



**University of  
Zurich** <sup>UZH</sup>

**Zurich Open Repository and  
Archive**

University of Zurich  
University Library  
Strickhofstrasse 39  
CH-8057 Zurich  
[www.zora.uzh.ch](http://www.zora.uzh.ch)

---

Year: 2013

---

**Comparing free-ranging and captive populations reveals intra-specific variation in aging rates in large herbivores**

Lemaître, Jean-François ; Gaillard, Jean-Michel ; Lackey, Laurie Bingaman ; Clauss, Marcus ; Müller, Dennis W H

DOI: <https://doi.org/10.1016/j.exger.2012.12.004>

Posted at the Zurich Open Repository and Archive, University of Zurich  
ZORA URL: <https://doi.org/10.5167/uzh-71300>  
Journal Article

Originally published at:

Lemaître, Jean-François; Gaillard, Jean-Michel; Lackey, Laurie Bingaman; Clauss, Marcus; Müller, Dennis W H (2013). Comparing free-ranging and captive populations reveals intra-specific variation in aging rates in large herbivores. *Experimental Gerontology*, 48(2):162-167.

DOI: <https://doi.org/10.1016/j.exger.2012.12.004>

## **ELECTRONIC APPENDIX**

### **Comparing free-ranging and captive populations reveals intra-specific variation in aging rates in large herbivores**

Jean-François Lemaître, Jean-Michel Gaillard, Laurie Bingaman Lackey, Marcus Clauss, Dennis W.H. Müller

**Table A1:** List of all species ( $n = 22$ ) included in the analysis. All variables are described in the methodology section of the paper.

Species	Diet	Data quality	Aging rate	Aging rate	Aging rate	Aging rate	Body mass (g)	Aging rate	Aging rate	Aging rate	Aging rate	Body mass (g)		
			<i>GAM</i> (wild)	<i>GAM</i> (zoo)	<i>Gompertz</i> (wild)	<i>Gompertz</i> (zoo)		<i>GAM</i> (wild)	<i>GAM</i> (zoo)	<i>Gompertz</i> (wild)	<i>Gompertz</i> (zoo)			
													Male	Female
Impala	<i>Aepyceros melampus</i>	60	1	0.0751	0.0064			55880	0.0784	0.0236			43660	Spinage 1972; Silva & Downing 1995
Moose	<i>Alces alces</i>	2	0	0.0611	0.0478			323000	0.0834	0.0145			257500	Ericson & Wallin 2001; Silva & Downing 1995
Pronghorn	<i>Antilocapra americana</i>	15	0	0.0839	0.0144	0.372	0.059	51500	0.0206	0.0036	0.240	0.111	41000	Byers 1997; Silva & Downing 1995
Gaur	<i>Bos gaurus</i>	66	0	0.1684	0.0150			880000	0.0272	0.0035			590000	Magomedov 2004; Weckerly 1998
Wild goat	<i>Capra hircus</i>	28	1	0.0591	0.0507			70100	0.0341	0.0251			42000	Magomedov 2004; Silva & Downing 1995
Alpine ibex	<i>Capra ibex</i>	60	0	0.0534	0.0190	0.384	0.289	87400	0.0175	0.0353	0.407	0.131	53000	Toigo 2007; Silva & Downing 1995
Roe deer	<i>Capreolus capreolus</i>	9	0	0.0537	0.0377	0.186	0.095	23580	0.0569	0.0555	0.214	0.196	23375	Gaillard et al. 2004; Silva & Downing 1995
Red deer	<i>Cervus elaphus</i>	47	0	0.0698	0.0206			160300	0.0393	0.0250			98733	Catchpole 2004; Silva & Downing 1995
Sikadeer	<i>Cervus nippon</i>	50	0	0.0730	0.0027			39450	0.0246	0.0038			27550	McCullough 2009; Silva & Downing 1995
Wildebeeste	<i>Connochaetes taurinus</i>	90	1	0.0413	0.0288			210000	0.0879	0.0177			170500	Atwell 1982; Silva & Downing 1995
Topi	<i>Damaliscus lunatus</i>	99	1	0.1800	0.0056			134000	0.1810	0.0258			122000	Mertens 1985; Silva & Downing 1995
Defassa Waterbuck	<i>Kobus ellipsiprymnus</i>	80	1	0.1154	0.0158			231000	0.0301	0.0241			174000	Spinage 1970; Weckerly 1998
Lechwe	<i>Kobus leche</i>	95	1	0.1142	0.0108			111750	0.1129	0.0108			86600	Sayer & Van Lavieren 1975; Silva & Downing 1995
Black-tailed deer	<i>Odocoileus hemionus</i>	11	1	0.0460	0.0497			112500	0.0107	0.0191			55500	Taber & Dasman 1957; Plard et al. 2011
Mountain goat	<i>Oreamnos americanus</i>	61	0	0.0469	0.0250	0.094	0.300	75000	0.0426	0.0357	0.220	0.206	70000	Festa-Bianchet & Côté 2009; Silva & Downing 1995
Soay sheep	<i>Ovis aries</i>	69	0	0.3679	0.0023	0.385	0.035	26000	0.0786	0.0114	0.280	0.169	20000	Catchpole 1998; Weckerly 1998
Bighorn sheep	<i>Ovis canadensis</i>	67	0	0.0711	0.0206	0.257	0.181	100000	0.0467	0.0090	0.171	0.099	60000	Loison 1999; Silva & Downing 1995
Dall mountain sheep	<i>Ovis dalli</i>	56	1	0.0796	0.0025			76000	0.0973	0.0296			48000	Murie 1944; Weckerly 1998
Reindeer	<i>Rangifer tarandus</i>	36	1	0.0590	0.0423			106500	0.0590	0.0216			76000	Reimers 1983, Leader-Williams 1988; Weckerly 1998
Chamois	<i>Rupicapra rupicapra</i>	74	1	0.0459	0.0008			40000	0.0440	0.0225			33500	Bocci 2010; Silva & Downing 1995
African buffalo	<i>Syncerus caffer</i>	90	1	0.0394	0.0181			667000	0.0466	0.0140			534000	Spinage 1972, Sinclair 1977, Mertens 1985, Silva & Downing 1995
Greater kudu	<i>Tragelaphus strepsiceros</i>	5	0	0.0566	0.0360	0.280	0.299	228000	0.0361	0.0360	0.377	0.176	157000	Owen-Smith 1990; Silva & Downing 1995

## References

- Ahrestani, F.S., Iyer, S., Heitkönig, I.M.A., Prins, H.H.T., 2011. Life-history traits of gaur *Bos gaurus*: a first analysis. *Mammal. Rev.* 41, 75-84.
- Attwell, C.A.M., 1982. Population ecology of the wildebeest *Connochaetes taurinus taurinus* in Zululand, South Africa. *Afr. J. Ecol.* 20, 147-168.
- Bocci, A., Canavese, G., Lovari, S., 2010. Even mortality patterns of the two sexes in a polygynous, near-monomorphic species: is there a flaw? *J. Zool.* 280, 379-386.
- Byers, J., 1997. *American Pronghorn: Social Adaptations and the Ghosts of Predators Past*. Chicago University Press, Chicago.
- Catchpole, E.A., Morgan, B.J.T., Freeman, S.N., Albon, S.D., Coulson, T.N., 1998. An integrated analysis of Soay sheep survival data. University of Kent.
- Catchpole, E.A., Fan, Y., Morgan, B.J.T., Clutton-Brock, T.H., Coulson, T., 2004. Sexual dimorphism, survival and dispersal in red deer. *JABES* 9, 1-26.
- Ericsson, G., Wallin, K., 2001. Age-specific moose (*Alces alces*) mortality in a predatorfree environment: Evidence for senescence in females. *Ecoscience* 8, 157-163.
- FestaBianchet, M., Côté, S., 2009. Mountain goats: ecology, behavior, and conservation of an alpine ungulate. Island Press, Washington, DC.
- Gaillard, J.M., Viallefont, A., Loison, A., Festa-Bianchet, M., 2004. Assessing senescence patterns in populations of large mammals. *Anim. Biodiv. Cons.* 27, 47-58.
- Leader-Williams, N., 1988. Reindeer on South Georgia: the ecology of an introduced population. Cambridge University Press, Cambridge.
- Loison, A., Festa-Bianchet, M., Gaillard, J.M., Jorgenson, J.T., 1999. Age-specific survival in five populations of ungulates: evidence for senescence. *Ecology* 80, 2539-2554.
- Magomedov, M.R.D., Akhemedov, E.G., Nazrullaev, N.I., 2004. Demographic structure of the bezoar goat, *Capra aegagrus* (Artiodactyla), population and regularities of its development in the eastern Caucasus. *Zoologichesky zhurnal* 83, 234-240.
- McCullough, D.R., Takatsuki, S., Kaji, K., 2009. Sika deer: Biology and Management of native and introduced populations. Springer, Tokyo.
- Mertens, H., 1985. Structures de population et tables de survie des buffles, topis et cobs de Buffon au Parc National des Virunga, Zaire. *Revue d'Ecologie (Terre et Vie)* 40, 33-51.
- Murie, A., 1944. The wolves of Mount McKinley. U.S. Natl. Park Serv. Fauna Natl. Parks U.S. Fauna Ser. No. 5.
- Owen-Smith, N., 1990. Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. *J. Anim. Ecol.* 59, 893-913.
- Plard, F., Bonenfant, C., Gaillard, J.M., 2011. Revisiting the allometry of antlers among deer species: male-male sexual competition as a driver. *Oikos* 120, 601-606.
- Sayer, J.A., Van Lavieren, L.P., 1975. The ecology of the Kafue lechwe population of Zambia before the operation of hydroelectric dams of the Kafue River. *Afr. J. Ecol.* 13, 9-37.

- Silva, M.B., Downing, J.A., 1995. CRC handbook of mammalian body masses. CRC Press.
- Sinclair, A.R.E., 1977. The African buffalo: a study of resource limitation of populations. The University of Chicago Press: Chicago and London.
- Spinage, C.A., 1970. Population dynamics of the Uganda defassa waterbuck (*Kobus defassa ugandae* Neumann) in the Queen Elizabeth Park, Uganda. *J. Anim. Ecol.* 39, 51-78.
- Spinage, C.A., 1972. African ungulates life tables. *Ecology* 53, 645-652.
- Reimers, E., 1983. Mortality in Svalbard reindeer. *Holar. Ecol.* 6, 141-149.
- Taber, R.D., Dasmann, R.F., 1957. The dynamics of three natural populations of the deer *Odocoileus hemionus columbianus*. *Ecology* 38, 233-246.
- Toïgo, C., Gaillard J.M., Festa-Bianchet, M., Largo, E., Michallet, J., Maillard, D., 2007. Sex and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. *J. Anim. Ecol.* 76, 679-686.
- Weckerly, F.W., 1988. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J. Mammal.* 79, 33-52.

**Table A2:** Analysis of the influence of environment (captive versus wild), diet (percentage of grass in the diet), body mass (log-transformed), data quality (longitudinal versus cross-sectional) and sex (male versus female) on aging rate ( $n = 22$  species). We compared models based on AIC and  $w_i$  (see material and methods section).  $\Delta$ AIC is the difference of corrected Akaike's criteria between the candidate model and the best model (in bold).

Independent variables	Deviance	AIC	$\Delta$ AIC	$W_i$
species	259.6	265.1	49.0	0.00
species + environment	214.1	222.1	6.0	0.04
species + body mass	258.8	266.8	50.7	0.00
species + sex	259.2	267.2	51.1	0.00
species + diet	259.4	267.4	51.3	0.00
species + quality	259.4	267.4	51.3	0.00
species + environment * body mass	212.4	224.4	8.3	0.01
species + environment + body mass	212.8	222.8	6.7	0.03
species + environment * sex	209.5	221.5	5.4	0.05
species + environment + sex	213.5	223.5	7.4	0.02
<b>species + environment * diet</b>	<b>204.1</b>	<b>216.1</b>	<b>0.0</b>	<b>0.81</b>
species + environment + diet	213.8	223.8	7.7	0.02
species + environment * quality	213.8	225.8	9.7	0.01
species + environment + quality	213.9	223.9	7.8	0.02
species + body mass * sex	257.5	269.5	53.4	0.00
species + body mass + sex	258.6	268.6	52.5	0.00
species + body mass * diet	258.4	270.4	54.3	0.00
species + body mass + diet	258.5	268.5	52.4	0.00
species + body mass * quality	258.7	270.7	54.6	0.00
species + body mass + quality	258.8	268.8	52.7	0.00
species + sex * diet	257.4	269.4	53.3	0.00
species + sex + diet	259.1	269.1	53.0	0.00
species + sex * quality	257.3	269.3	53.2	0.00
species + sex + quality	259.1	269.1	53.0	0.00
species + diet * quality	258.6	270.6	54.5	0.00
species + diet + quality	259.1	269.1	53.0	0.00

**Table A3:** Analysis of the influence of diet (percentage of grass in the diet), body mass (log-transformed) and data quality (longitudinal versus cross-sectional) on the difference in aging rate between wild and captive populations for females only ( $n = 22$  species). We compared models based on AIC and  $w_i$  (see methodology section).  $K$  represents the number of parameters in the model and  $\lambda$  the index of phylogenetic inertia.  $\Delta$ AIC is the difference of corrected Akaike's criteria between the candidate model and the best model (in bold).

Independent variables	k	$\lambda$	Deviance	AIC	$\Delta$ AIC	$w_i$
Null	3	< 0.001	56.7	58.73	0.81	0.24
Body Mass	4	< 0.002	55.98	61.08	3.16	0.07
<b>Diet</b>	<b>4</b>	<b>&lt; 0.003</b>	<b>52.82</b>	<b>57.92</b>	<b>0</b>	<b>0.35</b>
Quality	4	< 0.004	56.7	61.8	3.88	0.05
Body Mass * Diet	6	< 0.005	51.74	63.16	5.24	0.03
Body Mass + Diet	5	< 0.006	52.62	60.84	2.92	0.08
Body mass * Quality	6	< 0.007	55.86	67.27	9.35	0.00
Body mass + Quality	5	< 0.008	55.98	64.21	6.29	0.02
Diet * Quality	6	< 0.009	50.48	61.9	3.98	0.05
Diet + Quality	5	< 0.010	52.06	60.28	2.36	0.11

**Table A4:** Analysis of the influence of diet (percentage of grass in the diet), body mass (log-transformed) and data quality (longitudinal versus cross-sectional) on the difference in aging rate between wild and captive populations for males only ( $n = 22$  species). We compared models based on AIC and  $w_i$  (see methodology section).  $K$  represents the number of parameters in the model and  $\lambda$  the index of phylogenetic inertia.  $\Delta AIC$  is the difference of corrected Akaike's criteria between the candidate model and the best model (in bold).

Independent variables	k	$\lambda$	Deviance	AIC	$\Delta AIC$	$w_i$
Null	3	0.08	78.02	80.05	6.31	0.02
Body Mass	4	0.10	75.3	80.39	6.65	0.02
Diet	4	< 0.001	71.98	77.09	3.35	0.08
Quality	4	0.08	77.98	83.09	9.35	0.00
Body Mass * Diet	6	< 0.001	62.48	73.89	0.15	0.40
<b>Body Mass + Diet</b>	<b>5</b>	<b>0.08</b>	<b>65.54</b>	<b>73.77</b>	<b>0.00</b>	<b>0.43</b>
Body mass * Quality	6	< 0.001	74.82	86.23	12.49	0.00
Body mass + Quality	5	< 0.001	71.18	79.42	5.68	0.03
Diet * Quality	6	< 0.001	71.14	82.55	8.81	0.01
Diet + Quality	5	< 0.001	71.20	79.42	5.68	0.03



**Table A5:** Analysis of the influence of environment (captive versus wild), diet (percentage of grass in the diet), body mass (log-transformed), data quality (longitudinal versus cross-sectional) and sex (male versus female) on aging rate ( $n = 21$  species). Compared to Table S2, we excluded male *Ovis aries* from these models due to their particularly high aging rate. We compared models based on AIC and  $w_i$  (see methodology section).  $\Delta$ AIC is the difference of corrected Akaike's criteria between the candidate model and the best model (in bold).

Independent variables	Deviance	AIC	$\Delta$ AIC	$W_i$
species	243.6	249.6	46.9	0.00
species + environment	200	208	5.3	0.05
species + body mass	242.7	250.7	48	0.00
species + sex	243.2	251.2	48.5	0.00
species + diet	243.4	251.4	48.7	0.00
species + quality	243.4	251.4	48.7	0.00
species + environment * body mass	198.6	210.6	7.9	0.01
species + environment + body mass	198.6	208.6	5.9	0.04
species + environment * sex	196.9	208.9	6.2	0.03
species + environment + sex	199.4	209.4	6.7	0.03
<b>species + environment * diet</b>	<b>190.7</b>	<b>202.7</b>	<b>0</b>	<b>0.77</b>
species + environment + diet	199.8	209.8	7.1	0.02
species + environment * quality	199.2	211.2	8.5	0.01
species + environment + quality	199.8	209.8	7.1	0.02
species + body mass * sex	241.2	253.2	50.5	0.00
species + body mass + sex	242.5	252.5	49.8	0.00
species + body mass * diet	242.3	254.3	51.6	0.00
species + body mass + diet	242.3	252.3	49.6	0.00
species + body mass * quality	242.6	254.6	51.9	0.00
species + body mass + quality	242.6	252.6	49.9	0.00
species + sex * diet	241.1	253.1	50.4	0.00
species + sex + diet	243	253	50.3	0.00
species + sex * quality	240.9	252.9	50.2	0.00
species + sex + quality	243	253	50.3	0.00
species + diet * quality	242.4	254.4	51.7	0.00
species + diet + quality	243.1	253.1	50.4	0.00

**Table A6:** Analysis of the influence of environment (captive versus wild), diet (percentage of grass in the diet), body mass (log-transformed), and sex (male versus female) on aging rate estimated from Gompertz model ( $n = 7$  species). We compared models based on AIC and  $w_i$  (see methodology section).  $\Delta$ AIC is the difference of corrected Akaike's criteria between the candidate model and the best model (in bold).

Independent variables	Deviance	AIC	$\Delta$ AIC	$w_i$
species	103.7	109.7	17.3	0.00
species + environment	90.41	98.41	6.0	0.05
species + body mass	103.3	111.3	18.9	0.00
species + sex	100.8	108.8	16.4	0.00
species + diet	103.3	111.3	18.9	0.00
species + environment * body mass	89.68	101.7	9.3	0.01
<b>species + environment * sex</b>	<b>80.37</b>	<b>92.37</b>	<b>0.0</b>	<b>0.93</b>
species + environment * diet	88.03	100	7.6	0.02
species + body mass * sex	100.7	112.7	20.3	0.00
species + body mass * diet	101.6	113.6	21.2	0.00
species + sex * diet	100.3	112.3	19.9	0.00

**Table A7:** Analysis of the influence of diet (percentage of grass in the diet) and body mass (log-transformed) on the difference in aging rate estimated from Gompertz model between wild and captive populations for males only ( $n = 7$  species). We compared models based on AIC and  $w_i$  (see methodology section).  $K$  represents the number of parameters in the model and  $\lambda$  the index of phylogenetic inertia.  $\Delta AIC$  is the difference of corrected Akaike's criteria between the candidate model and the best model (in bold).

Independent variables	k	$\lambda$	Deviance	AIC	$\Delta AIC$	$W_i$
<b>Null</b>	<b>3.00</b>	<b>&lt;0.001</b>	<b>21.22</b>	<b>24.10</b>	<b>0.00</b>	<b>0.74</b>
Body Mass	4.00	<0.001	18.32	26.68	2.58	0.20
Diet	4.00	<0.001	21.20	29.56	5.46	0.05
Body Mass * Diet	6.00	<0.001	15.84	48.78	24.68	0.00
Body Mass + Diet	5.00	<0.001	18.24	35.17	11.07	0.00

**Table A8:** Analysis of the influence of diet (percentage of grass in the diet) and body mass (log-transformed) on the difference in aging rate estimated from Gompertz model between wild and captive populations for females only ( $n = 7$  species). We compared models based on AIC and  $w_i$  (see methodology section).  $K$  represents the number of parameters in the model and  $\lambda$  the index of phylogenetic inertia.  $\Delta AIC$  is the difference of corrected Akaike's criteria between the candidate model and the best model (in bold).

Independent variables	$k$	$\lambda$	Deviance	AIC	$\Delta AIC$	$W_i$
<b>Null</b>	<b>3</b>	<b>&lt;0.001</b>	<b>5.38</b>	<b>8.26</b>	<b>0.00</b>	<b>0.83</b>
Body Mass	4	<0.001	3.79	12.15	3.89	0.12
Diet	4	<0.001	5.38	13.74	5.48	0.05
Body Mass * Diet	6	<0.001	3.60	36.53	28.27	0.00
Body Mass + Diet	5	<0.001	3.76	20.68	12.42	0.00