the few human-caused mortalities ($n = 3$) as censored events, and also censored wolves that dispersed outside YNP ($n = 59$), went missing inside YNP ($n = 58$), or were alive at the end of the study ($n = 45$).

We estimated the survivor function, $S(t)$, which was the cumulative probability of survival of a wolf past age t, and the underlying hazard function, $h(t)$, which represented a wolf's instantaneous probability of death at age t, given survival to t. We obtained $h(t)$ by smoothing the Nelson-Aalen cumulative hazard function with the Epanechnikov kernel smoother (Klein & Moeschberger 2003) and tested the hypothesis that mortality risk increased with age by comparing parametric hazard models that express different forms of the baseline hazard function: exponential (constant hazard), Weibull (monotonic increase/decrease), and Gompertz (exponential increase/decrease). We tested for inter-sexual differences in the hazard function by comparing models with and without a term for sex.

Model equations are given elsewhere (Klein & Moeschberger 2003), but note that the dimensionless parameters θ and γ determine the shape of the Weibull and Gompertz hazard, respectively. When $\theta = 1$ and $\gamma = 0$, the hazard is constant and each model reduces to the exponential model. The hazard is decreasing when $\theta < 1$ and $\gamma < 0$ and increasing when $\theta > 1$ and $\gamma > 0$. We used a Wald test to evaluate H_o: $\theta = 1$ and H_o: $\gamma = 0$.

Age structure and kill rate

We evaluated the impact of predatory senescence on prey removal rates by analyzing the association between interannual (1998–2007; $n = 10$ years) variation in wolf population age structure (i.e. ratio of wolves > 3.0 years-old – see Results for justification) and ungulate kill rates. If older wolves were worse hunters, we expected kill rates to decline as the ratio of older wolves increased. We censused the YNP wolf population from aircraft each year just prior to reproduction (1st April) and recorded the ratio of radio-marked wolves > 3.0 years-old. The proportion of radio-marked wolves ranged from 42% to 61% of the total YNP census size (N_c; 59–142). Each 1st April estimate of age structure was paired with an estimate of average kill rate calculated from the number of ungulates killed by all YNP packs ($n = 7$–16) during the 30-day follow conducted the preceding March.

During each March, all YNP wolf packs were monitored from aircraft, and a subset of these packs, located mainly in the NR, was also followed from the ground (Smith *et al.* 2004). However, the estimates of kill rate reported in this study include only kills detected from aircraft since these were not biased by proximity to the road system. These estimates mostly included elk (90% of 694 kills) and occasional kills of bison (*Bison bison*; 7%), bighorn sheep (*Ovis canadensis*; < 1%), moose (*Alces alces*; 2%), and mule deer (*Odocoileus hemionus*; 1%).

We calculated the daily kill rate of each pack each March in four ways: the number, or biomass (kg), of kills made by a pack divided by either (1) the number of days during which that pack was observed (kills·pack^{-1}·day^{-1} or kg·pack^{-1}·day^{-1}) or (2) the product of the number of wolves in that pack times the number of days it was observed (kills·wolf^{-1}·day^{-1} or kg·wolf^{-1}·day^{-1}). Results for each calculation were then averaged across packs to derive four different estimates of mean daily kill rate each year. Means were weighted by the number of days each pack was observed to account for how search effort varied among packs due to inclement weather.

To assess the importance of predatory senescence as a predictor of kill rate, we compared models including one or more of the following covariates: senescent age structure (population ratio of wolves > 3.0 years-old), juvenile age structure (population ratio of pups), wolf abundance, elk abundance, ratio of wolf abundance to elk abundance, and winter severity. We fit all possible multivariate models and an intercept-only model for each of four model sets corresponding to a different estimate of kill rate. We explored the relationships between covariates with a correlation matrix and used Spearman rank correlations to account for the small sample. Analyses were limited to the NR because data for all covariates were unavailable for all YNP. Elk were annually counted in the NR by aerial survey in December or early January. Elk data from 1998 to 2004 were obtained from Vucetich *et al.* (2005) and data for the remaining years were taken from unpublished reports of the interagency Northern Range Working Group. Winter severity was indexed by snow water equivalent (i.e. water content of the snow) calculated from daily meteorological measurements recorded at three sites in the NR (Lamar Valley, Tower Falls, and Mammoth Hot Springs) and collected by P. Farnes (pers. comm.).

We conducted all analyses in STATA 10.1 and compared models using information-theoretic statistics (Burnham & Anderson 2002). The best-fit model was the one with lowest Akaike Information Criteria (adjusted for small sample size, AIC$_c$), smallest ΔAIC$_c$, and highest AIC$_c$ weight (W), though models with ΔAIC$_c$ < 2 were plausibly the best. We also used likelihood ratio statistics to test specific hypotheses among nested models, and results were considered significant at P < 0.05.

RESULTS

Individual predatory performance initially improved to a peak then declined with age (Fig. 1a–c). For each task, the best-fit model contained a linear spline for age with a single breakpoint and outperformed the intercept model (ΔAIC$_c$ = 6.61–18.40), simple linear model (ΔAIC$_c$ = 4.18–7.75), and quadratic model (ΔAIC$_c$ = 2.02–5.43; Table S1). The best-fit models did not significantly differ from similar models that included either a sex-by-age interaction after each breakpoint (likelihood ratio χ^2 = 0.03–2.76, d.f. = 1, P = 0.10–0.86) or an individual's age at last measurement (χ^2 = 0.36–2.47, d.f. = 1, P = 0.12–0.55), indicating that the pattern of decline was unaffected by gender or the selective disappearance of underperforming individuals at young ages. Results were also similar for a subset of observations that included data on the number and age of other wolves hunting alongside focal wolves. Neither factor altered a focal animal's age-specific performance.

The age at onset of predatory decline was task-specific. Models containing a single breakpoint with ΔAIC$_c$ < 2 suggest that the timing of predatory decline occurred at 1.0–1.1 years-old (attacking), 1.5–2.2 years-old (killing), and 2.1–3.5 years-old (selecting). The best-fit model for each respective task contained a breakpoint at 1.0-, 2.0-, and 3.0-years. The onset of decline could have been later if age-specific performance included a settled phase between the improvement and decline phases. However, models with two breakpoints did not outperform the best single breakpoint models (Table S1). But note that model uncertainty across each set of candidate 2-breakpoint models was high (attacking: ΔAIC$_c$ ≤ 2.30; selecting: ΔAIC$_c$ ≤ 3.65; killing: ΔAIC$_c$ ≤ 2.36; Table S1), indicating that we had insufficient data to resolve > 1 breakpoint.

Assuming that the single-breakpoint models best explained the effects of age on performance, the product of the models' population-averaged fitted values (Fig. 1a–c), which reflects the net effect of age across the different tasks (*sensu* MacNulty *et al.* 2009), reveals that overall performance declined after age 3.0 (Fig. 1d). This early and swift decline was consistent with the fast life history of YNP wolves, which included early first reproduction ($\bar{x}$ age at primiparity = 2.7 years [95% CI = ± 0.4 years]), short generation time ($\bar{x}$ age of breeding females = 4.2 years [95% CI = ± 0.2 years]), and high fecundity ($\bar{x}$ litter size = 4.8 pups·litter^{-1} [95% CI = ± 0.6 pups·litter^{-1}]) (n = 25 females).

Three lines of evidence support the hypothesis that declining predatory performance was due to senescence. First, the rate of decline was correlated with task difficulty (hence physical demand), which followed: selecting > killing > attacking [selecting was 30% more difficult than killing (P = 0.057), which was twice as difficult as attacking
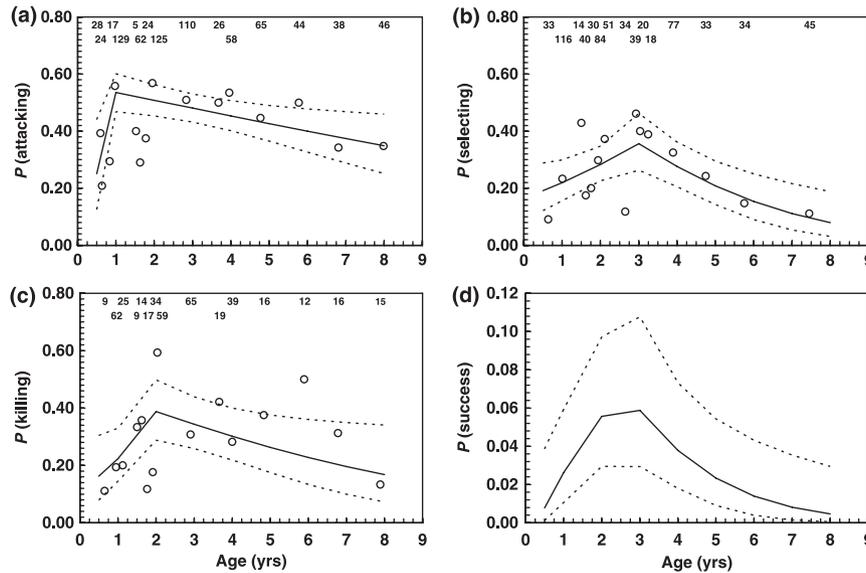
Figure 1 Effects of age (years) on the ability of individual wolves to attack (a), select (b), and kill (c) elk in Yellowstone National Park, 1995–2003. The number of wolves and wolf-elk encounters included in each analysis follows: 87 and 258 (a); 81 and 281 (b); 74 and 189 (c), respectively. Analyses of killing involved mainly adult elk (92% of 189 encounters). Solid lines are population-averaged fitted value lines from best-fit GLMM models with dotted lines indicating pointwise 95% confidence intervals. The estimated coefficients before and after each breakpoint are: 2.47 ± 0.93 ($P = 0.008$) and -0.11 ± 0.04 ($P = 0.013$) (a); 0.34 ± 0.16 ($P = 0.030$) and -0.37 ± 0.11 ($P = 0.001$) (b); 0.79 ± 0.34 ($P = 0.020$) and -0.19 ± 0.09 ($P = 0.032$) (c). Points are observed frequencies for each of 15 age categories determined via k-means cluster analysis with sample size indicated above each point. Analyses were performed on the raw binary data and not the illustrated points which are provided as a visual aid. The product of the fitted value lines and associated confidence intervals in (a), (b), and (c), representing the overall probability of success given an elk encounter and thus the net effect of age on predatory ability, is shown in (d).

($P < 0.001$)]. For each year beyond the onset of decline, individual ability decreased by 31% ($P = 0.001$), 17% ($P = 0.032$), and 10% ($P = 0.013$) in selecting, killing, and attacking, respectively. Thus, the most difficult task was also the most sensitive to ageing.

Second, the onset of decline in overall performance (Fig. 1d) coincided with a drop in serum albumin concentration (Fig. 2). A model with a breakpoint at age 3.75 provided the best fit to the serum data compared to the intercept model ($\Delta AIC_c = 13.51$), simple linear model ($\Delta AIC_c = 12.83$), quadratic model ($\Delta AIC_c = 2.16$), and other spline models with single breakpoints ($\Delta AIC_c = 2.52$–6.88) (Table S2). But because most of our sample was collected at the end of each annual age increment, it was possible that serum albumin levels dropped closer to age 3.0 than our results indicate. Only one 2-breakpoint model (ages 2.75 and 3.75) scored well ($\Delta AIC_c = 1.61$; Table S2), which supports the conclusion that serum albumin declined no later than age 3.75. There was no evidence of either an overall difference in serum albumin concentration between males and females ($\chi^2 = 0.11$, d.f. = 1, $P = 0.74$) or an intersexual difference in the rate of decline after age 3.75 ($\chi^2 = 2.49$, d.f. = 1, $P = 0.12$).
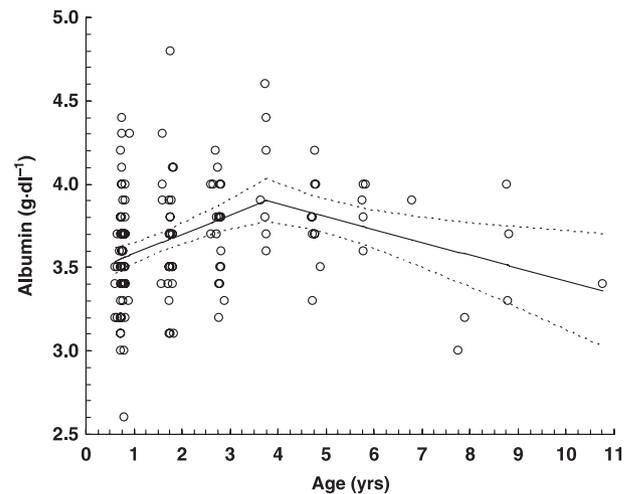

Figure 2 Effects of age (years) on serum albumin concentration ($g \cdot dl^{-1}$) for 149 wolves in Yellowstone National Park, 1997–2008. Solid line represents the fitted values from the best-fit simple linear regression model with dotted lines indicating pointwise 95% confidence intervals. The estimated coefficient before and after the breakpoint (age 3.75) is 0.12 ± 0.03 ($P < 0.001$) and -0.08 ± 0.03 ($P = 0.008$), respectively.

Third, ageing wolves experienced declining survival (Fig. 3a) and increasing mortality risk (Fig. 3b). Median survival time was 5.94 years (95% CI = 4.71, 7.20 years). The smoothed Nelson-Aalen cumulative hazard function illustrates a gradual increase in mortality risk between age 0.75 and 5.0, followed by an abrupt increase up to age 8 (Fig. 3b). The subsequent decline in the hazard was apparently due to the small sample in the tail of the distribution, which is evidenced by the large confidence intervals. Fitting the dataset to parametric models confirmed that mortality increased with age; the Weibull and Gompertz models outperformed the constant risk model (ΔAIC_c = 5.48; Table S3), and the dimensionless parameter that controls the shape of each function was significantly

larger than its respective null value ($\theta = 1.57 \pm 0.22$, $z = 3.26$, $P = 0.001$; $\gamma = 0.15 \pm 0.05$, $z = 2.82$, $P = 0.005$). The Gompertz model provided a marginally better fit than the Weibull model ($\Delta AIC_c = 0.20$) that was unaffected by gender ($\chi^2 = 0.22$, d.f. = 1, $P = 0.64$; Table S3).

We found little evidence that declining predatory performance reflected heightened caution with age rather than physical deterioration. Differences in the rate of decline between the different tasks mirrored differences in the risk of injury insofar as wolves were 3.57 ± 1.38 ($P = 0.001$) and 4.44 ± 1.38 ($P < 0.001$) times more likely to be struck by elk when selecting and killing than when attacking, respectively. But the large difference in injury risk between attacking and killing belied the comparatively small difference in the rate of decline between these tasks (−0.11 vs. −0.19). Moreover, the odds of injury when selecting tended to be less than when killing (odds ratio = 0.80 ± 0.32, $P = 0.57$) even though the rate of decline in selecting was nearly twice that of killing (−0.37 vs. −0.19). Taken together, these results suggest that age-related declines in predatory performance were not attributable to an elevated aversion to the risk of injury among older wolves.

Influence of senescent hunters on prey removal rate

Regardless of how wolf kill rate was calculated, it decreased as the population ratio of senescent hunters (wolves > 3.0 years-old) increased (Fig. 4). To be clear, a senescent hunter was defined as any wolf surviving ≥ 1 day beyond its 3rd birthday as illustrated in Fig. 1d. A multivariate analysis of the effects of different factors on wolf predation rate in the NR confirmed that senescent age structure was a top predictor of kill rate. When packs were the unit of measurement, the best-fit model included only senescent age structure and outperformed the intercept model (kills·pack^{-1}·day^{-1}: $\chi^2 = 8.27$, d.f. = 1, $P = 0.004$; kg·pack^{-1}·day^{-1}: $\chi^2 = 8.50$, d.f. = 1, $P = 0.004$), all other univariate models (kills·pack^{-1}·day^{-1}: ΔAIC_c = 3.47–7.47; kg·pack^{-1}·day^{-1}: ΔAIC_c = 4.09–8.09; Table 1), and all multivariate models, which included all combinations of covariates (kills·pack^{-1}·day^{-1}: ΔAIC_c = 3.32–55.09; kg·pack^{-1}·day^{-1}: ΔAIC_c = 4.64–56.59; Table S4).

When kill rate was estimated on a per capita basis, senescent age structure remained an important predictor, but there was evidence that other covariates were as much or more important. For instance, among models of kg·wolf^{-1}·day^{-1}, a univariate model including senescent age structure fit the data best and outperformed the intercept model ($\chi^2 = 6.33$, d.f. = 1, $P = 0.012$), but it was similar to a univariate model that included snow and to the bivariate models senescent + snow ($\chi^2 = 5.14$, d.f. = 1, $P = 0.023$) and senescent + pup ($\chi^2 = 5.12$, d.f. = 1,
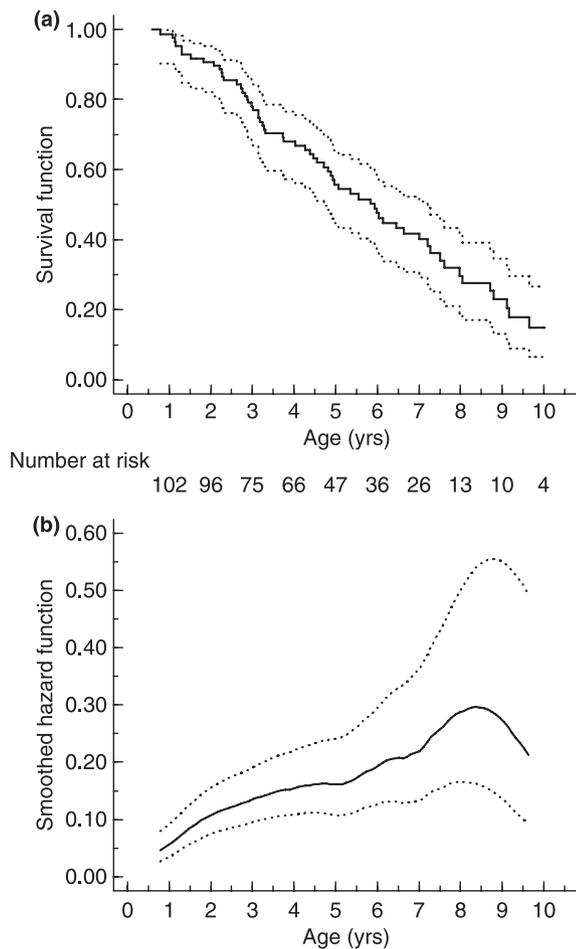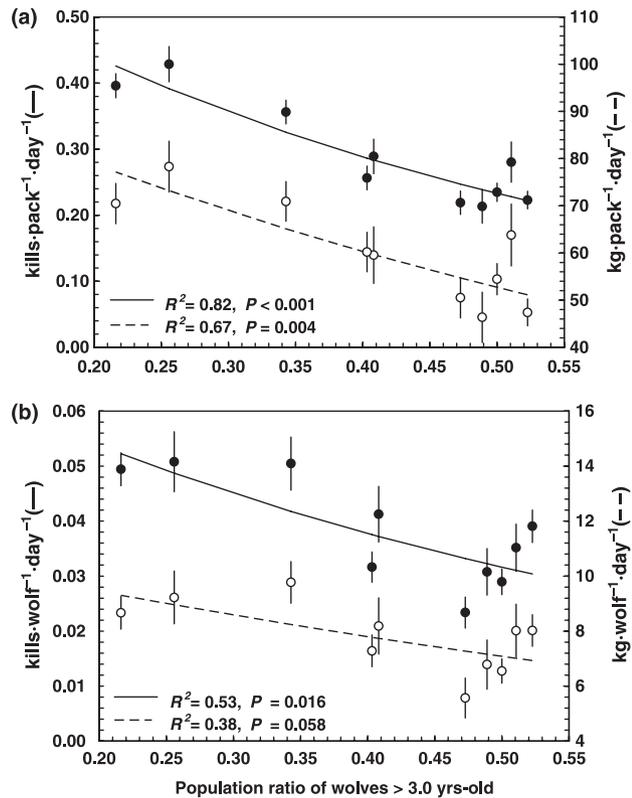
Figure 3 Kaplan–Meier survival function (a) and smoothed instantaneous hazard function (b) for 226 radio-marked wolves (≥ 0.75 year old) in Yellowstone National Park, 1998–2007. The hazard function is the estimated instantaneous risk of death as a function of wolf age. Dotted lines are 95% confidence bands and number at risk indicates the sample size at the beginning of each annual age increment.

Figure 4 Effects of wolf population age structure (ratio of wolves > 3.0 years-old) on average late winter (Mar) kill rate by packs (a) and wolves (b) in Yellowstone National Park, 1998–2007 (n = 10 years). Lines are back-transformed fitted values from regressions of log-transformed kill rates on age structure. Data points are observed means (± 95% CI) calculated as the number (●) or biomass in kg (○), of ungulates killed. Elk were the primary prey (90% of 694 kills).

P = 0.024; Table 1). Among models of kills·wolf^{-1}·day^{-1}, the best-fit model included only snow, but addition of the senescent term did improve model fit (χ^2 = 5.98, d.f. = 1, P = 0.015; Table 1).

Most covariates showed relatively low levels of collinearity (Spearman's rho < 0.41; Table S5), including senescent age structure and wolf abundance (Spearman's rho = 0.37, P = 0.29). The population ratio of senescent hunters was also unrelated to wolf population size across YNP (Spearman's rho = 0.49, P = 0.15).

DISCUSSION

Animals with rapid maturation and reproduction are expected to senesce earlier and faster than species with slow life histories because selection is too weak to maintain genetic health late in life (Hamilton 1966; Charlesworth 1980). Whereas it is established that this includes senescence

in survival and reproduction (Jones et al. 2008), our results suggest that senescence in predatory ability is similarly linked to life history as is broadly supported by other studies. For instance, an early decline in canid performance is also evident in the peak hunting success of some other wolves (age 4; Sand et al. 2006) and in the peak racing time of greyhounds (age 2.9; Taubert et al. 2007). By contrast, the hunting success of spotted hyena (*Crocuta crocuta*), which exhibits a slower life history (age at primiparity = 3–4 years, litter size = 1–2 cubs; Holekamp et al. 2007), appears to decline much later (age 9–10; Holekamp et al. 1997), as do the skills of aboriginal human hunters (age 45–50) who have an even slower life history (age at primiparity = 17.5 years, litter size = 1 child; Hill & Hurtado 1996; Walker et al. 2002; Gurven et al. 2006). Note, however, that none of the non-human studies were longitudinal and so may have underestimated the onset and rate of declining performance (Nussey et al. 2008). Nevertheless, the emerging pattern is that natural selection shapes senescence in predatory ability as well as survival and reproduction.

Our evidence that declining wolf hunting ability was due to physiological deterioration is also consistent with the findings of other studies. For example, the positive correlation between task difficulty and the rate of age-related decline in task performance has been observed among aboriginal human hunters (Walker et al. 2002; Gurven et al. 2006). In this case, the difficult task of killing prey declines more rapidly with age than does the easier task of finding prey. And like our results for wolves, the decline in aboriginal performance starts later as task difficulty increases. This is apparently due to learning, whereby hunters require more time to reach peak proficiency in the most difficult tasks. Indeed, the rate of juvenile improvement slows with increasing task difficulty for both wolves (see Fig. 1) and aboriginal hunters.

Strength measurements clearly show that declining performance in ageing aboriginal hunters is due to poor physical condition (Gurven et al. 2006). We used serum albumin to assess the physical condition of ageing wolves because lower serum albumin concentration has been associated with physiological ageing in dogs and other mammals, including humans (Rall et al. 1995; Lane et al. 2000). The age at which serum albumin declined in wolves is similar to some dogs (Mundim et al. 2007; Lawler et al. 2008). In ageing humans, reduced serum albumin relates to functional loss including diminished strength (Schalk et al. 2005) and mobility (Okamura et al. 2008). Similarly, ageing wolves show a close correspondence between peak serum albumin levels and peak performance of the most difficult predatory task (selecting).

Loss of physical function in ageing wolves can also be inferred from the age-related increase in mortality risk. Accelerated risk following declines in predatory perfor-

Table 1 Subset of models for multivariate analysis of wolf predation rate in northern Yellowstone National Park, 1998–2007

Model	kills·pack^{-1}·day^{-1}		kg·pack^{-1}·day^{-1}		kills·wolf^{-1}·day^{-1}		kg·wolf^{-1}·day^{-1}	
	ΔAIC$_c$	W	ΔAIC$_c$	W	ΔAIC$_c$	W	ΔAIC$_c$	W
Intercept	3.99	0.06	4.21	0.07	4.30	0.03	2.05	0.08
Senescent	**0.00**	**0.44**	**0.00**	**0.56**	2.75	0.07	**0.00**	**0.22**
Snow	5.88	0.02	7.26	0.01	**0.00**	**0.29**	0.52	0.17
Pup	3.96	0.06	4.09	0.07	8.41	0.00	6.23	0.01
Wolf	3.47	0.08	5.83	0.03	2.46	0.08	2.99	0.05
Elk	7.47	0.01	8.09	0.01	6.64	0.01	5.00	0.02
Wolf : elk	5.24	0.03	6.88	0.02	3.41	0.05	3.17	0.05
Senescent + snow	4.78	0.04	5.79	0.03	**0.02**	**0.28**	**0.86**	**0.14**
Senescent + pup	5.59	0.03	5.58	0.03	5.35	0.02	**0.88**	**0.14**
Senescent + wolf	3.32	0.08	5.31	0.04	4.77	0.03	4.66	0.02
Senescent + elk	5.56	0.03	4.64	0.05	8.63	0.00	6.00	0.01
Senescent + wolf : elk	5.66	0.03	5.98	0.03	6.65	0.01	5.41	0.01

Variables include senescent age structure (senescent = population ratio of wolves > 3.0 years-old), juvenile age structure (pup = population ratio of wolves < 1 year-old), wolf abundance (wolf), elk abundance (elk), ratio of wolf abundance to elk abundance (wolf : elk), and snow water equivalent (snow), which was an index of winter severity. Differences in AIC$_c$ compared to the best scoring model (ΔAIC$_c$), and AIC$_c$ weights (W) are given for each model; all best-supported models (i.e. ΔAIC$_c$ < 2.00) are presented here in boldface. Model selection results for the entire suite of candidate models is available as Supporting Information (Table S4).

mance and serum albumin concurs with the expectation that mortality risk increases with age due to breakdown in underlying maintenance traits (reviewed by Williams *et al.* 2006). However, the time lags between reduced overall performance (age 3) and accelerated mortality (age 5) and median life span (age 6) were not small. This might be the result of wolf social behaviour. Wolf packs are family groups that feed communally, so it is possible that younger hunters subsidized the survival of older, senescent (> 3.0-year old) hunters.

Our finding that adult ($\geq$ 2.0 years-old) wolves were maximally proficient predators for a fraction (*c.* 25%) of their lives challenges the prevailing view that the adults of a predator population are uniformly lethal. At the population-level, declining adult performance reduced the quantity of prey killed by wolves as the ratio of senescent hunters increased. This conforms to Maynard Smith and Slatkin's (MSS) prediction that interindividual differences in predatory ability limit predator impacts on prey (Maynard Smith & Slatkin 1973). But unlike the MSS model, the reduction in prey offtake in YNP arises not from the demise of sub-prime hunters, but from their relative increase, that is a shift in age structure. The MSS model assumes that age structure converges to a stable distribution, but our study adds to the list of free-living species that exhibit a fluctuating age structure; although, it is possible that YNP wolves are still approaching a stable age distribution 12 years post-reintroduction. Nevertheless, we believe this to be the first evidence that a fluctuating predator age structure has measurable effects on prey offtake. And because the ratio of senescent hunters varied independently of wolf popula-

tion size, wolf populations of equal size but different age structure may have different impacts on prey dynamics.

Variable age structure might also affect the non-consumptive effects of predators on prey. Studies proposing that elk alter their behaviour in response to wolves in ways that affect plant communities (e.g. Beyer *et al.* 2007; Ripple & Beschta 2007) equate predation risk with predator presence, assuming that each predator in a population is equally risky. But predatory senescence combined with a variable age structure may introduce substantial spatial and temporal variation in predation risk. Thus, the patchy release of woody plants in apparent response to wolf reintroduction in YNP (e.g. Beyer *et al.* 2007; Ripple & Beschta 2007) might reflect, in part, how elk response varies according to the presence of the most lethal wolves. Greater vigilance among elk living outside YNP compared to those inside YNP (Creel *et al.* 2008) may reflect a similar response given that wolves outside the park are often controlled to reduce livestock predation, thus skewing wolf age structure toward younger and therefore more lethal age classes (Sidorovich *et al.* 2007). Elk can distinguish between high- and low-risk predators, as indicated by their more aggressive response to adult coyotes (*Canis latrans*) than to juveniles (Gese 1999).

In summary, our results indicate that ageing impairs the athletic performance of a long-lived predator in accordance with its life history, and that this limits prey offtake via temporal fluctuations in predator age structure. Knowledge of predator age structure may therefore be necessary in order to accurately predict the impact of long-lived predators on prey populations.

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SUPPORTING INFORMATION

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

Table S1 Model selection results for models of age-specific predatory performance.
Table S2 Model selection results for models of age-specific serum albumin concentration.
Table S3 Model selection results for models of age-specific mortality risk.
Table S4 Model selection results for models of wolf predation rate.
Table S5 Spearman rank correlations between explanatory variables of wolf predation rate.

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