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Sex-specific actuarial and reproductive senescence in zoo-housed tiger (*Panthera tigris*): the importance of sub-species for conservation

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RUNING TITLE: Senescence patterns in zoo-housed tiger

RESEARCH HIGHLIGHTS

Accurate estimation of tiger demographic rates is needed to apply effective conservation plans.

Females of 7-9 years of age are crucial to consider controlling populations size.

Tiger sub-species might be considered separately for conservation goals.

ABSTRACT

A fifth of all known species are currently classified as threatened in the wild: the rate of biodiversity loss is rapid, continuous, and mostly due to anthropogenic activities. To slow down this decline, the accurate estimation of demographic parameters for threatened species is critical. With this aim, zoo institutions play an important role, giving access to data on zoo-housed animals, which aids researchers working on species life-history traits and intrinsic factors influencing the fitness of both sexes, such as age. While tigers (*Panthera tigris*) are particularly threatened in their natural environment, few of their demographic parameters have been determined because of their solitary and elusive nature as well as low population density. Using individual-based information for more than 9,200 tigers (from 1938 to 2018) recorded in the International Tiger Studbook 2018, we aimed to determine sub-species and sex-specific variability of survival and reproductive parameters with age. No significant sex-difference in actuarial senescence (i.e. decline of survival probabilities with age) was observed but males tended to have a higher juvenile mortality and a faster senescence than females. Reproductive senescence (i.e. decline of reproductive parameters with age) was more pronounced in females than males. Moreover, we observed sub-species-specific variation in mortality and reproductive patterns, pointing out the necessity to consider them independently for conservation goals. Our findings can provide meaningful improvements to the husbandry of zoo-housed tigers, emphasizing the importance of adult breeding females of 7-9 years-old to control zoo-housed population size, but also providing accurate demographic estimates, crucial to set up effective conservation plans.

Graphical Abstract

Actuarial senescence occurs in scientifically managed zoo-housed tigers of both sexes with very low adult mortality rate and a progressive increase of mortality rate after 10 years of age, leading to a longevity of 19 years. However, females only undergo reproductive senescence after 7-9 years of age. Photo credits: Alexander Sliwa.

KEYWORDS: demographic parameters; litter size; mortality rate; survival rate; tiger sub-species

INTRODUCTION

The Earth is currently facing a sharp decline of biodiversity (Hoffmann et al. 2010), and many critical decisions will have to be made to stop, or at least slow-down, this decline. With this aim, models of population dynamics and population viability analyses are critical to develop sound conservation strategies. However, these models require accurate demographic rates to provide meaningful results. For instance, the estimation of both reproduction and recruitment rates is required for population viability analysis (Smith and Mcdougal 1991; Staerk et al. 2019). These parameters are particularly necessary to quantify what human-induced mortality rates a wild population can withstand (Kenney et al. 1995; Smirnov and Miquelle 1999; Ahearn et al. 2001) to optimize human- and monetary-resources for conservation. In this respect, there is an urgent need to estimate accurate demographic parameters for threatened species. Although several long-term monitoring schemes for wild populations are now implemented (Clutton-Brock and Sheldon 2010), demographic rates are almost impossible to obtain in many threatened species, due to their elusive or solitary nature and low population densities. In particular, long-term data are missing to estimate sex- and age-specific variation in survival and reproductive parameters for long-lived species, which are especially vulnerable to extinction in the wild (Purvis et al. 2000).

Dynamics modelling and population viability analysis may be biased if we do not use demographic estimates that adequately account for factors structuring populations (e.g. Colchero et al. 2019). Age and sex are particularly important for the variation of demographic rates. Indeed, males and females may contribute differently to population dynamics (e.g. Barthold et al. 2016), such as in polygynous species where few males monopolize the access to reproductive females (e.g. in reindeer Mysterud et al. 2003). In addition, reproduction and survival (or mortality, corresponding to 1-survival probability) parameters vary with age in

most animals across the tree of life (Jones et al. 2014) showing an almost ubiquitous progressive decline of fitness at advanced age (e.g. Nussey et al. 2013; Tidière et al. 2016; Lemaître and Gaillard 2017). Actuarial and reproductive senescence patterns (i.e. progressive decline of survival or reproduction with increasing age, respectively) can be characterized by the rate of parameters declining, called the "rate of senescence". Determining senescence patterns for both sexes is fundamental to improve management of wild populations of threatened species as sex- and age-dependent patterns are expected to influence population dynamics and then probability to extinction (Robert et al. 2015).

Among the most threatened species in their natural environment, the tiger (*Panthera tigris*; Linné, 1758), considered as "endangered" by the IUCN Red List (Goodrich et al. 2015), is particularly difficult to study as a solitary, nocturnal, and elusive mammal (Sunquist and Sunquist 2002) with a wide home-range size and low-density populations (Goodrich et al. 2015). High anthropic pressure exerted on wild populations is the major threat, with key issues such as habitat destruction, the decline of prey base due to overhunting, commercial poaching (Horev et al. 2012) and overall poor tiger-human conflict management (Goodrich 2010). Numerous studies have faced the challenge of estimating hard-to-obtain tiger population parameters such as population size, density, survival and recruitment (Lynam et al. 2001; Azlan and Sharma 2003; Wan et al. 2003; Tilson et al. 2004; Bhagavatula and Singh 2006; Karanth et al. 2006; Goodrich et al. 2008; Barlow et al. 2009). However, for now, no age- and sex-dependent patterns of demographic rates are available for the wild tiger, although some demographic parameters have been obtained for the Amur sub-species (Kerley et al. 2003; Goodrich et al. 2008). Following survival and recruitment changes through time, their variability according to age and sex, and differences between the six genetically differentiated sub-species (Liu et al. 2018) will improve our understanding of the factors driving population dynamics in tigers (Williams et al. 2002). This will improve wild population dynamic models and population viability analysis, which are critical to help decision makers for conservation goals.

With abundant data available on animals living in human care, zoos and aquariums are precious allies to assist in the study of life-history traits and demographic rates for species which are difficult to access in the wild. Using the high-quality dataset of the International Tiger Studbook (Müller 2018), which compiles individual data from more than 10,000 zoo-housed pure-bred tigers from the six sub-species (current to 30th November 2018) in the last 80 years, we aimed to determine the age-dependent mortality and reproductive (litter size and cub survival) patterns of tigers living in human care, testing for a difference between sexes and sub-species. We estimate actuarial and reproductive senescence patterns as already highlighted in other zoo-housed mammalian populations (e.g. Bertschinger et al. 2008; Saunders et al. 2014; Tidière et al. 2015, 2017). Actuarial senescence has been shown to differ between sexes according to species mating system (e.g. in ungulates, Tidière et al. 2015): as a polygynous species (Horev et al. 2012), we expected that tiger males exhibit a faster actuarial senescence than females, resulting in a shorter longevity. In addition, age is a widely proposed factor to explain reproductive success variability in zoo-housed as well as free-ranging populations (Augustus et al. 2006; Hayward et al. 2014, 2015; Karniski et al. 2018; Tidière et al. 2018). Accordingly, as only females bear gestation and offspring care costs until cubs disperse (Sunquist and Sunquist 2002), we expected more marked reproductive senescence patterns for females than for males.

MATERIAL & METHODS

Study population

Data were obtained from the published International Tiger Studbook (Müller 2018), which compiles information from almost all regional studbooks for tigers around the world, including the majority of sub-specific pure-breed tigers living in human care in scientifically managed zoos worldwide from 1938 up to the 30th November 2018. Information accuracy may vary depending on the regional studbook as well as the interval of reporting information. The studbook provides individual-level information on sub-species, sex (male, female,

unknown), parental identities, date and location at birth, date and location of each inter-zoo transfer, and finally date and location at death, if the individual died before 1st January 2018. For some individuals, the monitoring was lost after a transfer: their capture-histories (i.e. their life histories) were right-censored at the given date. Hybrid individuals (i.e. individuals with parents belonging to different tiger sub-species) were excluded, as well as wild-captured individuals (due to a lack of precision in the date of birth) and individuals for which the sex and/or the year of birth were unknown. Data for a total of 9,210 tigers were analyzed (4,695 females and 4,506 males), spread over the six genetically differentiated sub-species (Liu et al. 2018) and subject to specific environmental selections (e.g. climates, habitats, prey densities): Amur tiger (*P. t. altaica*; Temminck, 1845; n=5,618 individuals), South China tiger (*P. t. amoyensis*; Hilzheimer, 1905; n=561 individuals), Indochinese tiger (*P. t. corbetti*; Mazak, 1968; n=48 individuals), Malayan tiger (*P. t. jacksoni*; Luo et al., 2004; n=294 individuals), Sumatran tiger (*P. t. sumatrae*; Pocock, 1929; n=1,564 individuals), and Bengal tiger (*P. t. tigris*; Linné, 1758; n=1,125 individuals).

Data analyses

Survival patterns

We first assessed the overall survival pattern of tigers, and then explored survival patterns per sex and per sub-species. First, for the general survival pattern, the history of each individual was built and loaded into a Bayesian model (with a modified version of the *'BaSTA'* package, Colchero et al, unpublished) with R version 3.5.1 (R Development Core Team 2016), to get reliable age-specific estimates of survival. Because of possible errors or typos when entering the data into the Studbook, some individuals' longevity may be overestimated. To avoid this, we performed the analysis removing the 0.1% longest lived individuals. A Siler model (Siler 1979) was used to describe tiger's survival pattern allowing the estimation of age-independent survival. The Siler model takes into account the three main phases of a mortality pattern

typical of mammalian species (i.e. infant, adult, and senescent phases; Caughley 1966; Engelman et al. 2014) with the following equation:

$$\mu(x) = e^{a_0 - a_1 x} + c + e^{b_0 + b_1 x}$$

with $\mu(x)$ the mortality rate at age x. The first part of the Siler model takes into account the decrease in mortality rates over infant and juvenile ages with e^{a_0} being the initial level and a_1 modelling the rate of decrease. The term c (also known as the Makeham term, (Makeham 1860) captures age-independent mortality and may be interpreted as the mean adult mortality rate. The last part of the equation corresponds to the Gompertz law (Gompertz 1825), commonly used to study mortality of mammals and birds living in human care (e.g. Ricklefs and Cadena 2007), assuming an exponential increase of mortality rate with age from an initial level e^{b_0} and b_1 being the rate of increase, also known as the rate of actuarial senescence. We then used a model selection procedure based on the Deviance Information Criterion (DIC, Ando 2011) to test sex- and sub-species-specific senescence patterns, where the model with the lowest DIC was retained. To highlight that actuarial senescence occurs in zoo-housed tigers, a simple exponential model (i.e. model with no effect of age on mortality rate) was performed and included in the selection procedure. Second, we tested for differences of mortality patterns between sexes (female vs male) and/or sub-species. The full model included the sex and the sub-species, and the two-way interactions between sex and sub-species. Finally, we estimated the tiger longevity, defined as the age reached by 10% of individuals (Moorad et al. 2012), from the life table estimated with the previously selected the Siler model.

Reproductive patterns

Two reproductive traits were used to investigate the reproductive pattern: litter size and cub survival. For each cub produced in a zoo, the studbook recorded the identity of the dam, the sire and the respective zoo at birth. All analyses of reproductive patterns were performed using generalized linear mixed models (*glmer()* function in the R *'lme4'* package, Bates et al.

2015). For these two reproductive traits, we used Akaike's Information Criterion (AIC, Burnham and Anderson 2002) for selecting fixed-effects included in the final models.

Litter size was measured as the number of cubs produced in each litter and varied from 1 to 6 cubs. We included litter size as the response variable (Poisson distribution with a log link). The full model included dam's age at litter birth, sire's age at litter birth, the sub-species (as a factor), dam's lifespan, sire's lifespan and one two-way interaction between dam's and sire's ages at litter birth. Including an interactive effect of parental ages allowed us to test for the possible effects of the age-difference between parents on breeding success (e.g. Tidière et al. 2018). Effects of parental ages at litter birth was tested for four types of age-specific models: parental age as a constant, linear, quadratic or threshold function. We fit two types of threshold models: one threshold model with one slope (i.e. constant effect of the parental age before or beyond the threshold) or two slopes (i.e. the slope coefficient of the parental age changes after the threshold) to account for the potential inability of quadratic models to reliably capture the full age-dependence (Gaillard et al. 2017). We selected threshold ages by comparing the maximum likelihood of models including all potential threshold ages across the tiger lifespan. Parental lifespans, included as correcting factors, accounted for the parental quality (van de Pol and Verhulst 2006) as robust individuals might live longer and produce bigger litters (e.g. Landes et al. 2019). Finally, we included the identity of the dam and the sire as random factors to avoid any pseudo-replication problem caused by repeated measures on the same individual (Hurlbert 1984), as well as the zoo at birth (anonymously) to take into account the possible influence of differences in care, experience, and management of tigers among zoos.

We also investigated the age-specific variation in cub survival which was defined as the probability for a cub at birth to reach sexual maturity (3.7 years, Müller 2018). We used the age at sexual maturity as threshold age because of its importance for zoo management practices: upon reaching sexual maturity, individuals may join a zoo-wide breeding population with the goal of promoting self-sustaining populations and genetic diversity

through managed pairing. Moreover, the probability at birth to reach sexual maturity indicates the energy allocated to reproduction as well as the quality of parental care after birth. We included cub survival per litter as a dependent variable for each litter (binomial distribution with logit link). The same covariates were included and same procedure was followed as for litter size.

RESULTS

Survival patterns

We identify for the first time an overall actuarial senescence pattern in zoo-housed tigers, for which the Siler model had a lower DIC than the exponential model (Table S1). Tigers displayed a mean first-year mortality of 0.367, and a mean adult mortality of 0.047 (Figure 1). Their rate of senescence was 0.40 ($IC_{95\%}$ [0.38,0.42], Table 1) and they lived up to 19 years (Figure 1). No significant between-sex or sub-species difference of actuarial senescence patterns were highlighted with the DIC method (Table S1). However, males tended to show a higher juvenile mortality and a faster rate of senescence than females (Table S2 and Figures S1 and S2). Moreover, Indochinese and Malayan tigers tended to have a lower juvenile mortality and a slower senescence, while Amur tigers a higher juvenile mortality and a faster senescence, than the three other tiger sub-species (Table S3, Figures S1 and S3).

Reproductive patterns

In human care, 20% of individuals reproducing successfully at least once in their life are observed successfully reproducing for the first time at 3 years of age. Zoo-housed tigers' mean litter size is of 2.34±0.02 cubs. The random effects of zoo at birth and parental identities explained in part the variability observed in cub survival while only zoo at birth influenced litter size (Table 2).

Litter size variability was explained, in addition to dam's and sire's lifespan, by a quadratic effect of female age and the sub-species (Table S4). Litter size increased with female's age

until reaching a maximum of 2.5 offspring per litter when females were 7 years-old, and decreasing thereafter (Table 2, Figure 2). Moreover, mean litter size varied between sub-species: on average, Bengal and Malayan tigers had the highest, while Indochinese tigers exhibited the lowest, litter size than other tiger sub-species (Table 2, Figure S4). Moreover, litter size was positively related to dam's as well as sire's lifespan (Table 2) confirming that individuals living longer were able to produce larger litters. Finally, the model including male's age had a lower AIC (ΔAIC=-1.03) indicating that litter size tended to decrease with increasing sire age (β=-0.006 [-0.013,0.001], t=-1.67).

The model selected to explain cub survival included, in addition to parental lifespans, a quadratic effect of female age (Table S5). Cub survival was positively related to female age until reaching a maximum for females of 9 years of age, and then decreasing after this age (Table 2, Figure 2). Moreover, cub survival was strongly positively correlated to dam's lifespan, and in a lesser extent to sire's lifespan (Table 2). With a difference of 0.79 units of AIC, the model including the sub-species as a factor had a lower AIC indicating that cubs of Malayan and Indochinese tigers tended to have a higher, while cubs of Amur and South China tigers a lower, probability to reach sexual maturity than other sub-species (Table 2, Figure S4).

DISCUSSION

We give the first evidence of actuarial senescence in tigers living in human care, with an overall longevity of 19 years. Moreover, our findings revealed that females undergo reproductive senescence after 7-9 years of age. Our results also showed sub-species-specific reproduction as well as mortality patterns, which are crucial to consider for conservation purposes.

Actuarial senescence

Our findings emphasized, for the first time to our knowledge, actuarial senescence in tigers (Figure 1). Juvenile (until 12 months-old) and adult mean mortality rates were significantly lower to observed estimates obtained in wild populations. For instance, in wild populations of the Amur tiger, juvenile mortality was estimated between 0.41 and 0.47 (Kerley et al. 2003) (0.37 in our study), and mean adult tiger mortality between 0.19 and 0.37 (for males and females, respectively, Goodrich et al. 2008) (0.047 in our study), revealing that tiger adult mortality is more impacted in the wild than juvenile mortality. Both studies (Kerley et al. 2003; Goodrich et al. 2008) showed that 57% of juvenile and more than 75% of adult mortalities were predominantly human-caused, strengthening the point that adult survival is a critical parameter to improve and maintain sustainable wild populations of tiger. Our results show a progressive increase of mortality rate with age accelerating after approximatively 10 years-old, and a longevity around 19 years. In the wild, female Amur tigers were observed to live to a maximum of 7 years and only few males are expected to live that long (Goodrich et al. 2008). Our findings are in line with the overall observation that zoo-housed carnivore species performed better in terms of survival parameters than their wild counterparts (Tidière et al. 2016), certainly due, for tigers, to the protection against anthropogenic-caused mortality, regular feeding and veterinary care provided by zoos.

Surprisingly, we did not find between-sex differences of actuarial senescence patterns, although males tend to show higher juvenile mortality and faster senescence than females (Figure S1B). This observation is supported by the survival estimates obtained from wild populations of the Amur tiger sub-species, where females exhibited a lower mortality rate than males (Goodrich et al. 2008). Males of polygynous species have a greater variance in reproductive success than females, resulting in a selection that would favor a 'high risk-high gain' strategy, promoting reproductive success but increasing mortality rate compared to females (Trivers 1985). For instance, in a wild population of a polygynous marine carnivore, the northern elephant seal (*Mirounga angustirostris*), females had a higher adult survival rate, began their senescence later, and lived 6 years longer than males (Condit et al. 2014).

However, as longitudinal data are not available for wild tiger populations, no results have been published concerning actuarial senescence parameters, and even less for a between-sex difference. We can hypothesize that between-sex difference of mortality and actuarial senescence parameters of zoo-housed tigers may be underestimated due to the highly protected environment provided by zoos (but see (Tidière et al. 2015). Indeed, these results may be interpreted according to the disposable soma theory (Kirkwood 1977) as, in zoos or in the wild, females undergo similar costs related to reproduction with gestation and lactation (Sunquist and Sunquist 2002), leading to a similar balance of energy allocation (between reproduction and survival). On the contrary, males do not undergo the cost of fighting or defending a territory to be able to reproduce in zoos. This saving of energy may lead to a higher amount of energy available for survival than in the wild, resulting in a slower actuarial senescence, explaining the non-significant between-sex difference of actuarial senescence rate and the lack of sex-difference of longevity in zoo-housed tigers.

Reproductive senescence

Female reproductive parameters increased with female age until reaching a maximum between 7 and 9 years of age, and then progressively declined thereafter (Figure 2). Similar patterns have been observed in wild populations of different carnivores (e.g. polar bear, *Ursus marimitus*, Folio et al. 2019; red wolf, *Canis rufus*, Lockyear et al. 2009) as well as other mammalian species (e.g. bottlenose dolphin, *Tursiops aduncus*, Karniski et al. 2018; alpine marmot, *Marmota marmota*, Berger et al. 2015), suggesting the possibility of common mechanisms driving mammalian reproductive success for females with increasing age. However, age-specific variation in litter size and cub survival might not be related to similar mechanisms: variation of litter size might be directly related to the female reproductive system and physiology, while offspring survival should be the consequence of maternal ability to provide offspring care. Then, the observed improvement of cub survival in females between 2 and 9 years of age might be due to experience gain, confirming results obtained by Saunders et al. (2014) showing that experienced tiger females exhibited higher breeding success.

However, the increasing mean litter size on the same age period cannot be related to a gain of female experience, but more to a progressive implementation of female reproductive system and physiology. In support of this, the minimum age at first reproduction of wild tigers was estimated around 4 years-old (Kerley et al. 2003) while our findings showed that 20% of females successfully reproduced for the first time between 2 and 3 years of age, which might be early in their developmental life. After 7-9 years-old, a progressive decline of mean litter size and cub survival was identified, indicating reproductive senescence in tiger females. The smaller litters observed for old females might suggest a general depreciation of the female reproductive system. However, no decline in ovarian cycle frequency had been identified in old female tigers (Saunders et al. 2014), indicating that our results might suggest a possible decrease of oocyte quality (Vom Saal et al. 1994), if not quantity. Moreover, the tendency of a progressive decline of cub survival might be related to a decreasing ability to provide fetus as well as cub care with age. In the wild, mothers' food acquisition seems to be strongly correlated to the quantity and quality of milk production in mammalian species with a direct influence on infant mortality (e.g. Elowe and Dodge 1989; Wright et al. 2008). If this argument is not valid in zoos, where food acquisition does not pose a problem, we can imagine a senescence in milk production physiology. A depreciation of the female reproductive system and a decrease of maternal ability to take care of cubs may not necessarily be inter-related, as observed in a zoo-housed population of cheetah (*Acinonyx jubatus*) where mean litter size was negatively influenced by maternal age but not cub survival (Augustus et al. 2006).

For male tigers, reproductive senescence was detected only as a slight decrease of litter size with age. Although no data or study were available for wild populations of tigers to compare, a similar negative correlation between litter size and male's age has been observed in other wild and zoo-housed carnivores (e.g. cheetah, Bertschinger et al. 2008; red wolf, Lockyear et al. 2009). This progressive decrease of litter size with increasing age may be related to a reduced quality of sperm with male aging, such as in cheetah for which litter size negatively

correlated to sire's age and sperm morphology count (Bertschinger et al. 2008). Finally, cub survival was not related to sire's age, which may not be surprising as only females provide offspring care in tigers.

Both reproductive parameters used in this study are positively correlated to parental lifespan. Lifespan may be an indicator of individual quality with longer-lived tigers being able to produce large litters with higher probabilities of cubs reaching sexual maturity, and then producing offspring in turn (van de Pol and Verhulst 2006). Moreover, individual lifespan may also be an indicator of institution husbandry practices and experience in managing zoo-housed tigers. Indeed, as transfers between institutions can be stressful for individuals with negative effects on their future reproduction, we can hypothesize that institutions taking care of a successful reproductive pair will keep them as long as possible and then acquire experience in tiger reproductive husbandry practices. This argument is supported by results provided by Saunders et al. (2014) showing an increased breeding success in zoos having a tiger litter within the previous five years.

Consequences in management practices and conservation of tiger: working at the sub-species level

Although the conservation priority is to protect the continuously shrinking wild population, optimal management of the zoo-housed meta-population has become an increasingly important tool for maintaining a viable global population (Conde et al. 2011). Today, fewer than 4,000 sexually mature free-ranging tigers are alive, covering only 7% of their historical range (Goodrich et al. 2015). In this context, scientifically managed zoological gardens may be seen as a lifeblood of tiger conservation through the management of individuals living in human care. Thanks to the partnership between zoos and researchers, our study allowed the characterization of sex- and sub-species-specific demographic parameters, providing tangible tools for tiger conservation. Our results strengthen the IUCN Red List recommendation made for wild tiger populations (Goodrich et al. 2015) to focus efforts on improving survival of

adult breeding females, as litter size and cub survival rely on them, to increase wild populations size. Moreover, our analysis of the actuarial and reproductive senescence patterns for males and females separately will improve estimates of population extinction risk as well and the accuracy of population viability analyses (Robert et al. 2015; Conde et al. 2019). In addition, understanding drivers of reproductive parameters in zoo-housed tigers will improve breeding programs and birth control as many zoos cannot keep an increasing number of tigers because of space limits (Seidensticker et al. 1999; Christie 2010).

Finally, our findings confirm the decision made by zoos to manage the six tiger sub-species separately, avoiding hybridization, as we revealed that the six sub-species presented differences of reproductive and survival patterns. Zoo-housed and wild populations of the six sub-species should not be concurrently managed but instead as different conservation units with specific genetic adaptations. The number and definition of tiger sub-species are still debated (Mazák and Groves 2006; Wilting et al. 2015; Liu et al. 2018) and solving this issue has serious implications for the conservation strategy of this threatened species. Indeed, one of the sub-species, the Indochinese tiger, is almost extinct in the wild (Azlan and Sharma 2003) and only a few individuals are still alive in zoos, while the South Chinese tiger is already possibly extinct in the wild (Goodrich et al. 2015). Moreover, zoo-housed populations maintain mitochondrial lineages which are currently rare or already absent in the wild (Sharma et al. 2009), whose maintenance ensures a minimum of genetic diversity critical for futur reintroduction plans. Our findings revealed that the South China tiger has the highest cub mortality rate as well as the smallest litter size, contrary to the Malayan tiger which has lower cub mortality and bigger litters than other sub-species. These lower reproductive performances in the South China tiger may be the sign of inbreeding depression already occurring in the zoo-housed population (e.g. in okapi *Okapia johnstoni* De Bois et al. 1990). However, a sufficient level of genetic diversity is present in the zoo-held South China tiger population, suggesting a potential for genetic restoration (Zhang et al. 2019). Moreover, Indochinese and Malayan tigers tended to senesce slower, while the Amur tiger senesced

faster than the other sub-species. These results indicate a possible difference in selection pressure between the sub-species. The differences between tiger sub-species confirms not only the importance of considering them separately in conservation plans but also the need to improve our knowledge on selective pressures driving the evolution of demographic parameters for each sub-species independently. However, this result should be taken with caution because of the high difference of sample size between sub-species (i.e. more than 5,000 for the Amur tiger and less than 50 for the Indochinese tiger). It is surprising as some of them benefit from higher scientific interest than others. For instance, we can retain from the literature cited here that most of demographic information available in the wild comes from the Amur sub-species, which is also the sub-species that is the most represented in zoos, currently and historically (578 out of 874 tigers alive in scientifically managed zoos in the 2018 International Tiger Studbook), while only 18 Indochinese tigers are currently alive in scientifically managed zoos (with a total of 48 individuals registered from 1993).

CONCLUSION

As the human population is constantly increasing, anthropic pressures will likely remain or even increase. In addition to *in situ* actions, conservation strategies may be reinforced with *ex situ* ones through the management of populations of threatened species maintained in zoos. Our findings revealed that actuarial and reproductive senescence occur in zoo-housed tigers, providing important fitness parameters for their management, but also enabling the improvement of population viability analyses modelling used to determine conservation plans. For instance, a focus on reproduction of adult females of 7-9 years seems to be critical to control zoo-housed tiger population size. Moreover, we highlight the importance of focusing on sub-species separately, to understand whether and how fitness parameters vary between them and to elaborate range-wide conservation plans. Finally, from the few data available from wild tigers, our results showed higher survival and reproductive parameters in zoos than in the wild, suggesting that zoo-housed populations could be seen as a lifeblood of tiger conservation through *ex situ* population management. As a flagship species, investment in

tiger conservation benefits not only this charismatic species, but also to protect a wide

diversity of lesser known species, such as other smaller threatened cat species or pangolins

(Pholidota), sharing the same ecosystem.

ACKNOWLEDGMENT

DATA AVAILABILITY

All data used in this study may be found in the International Tiger Studbook 2018 (Müller,

2018).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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Table 1. Siler model parameters obtained for the 9,201 tigers living in human care between 1938 and 2018. The first part of the Siler model takes into account a decrease in mortality rates over juvenile ages with e^{a_0} being the initial level and a_1 modelling the rate of decrease. The term c captures age-independent mortality and may be interpreted as the mean adult mortality rate. The last part of the equation corresponds to the Gompertz law assuming an exponential increase of mortality rate with age from an initial level e^{b_0} and b_1 being the rate of increase, also interpreted as the rate of actuarial senescence.

| Parameter	Mean	Standard Error	95% Confident Interval
a_0	2.467	0.027	2.415; 2.520
a_1	32.316	0.654	31.097; 33.593
c	0.047	0.001	0.044; 0.049
b_0	-0.297	0.195	-8.684; -7.906
b_1	0.400	0.011	0.378; 0.422

Table 2. Parameter estimates of litter size and cub survival for tigers living in human care between 1938 and 2018. For random factors, the variance is given as well as the standard deviation (Std. Dev.). Amur tiger (*P. t. altaica*) is used as reference. For random effects, only zoo at birth influences litter size while parental identities as well as zoo at birth influence cub survival.

Response variable	Fixed variables				Random effects			
	Variable	β	95%CI	z-value	Variable	N	Variance	Std. Dev.
Litter size	Intercept	0.494	0.342; 0.647	6.35	Female ID	110 2	0.000	0.000
N=3,794 litters	Female age	0.091	0.057; 0.125	5.21	Male ID	951	0.000	0.000
	Female age^2	-0.007	-0.009; -0.004	-6.22	Zoo ID	396	0.002	0.049
	P. t. amoyensis	-0.085	-0.183; 0.012	-1.71				
	P. t. corbetti	-0.267	-0.572; 0.038	-1.72				
	P. t. jacksoni	0.070	-0.060; 0.200	1.06				
	P. t. sumatrae	-0.103	-0.163; -0.043	-3.37				
	P. t. tigris	0.098	0.023; 0.173	2.55				
	Female lifespan	0.006	0.000; 0.011	2.01				
	Male lifespan	0.002	-0.004; 0.007	0.65				
Cub survival	Intercept	-3.028	-3.637; -2.418	-9.74	Female ID	105 2	0.946	0.973
N=3,124 litters	Female age	0.275	0.167; 0.384	4.99	Male ID	906	0.745	0.863
	Female age^2	-0.015	-0.022; -0.009	-4.64	Zoo ID	382	0.482	0.694
	Female lifespan	0.102	0.075; 0.128	7.55				
	Male lifespan	0.048	0.020; 0.075	3.40				

FIGURE LEGENDS
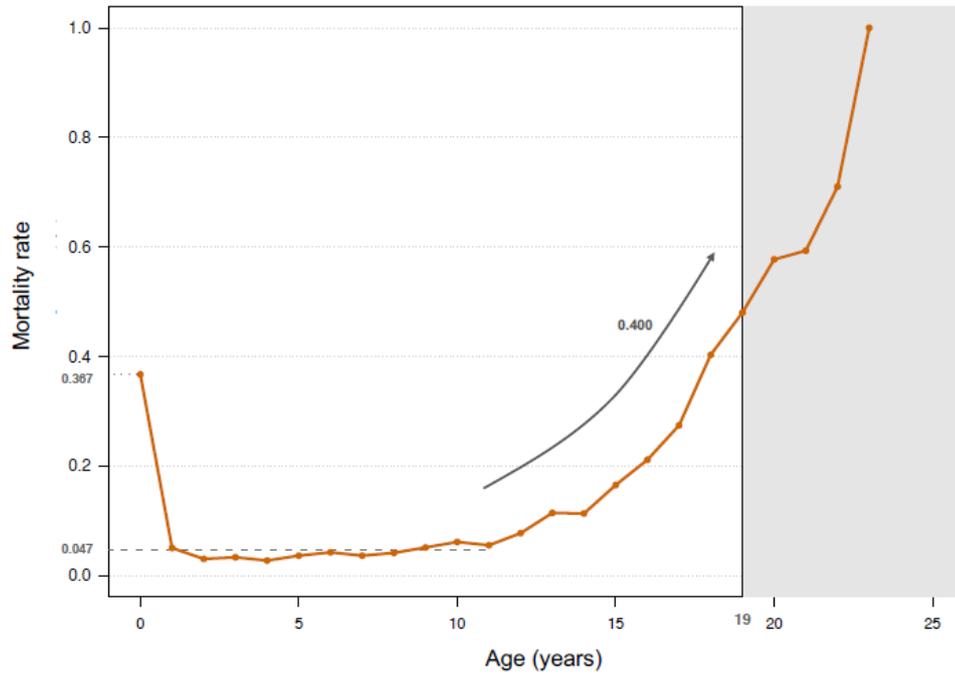
Figure 1. Actuarial senescence pattern of tiger estimated from 9,201 individuals living in zoo between 1938 and 2018. First-year mortality (dotted line), mean adult mortality (dashed line), rate of senescence (arrow) and longevity (full line) are indicated in grey. No sex or sub-species difference are identified.
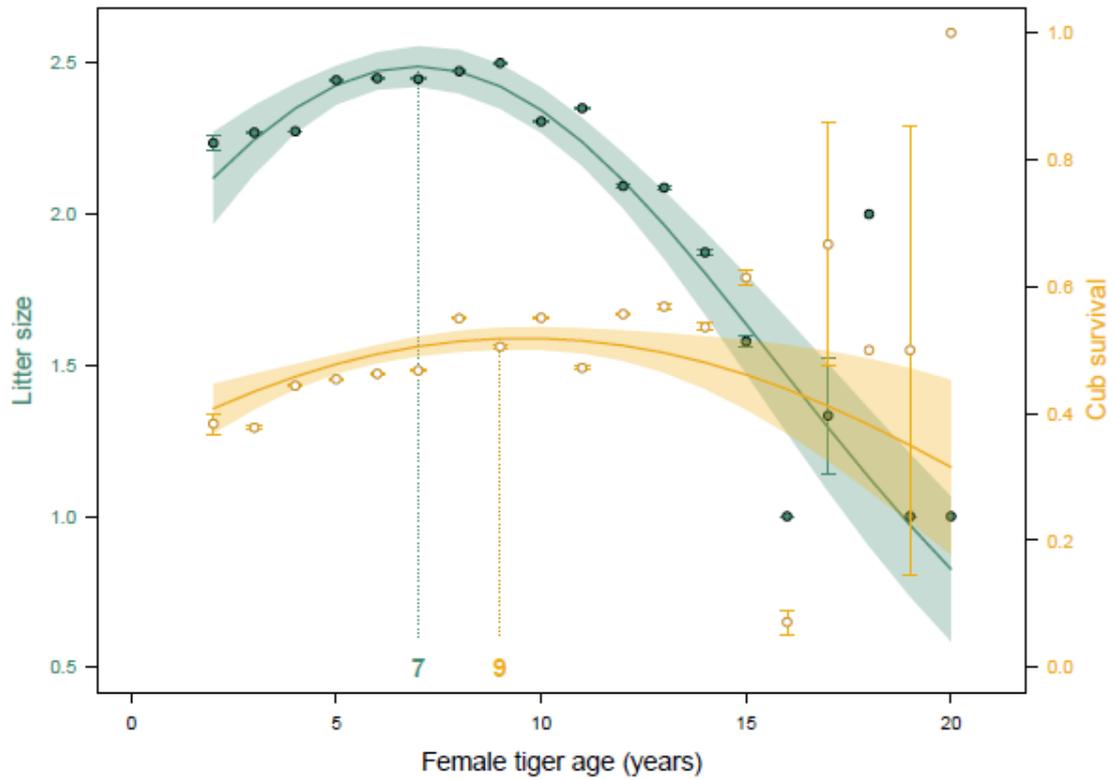
Figure 2. Reproductive pattern for zoo-housed tiger females according to mean litter size (dark color, full circle) and mean cub survival (light color, open circle) per age. Reproductive parameters increase with age until they reach a maximum between 7 and 9 years and decrease thereafter highlighting reproductive senescence. Predicted (solid line) and observed (dots) values are represented with their 95% confident interval.