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Supplementary Material

Measuring post-reproductive lifespan

An extensive literature search was conducted to identify all wild mammalian species for which reliable PRLS data is available using the following search term in Google Scholar (where ... is substituted for each mammalian taxonomic order): "Post reproductive lifespan" OR PRLS OR Menopause OR "Reproductive cessation" AND "...". When a hit was found for a given order, the search term was repeated for each genus within that order, and resulting hits were examined individually to assess the information contained in each.

We made an effort to standardise definitions of PRLS since most of our source publications used different methods and criteria. PRLS was quantified in two ways: 1. The average interval between last birth and death (only for females whose span between last live birth and death exceeded that of their own average inter-birth interval, plus two standard deviations). 2. The maximum lifespan minus the average age at reproductive cessation (where reproductive cessation was confirmed through the cessation of menstrual cycle, changes in ovarian anatomy, low/erratic progesterone levels or the absence of pregnancies in a population). Table S1 details the ways in which PRLS was determined for each study population. We note that definition 2, which considers the maximum lifespan and average age at reproductive cessation, could feasibly lead to a bias in which better sampled populations are more likely to find a particularly long-lived individual which leads to inference of PRLS being present. However, our data suggest that this is not a problem here as the median sample size for species found to have PRLS was actually slightly lower than that for species lacking PRLS (medians of 184 and 257 respectively). Also, the overall distributions of sample size in these two groups were greatly overlapping, again suggesting that we are not seeing such a bias. Nevertheless we stress that this measure more accurately reflects the presence of PRLS in some individuals within the population, rather than implying that it is commonly experienced by individuals (the prevalence within the population was also recorded – see below).

In order to measure the duration of PRLS, we calculated the proportion of maximum lifespan spent post-reproductive. This allowed us to include all species that show PRLS. In contrast, using the mean period post-reproductive would under-estimate the occurrence of PRLS in species with high early-life mortality, even when a substantial number of females showed PRLS (Cohen 2004). We therefore chose to measure intrinsic PRLS, even if it is realised in a relatively small (but non-zero) proportion of individuals. Data were also collected from the literature on the proportion of females experiencing PRLS.

While we considered using a combined index for PRLS, such as Levitis and Lackey's (2011) measure: PrR, this measure was not used for two reasons. First, the calculation of PrR requires life-history tables, which are not available for the vast majority of wild species. Second, by independently analysing three separate aspects of PRLS (presence, relative duration, and frequency) we are able to reveal factors that influence these components separately. In contrast, combining these different (and independent) aspects into one index, such as PrR, could easily obscure variation in one element of PRLS and also fails to acknowledge that different reasons could be behind these different aspects of the trait.

References

Cohen, A. A. (2004). Female post-reproductive lifespan: a general mammalian trait. *Biological Reviews*, 79(4), 733-750.

Levitis, D.A. and Lackey, L.B. (2011). A measure for describing and comparing postreproductive life span as a population trait. *Methods in Ecology and Evolution*, 2(5), 446-453.

Table S1. Life-history data obtained from the literature. Numbers after values indicate the literature source of the data. M abbreviated to pg: polygynous, pga: polygynandrous, mg: monogamous. PRLS definitions are coded as follows: (1) average birth and death, only for females whose span between last live birth and death exceeded that of their own average inter (2) maximum lifespan minus age at reproductive cessation. For definition 2, reproductive cessation was defined through (a) menstrual/oestrous cycle (b) changes in ovarian/uterine anatomy (c) last birth/ no more pregnant females / no more females recorded (d) low/erratic progesterone levels (e) no decrease in pregnancy rate with age (f) no changes in ovarian anatomy recorded (g) substantial decrease in pregnancy rate with age (but no data available on individual females - there may be just reduced success shortly before death)

Species	PRLS present	Relative duration PRLS (% max. lifespan)	Maximum lifespan	Mean group size	Frequency of PRLS (%)	Philopatry	Type of study population	Sample size	Definition of PRLS
Primates									
Common marmoset <i>Callithrix jacchus</i>	yes ₁	21.15 ₁	10 ₁	9 ₂	36.4% (of females reaching middle age) ₁	none _{3, 4}	captive	14 ₁	1
Vervet monkey <i>Chlorocebus</i>	no ₁	NA	17 ₁	40.5 ₂	NA ₁	female ₂	captive	12 ₁	1

<i>aethiops</i>									
Western lowland gorilla <i>Gorilla gorilla</i>	yes ₅	20 ₅	50 ₅	12 ₂	NA	none ₂	captive	NA	2d
	yes ₁	15.11 ₁	30 ₁	12 ₂	40% (of females reaching middle age) ₁	none ₂	captive	12 ₁	1
	yes ₆₃	16.15 ₆₃	52 ₆₃	12 ₂	23% (of geriatric females) ₆₃	none ₂	captive	22 ₆₃	2a
Golden lion tamarin <i>Leontopithecus rosalia</i>	yes ₁	32.22 ₁	12 ₁	9 ₂	47.4% (of females reaching middle age) ₁	none ₂	captive	21 ₁	1

Japanese macaque <i>Macaca fuscata</i>	yes ₆	13.64 (mean PRLS 4.5 years) ₆	33 ₆	47.25 ₆₆	50% (of old females) ₆	female ₂	wild (provisioned)	33 (total females), 14 old aged females (20+ years)	1*
	yes ₆	18 (mean PRLS 3.6 years) ₆	20 ₆	47.25 ₆₆	28.6% (20 of 70 females experienced post reproductive lifespan) ₆	female ₂	wild (non-provisioned)	9 old aged females (15+ years)	1*
Rhesus macaque <i>Macaca mulatta</i>	yes ₁	12.90 ₁	20 ₁	30 ₂	13.2% (of females that reached middle age) ₁	female ₂	captive	38 ₁	1

Pigtail macaque <i>Macaca nemestrina</i>	yes ₁	20.11 ₁	20 ₁	27.5 ₂	25.6% (of females that reached middle age) ₁	female ₂	captive	209 ₁	1
Bonnet macaque <i>Macaca radiata</i>	yes ₁	35.28 ₁	19 ₁	27.5 ₂	3.8% (of females that reached middle age) ₁	none ₂	captive	26 ₁	1
Barbary macaque <i>Macaca sylvanus</i>	yes ₇	21.43 ₇	28 ₇	35.5 ₂	NA	female ₂	captive	NA	2a
Ring-tailed lemur <i>Lemur catta</i>	no ₆₇	NA	17 ₆₅	11.5 ₆₄	NA	female ₇₀	wild	77 ₆₅	2e
Mouse lemur <i>Microcebus</i>	no ₈	NA	14 ₈	1 ₂	NA	none ₁₀	captive	NA	NA

<i>murinus</i>									
Chimpanzee <i>Pan troglodytes</i>	yes ₁₁	16.75 (based on average PRLS of 8.38) ₁₁	50 ₁₁	74 ₁₁	23.5% (of old females) ₁₁	male ₂	wild	34 old females ₁₁	1*
	yes ₁	19.28 ₁	48 ₁	74 ₁₁	60% (of females that reached middle age) ₁	male ₂	captive	15 ₁	1
	no ₆₂	NA	NA (last birth with 55) ₆₂	74 ₁₁	NA	male ₂	wild	165 ₆₂	NA

Olive baboon <i>Papio anubis</i>	yes ₁₂	11.11 (fertility ceases at 24 years) ₁₂	27 ₁₂	50 ₂	NA	female ₂	wild	NA	2a
Orangutan <i>Pongo</i>	yes ₁	18.64 ₁	38 ₁	2 ₂	31.9% (of females that reached)	none ₂	captive	53 ₁	1

<i>pygmaeus</i>					middle age) ₁				
Milne-Edward's sifaka <i>Propithecus diadema edwardsi</i>	no ₁₃	NA	32 ₁₃	6 ₂	NA	female ₂	wild	NA	2f
Saddleback tamarin <i>Saguinus fuscicollis</i>	yes ₁	33.54 ₁	12 ₁	6.5 ₂	47.4% (of females that reached middle age) ₁	none ₁₄	captive	6 ₁	1
	yes ₁₅	16.67 ₁₅	20.4 ₁₅	6.5 ₂	100% (of old females *)	none ₁₄	captive	6 ₁₅	2a,2b,2d
Cotton-top tamarin <i>Saguinus oedipus</i>	yes ₁₅	6.59 ₁₅	18.2 ₁₅	8 ₂	100% (of old females *)	none ₁₆	captive	6 ₁₅	2a,2b,2d

Hanuman Langur <i>Semnopithecus entellus</i>	Yes ₁₇	14.57 (5.1 average PRLS) ₁₇	35 ₁₇	38.5 ₁₇	16.13 % (includes all observed females, not only aged females)	female ₁₇	Wild (1/3 of foraged food provisioned)	31	1
Squirrel monkey <i>Saimiri sciureus</i>	yes ₁	17.29 ₁	19 ₁	32 ₂	32.1% (of females that reached middle age)	female ₂	captive	28 ₁	1
Humans <i>Homo sapiens</i> Ache people, Paraguay	yes ₅₈	45.45 ₅₈	77 ₅₈	168 ₅₈	-	male ₁₀₂	wild	292 ₅₈	2a
!Kung Bushmen, Botswana	yes ₅₉	60.23 ₅₉	88 ₅₉	35 ₆₁	80% ₅₉	male ₁₀₂	wild	500 ₅₉	2a

(Krummhorn, Germany, 18 th & 19 th Century)	yes ₁	30.18 ₁	97 ₁	NA	97% (of females that reached middle age) ₁	male ₁₀₂	wild	106 ₁	1
Cetaceans									
Antarctic minke whale <i>Balaenoptera acutorostrata</i>	no ₁₈	NA	50 ₂₀	2 ₁₉	NA	none ₁₉	wild	>12000 ₁₈	2e
Antarctic fin whale <i>Balaenoptera physalus</i>	no ₉₆	NA	85 ₉₆	1.56 ₉₇	NA	NA	wild	1422 ₉₆	2e
Sei whale <i>Balaenoptera borealis</i>	no ₁₈	NA	60 ₂₁	3 ₁₉	NA	NA	wild	1521 ₁₈	2e

Short-finned pilot whale <i>Globicephala macrorhynchus</i>	yes ₂₂	45.24 ₂₂	63 ₂₂	27.5 ₁₉	25% ₂₄	both ₂₃	wild	245 ₂₂	2b, 2c
Long-finned pilot whale <i>Globicephala melas</i>	yes ₂₄	0.32 ₂₄	59 ₂₄	30 ₁₉	4.4% (of mature females) ₂₄	both _{25, 26}	wild	1070 ₂₄	2a, 2b
Killer whale <i>Orcinus orca</i> Northern	yes ₂₈	54.44 (50% post reproductive at 41 years) ₂₈	90 ₂₈	9.7 ₂₈ / 26 ₈ *	10% of population ₂₈	both ₂₃	Wild	63 ₂₈ / 41 ₂₈ *	2c
Franciscana <i>Pontoporia blainvillei</i>	no ₃₀	NA	19 ₃₀	NA	NA	female ₃₂	Wild	97 ₃₀	2f
False killer whale	yes ₁₈	NA	NA	30 ₁₉	17.91% (of all mature	female ₆₈	wild	67 (mature females) ₁	2c

<i>Pseudorca crassidens</i>					females) ₁₈			8	
Estuarine dolphin <i>Sotalia guianensis</i>	yes ₃₃	16.67 ₃₃	30 ₃₄	12.4 ₃₅	NA	NA	wild	23 ₃₃	2b
Spinner dolphin <i>Stenella longirostris</i>	yes ₉₈	NA	536 ₉₈	211 ₆₉	0.74% (of adult females) ₁₀₁	Variable ₇₀	wild	536 ₉₈	2b
Spotted dolphin <i>Stenella attenuata</i>	yes ₃₆	55.43 ₃₆	46 (mean LS) ₃₇	252.5 ₁₉	NA	Uncertain ₇₁	wild	257 ₃₆	2c

Bottlenose dolphin <i>Tursiops truncatus</i>	no ₁₈	NA	40 ₁₈	13 ₁₉	NA	female ₃₈	wild	151 ₁₈	2e
Perissodactyla									
Domestic horse <i>Equus caballus</i>	Yes ₇₃	6.67 ₇₃	45 ₇₃	4.52 ₇₂	NA	none ₇₄	captive (domestic)	NA	2c
Artiodactyla									
Domestic cattle <i>Bos primigenius Taurus</i>	yes ₄₀	25	20 ₄₀	10.5 ₄₁	>50% (infertile at 15 years)	female ₄₂	captive	152 ₄₀	2c
White-tailed deer	no ₄₄	NA	17.50 ₄₄	3 ₄₇	NA	female ₄₅	wild	284 ₄₄	2e

<i>Odocoileus virginianus</i>									
Bighorn sheep <i>Ovis canadensis</i>	Yes ₇₅	5.26 ₇₅	19 ₇₅	10 ₇₅	0.75% ₇₅	female ₇₈	wild	265 ₇₅	2c
Soay sheep <i>Ovis aries</i>	Maybe ₉₁	NA	12 ₉₁	NA	NA	NA	wild	894 ₉₁	2f

Red deer <i>Cervus elaphus</i>	yes _{92, 93}	> 9.52 ₉₃	> 21 (females were culled at 21 years) ₉₃	30 ₉₅	47.5% (of population) ₉₃	female ₉₈	captive	40 ₉₃	2c
	maybe ₉₄	NA	18 (very few females live beyond this age)	30 ₉₅	NA	female ₉₈	wild	551 ₉₅	2f

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Carnivora

Cat <i>Felis catus</i>	Yes ₈₂	30 ₈₂	20 ₈₅	Variable ₈₃ (solitary and group-living)	NA	none ₈₃	captive (domestic)	NA	NA
Polar bear <i>Ursus maritimus</i>	yes ₄₈	33.33 ₄₈	30 ₄₈	1 ₄₉	2.2%*	none ₄₉	wild	402 ₄₈	2c
African lion <i>Panthera</i>	yes ₁₂	14.27 ₁₂	19.83 ₁₂	4.64 ₇₇	1.7% (pers. com. Prof C Packer)	female/none ₇₆	wild	123 ₁₂	2c

<i>leo</i>									
Banded Mongoose <i>Mungos mungo</i>	no ₆₁	NA	10.50 ₆₁	14 ₆₁	NA	none ₆₁	wild	NA	1
Meerkat <i>Suricata suricatta</i>	maybe ₈₀	NA	12 ₈₀	16.7 ₈₁	NA	none ₈₁	Wild	42 (dominant females) ₈₀	2f

Dog <i>Canis familiaris</i>	yes ₇₃	43.75 ₇₃	16	4 ₇₈	<50% ₇₉	none ₇₈	captive (domestic) ₇₃	NA	2c
Proboscidae									
African elephant <i>Loxodonta africana</i>	no ₅₀	NA	65 ₅₀	9 ₅₁	NA	female ₅₂	wild	546 (38 survived reached >50) ₅₀	2e
Asian elephant <i>Elephas maximus</i>	Yes ₈₅	12.5 ₈₅	79.64 ₈₅	8 ₈₄	32.95% (457/1040) live past 40 years: age when 75% of females ceased to reproduce) ₈₅	female ₈₄	Mixed ₈₄	1040 ₈₅	Mean lifespan – mean age at last reproduction

	No/maybe ₈₅	17.01(54 oldest reproducing female) 54.11 (Mean age at last reproduction 29.88) ₈₅	65.11 ₈₅	8 ₈₄	NA	female ₈₄	captive	471 ₈₅	1*
	Yes ₈₅	56.49 (mean age at last reproduction 34.65) ₈₅	79.64 ₈₅	8 ₈₄	32.95% ₈₅	female ₈₄	wild	569 ₈₅	1*
Lagomorpha									
Domestic rabbit <i>Oryctolagus</i>	yes ₈₆	66.67 ₈₆	15 ₈₆	7 ₉₀	NA	female ₈₇	captive (domestic)	NA	2 (method NR)

<i>cuniculus</i>									
Rodontidae									
Lab mouse <i>Mus musculus</i>	yes ₇₃	60.00 ₇₃	4.17 ₇₃	1 ₈₈	NA	none ₈₈	captive (domestic)	NA	2c
Lab rat <i>Rattus norvegicus</i>	yes ₇₆	52.00 ₇₃	4.17 ₇₃	Variable (solitary when food dispersed, in urban environments mean groups of 22.5) ₈₉	NA	none ₉₀	captive (domestic)	NA	2c
Chinese hamster <i>Cricetulus</i>	no ₅₃	NA	1.75 ₅₃	NA	NA	NA	captive	25 (aged females) ₅₃	2c, g

<i>griseus</i>									
Columbian ground squirrel <i>Spermophilus columbianus</i>	no ₅₄	NA	9 ₅₄	29 ₅₇	NA	female ₅₅	wild	229 ₅₄	2g

References for Table S1

1. Caro, T. M., Sellen, D. W., Parish, A., Frank, R., Brown, D. M., Volland, E., Mulder, M. B. 1995 Termination of reproduction in human female primates. *International Journal of Primatology*, **16**, 205-220.
2. Rowe, N., Goodall, J., Mittermeier, R. 1996 *The pictorial guide to the living primates* (Vol. 9). New York: Pogonias Press.
3. Pontes, A. R. M., da Cruz, M. A. O. M. 1995 Home range, intergroup transfers, and reproductive status of common marmoset (*Callithrix jacchus*) in a forest fragment in North-Eastern Brazil. *Primates*, **36**, 335-347.
4. de Sousa, M. B. C., da Rocha Albuquerque, A. C. S., Yamamoto, M. E., Araújo, A., de Fátima Arruda, M. 2009 Emigration strategy of the common marmoset (*Callithrix jacchus*). *The Smallest Anthropoids*. Springer US.
5. Walker, M. L., & Herndon, J. G. 2008 Menopause in nonhuman primates?. *Biology of reproduction*, **79**, 398-406.
6. Pavelka, M. S. M., Fedigan, L. M., & Zohar, S. (2002). Availability and adaptive value of reproductive and postreproductive macaque mothers and grandmothers. *Animal Behaviour*, *64*(3), 407-414.
7. Paul, A., Kuester, J., Podzuweit, D. 1993 Reproductive senescence and terminal investment in female Barbary macaque at Salem. *International Journal of Primatology*, **14**, 105-124.
8. Bons, N., Rieger, F., Prudhomme, D., Fisher, A., Krause, K. H. 2006 *Microcebus murinus*: a useful primate model for Parkinson's and Alzheimer's disease?. *Genes, Brain and Behavior*, **5**, 120-130.
9. Radespiel, U. 2000 Sociality in the gray mouse lemur (*Microcebus murinus*) in northwestern Madagascar. *American Journal of Primatology*, **51**, 21-40.
10. Radespiel, U., Lutermann, H., Schmelting, B., Bruford, M. W., & Zimmermann, E. 2003 Patterns and dynamics of sex roles in a nocturnal primate, the grey mouse lemur, *Microcebus murinus*. *Animal Behaviour*, **65**, 709-719.
11. Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., Zamma, K. 2003 Demography, fecundity, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology*, **59**, 99-121.
12. Packer, C., Tatar, M., & Collins, A. 1998 Reproductive cessation in female mammals. *Nature*, **392**, 807-811. And per Parker, C.
13. Wright, P., King, S., Baden, A., Jernvall, J. 2008 Aging in wild female lemurs: sustained fertility with increased infant mortality. *Evolution*, **62**, 100-110.
14. Garber, P. A. 1997 One for all and breeding for one: cooperation and competition as a tamarin reproductive strategy. *Anthropology: Issues, News, and Reviews*, **5**, 187-199.
15. Tardif, S. D., & Ziegler, T. E. 1992 Features of female reproductive senescence in tamarins (*Saguinus spp.*), a New World primate. *Reproduction and fertility*, **94**, 411-421.
16. Savage, A., Giraldo, L. H., Soto, L. H., Snowdon, C. T. 1996 Demography, group composition, and dispersal in wild cotton-top tamarins (*Saguinus oedipus*) groups. *American Journal of Primatology*, **38**, 85-100.

17. Sommer, V., Srivastava, A., Borries, C. 1992 Cycles, sexuality, and conception in free-ranging langurs (*Presbytis entellus*). *Journal of Primatology*, **28**, 1-27.
18. Marsh, H., Kasuya, T. 1986 Evidence for reproductive senescence in female cetaceans. *Report of the International Whaling Commission*, **14**, 57-74.
19. Evans, P. G. 1987 *The natural history of whales & dolphins*. Helm.
20. Carey, J., Judge, D. 2002 Longevity records: life spans of mammals, birds, amphibians, reptiles, and fish. *On-line*. *Marine Demographic Research*. Accessed June, **13**, 2005. **Cited in** Samuels, D. C. 2005 Life span is related to the free energy of DNA. *Mechanisms of ageing and development*, **126**, 1123-1129.
21. Kanda, N., Goto, M., Pastene, L. A. 2006 Genetic characteristics of western North Pacific sei whales, *Balaenoptera borealis*, using microsatellites. *Marine Biotechnology*, **8**, 86-93.
22. Kasuya, T., Marsh, H. 1984 Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, on the Pacific coast of Japan. *Report of the International Whaling Commission*, **6**, 259-310.
23. Johnstone, R. A., & Cant, M. A. 2010 The evolution of menopause in cetaceans and humans: the role of demography. *Royal Society B: Biological Sciences*, **277**, 3765-3771.
24. Martin, A. R., Rothery, P. 1993 Reproductive parameters of female long-finned pilot whales (*Globicephala melas*) and their calves in the Azores Islands. *Rep. Int. Whal. Comm.*, **14**, 263-304.
25. De Stephanis, R., Verborgh, P., Pérez, S., Esteban, R., Minvielle-Sebastia, L., Guinet, C. 2008 Long-term social structure of pilot whales (*Globicephala melas*) in the Strait of Gibraltar. *Acta Ethologica*, **11**, 81-94.
26. Amos, B., Bloch, D., Desportes, G., Majerus, T. M., Bancroft, D. R., Barrett, J. A., Dover, G. A. 1993 A review of the morphology and behavior relating to social organisation and breeding system in the long-finned pilot whale. *Report of the International Whaling Commission*, **21**, 209-217.
27. Ward, E. J., Parsons, K., Holmes, E. E., Balcomb III, K. C., Ford, J. K., Altenburger, A., Gunz, P. 2009 The role of menopause and reproductive senescence in a long-lived social mammal. *Frontiers in zoology*, **6**, 1-11.
28. Olesiuk, P. F., Ellis, G. M., & Ford, J. K. 2005 *Life history and population dynamics of northern resident killer whales (Orcinus orca) in the Strait of Georgia, British Columbia*. Canadian Science Advisory Secretariat.
29. Pilot, M., Dahlheim, M. E., Hoelzel, A. R. 2010 Social cohesion among kin, gene flow without dispersal and the evolution of genetic structure in the killer whale (*Orcinus orca*). *Journal of evolutionary biology*, **23**, 20-31.
30. Danilewicz, D. 2003 Reproduction of female franciscana (*Pontoporia blainvillei*) in Rio Grande do Sul, southern Brazil. *Journal of Aquatic Mammals*, **2**, 67-78.
31. Panebianco, M. V., Negri, M. F., Cappozzo, H. L. 2012. Reproductive aspects of male franciscana dolphins (*Pontoporia blainvillei*) in Argentina. *Animal Reproduction Science*, **131**, 41-48.

32. Costa-Urrutia, P., Abud, C., Secchi, E. R., Lessa, E. P. 2012 Population genetic structure and social kin associations of *Pontoporia blainvillei*. *Journal of Heredity*, **103**, 92-102.
33. Weber Rosas, F. C., Monteiro-Filho, E. L. 2002 Reproduction of the estuarine dolphin (*Sotalia guianensis*) on the coast of Brazil. *Journal of Mammalogy*, **83**, 507-515.
34. Rosas, F. C. W., Barreto, A. S., Monteiro, E. L. D. 2003. Age and growth of the estuarine dolphin (*Sotalia guianensis*) on the Paraná coast, southern Brazil. *Fishery Bulletin*, **101**, 377-383.
35. Santos, M. D. O., Rosso, S. 2007 Ecological aspects of marine tucuxi dolphins (*Sotalia guianensis*) based on group size in the Cananéia estuary, southeastern Brazil. *Latin American Journal of Aquatic Mammals*, **6**(1), 71-82.
36. Kasuya, T. 1985 Effect of exploitation on reproductive parameters of the spotted and striped dolphins off the Pacific coast of Japan. *Scientific Reports of the Whales Research Institute*, **36**, 107-138. **Cited in** Marsh, H., & Kasuya, T. 1986 Evidence of reproductive senescence in female cetaceans. *Report of the International Whaling Commission*, **8**, 57-74.
37. Nowak, R. M. (Ed.). 2003 *Walker's marine mammals of the world*. JHU Press.
38. Möller, L. M., Beheregaray, L. B. 2004 Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). *Molecular Ecology*, **13**, 1607-1612.
39. Scott, M. D., Wells, R. S., Irvine, A. B. 1990 A long-term study of bottlenose dolphins on the west coast of Florida 11. *Dolphin*, **235**.
40. Erickson, B. H., Reynolds, R. A., Murphree, R. L. 1976 Ovarian characteristics and reproductive performance of the Atlantic bottlenose dolphin. *Reproduction*, **15**, 555-560.
41. Hernández, L., Barral, H., Halffter, G., & Colón, S. S. 1999 A note on the behavior of feral cattle in the Chihuahuan Desert. *Animal Behaviour Science*, **63**, 259-267.
42. Reinhardt, V., Reinhardt, A. 1981 Cohesive relationships in a cattle herd (*Bos indicus*). *Behaviour*, **77**, 121-151.
43. Lazo, A. 1995 Ranging behaviour of feral cattle (*Bos taurus*) in Donana National Park, SW Spain. *Journal of Zoology*, **235**, 1-10.
44. DelGiudice, G. D., Lenarz, M. S., Powell, M. C. 2007 Age-specific fertility and fecundity in northern free-ranging white-tailed deer: evidence for reproductive senescence? *Journal of Mammalogy*, **88**, 427-435.
45. Jarman, P. 1974 The social organisation of antelope in relation to their ecology. *Behaviour*, **48**, 215-267.
46. DeYoung, R. W., Demarais, S., Gonzales, R. A., Honeycutt, R. L., Gee, K. L. 2002 Multiple paternity in white-tailed deer (*Odocoileus virginianus*) revealed by DNA microsatellites. *Journal of Mammalogy*, **83**, 884-892.
47. Lagory, K. E. 1986 Habitat, group size, and the behaviour of white-tailed deer. *Behaviour*, **98**, 168-179.
48. Ramsay, M. A., Stirling, I. 1988 Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *Journal of Zoology*, **224**, 1-10.
49. Derocher, A. E., Andersen, M., Wiig, Ø., Aars, J. 2010 Sexual dimorphism and the mating ecology of polar bears (*Ursus maritimus*) in Svalbard. *Behavioral Ecology and Sociobiology*, **64**, 939-946.

50. Moss, C. J. 2001 The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Applied Ecology*, **38**, 150-156.
51. Leuthold, W. 1976 Age structure of elephants in Tsavo National Park, Kenya. *Journal of Applied Ecology*, **13**, 435-444.
52. Rasmussen, L. E. L., Schulte, B. A. 1998 Chemical signals in the reproduction of Asian (*Elephas maximus*) and African elephants. *Animal Reproduction Science*, **53**, 19-34.
53. Parkening, T. A. 1982 Reproductive senescence in the Chinese hamster (*Cricetulus griseus*). *Journal of Gerontology*, **37**, 105-110.
54. Broussard, D. R., Risch, T. S., Dobson, F. S., Murie, J. O. 2003 Senescence and age-related reproduction of female Columbian ground squirrels. *Journal of Animal Ecology*, **72**, 212-219.
55. Wiggett, D. R., & Boag, D. A. 1989 Intercolony natal dispersal in the Columbian ground squirrel. *Canadian Journal of Zoology*, **67**, 100-105.
56. Raveh, S., Heg, D., Viblanc, V. A., Coltman, D. W., Gorrell, J. C., Dobson, F. S., ...Neuhaus, P. 2011 Male reproductive senescence and paternity in the polygynandrous Columbian ground squirrel (*Urocitellus columbianus*). *Behavioral Ecology and Sociobiology*, **55**, 103-111.
57. Fairbanks, B., Dobson, F. S. 2007 Mechanisms of the group-size effect on vigilance in Columbian ground squirrels: direct effects on detection. *Animal Behaviour*, **7**, 115-123.
58. Hill, K. R., Hurtado, A. M. 1996 *Ache life history: The ecology and demography of a foraging people*. Transaction Publishers, New York.
59. A. A. 2004 Female post-reproductive lifespan: a general mammalian trait. *Biological Reviews*, **79**, 733-750.
60. Howell, N. 1979 *Demography of the Dobe !Kung*, New York: Academic Press
61. Draper, P. 1974 Crowding among hunter-gatherers: the !Kung Bushmen. *Crowding and Behavior*, **2**, 226.
62. Personal communication, Vitikainen, E., based on a 20 year study of a population of over 2000 individuals.
63. Thompson, M. E., Jones, J. H., Pusey, A. E., Brewer-Marsden, S., Goodall, J., Marsden, D., Wrangham, R. W. 2007 Age-related changes in wild chimpanzees provide insights into the evolution of menopause. *Current Biology*, **17**, 2150-2156.
64. Margulis, S. W., Atsalis, S., Bellem, A., Wielebnowski, N. 2007 Assessment of reproductive behavior and hormonal cycles in western Lowland gorillas. *Zoo biology*, **26**, 117-139.
65. Gould, L., Sussman, R. W., & Sauther, M. L. 2003 Demographic and life-history patterns in a population of ring-tailed lemurs at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. *American Journal of Physical Anthropology*, **120**, 182-192.
66. Ichino, S., Soma, T., Miyamoto, N., Chatani, K., Sato, H., Koyama, N., Takahata, Y. 2015 Lifespan and reproductive senescence in a free-ranging ring-tailed lemur (*Lemur catta*) population at Berenty, Madagascar. *Folia Primatologica*, **86**, 134-139.
67. Takasaki, H. 1981 Troop size, habitat quality, and home range area in Japanese macaques. *Behavioral Ecology and Sociobiology*, **10**, 1-10.
68. Gould, L. 1997 Intermale affiliative behavior in ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. *Primate*, **15**, 15-30.
69. Foote, A. D. 2008 Mortality rate acceleration and post-reproductive lifespan in matrilineal whale species. *Biology Letters*, **4**, 100-103.
70. Karczmarski, L., Würsig, B., Gailey, G., Larson, K. W., Vanderlip, C. 2005 Spinner dolphins in a remote Hawaiian atoll: population structure. *Behavioral Ecology*, **16**, 675-685.

70. Andrews, K. R., Karczmarski, L., Au, W. W., Rickards, S. H., Vanderlip, C. A., Bowen, B. W., ...Toonen, R. J. 2010 Rolling homes: social structure, habitat diversity and population genetics of the Hawaiian spinner dolphin (*Stenella longirostris*). *Ecology*, **19**, 732-748.
71. Courbis, S. S. 2011 *Population structure of island-associated pantropical spotted dolphins (Stenella attenuata) in Hawaii*. State University.
72. Linklater, W. L., Cameron, E. Z., Stafford, K. J., Veltman, C. J. 2000 Social and spatial structure and range use by Kaimanawa horses (*Equus caballus*: Equidae). *New Zealand Journal of Ecology*, 139-152.
73. vom Saal, F. S., Finch, C. E., Nelson, J. F. 1994 Natural history and mechanisms of reproductive aging in humans, laboratory mice, and other selected vertebrates. *The physiology of reproduction*, **2**, 1213-1314.
74. Monard, A. M., Duncan, P. 1996 Consequences of natal dispersal in female horses. *Animal behaviour*, **52**, 565-579.
75. Berube, C. H., Festa-Bianchet, M., Jorgenson, J. T. 1999 Individual differences, longevity, and reproductive senescence in wild sheep. *Ecology*, **80**, 2555-2565.
76. Pusey, A. E., Packer, C. 1987 The evolution of sex-biased dispersal in lions. *Behaviour*, **101**, 275-310.
77. Mosser, A., Packer, C. 2009 Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, **78**, 367-370.
78. Boitani, L., Ciucci, P. 1995 Comparative social ecology of feral dogs and wolves. *Ethology Ecology & Evolution*, **7**, 49-64.
79. Cohen, A. A. 2004 Female post-reproductive lifespan: a general mammalian trait. *Biological Reviews*, **79**, 733-750.
80. Sharp, S. P., Clutton-Brock, T. H. 2010 Reproductive senescence in a cooperatively breeding mammal. *Journal of Animal Ecology*, **79**, 177-183.
81. Clutton-Brock, T. H., Hodge, S. J., Flower, T. P. 2008 Group size and the suppression of subordinate reproduction in meerkats. *Animal Behaviour*, **76**, 689-700.
82. Marshall, F. H. A. 1964 *The Physiology of Reproduction*, 3rd Edn. Longmans, London. **Cited in** Cohen, A. A. 2004 Female post-reproductive lifespan: a general mammalian trait. *Biological Reviews*, **79**, 733-750.
83. Jones, E., Coman, B. J. 1982 Ecology of the Feral Cat, *Felis catus* (L.), South-Eastern Australia III. Home Ranges and Population Density in a Semiarid North-West Victoria. *Wildlife Research*, **9**, 409-420.
84. Vidya, T. N. C., Sukumar, R. 2005 Social organization of the Asian elephant (*Elephas maximus*) in southern India inferred from mitochondrial DNA. *Journal of Ethology*, **23**, 205-210.
85. Lahdenperä, M., Mar, K. U., Lummaa, V. 2014 Reproductive cessation and post-reproductive lifespan in Asian elephants and humans. *Frontiers in zoology*, **11**, 1-14.
86. Comfort, A. 1979 *The Biology of Senescence*, 3rd Edn., New York: Elsevier, **Cited in** Cohen, A. A. 2004 Female post-reproductive lifespan: a general mammalian trait. *Biological Reviews*, **79**, 733-750.

87. Surridge, A. K., Bell, D. J., Hewitt, G. M. 1999 From population structure to individual behaviour: genetic analysis of European wild rabbit (*Oryctolagus cuniculus*). *Biological Journal of the Linnean Society*, **68**, 57-71.
88. Latham, N., Mason, G. 2004 From house mouse to mouse house: the behavioural biology of free-living *Mus musculus* the laboratory. *Applied Animal Behaviour Science*, **86**, 261-289.
89. Barnett, S. A., Spencer, M. M. 1951 Feeding, social behaviour and interspecific competition in wild rats. *Behaviour*, **2**, 1-10.
90. Lynn, D. A., Brown, G. R. 2009 The ontogeny of exploratory behavior in male and female adolescent rats (*Rattus norvegicus*). *Developmental psychobiology*, **51**, 513.
91. Hayward, A. D., Wilson, A. J., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M., Kruuk, L. E. 2013 Reproductive senescence in Soay sheep: variation across traits and contributions of individual ageing and selective disappearance. *Functional Ecology*, **27**, 105-114.
92. Fisher M.W., McLeod B.J., Mockett BG, Moore GH, Drew K.R. 1996 Reproductive senescence in aged red deer hinds. *New Zealand Society of Animal Production*, **56**, 344-346
93. Fisher, M. W., McLeod, B. J., Heath, D. A., Lun, S., Hurst, P. R. 2000 Role of ovarian failure in reproductive senescence in (Cervus elaphus) hinds. *Journal of reproduction and fertility*, **120**, 211-216.
94. Nussey, D. H., Kruuk, L. E., Morris, A., Clements, M. N., Pemberton, J. M., Clutton-Brock, T. H. 2009 Inter-and intraspecific patterns across reproductive traits in a wild red deer population. *The American Naturalist*, **174**, 342-357.
95. Coulson, T., Albon, S., Guinness, F., Pemberton, J., Clutton-Brock, T. 1997 Population substructure, local density, and reproductive success in red deer (*Cervus elaphus*). *Ecology*, **78**, 852-863.
96. Mizroch, S. A. 1981 Analysis of some biological parameters of the Antarctic fin whale (*Balaenoptera physalus*). *Report of the Whaling Commission*, **31**, 425-434
97. Notarbartolo-di-Sciara, G., Zanardelli, M., Jahoda, M., Panigada, S., Airoldi, S. 2003 The fin whale *Balaenoptera physalus* in the Mediterranean Sea. *Mammal Review*, **33**, 105-150.
98. Perrin, W. F., Holts, D. B., Miller, R. B 1977 Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenodelphis longirostris* in the eastern tropical Pacific. *Fishery bulletin* **75**, 725-750.
99. Cant, M. A., Johnstone, R. A. 2008 Reproductive conflict and the separation of reproductive generations in humans. *National Academy of Sciences*, **105**, 5332-5336.

PRLS. We coded the absence or presence of PRLS as having states 0 and 1 respectively and used this as our response variable. Estimated coefficients and 95% confidence intervals are given, and significant predictors are highlighted in bold. N is the number of species included in the model. Species that had missing data for a particular variable were excluded from the relevant models (i.e. those models that included that variable). We considered a variable to be a significant predictor of the presence of PRLS when $P \leq 0.05$.

natural history variable	β	lower 95% CI	upper 95% CI	P	N
Maximum lifespan	3.186	-1.872	9.211	0.190	27
Group size	1.740	-0.062	3.504	0.073	26
Male philopatry	340.523	39.603	632.792	0.018	25
Female philopatry	-59.950	-375.380	292.930	0.692	25

Table S3. Results from GEEs testing for effects of four natural history variables on the relative duration of PRLS and on the frequency with which PRLS is experienced in the population. Estimated coefficients (\pm SE) are given, and significant predictors are highlighted in bold. Species that had missing data for a particular variable were excluded from the relevant models (i.e. those models that included that variable). N is the number of species included in the model.

Response term	Natural history variable	$\beta \pm SE$	t	P	N
Relative duration of PRLS	Maximum lifespan	0.038\pm0.011	3.482	0.007	25
	Group size	0.009 \pm 0.005	1.841	0.100	24
	Male philopatry	1.394 \pm 0.676	2.063	0.071	22
	Female philopatry	-1.573\pm0.681	-2.308	0.048	22
Frequency with which PRLS is experienced in population (proportion of females that experience PRLS)	Maximum lifespan	0.0376 \pm 0.0159	2.364	0.052	16
	Group size	0.0515\pm0.0137	3.762	0.007	17
	Male philopatry	1.900\pm0.786	2.418	0.047	17
	Female philopatry	-0.914 \pm 0.828	-1.104	0.307	17