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Sustainable trophy hunting of African lions

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In most species, sport hunting of male trophy animals can only reduce overall population size when the rate of removal of males is so high that females can no longer be impregnated[1]. However, where males provide extensive paternal care, the removal of even a few individuals could harm the population as a whole[2,3]. In species such as lions, excessive trophy hunting could theoretically cause male replacements (and associated infanticide[4,5]) to become sufficiently common to prevent cubs reaching adulthood. Here we simulate the population consequences of lion trophy hunting using a spatially explicit, individual-based, stochastic model parameterized with 40 years of demographic data from northern Tanzania. Although our simulations confirm that infanticide increases the risk of population extinction, trophy hunting could be sustained simply by hunting males above a minimum age threshold, and this strategy maximizes both the quantity and the quality of the long-term kill. We present a simple non-invasive technique for estimating lion age in populations lacking long-term records, and suggest that quotas would be unnecessary in any male-only trophy species where age determination could be reliably implemented.

Male lions reach sexual maturity at about 2.5 yr of age and live to a maximum of about 15 yr in nature[6]. The lion's mane reaches full size at about 4 yr (ref. 7), and peak reproductive success is attained by about 8 yr (ref. 8). African lions live in stable social groups ('prides') containing an average of six breeding females and a coalition of 2–3 adult males. The resident coalition sires all cubs born during their tenure[9], but most coalitions only remain resident for about 2 yr on average—long enough to rear a single cohort of young to independence[10]. Rather than wait for mothers with dependent offspring to rear their current brood, incoming males typically kill all cubs ≤9 months of age and evict older subadults when they first take over a pride[4,5]. Trophy hunting is expected to increase the rate of male takeovers, as larger coalitions dominate smaller ones[11] and the loss of even one male from a resident coalition renders it more vulnerable to being ousted[12].

We developed a comprehensive simulation model that tracks the fate of each individual in a population[13] (see Methods), and we present results based on 'populations' comprising a maximum of ten prides of ≤9 females per pride. Outcomes of hunting should be most sensitive to factors that limit population size: the maximum number of prides in the population, maximum pride size, and the incidence of infanticide. We therefore ran simulations of populations containing a maximum of five prides with ≤10 females and ten prides with ≤7 females, and our conclusions were unchanged. The impact of infanticide is emphasized below (see Fig. 1). At each six-month time step, animals survive and breed according to probabilities observed in the long-term lion studies in the Serengeti National Park and in Ngorongoro Crater[14,15]. Demographic parameters depend on the age, sex and social status of individual lions. Probability of female recruitment depends on the number of adult females in the pride, whereas probability of male takeovers depends on the size and age of resident coalitions versus challenging nomadic coalitions. An emerging property of these interactions is a density-dependence that leads to a quasi-equilibrium where the total population size fluctuates slightly (with demographic stochasticity) around a well-defined average. Preliminary trials started the populations with an arbitrary set of individuals and an arbitrary age

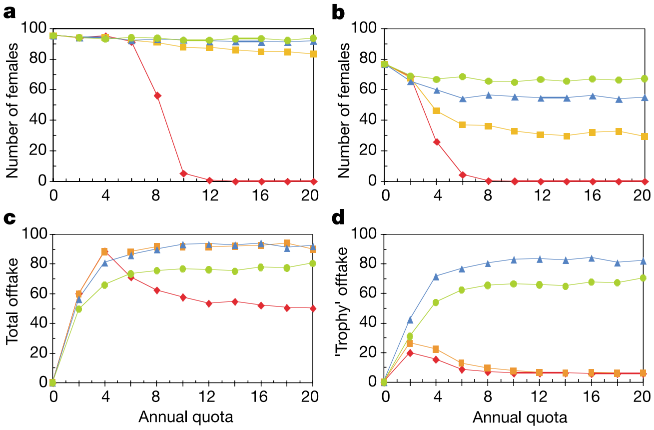

Figure 1 Effects of trophy hunting as a function of quota size and male age. Average outcome after 100 runs is shown from shooting males of the following ages: ≥3 yr old (red), ≥4 yr (orange), ≥5 yr (blue), ≥6 yr (green). **a**, Number of adult females after 30 yr in hypothetical populations where males are non-infanticidal. **b**, Number of females in infanticidal populations; note that infanticidal populations are smaller and more vulnerable to trophy hunting. **c**, Total number of males harvested over 30 yr in infanticidal populations. **d**, Total number of 5–6-yr-old 'trophies' harvested in infanticidal populations.

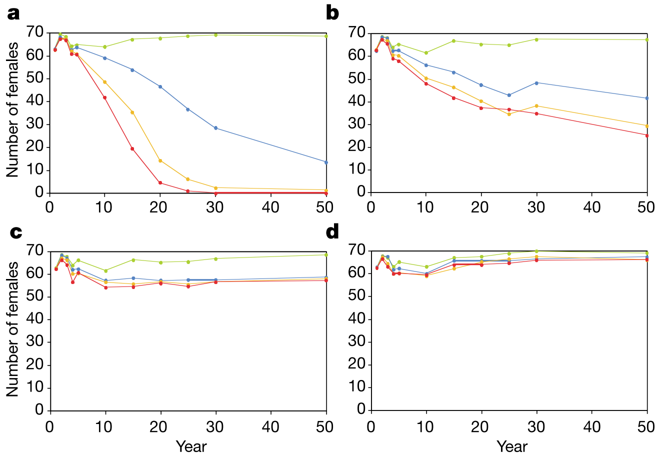

Figure 2 Female population size through time as a function of quota size and male age in infanticidal populations. Red indicates average outcome over 100 runs from an annual quota of 10 males, orange from a quota of 6 males, blue from a quota of 4, and green from a quota of 2. **a**–**d**, Female population size when hunters shoot males that are ≥3 yr old (**a**), ≥4 yr (**b**), ≥5 yr (**c**) and ≥6 yr (**d**).

distribution, and proceeded (without trophy hunting) until the population reached a stable size and age-structure that served as the standardized starting point for all simulations.

Trophy-hunting strategies were varied in two ways. First, the minimum age of eligible males ranged from ≥3 yr to ≥6 yr. Second, quotas could range from 0 to 20 males per year. Individual males were removed according to the age minimum, but at random with respect to pride or nomadic status. Figure 1 illustrates the effects of these strategies after 30 yr (as start-up populations required 20–25 yr to equilibrate). Figure 1a and b shows that if offtake included males as young as three years of age, the female population would invariably collapse if quotas were too high. But as the minimum age of trophy males was raised, the chances of population persistence increased markedly—to the point where removing males ≥6 yr in age had no substantial effect, regardless of quota size. Note that the sensitivity to over-hunting is exacerbated by infanticide: if we eliminate infanticide from the model, the resultant populations are always larger regardless of hunting strategy (Fig. 1a)—but removing too many young males will still drive the population to extinction because females are eventually unable to mate. Figure 2 shows the average size of the female population through time as a function of male age and quota size. Shooting too many young males leads to an inevitable decline in population size, whereas quota size is irrelevant when hunting is restricted to older males. Running the simulations for 50 yr in infanticidal populations, quotas of more than two ≥3- or ≥4-yr-old males per year produced at least one case of extinction per 100 runs, whereas there were no extinctions when hunting was restricted to ≥5- or ≥6-yr-olds.

By only removing ≥5- or ≥6-yr-old males, younger males have the opportunity to remain resident long enough to rear a cohort of young. By removing males in a manner that sustains population growth, the population can yield more males in the long run. Figure 1c and d shows that the cumulative number of males harvested over 30 yr is also sensitive to male age and quota, but, again, the detrimental impact of trophy hunting is largely avoided by maintaining a minimum age of 5–6 yr, and the total number of high-quality 'trophies' (large-maned males of 5–6 yr) taken at random from these populations is also highest. Hunting fees are highest in reserves with greater opportunities to shoot trophy animals, so it is noteworthy that the most impressive males are so 'expendable' to the population. Figure 3 shows the expected annual harvest of 'trophy males' through time. By restricting offtake to ≥5- or ≥6-yr-old males, hunters harvest a greater cumulative number of trophy males and are likely to gain a steadier offtake each year.

Hunters often estimate male age on the basis of mane size or colouration, but these phenotypes are only loosely correlated with age and vary greatly across the geographic range of the lion[7]. The most reliable index in the Serengeti/Ngorongoro lions is the extent of dark pigmentation in the tip of the nose, which becomes increasingly freckled with age (Fig. 4). Individual variation in nose colouration is sufficiently low that age can be estimated up to 8–9 yr (Table 1). The noses of 5-yr-old males are 50% black, so a simple rule of thumb would be to restrict all trophy hunting to males with noses that are more than half black. However, the noses of Ngorongoro males darkened more slowly than Ngorongoro females and Serengeti males/females (Fig. 4), thus site-specific data may be necessary to provide accurate age estimates. However, in areas with slower rates of nose darkening, the 50% rule would safely restrict hunting to ≥8-yr-old males.

Detailed predictions of these simulations should be interpreted

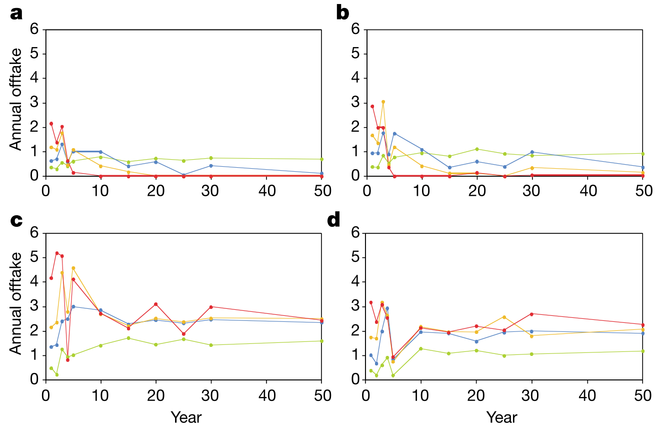

Figure 3 Annual offtake of 5–6-yr-old 'trophy' males as a function of quota size and male age in infanticidal populations. Red indicates average outcome of 100 runs from an annual quota of 10 males, orange from a quota of 6 males, blue from a quota of 4, and green from a quota of 2. Annual offtake of trophies when hunters shoot males that are ≥3 yr old (**a**), ≥4 yr (**b**), ≥5 yr (**c**) and ≥6 yr (**d**).

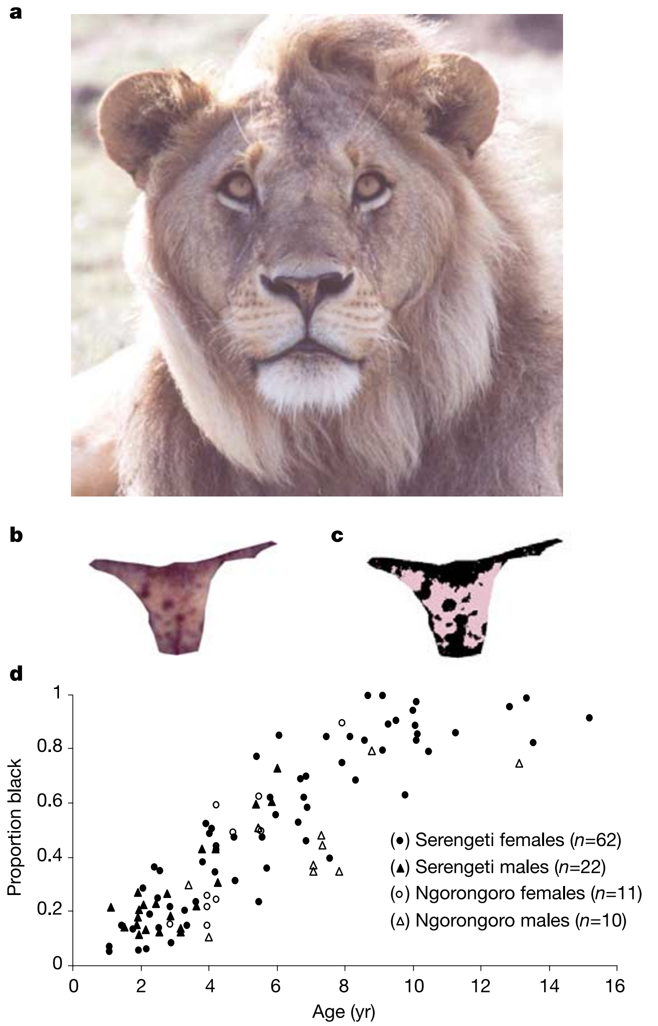

Figure 4 Age estimation for adult lions using nose colouration. **a**, Identification photograph of a 3-yr-old Serengeti male. **b**, Excised photo of nose tip. **c**, GIS rendering of nose colouration. **d**, Age-change of nose colouration for males and females in two separate populations. After controlling for age, there was no effect of sex on nose colour in the Serengeti, but Ngorongoro males had lighter noses than Ngorongoro females ($P = 0.0485$) and Serengeti males ($P = 0.0281$).

with caution, because they rely on demographic patterns in two adjacent populations in northern Tanzania and may not apply to every situation. Nevertheless, our results do point to possible conflicts between conservation and consumption. Figures 1b and 2 suggest that lion populations will be larger if trophy hunting is restricted to males ≥6 yr, but this strategy entails an opportunity cost: long-term harvests are highest from hunting males with ages ≥5 yr (Fig. 1c and d, Fig. 3). Our analysis also treats the lion population as a ‘closed system’, sustained solely by birth rates of the resident females, which exemplifies populations most at risk from overexploitation. ‘Open’ systems involve game reserves immediately adjacent to national parks where excess males and females can freely disperse from protected areas into low density hunting areas. Our analysis also assumes that trophies are removed at random according to residence status. If hunters followed a more sophisticated approach by selectively targeting nomadic males or resident males whose cubs have recently reached independence, trophy hunting could greatly reduce the incidence of infanticide, and population sizes would approach the levels predicted by Fig. 1a.

Assuming an average pride range of 100 km^2, our simulated population of ten prides would yield fewer than three males per 1,000 km^2 per year (Fig. 1c). Hunting quotas in 34 reserves in Tanzania in 1995 were set at an average of 3.8 males per 1,000 km^2 (median, 2.8; range, 0.5–13.4). Although the expectations from these concessions were generally set at an appropriate order of magnitude, quotas have increased in many Tanzanian reserves since 1995, and quotas are even higher in parts of Africa where lion population densities are considerably lower. Therefore, realistic lion harvests for most areas may not generate sufficient revenue to be economically viable in the long term unless concessions establish an auction system[16] or sell hunting ‘opportunities’ (which may or may not succeed in killing a lion) rather than attempt to base their income exclusively on successful hunts.

Our model shows clearly that age is a critical variable enabling the persistence of trophy species with extensive paternal care. As long as hunting is restricted to a safe minimum age (and the rule is honestly enforced[17]), there is no risk of setting excessive quotas even in areas where it is impossible to estimate the overall population size[18]. Lions’ noses continue to darken until they are at least 9 yr old, so rough estimates of male age can easily be made (Table 1). Thus despite the complexity of lion social structure and the complex consequences of male removal, populations can be sustained by following a simple harvest rule, combined with a simple technique for age-assessment.

Although our model was designed to examine the impact of trophy hunting in only one species, our findings have broad significance. First, highly valued ‘trophy’ animals are individuals with unusually well-developed secondary sexual characteristics, such as large antlers, horns, tusks or mane. Although these traits generally grow with age, high-quality individuals may show precocious physical development and thus be shot before they are able to breed—with negative evolutionary effects on the population as a whole[19]. Thus it is particularly important to assess age independently from the ‘trophy’ phenotype, and to set age thresholds high enough to ensure successful breeding by the best males. Second, the hunting industry has always been based on some sort of quota system, even though quotas are generally viewed as arbitrary and difficult to enforce[16,20,21]. Our analysis suggests that quotas could eventually become irrelevant to the conservation of lions hunting is restricted to males. With basic information on breeding biology and social behaviour (such as infanticide and other quirks of male behaviour[22]), an age-threshold criterion could be calculated that would minimize the adverse effects from killing all of the eligible males each year. By excluding the younger adult males from the annual kill, females would always be impregnated and vulnerable offspring would generally be protected by their fathers. ☐

Table 1 **Statistical relationship between nose blackness and age**

Proportion black	Estimated age in years (s.e.)	95% p.i.	75% p.i.	50% p.i.
0.10	2.66 (1.24)	0.17–5.15	1.21–4.10	1.81–3.50
0.20	3.25 (1.24)	0.77–5.72	1.81–4.69	2.41–4.09
0.30	3.84 (1.23)	1.37–6.30	2.40–5.27	3.00–4.68
0.40	4.42 (1.23)	1.97–6.89	3.00–5.86	3.59–5.26
0.50	5.02 (1.23)	2.56–7.48	3.59–6.45	4.18–5.85
0.60	5.61 (1.23)	3.14–8.07	4.18–7.04	4.77–6.44
0.70	6.20 (1.23)	3.73–8.66	4.77–7.63	5.36–7.04
0.80	6.79 (1.24)	4.32–9.26	5.35–8.23	5.95–7.63
0.90	7.38 (1.24)	4.90–9.87	5.94–8.82	6.54–8.22
1.00	7.97 (1.25)	5.58–10.47	6.52–9.42	7.12–8.82

s.e., standard error; p.i., predicted interval. Predicted values are based upon the least-squares regression of a truncated data set for 63 known-aged females in the Serengeti and Ngorongoro aged ≤10 yr ($y = 2.0667 + 5.9037\arcsin(x)$; $r^2 = 0.75$, $P < 0.0001$). Predicted intervals at 95%, 75% and 50% are included for upper and lower bounds.

Methods

Simulation model

In the Windows-driven C++ model[12], female lions and their dependent offspring are organized into ‘prides’ that defend spatially arranged and interconnected territories. The model ignores environmental stochasticity, so the maximum number of territories and maximum pride size is held constant for a given set of simulations. The model distinguishes between sex and age class (cubs <6 months, cubs 6–12 months, cubs 12–24 months, subadult males and females, adult males and females) and tracks individuals by social and reproductive status. Only 3–13-yr-old females produce cubs; females are not able to breed again until they lose their entire litter or their surviving offspring reach 2 yr of age. Males are classified as either subadult, nomadic or resident; lone males may join up with other lone males or groups of two. Nomadic and subadult males move freely between and within pride territories a specified number of times per time step, but do not breed with females. Residents may be affiliated with up to three prides at once. Competition for pride residence is determined by using a competition matrix[23] that weights overall competitive strength according to male age and coalition size. Cubs are killed with an age-specific probability when new males first enter a pride.

At each time step, the model simulates cub production using a random number for each eligible female that draws her litter size from a distribution, determines individual survival (assigned by random number according to the observed survival rate for animals of that age, sex and social status—see Supplementary Information), updates ages for survivors, organizes 2-yr-old males in each pride into subadult male groups, promotes 3-yr-old males into nomadic groups, and determines the fate of subadult females. Recruitment of females into their natal pride depends on the number of adult females already in the pride and the specified upper limit for that pride (which can be temporarily exceeded by no more than two females). If the subadult females cannot be accommodated in their natal pride, they are allowed to search for empty territories, but they die if they cannot find any vacancies. At ‘equilibrium’, the simulated populations closely matched real populations in terms of the male:female:cub ratio, the average age of resident males, and the size range of subadult cohorts. To test the effects of trophy hunting, each simulation ran for 30 or 50 yr with 100 replicates. The initial age structure, reproductive history, pride affiliation, and distribution were identical for each replicate. Harvesting occurred at random (within the rules) every 6 months, although it was not always possible to meet the quota.

Nose assessments

Close-up colour photographs ($n = 189$) were taken of 105 known-aged lions, including 73 females and 32 males from the Serengeti National Park and Ngorongoro Crater, Tanzania, between 1999 and 2002. Each photograph was first digitized at high resolution into a .tif file, and the fleshy part of the nose (‘nose tip’) from each image was excised using Adobe Photoshop 4.01 LE. We then used the Spatial Analyst extension of ESRI Arcview 3.2 to rasterize each cut-out nose tip and assign each newly created ‘grid’ a range of colour values. By limiting the colour values to either ‘black’ or ‘not black’, the nasal pigmentation pattern was ‘mapped’ and quantified for the percentage of readable pixels that contained ‘black’. We used linear multiple regression to assess the effect of age, sex, habitat and population on pigmentation. In cases where multiple photographs were available for the same individual, the mean pigmentation score was regressed against mean age.

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1. Milner-Gulland, E. J. *et al.* Reproductive collapse in saiga antelope harems. *Nature* **422,** 135 (2003).
2. Swenson, J. E. *et al.* Infanticide caused by hunting of male bears. *Nature* **386,** 450–451 (1997).
3. Greene, C., Umbanhowar, J., Mangel, M. & Caro, T. in *Behavioral Ecology and Conservation Biology* (ed. Caro, T.) 271–305 (Oxford Univ. Press, Oxford, 1998).
4. Bertram, B. C. R. Social factors influencing reproduction in wild lions. *J. Zool.* **177,** 463–482 (1975).
5. Packer, C. Infanticide is no fantasy. *Am. Anthropol.* **102,** 829–831 (2000).
6. Schaller, G. B. *The Serengeti Lion* (Univ. Chicago Press, Chicago, 1972).

7. West, P. M. & Packer, C. Sexual selection, temperature and the lion's mane. *Science* **297,** 1339–1343 (2002).
8. Packer, C. *et al.* in *Reproductive Success* (ed. Clutton-Brock, T. H.) 363–383 (Univ. Chicago Press, Chicago, 1988).
9. Packer, C., Gilbert, D., Pusey, A. E. & O'Brien, S. J. A molecular genetic analysis of kinship and cooperation in African lions. *Nature* **351,** 562–565 (1991).
10. Packer, C. & Pusey, A. E. Male takeovers and female reproductive parameters: a simulation of oestrus synchrony in lions (*Panthera leo*). *Anim. Behav.* **31,** 334–340 (1983).
11. Bygott, J. D., Bertram, B. R. C. & Hanby, J. P. Male lions in large coalitions gain reproductive advantages. *Nature* **282,** 838–840 (1979).
12. Grinnell, J., Packer, C. & Pusey, A. E. Cooperation in male lions: kinship, reciprocity or mutualism? *Anim. Behav.* **49,** 95–105 (1995).
13. Quadling, H. S. & Starfield, A. M. Exploiting object-orientated programming structures in the quest for an individual-based lion population model with an attractive user interface. *S. Afr. J. Sci.* **98,** 449–454 (2002).
14. Packer, C., Tatar, M. & Collins, D. A. Reproductive cessation in female mammals. *Nature* **392,** 807–811 (1998).
15. Packer, C., Pusey, A. E. & Eberly, L. Egalitarianism in female African lions. *Science* **293,** 690–693 (2001).
16. Leader-Williams, N., Kayera, J. A. & Overton, G. L. *Tourist Hunting in Tanzania* (IUCN Species Survival publication no. 14, Gland, Switzerland, 1996).
17. Smith, R. J., Muir, R. D. J., Walpole, M. J., Balmford, A. & Leader-Williams, N. Governance and the loss of biodiversity. *Nature* **426,** 67–70 (2003).
18. Hillborn, R. & Walters, C. J. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty* (Chapman & Hall, New York, 1992).
19. Coltman, D. W. *et al.* Undesirable evolutionary consequences of trophy hunting. *Nature* **426,** 655–658 (2003).
20. Caro, T. M. *et al.* The impact of tourist hunting on large mammals in Tanzania: an initial assessment. *Afr. J. Ecol.* **36,** 321–329 (1998).
21. Sutherland, W. J. Sustainable exploitation: a review of principles and methods. *Wildl. Biol.* **7,** 131–140 (2001).
22. Slotow, R., Van Dyk, G., Poole, J., Page, B. & Klocke, A. Older bull elephants control young males. *Nature* **408,** 425–426 (2000).
23. Starfield, A. M., Furniss, P. R. & Smuts, G. L. in *Dynamics of Large Mammal Populations* (ed. Fowler, C. W.) 121–134 (Wiley, New York, 1981).

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Fitness benefits of prolonged post-reproductive lifespan in women

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Most animals reproduce until they die, but in humans, females can survive long after ceasing reproduction[1,2]. In theory, a prolonged post-reproductive lifespan will evolve when females can gain greater fitness by increasing the success of their offspring than by continuing to breed themselves[3–6]. Although reproductive success is known to decline in old age[1–6], it is unknown whether women gain fitness by prolonging lifespan post-reproduction. Using complete multi-generational demographic records, we show that women with a prolonged post-reproductive lifespan have more grandchildren, and hence greater fitness, in pre-modern populations of both Finns and Canadians. This fitness benefit arises because post-reproductive mothers enhance the lifetime reproductive success of their offspring by allowing them to breed earlier, more frequently and more successfully. Finally, the fitness benefits of prolonged lifespan diminish as the reproductive output of offspring declines. This suggests that in female humans, selection for deferred ageing should wane when one's own offspring become post-reproductive and, correspondingly, we show that rates of female mortality accelerate as their offspring terminate reproduction.

Life-history theory generally predicts that there should be no selection for living beyond one's reproductive capacity[1,2]. That female humans show a prolonged post-reproductive lifespan is therefore puzzling. The most compelling hypothesis so far predicts that selection will favour a prolonged post-reproductive lifespan if this enables individuals to increase their fitness through assisting their own offspring to reproduce successfully (the grandmother hypothesis)[3,4]. Such helping by post-reproductive individuals is unusual in the animal kingdom: helpers are typically pre-reproductive offspring that delay their own dispersal and help their parents to breed[7]. Nevertheless, evidence of helper effects from cooperatively breeding animals can be used to predict the benefits that mothers may confer by helping offspring to reproduce. Helpers may 'lighten the reproductive load' of breeders (allowing them to breed earlier and/or more often[8,9]) or provide care that is additive to breeders (causing survival improvements to their offspring[9–11]).

Previous research on humans provides some evidence that post-reproductive mothers can benefit the reproductive output of their offspring[12–15]. However, it has not yet been possible to test whether prolonged post-reproductive longevity in humans is associated with greater grandchild production, and hence greater fitness, because data covering the complete reproductive histories of several generations of individuals are scarce. Here we investigate the fitness benefits of prolonged post-reproductive lifespan using complete, multi-generational individual-based data sets from humans living in two different countries (Finland, $n = \sim500$ women and Canada, $n = \sim2{,}300$ women) during the eighteenth and nineteenth centuries (see Methods). We concentrate on the fitness benefits of post-reproductive lifespan for females, because the post-reproductive lifespan of males cannot easily be defined. Our data come from historical farming communities, where grandparent(s) are known to have been an integral part of the family, residing in the same house as at least one of their offspring and near to virtually all others[16,17]. Evidence from contemporary human populations shows that grandparents may assist philopatric offspring by transferring knowledge and participating in household tasks and child care, and that such help may increase offspring breeding probability[12], and grandchildren nutrition and survival[4,14].

We first investigate the effect of a woman's post-reproductive lifespan (age at death after ~50, see Methods) on the number of grandchildren that she leaves in the population (that is, fitness). Second, using the Finnish data set, we investigate the effect that the presence of a post-reproductive mother has on the lifetime reproductive performance of all her offspring: lifetime fecundity, lifetime reproductive success (number of children produced and raised to 15) and individual λ[18] (a fitness measure incorporating the timing of reproduction and the lifetime reproductive output) (see Methods). Third, we investigate the mechanism(s) through which post-reproductive females influence the fitness of their offspring (and hence themselves) by comparing the effect of post-reproduc-