

**IDEA AND  
PERSPECTIVE**

# Lifespan is unrelated to investment in reproduction in populations of mammals and birds in captivity

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## Abstract

We examined the relationship between number of offspring produced to a certain age and subsequent longevity in captive zoo populations of 18 species of mammal and 12 species of bird. The age cut-offs in each analysis were set to include 50%, 75% and 90% of the offspring produced in each of the population samples. Only one of 68 regressions was significant, and its slope was positive. In addition, we examined the relationship between age at first reproduction up to a certain age and longevity after that age, generally 5 years (3–8), among 17 species of mammal and 12 species of bird. Only one of these regressions had a significantly positive slope, indicating that early reproduction rarely reduces lifespan. Overall, we found no evidence that producing offspring in a zoo environment influences the age at death. Thus, although trade-offs might apply in natural populations under resource limitation, neither pregnancy, growth of the foetus and lactation in mammals, nor egg production in birds, reduces lifespan in the absence of such stress. If genetically based or other intrinsic antagonistic pleiotropy underlies the evolution of senescence, it was not evident in our analyses.

## Keywords

Aging, antagonistic pleiotropy, disposable soma, senescence, survival, trade-off, zoo populations.

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## INTRODUCTION

The disposable soma theory of aging (Kirkwood & Holliday 1979; Kirkwood 1990) and the antagonistic pleiotropy theory of aging (Williams 1957; Rose 1991) predict that reproductive success and lifespan are constrained by physiological trade-offs that prevent both from being increased simultaneously (Reznick 1985; de Jong & van Noordwijk 1992; Harshman & Zera 2006). Such trade-offs underlie all life-history theory (Roff 1992; Stearns 1992) but have been difficult to demonstrate in the case of lifespan and number of offspring. Westendorp & Kirkwood (1998) analysed births and lifespan of British aristocracy and showed that longevity of women after 60 years of age was negatively influenced by a large number of offspring and early childbirth (Mineau *et al.* 2002; Smith *et al.* 2002). Numerous subsequent studies have found conflicting and generally weak results (Hurt *et al.* 2006). Surprisingly, many analyses revealed positive relationships between number of offspring and lifespan (Korpelainen 2000; McArdle *et al.* 2006), which likely reflect differences among individuals in overall health status (Doblhammer & Oeppen 2003).

In studies of human populations, negative impacts of childbearing on longevity appear to be most pronounced among lower income groups in which general health is poor (Lycett *et al.* 2000; Dribe 2004) or pre-industrial groups without adequate access to health care (Penn & Smith 2007). The common finding that female longevity is directly related to late births has led to the idea that long life is tied to prolonged activity of the female reproductive system (Muller *et al.* 2002), which has been confirmed experimentally in mice by transplantation of the ovaries of young females into older individuals (Cargill *et al.* 2003).

Although the concept of constraint and trade-off has shaped investigations of reproductive success and mortality in natural populations for decades (Reznick 1985; de Jong & van Noordwijk 1992; Stearns 1992; Tavecchia *et al.* 2005), few studies have considered the influence of birth *per se* on long-term female condition and aging. In any non-experimental study, the relationship between number of offspring and lifespan is likely to be influenced in opposite directions by variation in the innate quality of mothers (positive) and by external stresses resulting from poor environmental conditions (negative). Thus, the consequences of producing

offspring for longevity, owing to direct physiological and genetic connections between reproductive activities and aging, cannot be assessed unambiguously in most contexts. For example, in a long-term study of reindeer (*Rangifer tarandus*), Weladji *et al.* (2006) found a positive correlation in females between breeding success and longevity, suggesting that variation in overall quality of the mother influenced both reproduction and longevity in parallel. Any negative effects of birth on lifespan might have been obscured. In contrast, Nussey *et al.* (2006) recently reported that early reproduction accelerates reproductive senescence in red deer (*Cervus elaphus*).

In this study, we attempt to avoid several potentially confounding effects by examining the relationship between number of offspring and age at death in zoo populations of non-domestic mammals and birds. The advantages of captive populations for this purpose are that high-quality animal care reduces the effect of trade-offs resulting from nutritional and other external stresses and that variation in number of births is largely the result of decisions on the part of zoo personnel and is at least partly independent of individual quality. In addition, individual quality probably has reduced impact on health and survival in an environment with abundant food and high-quality care. Consequently, any relationship between number of births and lifespan should reflect direct consequences of producing offspring, including alteration of hormone profiles and intrinsic stresses of embryo development, parturition and lactation in mammals, or egg production in birds, on subsequent survival.

## MATERIALS AND METHODS

We analysed a dataset maintained by the International Species Information System (ISIS; <http://www.isis.org>), and generously provided by Dr Nate Flesness with the permission of the ISIS Board of Directors. The ISIS database contains detailed records of zoo animals that allows one to compile the reproductive history of each individual, including the number of offspring produced, the age at parity, and the age at death. However, opinions differ concerning the accuracy and utility of ISIS data (see, for example, Earnhardt *et al.* 1995a,b; Flesness *et al.* 1995). Accordingly, we performed extensive cleanup of the raw ISIS data prior to analysis. Earnhardt *et al.* (1995a) cited numerous errors with regard to parent identity (ID), which would confound analyses of parent longevity in relation to offspring production. These discrepancies (their appendix A) included the use of local zoo ID numbers, which pertains to individuals transferred between institutions, and offspring for which parents are listed as unknown (UNK).

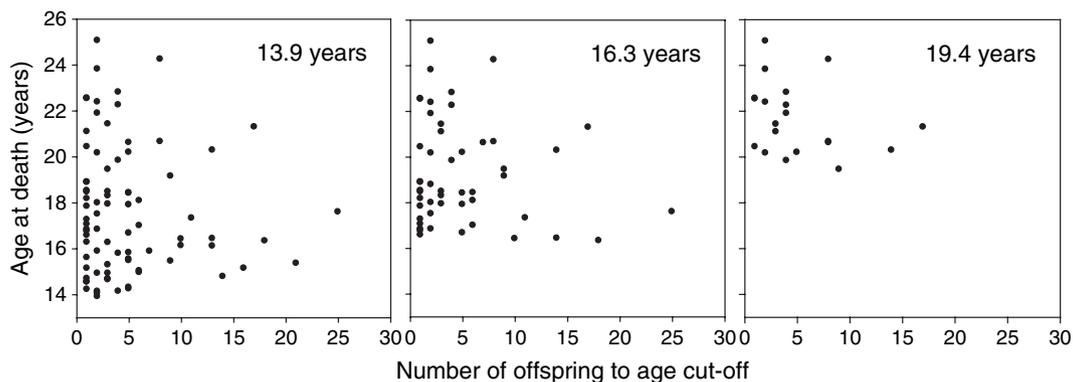
To avoid problematic data, we scanned all the birth, transfer and death records for each individual for

discrepancies in age and location. Records that could not be reconciled were deleted from analyses. With respect to zoo ID, most individuals of the species in our analysis were given permanent ID numbers that were transferred between institutions. Where these numbers changed, this could be recognized by transfer information. If the ID number could not be tracked at a new location following a transfer, we could not obtain an age at death and the record was not included in our analysis. With respect to UNK, this is a common ISIS ID for individuals of many species, particularly when individuals are captured in the wild or are maintained in groups. These individuals were not included in our analysis. Based on reproductive histories obtained from the cleaned ISIS data for species with large zoo populations, we assessed the relationship between reproduction and age of death for 18 species of mammal and 12 species of bird.

Even in zoo populations, differences in general health and mortality selection tend to produce positive relationships between number of offspring and lifespan and therefore dampen negative effects of reproduction on longevity (Doblhammer & Oeppen 2003). Furthermore, if zoo personnel selected the healthiest individuals for breeding, deleterious effects of breeding on lifespan could be obscured. Administration of birth control medications to reduce pregnancy also might influence longevity through direct endocrine effects. To minimize these statistical effects in the entire dataset, we considered the relationship between number of offspring produced up to a given arbitrary age, and the subsequent survival of mothers past that age. Although this approach does not eliminate general health effects among mothers surviving to a particular age, it restricts number of offspring to a set period of life and examines survival after that point, creating a degree of independence between the two. To determine whether these relationships might change with age, we conducted separate analyses that included individuals alive after 50%, 75%, and 90% of the offspring in the sample had been born. For each of these subsets of data, we regressed age at death on number of offspring produced up to the cut-off age using the SAS statistical procedure GLM. We also asked whether early reproduction might be particularly costly in terms of longevity by using linear regression to test the relationship of longevity past a certain age (generally 5 years, range 3–8) to the age at first parturition or egg laying up to that age. The cut-off age was chosen to provide the largest possible sample of individuals.

## RESULTS

We found no evidence that reproduction early in life influences, either positively or negatively, lifespan in zoo populations of non-domestic mammals and birds.



**Figure 1** Relationship between age at death of mothers and number of offspring produced to a particular age in zoo populations of the lion *Panthera leo*. Sample sizes are 82, 50 and 21 mothers. Only individuals producing at least one offspring are included in the dataset. The slopes of the regressions were  $-0.053$ ,  $-0.059$ , and  $-0.194$  years per offspring, respectively, but none was significant ( $P = 0.23, 0.35, 0.13$ ).

The largest dataset available was for the lion *Panthera leo*, which is shown in Fig. 1. The age of mothers at which half the offspring in the sample had been born (50% cut-off) was 13.9 years. The 75% and 90% cut-offs occurred at 16.3 and 19.4 years, respectively. Although the regressions between age at death and number of offspring were negative (Table 1), none differed significantly from a slope of 0. In addition, age at death after 5 years was unrelated to age at first reproduction up to 5 years ( $n = 81$ ,  $P = 0.66$ ).

Of 68 regressions, only the golden lion tamarin produced a significant relationship between number of offspring and age at death, and the slope of the relationship was positive (Table 1; Fig. 2). At the 50% cut-off point of 11.68 years, females that had produced greater than 15 offspring survived longer than those that had produced fewer than 15 offspring ( $P = 0.006$ ). However, at the 75% cut-off point (15.01 years), this advantage had disappeared ( $P = 0.22$ ) because the subset of low-fecundity females with earlier deaths had been removed from the sample. Few of the high-fecundity females died before reaching 15 years of age. The smaller number of offspring produced by several females with shorter lifespans might have resulted from the early termination of active reproduction by injury or disease.

Obtaining one significant result of 68 does not deviate from what one would expect by chance (type I error; binomial probability = 0.14). Indeed, the probabilities of the individual regression coefficients were nearly uniformly distributed between 0 and 1, indicating an essentially random relationship between number of offspring and age at death in the sample as a whole. Among mammals, 22 of 49 regression coefficients were negative, whereas among birds 16 of 19 coefficients were negative ( $G_{\text{adj}} = 17.6$ , d.f. = 1,  $P < 0.0001$ ). Although the number of negative regressions for mammals did not differ significantly from an even distribution ( $P = 0.28$ ), the bird data exhibited

significantly more negative values than expected by chance ( $P < 0.001$ ), even though not one individually was significant. Thus, in birds, there might be a weak tendency for egg production, incubation and chick rearing to reduce lifespan.

We also examined the relationship between number of offspring and age at death of fathers, using the same analysis approach as for females, for four species of mammal (*Panthera leo*, *Leontopithecus rosalia*, *Capra hircus*, *Canis lupus*) and two species of bird (*Leucopsar rothschildi*, *Rollulus roulroul*). None of 18 correlations was significant at the  $P < 0.05$  level. Eight of 18 correlations were negative.

With respect to the relationship between lifespan and age at first reproduction, three species of mammals of 17 exhibited significant relationships ( $0.01 < P < 0.05$ : spotted deer *Axis axis*, slope =  $2.48 \pm 0.87$ ; Common Marmoset *Callithrix jacchus*, slope =  $-0.68 \pm 0.29$ ; Golden Lion Tamarin *Leontopithecus rosalia*, slope =  $-1.16 \pm 0.54$ ), only the first of which suggested that delaying first reproduction resulted in prolonged lifespan. Ten of 17 regression slopes were positive ( $P > 0.5$ ). Among 12 species of birds, seven regression slopes were positive ( $P > 0.5$ ) and none were significant.

## DISCUSSION

Our analyses failed to reveal a significant relationship between number of offspring produced up to a given age and subsequent survival in either birds or mammals. Age at first reproduction also did not appear to influence age at death. Thus, neither individual quality, which would produce a positive correlation between reproductive investment and lifespan, nor constraints imposed by limited resources, which would produce a negative relationship, appear to be operating in zoo populations. The absence of these relationships is not surprising because zoo animals are provided abundant food and excellent care, on the one

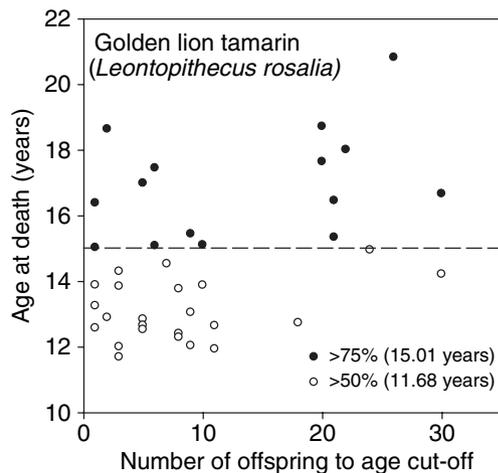
**Table 1** Regression statistics for the relationship between subsequent longevity and number of offspring produced up to a particular age corresponding to ages of mothers at the completion of 50%, 75% and 90% of the offspring in the population sample

Species	50%			75%			90%		
	d.f.	Slope	<i>P</i> -value	d.f.	Slope	<i>P</i> -value	d.f.	Slope	<i>P</i> -value
<b>Mammals</b>									
Red Kangaroo <i>Macropus rufus</i>	46	0.219	0.242	18	0.227	0.943	5	0.909	0.084
Amur Tiger <i>Panthera tigris altaica</i>	56	0.226	0.490	26	0.002	0.937	7	-0.048	0.209
Reindeer <i>Rangifer tarandus</i>	47	0.012	0.933	25	0.101	0.389	7	-0.587	0.127
Cheetah <i>Acinonyx jubatus</i>	44	0.002	0.964	24	-0.013	0.767	7	-0.067	0.206
Lion <i>Panthera leo</i>	81	-0.053	0.231	49	-0.059	0.352	20	-0.194	0.126
Patagonian Cavy <i>Dolichotis patagonum</i>	49	0.138	0.130	18	0.036	0.609	6	0.067	0.387
Golden Lion Tamarin <i>Leontopithecus rosalia</i>	37	0.115	0.006	12	0.052	0.218	-	-	-
Cotton-top Tamarin <i>Saguinus oedipus</i>	50	-0.029	0.753	27	0.029	0.821	8	0.105	0.507
Capibara <i>Hydrochaeris hydrochaeris</i>	37	0.007	0.902	18	-0.041	0.386	8	0.042	0.629
Leopard <i>Panthera pardus</i>	56	0.044	0.444	26	0.072	0.206	6	-0.238	0.569
Domestic Goat <i>Capra hircus</i>	38	-0.266	0.173	22	0.160	0.546	11	0.001	0.997
Blackbuck <i>Antelope cervicapra</i>	28	-0.148	0.431	14	0.506	0.268	5	0.131	0.645
Gray Wolf <i>Canis lupus</i>	36	-0.042	0.458	20	-0.004	0.932	-	-	-
Barbary Sheep <i>Ammotragus lervia</i>	29	-0.084	0.424	15	-0.015	0.917	5	-0.057	0.800
Spotted Deer <i>Axis axis</i>	14	-0.198	0.735	8	-1.240	0.303	-	-	-
Slender-tailed Meerkat <i>Suricatta suricatta</i>	23	0.056	0.328	11	-0.034	0.550	-	-	-
Ring-tailed Lemur <i>Lemur catta</i>	34	0.431	0.356	15	0.750	0.051	-	-	-
Common Marmoset <i>Callithrix jacchus</i>	30	0.150	0.057	11	-0.115	0.276	5	-0.110	0.556
<b>Birds</b>									
Bali Myna <i>Leucopsar rothschildi</i>	42	-0.019	0.665	23	-0.047	0.316	9	-0.091	0.188
Jackass Penguin <i>Spheniscus demersus</i>	22	-0.029	0.791	13	-0.053	0.520	-	-	-
Crested Wood Partridge <i>Rollulus roulroul</i>	25	-0.003	0.924	12	-0.019	0.509	7	0.103	0.207
Golden Pheasant <i>Chrysolophus pictus</i>	20	-0.004	0.791	8	-0.007	0.315	-	-	-
North American Wood Duck <i>Aix sponsa</i>	6	-0.014	0.981	-	-	-	-	-	-
Hooded Merganser <i>Mergus cucullatus</i>	6	-0.085	0.287	-	-	-	-	-	-
Ostrich <i>Struthio camelus</i>	9	-0.038	0.901	-	-	-	-	-	-
Mandarin Duck <i>Aix galericulata</i>	12	-0.131	0.199	11	-0.079	0.375	-	-	-
Gouldian Finch <i>Chloebia gouldiae</i>	12	-0.014	0.592	-	-	-	-	-	-
Scarlet Ibis <i>Eudocimus ruber</i>	11	-0.428	0.698	-	-	-	-	-	-
Humboldt Penguin <i>Spheniscus humboldti</i>	15	0.112	0.516	-	-	-	-	-	-
Superb Starling <i>Lamprolornis superbus</i>	12	0.011	0.699	-	-	-	-	-	-

hand, and reproduction is controlled by zoo personnel at least in part independently of individual quality, on the other hand. Abundant food and excellent care should reduce the effect of differences in individual quality on survival and reproduction, which likely appear primarily under stressful conditions when low-quality individuals would perform poorly in all respects. Favourable zoo conditions are also likely to reduce any negative consequences for the stress of reproduction on longevity.

Other attributes of zoo populations might influence analyses of the kind presented in this study. For example, variation in animal husbandry between institutions might create variation in individual quality that would obscure a negative relationship of longevity with reproductive output, which would appear as a statistical interaction between institution and number of offspring influencing longevity.

Unfortunately, the ISIS dataset includes too few individuals per zoo for a meaningful analysis. Captivity imposes unique stresses on animals (Terio *et al.* 2004) that might influence both reproduction and survival, but also cannot be sorted out in our analyses. In addition, because of the small number of individuals held in captivity, inbreeding leading to genetic differences between zoological institutions, and the exposure of deleterious genetic variation within institutions is a concern (Frankham 2005). However, zoological institutions have made substantial efforts to reduce inbreeding through genealogical analyses and exchanges of captive animals between zoos for breeding purposes. We do not believe that this is a critical problem. Several of the species, such as the Amur tiger, cheetah, golden lion tamarin and Bali myna, are endangered in the wild and are highly managed in zoological institutions. This might create variation in reproductive



**Figure 2** Relationship between age at death and number of offspring produced to the 50% age cut-off among female golden lion tamarins. Females that reached the 75% age cut-off are represented by filled circles; although several of these females produced additional offspring, the relationship between offspring number and age at death did not change substantially.

schedules that could skew our results. While it would be difficult to address all the species-specific nuances of the care and management of captive populations, we are impressed that none of the species exhibits a negative relationship between longevity and reproduction.

While we acknowledge that many uncontrolled factors can influence reproduction and longevity in captive populations, the failure to find a relationship between number of offspring and longevity nonetheless suggests that the act of reproduction itself does not influence the probability of death or aging through direct physiological links (Harshman & Zera 2006). Our results also fail to support a direct genetic connection between fecundity and lifespan. Thus, if the production of offspring reduced lifespan in nature (Reid *et al.* 2003), this constraint would have to occur through stresses and risks imposed on short-term survival by limited resources, and through physiological effects of such stresses on the rate of aging, to affect potential long-term survival. Negative correlations between reproduction and longevity in human populations living in relatively benign environments (Westendorp & Kirkwood 1998; Smith *et al.* 2002) suggest that long-term effects of reproduction are possible, although none were detected in this study. Other analyses of human data emphasize that negative correlations between number of offspring and longevity only appear in segments of the population that are under nutritional or other stresses associated with low economic status (Lycett *et al.* 2000; Dribe 2004). It seems clear, however, that under favourable conditions, reproduction itself does not shorten lifespan through intrinsic constraints or trade-offs independent of external conditions of the environment.

If genetically based antagonistic pleiotropy – between number of offspring or age at first reproduction and lifespan – underlies the evolution of senescence (Rose 1991), as suggested by analyses of one species in nature by Charmanier *et al.* (2006), it is not evident in our analyses. Our results also provide no evidence that hormonal changes and intrinsic physiological stresses associated with allocation of resources to reproduction (Ricklefs & Wikelski 2002; Harshman & Zera 2006) influence aging and longevity. The disposable soma theory of aging postulates constitutive mechanisms of damage prevention or repair that would not be detected by an analysis such as ours. Nonetheless, the analysis of reproductive output and age at death in captive populations and zoos allows us to reject intrinsic trade-offs connecting reproduction and death as important constraints on the life histories of mammals and birds. That is, nothing inherent to producing offspring *per se* appears to reduce longevity. Accordingly, trade-offs observed in nature would arise through the interaction of individuals with their environments under conditions of limited resource availability.

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## COMMENTARY ON RICKLEFS & CADENA (2007): REPRODUCTIVE INVESTMENT AND LIFESPAN

Ricklefs & Cadena (2007) conclude that their analyses of 30 zoo populations allow them to 'reject intrinsic trade-offs connecting reproduction and death as important constraints on the life histories of mammals and birds'. While we agree that trade-offs might not be expected in benign environments such as zoos, we remain unconvinced that their analysis of phenotypic data shows that there are no intrinsic trade-offs constraining life-history evolution within or among species. Several confounding factors have not been adequately addressed in their analyses.

1. As discussed by Ricklefs & Cadena (2007), great care is needed when using zoo breeding data for life-history analyses. ISIS data are compiled from submissions from zoos and inevitably contain errors and omissions, such as missing records for births and deaths, and for animals lost to audit as they move between institutions. Researchers would be expected to clean up ISIS data prior to analysis to remove these errors as far as possible (Earnhardt *et al.* 1995; Flesness *et al.* 1995; Kalinowski & Hedrick 2001). This should entail cross-checking to individual zoo records rather than just internal checking of the database, because of the likelihood that some birth and death records are