



## Longevity in cheetahs: the key to success?

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An understanding of the factors governing reproductive success has fundamental implications for population demography, conservation, selection and adaptation. Although a consistent positive correlation between lifetime reproductive success and longevity has been reported for many iteroparous organisms, few studies have explored how longevity influences annual individual performance. In this study we show (1) that longevity and lifetime reproductive success are positively but not linearly correlated, (2) that short-lived individuals have higher annual reproductive success, (3) that the generally lower success of the last breeding occasion increased with females' longevity, and (4) that long-lived females have higher chances of rearing long-lived females. We suggest that experience and the increase in the number of reproductive events with longevity are key processes leading to a strong correlation between (1) lifetime reproductive success and longevity and (2) mother and daughter longevities. Our results demonstrate the importance of long term studies that follow multiple generations in gaining a full understanding of the factors affecting reproductive success.

Understanding how and why reproductive success varies between individuals, including how much different components of breeding success contribute to the variance in reproductive success, and identifying phenotypic, environmental, developmental or genetic factors affecting reproductive success has been a common focus of ecological research over the last decades. Such an understanding has implications for population demography and conservation (Begon et al. 1996), selection (Stearns 1992) and adaptation (Williams 1966).

In the last two decades, considerable information has accumulated on the various factors affecting annual reproductive success and lifetime reproductive success in mammals (Boyce and Boyce 1988, Clutton-Brock et al. 1988, Smith and MacDougal 1991, Ribble 1992, Konig 1994, Wauters et al. 1994): age (Le Boeuf and Reiter 1988), environmental conditions (Packer et al. 1988), density (Clutton-Brock et al. 1988), predation avoidance (Durant 2000a), and mother quality as indexed by rank (Dunbar 1980, Malcolm and Marten 1982, Packard et al. 1983, Holekamp et al. 1996), body mass (Festa-Bianchet et al. 1998) or longevity (Weladji

et al. 2006) have all been reported to affect annual reproductive success. Predation risk during life (Kjellander et al. 2004) and mother quality as indexed by body mass (Newton 1989, Festa-Bianchet et al. 2000), rank (White 2005) or longevity (Berube et al. 1999) have also been reported to affect lifetime reproductive success.

Weladji et al. (2006) recently reported that a consistently reported positive effect of longevity on lifetime reproductive success (Clutton-Brock 1988, Newton 1989, Stearns 1992, Korpelainen 2000, Thomas et al. 2000) could be accounted for by processes other than just a positive association between longevity and the mother quality. In fact, three different, non exclusive, processes can be involved—the correlation between longevity and time, i.e. the number of possible breeding attempts (1), the correlation between longevity and experience (2), and the correlation between longevity and the intrinsic quality of the individual (3). Weladji et al. (2006) assessed empirically the relative influence of these processes – time, experience; and quality – on the relationship between longevity and lifetime reproductive success and showed

that all three played a role in the positive relationship between longevity and lifetime reproductive success in semi-domesticated reindeer *Rangifer tarandus*. More specifically, they demonstrated a positive effect of age on reproductive success, and showed that long-lived individuals had higher reproductive success at all ages, especially during the last breeding attempt.

To our knowledge, however, this type of approach (i.e. disentangling the effects of experience, time and quality on the relationship between longevity and lifetime reproductive success) has not been undertaken on other large mammals. Moreover, there is still less information on whether the relationships between lifetime reproductive success and longevity are passed down through generations: if longevity exhibits such a correlation with lifetime performance, there is strong potential for natural selection to act on differences in individual quality through the inheritance of genetic factors that affect lifespan (Edney and Gilt 1968). This neglect is understandable, since assessing reproductive success over the lifetime of large mammals requires a long term investment in monitoring individuals over their lifespan, and there are few such studies in existence. Still fewer are able to track individuals through multiple generations. What studies exist often focus on confined populations not exposed to a full suite of ecological and environmental effects which exert impacts on reproductive success and survival in free ranging populations. In particular, predation, neglected from such studies, is likely to play a critical role in its impacts on reproductive success that is quantitatively and qualitatively different to the role of other impacts such as foraging success and maternal dominance. Whether Weladji's demonstrated relationship between longevity and reproductive success holds for freely foraging, predated populations has therefore never been tested.

Cheetah *Acinonyx jubatus* in the Serengeti plains represent an ideal opportunity to explore such issues in carnivores – a taxon where few data on lifetime reproductive success and its determinants are available—since the population has now been monitored for over 30 years (Caro 1994) and much information has been gathered on individual reproductive success, lifetime reproductive success and genetic links among individuals.

Like many other organisms, age has been demonstrated to affect annual reproductive success in cheetahs: it was previously demonstrated that as age increases, reproductive success increases, reaching a peak at 6–7 years and then declining into later years (Kelly et al. 1998, Durant et al. 2004). Longevity was not previously reported to affect annual reproductive success in terms of number of cubs or litters raised to independence (Kelly et al. 1998). Those results seem to indicate that, contrary to results gathered on reindeer, only

experience (indexed by age) and the increase of breeding opportunities with time influence the positive relationship between longevity and lifetime reproductive success in this species, and not individual intrinsic quality. However, these studies did not take into account the outcome of the last reproductive event which can make a substantial contribution to lifetime reproductive success. In reindeer, long-lived females had higher average annual success than short-lived ones at a given age, but the difference between females increased during the last reproductive event (Weladji et al. 2006).

We aim here (1) to examine the importance of mother quality in determining reproductive success in cheetahs. We proceeded in two steps: (1) we re-evaluated the relationship between lifetime reproductive success and longevity, (2) we investigated whether annual reproductive success varied according to individual intrinsic quality, as indexed by longevity (Descamps et al. 2006, Weladji et al. 2006). We also included the last reproductive event as a possible factor affecting annual reproductive success. We finally explored (2) whether long-lived females produce long-lived daughters.

## Material and methods

### Study area and data

Cheetah of the south eastern plains of the Serengeti National Park, Tanzania, have been studied nearly continuously since 1974 (Caro 1994), and the entire population systematically tracked since 1982, after which the population fluctuated between 50 and 80 adult cheetah. Cheetah in the study area are located by eye by scanning through binoculars from high vantage points. Once located, they are approached slowly, and individually identified according to unique spot patterns on their pelage (Caro and Durant 1991), and details about their location, reproductive status and the presence and identification of dependent cubs are recorded (Durant et al. 2004). In this manner the history of individual cheetah are tracked through their lifetimes.

We restricted our analysis to females of known age, i.e. those who were monitored since they were cubs. Females' annual reproductive success ( $n = 444$  for 99 females) was assessed by the number of cubs reaching a year (Durant et al. 2004), since independence does not occur before this time and because most juvenile mortality occurs before one year (Laurenson 1994). Cheetahs do not reproduce seasonally and can breed all year long, and early litter losses are rarely detected. Failure to produce cubs that reach one year of age (annual reproductive success = 0) could then be linked

to (1) not having produced cubs or (2) having produced cubs that died.

Because cheetah are located by sight, intervals between sightings are unpredictable. Hence to reduce the probability that cubs are deemed to have not survived to a year, when in fact they may have survived but are simply not seen, we neglected litters from the analysis if the mother was not resighted within 10 months of the first sighting. We neglected adopted cubs from all analyses.

This individual variation in sighting intervals, as well as the fact that litters are generally not observable before cubs start to leave the lair (around 3 months of age), present challenges in the identification of the the last reproductive event for cheetahs. We defined the last reproductive event as the reproductive event occurring during the year when the female was last seen. The last reproductive event was included as a binomial fixed factor (0/1) in our analysis.

Longevity was assessed following the methods described by Durant et al. (2004). Lifetime reproductive success is always more difficult to assess than annual reproductive success, since regular yearly sightings of known age females are required. We were able to assess lifetime reproductive success for 57 females, whose longevity spanned from 3.5 to over 14 years. Eighty-nine sets, where the longevity of both the mother (38 different females, with an average of  $2.34 \pm 1.17$  cubs per mother) and the daughter were known, were also available. Since juvenile mortality is high, only females reaching at least two years were considered.

Age was used as a proxy of experience. The number of reproductive events undertaken by each female could also be used as a proxy of experience. Since cheetahs reproduce all year round and since early litter losses are rarely detected, we could not however access this information.

Rainfall was previously reported to affect annual reproductive success (Durant et al. 2004). Annual rainfall from monthly records (1980–1999) was obtained from a rain gauge at the Serengeti Wildlife Research Center, near Seronera (station 35, mean, range). Estimates from missing months were calculated using the mean for that month over the years where data were available.

## Statistical analyses

The relationship between lifetime reproductive success (log-transformed) and longevity was assessed using linear modelling. Initial use of additive models (Pinheiro and Bates 2000) with smoothing splines was made to explore possible non-linear relationships. Polynomials were chosen for modelling non-linear relationships.

The relationship between annual reproductive success and female age, longevity and last reproductive event was assessed using generalized linear mixed models, with annual reproductive success expected to follow a Poisson distribution and female individual identity as a random factor. Polynomials were chosen for modelling non-linear relationships, such as the previously described relationship between age and annual reproductive success. Annual rainfall was previously described as affecting annual reproductive success (Durant et al. 2004) and was accounted for in the analysis.

Finally, the link between the longevity of the mother and the longevity of the daughter was assessed using linear mixed models controlling for the identity of the mother.

All statistical analyses were performed in the statistical package R ([www.r-project.org](http://www.r-project.org)).

## Results

Lifetime reproductive success increased non linearly with longevity: the best model involved a second order polynomial relationship between success and longevity (longevity: L.S. means =  $2.12 \pm 0.24$ ,  $T = 8.87$ ,  $p < 0.001$ ; longevity<sup>2</sup>: L.S. means =  $-0.58 \pm 0.24$ ,  $T = -2.42$ ,  $p = 0.02$ ; Fig. 1), resulting in an increase in lifetime reproductive success up until 11 years of longevity, and then levelling off up to 14 years (the oldest age recorded in this study).

As previously reported, rainfall and age influenced annual reproductive success. Annual reproductive success increased with age until seven years of age, and then decreased with female's age (Appendix 1). Annual reproductive success decreased with female longevity (Table 1). Reproductive success during the last reproductive event before death was generally lower than during other reproductive events, but increased with the longevity of the females (Table 1, Fig. 2).

Finally the longevity of the daughter was finally significantly positively correlated with the longevity of the mother (slope =  $0.39 \pm 0.14$ ,  $t = 2.73$ ,  $p = 0.01$ ; Fig. 3).

## Discussion

From this study we show (1) that lifetime reproductive success is positively but non linearly linked to longevity in cheetahs, (2) that long-lived females have lower annual reproductive success than short-lived ones, (3) that the success of the terminal-breeding occasion in cheetahs is lower than the reproductive success of previous years, but increased with the longevity of the

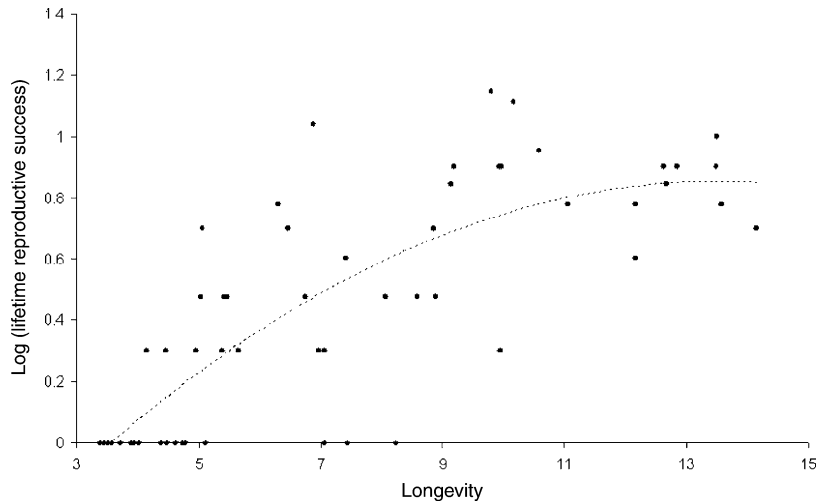


Fig. 1. Relationship between lifetime reproductive success (number of cubs produced reaching a year) and longevity (in years) in cheetahs. Lifetime reproductive success was assessed for 57 females, whose longevity spanned from 3.5 to over 14 years.

female, and (4) that mother and daughter longevitys are positively correlated.

As in most previous studies of the relationship between reproductive success and longevity (Stearns 1992, Berube et al. 1999, Korpelainen 2000, Thomas et al. 2000, Kjellander et al. 2004, Descamps et al. 2006), cheetah females that live the longest enjoyed the highest lifetime reproductive success. However, we report a positive but non-linear relationship between lifetime reproductive success and longevity in this species. A non-linear relationship between individual fitness and longevity was also reported for reindeer (Weladji et al. 2006). Such a non linear relationship could be accounted by senescence (Gaillard et al. 2004), a process already suggested for cheetahs: annual reproductive success indeed decreases with advanced age in this species (Durant et al. 2004, Appendix 1), following a similar pattern to that reported for many long-lived vertebrates (Pianka and Parker 1975, Clutton-Brock 1984, Packer et al. 1988). Such a decrease could explain why lifetime reproductive success seems to level off with longevity.

Contrary to previous results on cheetah, we also report an effect of longevity on reproductive success, and interestingly, the main effect of longevity on annual reproductive success is negative, suggesting that the annual reproductive success of long-lived individuals is lower than the reproductive success of short-lived ones. Such results were previously reported by Descamps et al. (2006) on red squirrels *Tamiasciurus hudsonicus*: in this species, lifetime reproductive success was also positively correlated with longevity, but short-lived individuals bred earlier and had higher number of juveniles weaned per breeding attempts. In this species, high quality individuals accessing high lifetime reproductive success were therefore not the ones that had high annual reproductive success, but the ones that lived long enough to access a higher number of reproductive opportunities. The same conclusion might apply for cheetahs, since, for this species also, long-lived individuals have lower annual reproductive success.

“Good reproducers” thus seem to die young in this species. This might be explained by the existence of annual tradeoffs between reproduction and survival, as

Table 1. Relationship between annual reproductive success (indexed as the annual number of cubs reaching a year), rainfall (in mm), the last reproductive event and longevity (in years). The identity of the mother was controlled for (generalized linear mixed model).

Parameters	L.S. means	SE	T	p
Intercept	1.56	0.57	2.75	0.006
Age	3.49	2.67	1.31	0.19
Age <sup>2</sup>	-9.55	2.06	-4.64	<0.001
Age <sup>3</sup>	4.99	1.83	2.72	0.006
Annual rainfall	-0.002	0.0005	-3.32	0.0009
Longevity	-0.08	0.04	-2.34	0.02
Last reproduction	-3.86	1.12	-3.46	0.0005
Last reproduction: longevity	0.33	0.11	2.90	0.004

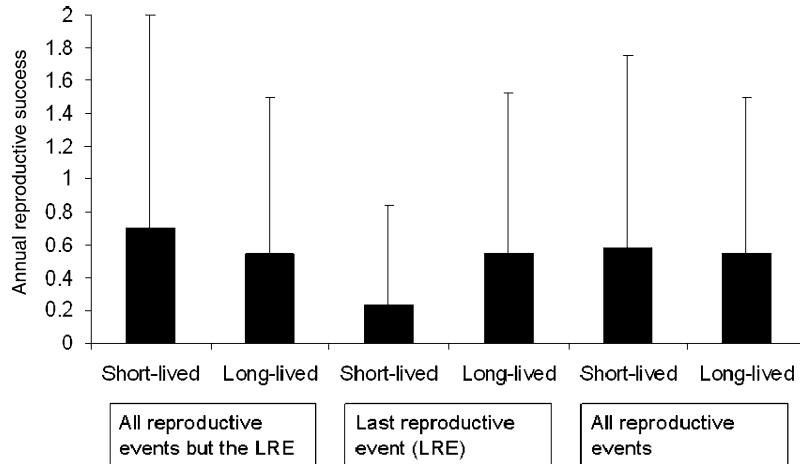


Fig. 2. Average annual reproductive success (with standard errors) during all the reproductive events but the last one, during the last reproductive event, and during all the reproductive events. The median longevity in our dataset was 10.18 years. All animals with a longevity below that threshold were considered as short-lived animals.

recently suggested in the context of senescence in red deer *Cervus elaphus* (Nussey et al. 2006). Selective disappearance (van de Pol and Verhulst 2006) of good quality phenotypes might indeed happen, such that the oldest age classes have a higher proportion of poorer quality individuals (if annual reproductive success is used as a proxy of individual quality). This mechanism could then also explain our Fig. 1: if long-lived individuals are of poorer quality, then lifetime reproductive success will tail off beyond a certain age. This is a distinct hypothesis from the within-individual senescence previously mentioned, since individual females

may not need to show any decline in annual reproductive success with age (no senescence involved).

The success of the terminal breeding occasion was dependent on longevity in this species. While short-lived females generally experienced a strong decrease in reproductive success during their last attempt, long-lived females were able to maintain a similar level of success. The interaction between longevity and the last reproductive event could be the result of a tradeoff between early and late reproduction, so that females with high output early on both die younger and have reduced success in the last year. This hypothesis is

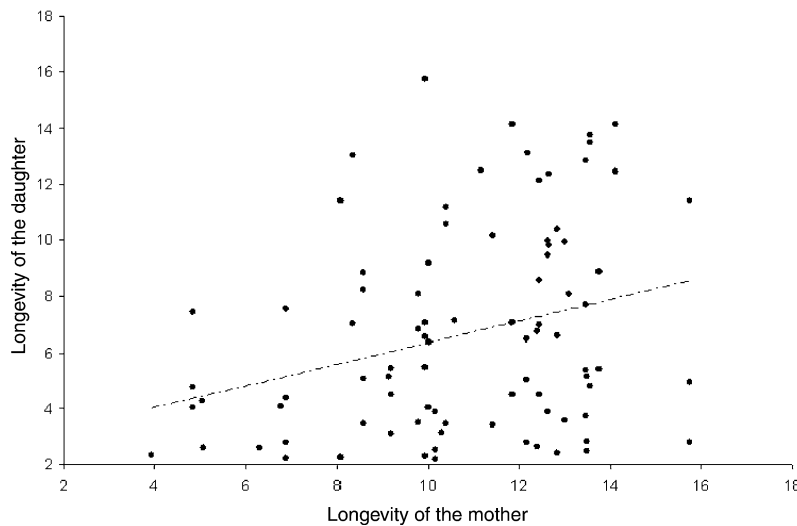


Fig. 3. Relationship between longevity of the mother (in years) and longevity of the daughter in cheetahs (in years). Eighty-nine sets, where the longevity of both the mother (38 different females, with an average of  $2.34 \pm 1.17$  cubs per mother) and the daughter were known, were used to generate this figure.

supported by the fact that short-lived females reached higher average annual reproductive success prior to their last reproductive event. However, this result could also be accounted for by a correlation between high average annual reproductive success and risk taken by the mothers, so that “good” reproducers are more likely to take risks and die dramatically due to accidents whilst catching prey or predation whereas “less risky” females are more likely to live longer and die slowly due to decreasing condition, such as might happen due to tooth loss or some pathogens. In that case, the sudden disappearance of the “risky” females would directly lead to the whole litter loss, while the slow decreasing condition of the “less risky” females would allow them to raise their cubs before dying.

A low percentage (7.6%) of the variation in the annual reproductive success in cheetahs is actually explained by our model. Cheetah show particularly high levels of juvenile mortality, with only 5% of cubs born reaching independence (Laurenson 1994). Under four months, cubs are particularly susceptible to predation since they are not fast enough to outrun all predators. Lions *Panthera leo* are the primary predators of cubs in the lair, while spotted hyenas *Crocuta crocuta* and lions appear to kill emergent cubs in equal proportions (Laurenson 1994). Another cause of death in the lair was due to the abandonment of lairs by mothers, due to a paucity of prey close to the lair, a common factor in migratory systems such as the Serengeti. Considering the low percentage of variance explained by our model, we can hypothesize that local environmental variables such as abundance of predators or prey around the lair at the time of denning might have strong impacts on the percentage of variance explained in annual reproductive success. Local predator abundance might have similar impacts for the first two months after emergence. However, it would be impossible to collect data at this level for this species, and hence no such data were available for analysis here.

Traits other than longevity have been proposed to index mother quality: body mass (Ribble 1992, Berube et al. 1999), age at first reproduction (Kruuk et al. 2000), or social rank (White 2005) have all been suggested as proxies for phenotypic quality and have been shown to influence lifetime reproductive success. However, in many cases those traits correlate with longevity (Wauters and Dhondt 1989, Berube et al. 1999), so that, although they correlate with lifetime reproductive success, they sometimes do not influence the annual reproductive outcome when longevity is taken into account (Gaillard et al. 2000 for body mass). In rodents for example, heavy females have been reported to produce more offspring than light females, but this was primarily due to their greater longevity (with body mass influencing survival and thus longevity; Ribble 1992). In bighorn *Ovis canadensis* ewes,

body mass was associated with longevity, better survival of old ewes and lower fitness costs of reproduction (Festa-Bianchet et al. 1997, 1998). As pointed out by Weladji et al. (2006), longevity is one component within a whole set of factors that shape among-individual differences in performance.

This study thus pinpoints longevity as playing an important role in determining lifetime performance in cheetahs. Our results show moreover that this trait is also influenced by the mother’s identity. Once a female reaches independence, the life expectancy of a daughter is positively linked to the longevity of its mother. Similar results have previously been reported for red deer where the identity of the mother has been reported to impact total fitness, longevity, birth weight and breeding success (Kruuk et al. 2000), however this is the first report of such results in a large carnivore exposed to predation. Various mechanisms might explain this positive correlation: long-lived mothers might, for example, be females that have learned to avoid predators (Durant 2000b), that inhabit a certain type of habitat, that have better foraging abilities, or that are more efficient at ensuring those skills are passed on to their offspring.

However, only 8% of the variability in daughters’ longevities is explained by the mother’s longevity. Moreover, there is an evident difference in mothers’ and daughters’ distribution of longevities: while more than 50% of the mothers live longer than eight years of age, more than 50% of the daughters die before this age. It seems therefore that “being able to produce an independent female” is already linked to longevity. The positive correlation we observed might thus simply reflect the fact that the longer a female lives, the higher number of independent females she produces, the higher chances she has to produce a long-lived female.

Our results, together with those of Weladji et al. (2006) and Kruuk et al. (2000), demonstrate the importance of long term studies for a full understanding of the factors affecting lifetime reproductive success. In particular, the study reinforces the significance of the last breeding attempt in its contribution to the reproductive success of individuals, since it demonstrates its importance in two fundamentally different species such as cheetah and reindeer which survive in very different ecosystems and environments – tropical and temperate. A reduced success in the terminal-breeding occasion than during previous years has been previously reported in birds (Rattiste 2004) and ungulates (Weladji et al. 2006) and interpreted as disease-related or condition-related problem. Long-lived large mammals generally have few opportunities to produce independent offspring due to a prolonged period of dependence on the mother by surviving cubs. Cheetah cubs are generally dependent on their mother for 18 months. As cheetah females begin to breed at two

years and can continue to reproduce until 12 years (no female older than 12 has ever been recorded to breed in the wild), this means they can produce a maximum of seven litters in their lifetime, making the last breeding attempt likely to provide a minimum contribution of 14% to lifetime reproductive success in even the most reproductively active and long lived females. In our dataset on annual reproductive success, average longevity was  $7.47 \pm 3.20$  years, making the last breeding attempt likely to provide a minimum contribution of 20–25% (1/4) to lifetime reproductive success. In most situations the last breeding attempt makes an even larger contribution. Given such effects can not be picked up by any study of less than the maximum lifespan of the species, then the role of longevity in reproductive success in long lived mammals may be overlooked by any short, or even medium, term study. This could lead to fundamentally different conclusions about the relative role that experience versus quality plays in reproductive success, and hence in population dynamics, and ultimately adaptation and evolution.

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Appendix 1. Average annual reproductive success (ARS) and cheetahs' age when the annual reproductive success is estimated (in years). Since annual reproductive success is defined in this study as the number of cubs reaching a year, three year old females are in fact females which started to reproduce at two years of age.

Age	Average ARS
3	0.21
4	0.58
5	0.63
6	0.83
7	0.91
8	0.69
9	0.42
10	0.58
11	0.55
12	0.35
13	0.33
14	0.00