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# Retrospective study of captive jaguar *Panthera onca* mortality in the European breeding population from 1998 to 2018

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**Abstract**
The jaguar *Panthera onca* is classified as Near Threatened by the IUCN, and the population in the wild is decreasing. To date, no studies on the causes of mortality in jaguars in European zoos have been completed. Therefore, this study was conducted to determine the most common causes of mortality in captive jaguars in the European breeding population between 1998 and 2018. A total of 206 jaguars died during the study period. Causes of death were obtained for 53.8% of the population. Most deaths (51.4%) occurred in geriatric animals, while cubs accounted for 22.3% of deaths. Trauma was the leading known cause of death for the study population (21.6%), affecting primarily cubs and characterised by lethal wounds inflicted by the dam or sire. Cub survival was unaffected by dam parity (P=0.21, OR=0.8, CI=0.46–1.2) or litter size (P=0.09, OR=0.6, CI=0.42–1.28). It is likely that factors such as underlying disease, zoo management and husbandry could influence cub survival. Neoplasia is an important cause of death for the study population (19.8%) and evidence of metastasis was found in over half of those cases. Mammary and liver carcinoma were the most common tumours. This study identifies recent trends in mortality in the European breeding population of jaguars, which can be used to guide preventive medicine programmes. Inconsistencies in record-keeping suggest that a unified necropsy protocol for jaguars in European zoos is needed to gather standardised information and improve understanding of jaguar mortality.

## Introduction

The jaguar *Panthera onca* is the largest neotropical felid and the only surviving species of the genus *Panthera* in the New World (Culver and Hein 2016). The jaguar is classified as Near Threatened by the International Union for Conservation of Nature's Red List of Threatened Species, with a decreasing population trend (Quigley et al. 2017). However, this classification was based on population assessments that were mostly carried out in geographic areas known for having high population densities; hence, the overall jaguar population could have been overestimated (Tobler and Powell 2013). Habitat loss and fragmentation are the main threats faced by the jaguar (Paviolo et al. 2008).

### *Ex-situ conservation and captive breeding programs*

The jaguar is a popular felid species for zoological institutions and provides a high-impact exhibit for the public. Zoological institutions worldwide have held jaguars in captivity for many decades to educate the public about threats to their existence and to highlight population decline (Law 2013).

Given the conservation status of the jaguar, the limited knowledge of its biology, and the vital role it plays in the ecosystem, captive populations are an essential source of knowledge for the species and could even be regarded as a genetic safety net for the wild population. Jaguars are a species of conservation interest for the European Association of Zoos and Aquaria (EAZA). Therefore, there is a European Endangered Species Programme (EEP) for jaguars. The goal of the jaguar

EEP to maintain a self-sustaining and healthy population to fulfil the need of zoos to hold jaguars for exhibition, education and conservation research is currently being met (Biddle 2017).

***Mortality in captive jaguars***

Little has been recorded about captive jaguar mortality; the only published study evaluated morbidity and mortality of the North American captive population from 1982 to 2002 (Hope and Deem 2006). In that study, 24% (21/87) of deaths were in the cub and juvenile age group (less than two years of age). Cub and juvenile deaths were predominantly caused by stillbirths, unexplained neonatal deaths, trauma and pneumonia (Hope and Deem 2006). In the same study, the geriatric group (>16 years), accounted for the highest proportion of deaths (45%, 39/87) among all age groups. Reproductive and musculoskeletal diseases were the most common causes of mortality amongst geriatric animals (Hope and Deem 2006). The study also reported that in 13% (11/87) of cases, the cause of death could not be ascertained due to insufficient data (Hope and Deem 2006).

To date, no study has analysed the causes of mortality in captive jaguars within the European breeding population. Furthermore, veterinary guidelines for the care of jaguars in EAZA collections are lacking. Routine post-mortem examinations of animals are an important part of any preventive medicine programme, as their interpretation could lead to the identification of unexpected health events in a specific population (Küker et al. 2018; Riley 2014). Therefore, the interpretation of post-mortem reports (PMR) in mortality studies is beneficial for the zoological medicine field, as PMRs show trends in population mortality, and thus allow inferences of the health status of the captive population (Hope and Deem 2006). Moreover, once the common causes of mortality have been identified, recommendations can be made to drive changes in husbandry and implement preventive medicine programmes to reduce deaths related to foreseeable causes.

This study aimed to determine the most common causes of mortality in captive jaguars in the EEP between 1998 and 2018 and to determine recommendations to improve the healthcare and welfare of the population. The objectives of this study were to determine the most common causes of death within the population and compare them between age groups and sexes; to identify median age of death and compare it between sexes; to determine if parity, litter size and maternal experience influenced cub survival; and to assess whether histopathology is a useful method to evaluate the cause of death.

## Materials and methods

***Data collection and categorisation***

To evaluate the recent causes of death for the European captive jaguar population and to highlight current trends in age at death, the period between 1998 and 2018 was selected. All the collections that reported jaguar deaths in the EEP during the selected study period were contacted by email through the EEP coordinator (R.B.), and for each animal that had died, a formal request was made for its medical records and PMR. The information was voluntarily submitted by the collections that wished to participate in the study, and data were treated anonymously.

Sex, date of birth and date of death were obtained for all animals from studbook records. Animals whose records did not specify day and month of birth or death were assigned 1 July of the reported year as their birth or death date. The middle of the year (1 July) was selected to limit the error in the calculation of age at death to a maximum of six months. The error obtained by assigning a set day of birth or death is unlikely to bias data analysis since age groups, rather than precise ages, were used for statistical analyses. To allow for statistical analysis, the age at death was grouped using a modified version of the age groups described by Hope and Deem (2006), dividing 'cubs to juvenile' into two different groups. Age at death was categorised into five age groups: jaguars that died before the average age of weaning (6 months) were listed as 'cubs', animals that survived past the cub stage but did not reach the mean age for sexual maturity (2 years) were defined as 'juveniles', and animals that died in the reproductive stage were divided into two categories, 'young adults' (2–5 years) and 'adults' (6–16 years). Finally, animals that survived beyond reproductive age (>16 years) were classified as 'geriatric'.

Sex was categorised as female, male or undetermined. The cause of death was ascertained by the interpretation of the PMR or medical records by an author (M. Duque-Correa) in conjunction with the jaguar EEP Veterinary Advisor or retrieved from the studbook. Causes of death were categorised following Heaver and Waters (2019), using a modified version of the World Health Organization's International Classification of Diseases (WHO 2018), into one of the following categories: infectious, neoplastic, endocrine, metabolic, neurological, cardio-circulatory, respiratory, digestive, cutaneous, musculoskeletal, genitourinary, pregnancy-related (including abortion/stillbirth), congenital, trauma or other. If the animal was euthanised, the reason for euthanasia was recorded as the cause of death. Additionally, if the cause of death could not be identified due to lack of evidence, it was classified as 'insufficient data' or 'institution abstinence' when zoos did not respond to the request, as defined by Heaver and Waters (2019). Owing to the lack of pedigree data for the population, the effect of inbreeding on mortality could not be assessed. Finally, analysis of the PMRs included whether histopathology was undertaken and on how many organ systems, in order to assess how often it was performed and to better understand how this tool is used when establishing cause of death.

***Statistical analyses***

Data were analysed using R (version 3.6.0, R Core Team 2019); results were considered significant if $P<0.05$. Mortality rate (number of animals that died each year divided by the total number of animals alive during that year) was calculated for each year of the study period and the mean mortality rate was calculated for the entire study period and expressed as a percentage. Data on yearly deaths and live animals per year were retrieved from studbook records. The median age of death was calculated for the whole population and each sex, including only animals that had died during the study period. The interquartile range (IQR) was utilised to describe median variation. The frequency of each cause of death was determined for the population, for each sex and per age group. The chi-square test was used to assess significant variation between the causes of mortality for sex; animals of undetermined sex were excluded from this analysis. Given that in this study and previous work carried out by Hope and Deem (2006) cubs accounted for a high number of deaths, further analysis was instigated into the causes of cub death. The roles of parity (number of litters per dam), maternal experience (inexperienced=two or fewer litters; experienced=three or more litters) (Metz et al. 2017) and litter size (number of cubs per litter) in cub survival were investigated using generalised estimating equations (GEEs). GEEs were used as a binomial logistic regression model accounting for litters as repeated measures. For this analysis, animals born between 1998 and 2018 were included (n=207), and survival beyond weaning age (6 months) was recorded and used as a binary output variable. GEEs were performed using R package 'geepack' (Højsgaard et al. 2006).

The Kaplan-Meier method (Bland and Altman 1998) was used to determine if there was a difference in survival age between females and males that died during the study. Survival analysis was performed using R packages 'survival' (Therneau and

**Table 1.** Results from generalised estimating equations (GEE) analysing the influence of litter number, maternal experience and litter size on cub survival past weaning age in captive jaguars *Panthera onca.* Parity=number of litters per dam, maternal experience (inexperienced=two or fewer litters; experienced=three or more litters) and litter size=number of cubs per litter.

| Predictor variable | β estimate±SE | 95% CI | Odds ratio | P-value |
|---|---|---|---|---|
| Parity | -0.223±0.181 | (-0.57, 0.13) | 0.8 | 0.21 |
| Maternal experience | -0.420±0.528 | (-1.45, 0.61) | 0.6 | 0.42 |
| Litter size | -0.511±0.305 | (-1.10, 0.08) | 0.6 | 0.09 |

**Table 2.** Distribution of litters included in the study (n=124) by dam parity. Parity=1 indicates a dam giving birth to her first litter, parity=2 is a dam giving birth to her second litter.

| Dam parity | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| Number of litters | 51 | 33 | 18 | 10 | 5 | 3 | 3 | 1 |

Lumley 2019), ‘survminer’ (Kassambara et al. 2019) and ‘ggplot2’ (Wickham 2016). To analyse if there were significant differences in the use of histopathology in post-mortem examinations between sexes and age classes, two-sided Fisher’s exact tests were used.

## Results

During the study period, 212 animals died in 71 different European zoos and were reported to the EEP coordinator. By the end of the study period (31 December 2018) there were 91 live jaguars in 40 zoos. Six animals were excluded from the data analyses as there was no reliable information regarding their age. Therefore, 206 animals were included in the mortality review. Of these, 50% (103/206) were female, 43.6% (90/206) male and 6.3% (13/206) of undetermined sex. The median age at death for the population was 16.46 years (IQR=0.9–20.0). The oldest animal in the study was a female that died when she was 25 years 9 months and 6 days old. The mean annual mortality rate during the entire study period was 9% (range=4–15%, Figure 1).

### *Age*

Median age at death was 16.7 years (IQR=4.6–20.0) for females, 16.8 years (IQR=8.2–20.4) for males and 4 days (IQR=1.0–16.5) for animals of undetermined sex. The Kaplan-Meier method (Figure 2) showed no statistical difference (P=0.86) in the age of death between females and males.

More than half of the deaths (51.4%, 106/206) occurred in geriatric animals. Cubs had the second highest proportion of deaths (22.8%, 47/206) and 19.4% of deaths (40/206) were from the adult group. Juveniles and young adults accounted for the lowest number of deaths, with 3.8% (8/206) and 2.9% (6/206), respectively. To further analyse cub mortality, data from 207 cubs born in 124 litters from 1998 to 2018 were analysed. The GEE found that cub survival was not significantly affected by parity, maternal experience or litter size (Table 1). The distribution of litters related to dam parity can be seen in Table 2. Litter size ranged from one to four animals; 50% (62/124) of the litters had only one cub, while 33.8% (42/124), 15.3% (19/124) and 0.8% (1/124) of the litters had two, three and four cubs, respectively.

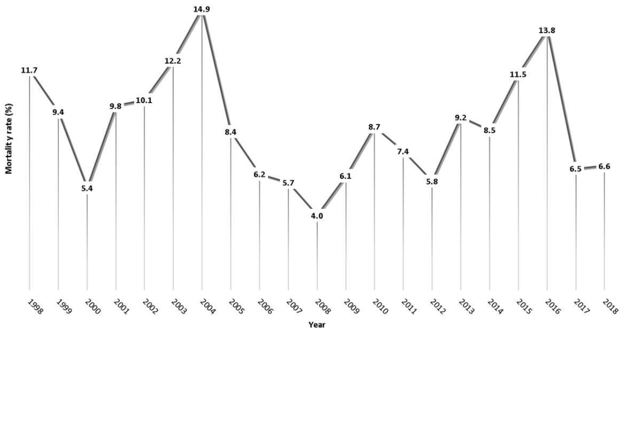


**Figure 1.** Mortality rate per year of captive jaguars *Panthera onca* in the European breeding population between 1998 and 2018. Mortality rate (%) was calculated as the number of animals that died each year divided by the total number of animals that lived during the same year.

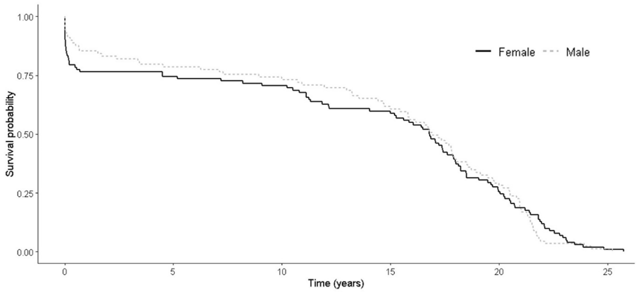


**Figure 2.** Kaplan-Meier survival curve for female and male jaguars *Panthera onca* in the European breeding population between 1998 and 2018. There was no statistical difference (P=0.86) in the age of death between sexes. Females are represented by the continuous black line and males by the dashed grey line.

**Table 3.** Causes of death in jaguars *Panthera onca* for which a cause of death was identified (n=111), stratified by age group. Percentages represent the proportion of animals that died from that cause in each age group.

| Cause of death | Cubs | Juveniles | Young adults | Adults | Geriatric | Total |
|---|---|---|---|---|---|---|
| Trauma | 17 (62.9%) | 4 (80%) | - | 3 (16.6%) | - | 24 (21.6%) |
| Neoplasia | - | - | 1 (20%) | 2 (11.1%) | 19 (33.9%) | 22 (19.8%) |
| Genitourinary | - | - | - | 5 (27.7%) | 13 (23.2%) | 18 (16.2%) |
| Infectious | - | 1 (20%) | - | 2 (11.1%) | 9 (16%) | 12 (10.8%) |
| Musculoskeletal | - | - | - | - | 7 (12.5%) | 7 (6.3%) |
| Digestive | - | - | 1 (20%) | 2 (11.1%) | 4 (7.1%) | 7 (6.3%) |
| Respiratory | 3 (11.1%) | - | - | - | 2 (3.5%) | 5 (4.5%) |
| Metabolic | 2 (7.4%) | - | 2 (40%) | - | - | 4 (3.6%) |
| Pregnancy-related | 3 (11.1%) | - | - | - | - | 3 (2.7%) |
| Cardio-circulatory | - | - | 1 (20%) | 2 (11.1%) | - | 3 (2.7%) |
| Neurological | 1 (3.7%) | - | - | - | - | 1 (0.9%) |
| Endocrine | - | - | - | - | 1 (1.7%) | 1 (0.9%) |
| Congenital | 1 (3.7%) | - | - | - | - | 1 (0.9%) |
| Other | - | - | - | 2 (11.1%) | 1 (1.7%) | 3 (2.7%) |
| Total per age group | 27 | 5 | 5 | 18 | 56 | 111 |

***Cause of death***

Information on whether the death of the individuals occurred naturally or by euthanasia was reported in 60% (124/206) of the cases. Of these animals, 57.2% (71/124) were euthanised and the remainder 42.7% (53/124) died naturally. Cause of death could not be ascertained for 46.1% (95/206) of the population due to 'institution abstinence' (33.4%, 69/206) or 'insufficient data' (12.6%, 26/206). The cause of death was obtained for 53.8% (111/206) of the jaguars. Most causes of death were obtained by interpretation of PMRs (65.7%, 73/111) and the remaining causes (34.2%, 38/111) were obtained by analysing the clinical records of the animals or were retrieved from data recorded in the studbook.

The causes of death per age group for the study population are shown in Table 3. The leading cause of death for this population was trauma (21.6%, 24/111), affecting mostly the younger groups: 62.9% (17/27) of cubs and 80% (4/5) of juveniles. The second most common cause of mortality was neoplasia (19.8%,

**Table 4.** Causes of death in jaguars *Panthera onca* for which a cause of death was identified (n=111) by sex. Percentages represent the proportion of animals from each sex that died from that cause.

| Cause of death | Female | Male | Undetermined | Total |
|---|---|---|---|---|
| Trauma | 11 (18.9%) | 8 (17%) | 5 (83.3%) | 24 (21.6%) |
| Neoplasia | 13 (22.4%) | 9 (19.1%) | - | 22 (19.8%) |
| Genitourinary | 9 (15.5%) | 9 (19.1%) | - | 18 (16.2%) |
| Infectious | 5 (8.6%) | 7 (14.8%) | - | 12 (10.8%) |
| Musculoskeletal | 1 (1.7%) | 6 (12.7%) | - | 7 (6.3%) |
| Digestive | 4 (6.8%) | 3 (6.3%) | - | 7 (6.3%) |
| Respiratory | 5 (8.6%) | - | - | 5 (4.5%) |
| Metabolic | 4 (6.8%) | - | - | 4 (3.6%) |
| Pregnancy-related | 1 (1.7%) | 1 (2.1%) | 1 (17.6%) | 3 (2.7%) |
| Cardio-circulatory | 1 (1.7%) | 2 (4.2%) | - | 3 (2.7%) |
| Neurological | 1 (1.7%) | - | - | 1 (0.9%) |
| Endocrine | - | 1 (2.1%) | - | 1 (0.9%) |
| Congenital | 1 (1.7%) | - | - | 1 (0.9%) |
| Other | 2 (3.4%) | 1 (2.1%) | - | 3 (2.7%) |
| Total | 58 | 47 | 6 | 111 |

22/111), with tumours commonly seen in the reproductive tract and liver; mammary adenocarcinomas and liver carcinomas were most frequently described. Over half (54.5%, 12/22) of neoplastic cases showed evidence of widespread metastasis. Genitourinary diseases were also an important cause of death (16.2%, 18/111); conditions leading to death included interstitial nephritis and chronic renal failure. Infectious diseases were varied. However, the causative agent was only explicitly listed in three cases, while the other cases were listed as having bacterial origin without a known aetiological agent. Infections were found to be related to a variety of pathological processes, such as bronchopneumonia, enteritis, hepatitis and cholangiohepatitis. Musculoskeletal diseases accounted for 6.3% (7/111) of deaths and were mostly related to chronic arthritis that led to euthanasia for welfare reasons. Deaths due to digestive disease were caused either by aseptic or infectious peritonitis or intestinal perforation by prey items. Causes of death listed as 'other' included two heat-strokes, and a female that was euthanised due to central blindness caused by an astrocytoma. The remaining causes of death are detailed in the age group sections.

*Cubs*
Remarkably, half of the deaths in this age group occurred in the first 17 days of life. Cub deaths were mostly caused by trauma (62.9%, 17/27) predominantly characterised by lethal bites or non-lethal bite wounds that required euthanasia for welfare reasons. Stillbirths caused all pregnancy-related deaths. Respiratory deaths included two cases of atelectasis and infectious disease. Other deaths corresponded to poor nutritional status (metabolic), congenital abnormalities and one cub that presented with hindquarter paralysis (neurological) and that was euthanised.

*Juveniles*
Similarly to cubs, the leading cause of death for juveniles was trauma (80%, 4/5), which in all cases was caused by lethal bites by the dam or sire. *Klebsiella* was isolated from the remaining juvenile, which died as a result of infectious disease.

*Young adults*
Metabolic causes were the most predominant cause of death in young adults (40%, 2/5), related to poor nutritional status. The other cases involved a liver haemangioma, a digestive obstruction and a cardiac arrest.

*Adults*
The leading cause of death in adults was genitourinary disease (27.7%, 5/18); renal disease was the illness most frequently reported. The traumatic deaths corresponded to two adult females and a male that died due to bites inflicted by their male partners. Mammary carcinomas were reported in two out of three neoplasia cases. Three animals died due to infectious processes, but the specific infectious agents were not listed in the PMRs. Deaths related to the digestive system were due to an intestinal perforation by a food item and a case of acute hepatitis.

*Geriatric*
Neoplastic deaths were the most common in this age group (33.9%, 19/56) and liver and mammary carcinomas were the most commonly described tumours (5/19 each). Other types of tumours were found in the muscle, gallbladder and spleen. Genitourinary diseases accounted for 23.2% (13/56) of the deaths; illnesses leading to death included chronic renal failure and chronic interstitial nephritis. Infectious processes were also common in this group, but the agents were only identified in two cases (*Proteus mirabilis* and *Mycobacterium* sp.). The respiratory and digestive systems had the highest number of fatal infections. Musculoskeletal deaths were found solely among geriatric animals; the leading cause was arthritis in various joints, including hips, shoulders, knees and the vertebral column.

***Sex***
The causes of death of females and males can be seen in Table 4. Individuals of undetermined sex mostly died of trauma (83.3%, 5/6) and one was a stillbirth (16.6%, 1/6). The leading cause of death for females was neoplasia (22.4%, 13/58); for males it was both neoplasia and genitourinary conditions (19.1%, 9/47 each). No significant differences were found for the causes of death between females and males ($\chi^2$(4, n=85)=1.22, P=0.87).

***Histopathology***
Histopathology was undertaken in 78% (57/73) of post-mortem examinations. No significant difference was found in the number of histological examinations performed between females and males (P=0.63). However, a significant difference was found in the proportion of histological procedures performed by age class (P<0.001), with significantly less histopathological examinations of cubs and juveniles than for all other age groups (Table 5).

**Table 5.** Number of cases in which histopathology was carried out in post-mortem examinations, by age group.

| Histopathology | Age class | | | | | Total |
|---|---|---|---|---|---|---|
| | Cubs | Juveniles | Young adults | Adults | Geriatric | |
| No | 16 (72.7%) | 4 (100%) | - | 4 (33.3%) | 4 (8.6%) | 28 (32.9%) |
| Yes | 6 (27.2%) | - | 1 (100%) | 8 (66.6%) | 42 (91.3%) | 57 (67%) |
| Total | 22 | 4 | 1 | 12 | 46 | 85 |

## Discussion

This retrospective study offers an overview of recent mortality trends in the jaguar EEP population. The geriatric group accounted for most of the deaths (51.4%, 106/206), which were mostly due to age-related diseases such as neoplasia and nephropathy. Cubs accounted for 22.3% (46/206) of deaths in the study population, with half of these deaths occurring in the first 17 days of life. The jaguar EEP population is managed to be self-sustaining; therefore, it is of the utmost importance to minimise cub deaths and optimise breeding potential.

### *Age*

The geriatric group presented the highest mortality rate (51.4%, 106/206) of the study population. This is consistent with captive jaguar mortality in North America, where almost half of the dead individuals belonged to this age group (Hope and Deem 2006). Furthermore, the maximum age of death for this population (25 years and 9 months) is similar to the maximum age of death in the North American population (up to 25 years). The number of deaths of cubs and juveniles combined (26.6%, 55/206) was similar to the number of deaths registered in the same age groups in the North American population (24%) (Hope and Deem 2006). Additionally, other studies of several *Panthera* species have found that cubs and juveniles account for a large proportion of deaths, showing that animals that survive past juvenile age have a high probability of reaching geriatric age (Napier et al. 2018).

A study of Asiatic lion *Panthera leo persica* mortality found that over 50% of the deaths occurred in the neonate group (<1 month of age); the leading causes of neonatal death were lack of parental care (i.e., cub abandoned or not cared for by the dam) and trauma (Metz et al. 2017). That study found that the likelihood of cubs surviving past one year of age was directly influenced by the number of litters raised by a dam. However, in the current study, maternal experience (P=0.42) and litter size (P=0.09) had no significant effect on cub survival. This difference might be related to better maternal care in jaguars than in Asiatic lions, evidenced by the absence of cub deaths due to lack of care in this study population. Zoos with recent tiger *Panthera tigris* litters presented higher cub survival than zoos without recent births (Saunders et al. 2014). Husbandry factors, such as prioritising the reproduction of experienced females or pairs with recent litters could increase cub survival.

### *Causes of death*

The cause of death was obtained for only 53.8% (111/206) of the population despite data requests being mediated by the EEP coordinator. Therefore, improving communication between the institutions that hold jaguars and the EEP coordinator is necessary; a constant and reliable flow of information will benefit the whole captive jaguar population in Europe. Euthanasia accounted for 57.2% (71/124) of the deaths in the study population. This could be correlated to the high proportion of geriatric mortality due to degenerative causes and the fact that humane euthanasia is advised for jaguars when the quality of life has been impaired due to medical or welfare reasons (AZA Jaguar Species Survival Plan 2016). The analysis of PMRs allowed the establishment of cause of death for 65.7% (73/111) of cases. The quality of PMRs and medical records varied considerably across institutions. Although analysing the quality of records was beyond the scope of this study, institutions should strive to improve record keeping, as valuable information can be obtained through retrospective analysis of these documents. Loss of data was evident in this study, as a third of deaths was classified as unknown.

Trauma was the leading cause of mortality for this population (21.6%, 24/111), and most trauma cases (17/24) involved cubs. Fatal wounds inflicted by the dam (7/10) or sire (3/10) were the primary cause of traumatic deaths. Other populations of captive wild felids also reported high rates of neonate and juvenile mortality due to trauma inflicted by the parents (Metz et al. 2017; Napier et al. 2018). In the wild jaguar, infanticide has been recorded. For example, Soares et al. (2006) provided evidence of a male, subsequently proven to be the sire, that killed two 9-month-old cubs. The main difference between infanticide events in the wild and in captivity is the age at death. In captive populations these events occur when the animals are very young (<2 months), whereas in the wild it has been reported in older cubs that were already weaned and aged 5 to 9 months (Tortato et al. 2017). Causes of infanticide are not well understood but have been hypothesised to be linked to adverse environmental conditions or as a mechanism of regulation of the carnivore population (Soares et al. 2006).

Most births in the study period were from first- and second-time mothers, as breeding recommendations are given to adult pairs that have not bred before. Maternal experience does not seem to be related to cub survival in this population (P=0.21) and as populations are carefully managed in zoological institutions, these factors are unlikely to be an underlying cause of infanticide. Furthermore, as has been described in other species, other factors such as underlying diseases could influence infanticide rates (Acton et al. 2000). Therefore, thorough post-mortem examinations of cubs are required to understand the role that underlying diseases play in traumatic deaths in jaguars, as it is a substantial cause of mortality.

Neoplasia was the second most common cause of mortality for this population (19.8%, 22/111); its presentation increased with age, with more cases reported in geriatric animals than in adults and young adults, and none in juveniles or cubs. Furthermore, more than half (54.5%) of the neoplastic cases showed evidence of metastasis. Similarly, a study of *Panthera* species found that 50% of the animals in sanctuaries in North America had neoplastic disease, with a higher incidence in older animals suggesting that increasing age likely influences tumour prevalence (Kloft et al. 2019). In that study, 35% of the tumours metastasised (Kloft et al. 2019). Owing to the high rate of neoplastic disease in jaguars and the frequent occurrence of metastasis, routine health examinations in aging jaguars are advised. Furthermore, monitoring for disease spread and quality-of-life assessments are also recommended.

The mammary gland and liver were the organs most affected by neoplasia. Other studies in *Panthera* species have reported that the reproductive system was commonly affected by neoplasia (28%, 47/168) and mammary carcinoma was the most prevalent tumour type (Kloft et al. 2019). Furthermore, studies on mammary cancer in captive wild felids have found contradictory evidence linking contraception and malignant mammary neoplasms (Harrenstien et al. 1996; Kloft et al. 2019). A study in North America found that 94% of the felids that had been given contraception with megestrol acetate (MGA) developed mammary cancer (Harrenstien et al. 1996). However, Kloft et al. (2019) suggested that MGA might not be a risk factor for mammary cancer in *Panthera* species, as none of the animals in their study population received contraception but the animals still presented with mammary tumours. Therefore, other factors could be associated with mammary neoplasia.

Owing to similarities in the rates of mammary and ovarian cancer in humans and jaguars, researchers are aiming to sequence the BRCA1 gene (Munson and Moresco 2007). In humans the BRCA1 gene regulates progesterone receptor signalling in mammary epithelial cells and has been associated with mammary and ovarian cancers (Ma et al. 2006). In jaguars an altered BRCA1 function could result in increased progestin activity in the mammary gland, resulting in a predisposition to cancer (Munson and Moresco 2007). Contraception history for the study population was not analysed. However, since the EEP has a non-breeding recommendation for the majority of animals (Biddle 2017), it can be assumed that contraception has been used widely in the population. Nonetheless, further studies are needed to evaluate the effects of contraception and genetics on mammary neoplasia in jaguars.

Genitourinary disease contributed to 16% of the deaths in the study population due to kidney diseases of different aetiologies. Remarkably, renal disease contributed to only 6% of jaguar deaths in the Association of Zoos and Aquariums (AZA) population in the US (Hope and Deem 2006). Nevertheless, 17.6% of European jaguars experienced various non-fatal renal diseases during the study period. A study that analysed necropsy results of felids in German zoological gardens found that 87% (33/38) of the animals had renal lesions at the time of death (Junginger et al. 2015). However, all the animals in that study were considered as a single population, possibly biasing results due to the overrepresentation of some species. Chronic kidney disease is common in geriatric wild felids (Newkirk et al. 2011). However, genitourinary disease accounted for only 6–22% of deaths in different species of captive wild felids (Heaver and Waters 2019; Hope and Deem 2006; Metz et al. 2017). Further research is needed to better characterise the importance of renal disease in morbidity and mortality in captive wild felids.

Musculoskeletal and neuromuscular diseases were the main reasons for euthanasia in male jaguars (24%, 9/38) in the AZA population (Hope and Deem 2006). In the present study musculoskeletal disease only accounted for 6% of the deaths, but it seems that joint disease affected males more commonly than female jaguars. Weight could influence the presentation of musculoskeletal deaths, as male jaguars (77–100 kg) are known to be heavier than females (45–68 kg) (USFWS 2012). Moreover, most of the males in this study that presented with arthrosis or arthritis were reported to be overweight. These assumptions are supported by the hypothesis that the stress of locomotion in large mammals could lead to persistent inflammatory responses in joints (Nunn et al. 2007). However, it is unlikely that body weight and size are the only factors related to musculoskeletal disease (Nunn et al. 2007).

### *Histopathology*

Histopathological examinations were carried out in most necropsies (78%, 57/73). However, the use of histopathology was dependent on the age group. Most PMRs of geriatric animals included histopathology (91.3%, 42/46), in contrast to cubs for which only a small proportion was further examined in this manner (27.2%, 6/22). The lack of histopathology in the cub group could be associated with the fact that the leading cause of death was trauma, a diagnosis that does not require the use of specialised diagnostic techniques. However, the histopathological examination of captive red wolves *Canis rufus* found that most of the neonates that were fatally injured by their parents (8/12) had an underlying disease, suggesting that maternal culling of unhealthy neonates could be the underlying cause of traumatic deaths (Acton et al. 2000). Therefore, concurrent diseases or congenital problems were possibly missed in the jaguar cubs for which histopathology was not undertaken. Furthermore, microscopic lesions may have been missed in the cases where histopathology was only used in the organs with macroscopic lesions. Thus, performing standardised histopathological examinations in all jaguars in the EEP, including cubs, is highly recommended.

### *Limitations*

The cause of death was established for only 53.8% (111/206) of cases. Therefore, some causes of death could be over- or underrepresented. Despite data requests being mediated by the EEP coordinator, 'institution abstinence' was the leading reason for not establishing a cause of death (33.4%, 69/206). Insufficient data accounted for 12.6% (26/206) of the cases without a known cause of death, as some PMRs were lost or lacked details. Therefore, a constant and reliable flow of information will improve current knowledge regarding the health of the captive jaguar population.

## Conclusions

This study highlights the leading causes of death in jaguars housed in European zoos and identifies the age groups with the highest rates of death. The results of this investigation could improve the care of captive jaguars in the EEP, as the information provided can be used as guidelines for preventive medicine.

One of the most significant findings of this study is that jaguars that survive past cub age often live to reach adult or geriatric age. Trauma was the leading cause of death for cubs (62.9%, 17/27). Underlying disease, institutional experience with litters, husbandry and population management are probable factors leading to infanticide of jaguars. Monitoring and recording of the first weeks of life and conducting histopathological examinations on dead cubs are necessary for a comprehensive understanding of the conditions leading to traumatic cub death. Owing to the high rate of neoplasia and metastasis found in this study, frequent medical check-ups are advisable. The high rate of mammary neoplasia in this population is similar to that found in previous studies on mammary cancer in this species. However, the specific causes of tumours require further investigation. Once animals reach adulthood, it becomes increasingly important to frequently monitor renal function and continue to do so throughout the animals' lives, as genitourinary disease proved to be a substantial cause of death in both adult and geriatric animals. A unified necropsy protocol that includes routine histopathology is needed for the institutions that hold jaguars in the EEP, to improve diagnoses and gather standardised information regarding the death of animals in the European jaguar population. Stronger communication between the EEP and participating collections would be beneficial for future research. A constant flow of data would ensure that more accurate and updated information is obtained in a reliable way, avoiding loss of data.

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