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Research Article

A 31-year retrospective analysis on breeding success and cub mortality of African lions [Panthera Leo] in the Australasian captive population

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Abstract

Studbooks are the foundation for managing and preserving threatened species in captivity and provide conservation managers with the ability to appropriately plan breeding activities to maintain self-sustaining populations. The African lion [Panthera Leo] is a priority species within Australasian zoos and is included in the Australian Regional Species Plan. This study used a regional studbook to not only describe basic reproductive parameters, but also to compare the differences in reproductive success for lions that were transferred between facilities, relative to their social grouping, life stage, and the presence of littermates. Results showed that lionesses that stayed in their natal institution or those transferred before maturity as a singleton were more successful breeders than females transferred as a cohort group, while the reproductive success of male lions did not appear to be influenced by such factors. The sex ratio of litters and the net reproductive rate was influenced by the social groupings of breeding animals. Lionesses that stayed in their natal pride tended to produce more male cubs, while females that were transferred as singletons had more female cubs. Collectively the findings from this study have important implications for the captive management of lions.

Keywords: African lion; reproduction; sex ratio, social grouping; mortality

Introduction

Biological information collected from captive populations can significantly improve the breadth of knowledge for individual species, particularly when there is a limited understanding of what can influence a population's structure [1]. The African lion, Panthera Leo, is currently listed as Vulnerable by the International Union for Conservation of Nature [IUCN] and has been identified as a species in crisis, resulting from notable historical population declines over the last several decades [2-4]. The main threatening processes experienced by this species are habitat loss, a reduction in prey biomass, excessive harvest quotas and indiscriminate killing through human-wildlife conflict [5]. Further to this is the emerging threat involving the trade in bones and other body parts for traditional medicine both in Africa with exports to Asia [6,7]. Lions form relatively cohesive social units that undergo periods of fission and fusion [8]. A pride is generally comprised of related females and their young [1-20 individuals], and a cohort of immigrant males whose group size can range from 1-9 individuals [9-11].

Most females stay with their natal pride their whole life with emigration or expulsion of subadult females occurring less frequently. Females that have left the pride may be accepted back into the social group, while unfamiliar or strange females are rarely accepted into an established pride [12,13]. As an inbreeding avoidance mechanism, male coalitions typically disperse from their natal pride as they approach maturity, between 25-48 months and lead a relatively nomadic existence before challenging the males of a resident pride for territorial and breeding rights [14]. In free ranging populations, the reproductive success of each sex depends on the number of individuals within each single sex group. For lionesses, kin selection plays an important role in collectively rearing young, hunting co-operatively and territorial defense [15-17]. Solitary females are unable to maintain exclusive home ranges and experience low reproductive success [18]. Conversely, the total number of consorts a male has directly influences his individual reproductive success; while the overall reproductive success of pride males is enhanced by an increase in coalition size [19,20].

Despite males becoming sexually mature at around two years of age [21], they are unlikely to breed before the age of four and only have a reproductive lifespan in the wild of approximately three years. Male reproduction generally ceases after their pride tenure is lost but males as old as 16 years can still produce viable sperm [22]. Synchronous breeding is a strategy that can increase cub survival, especially when similar aged litter are communally raised. Breeding synchrony can occur as part of a within-pride mechanism of simultaneous estrus cyclin or after the loss of dependent offspring resulting from a male takeover and aligned mating activity [23]. The age of first reproduction for lionesses in the wild can be as young as 32 months with most females giving birth by the time, they reach four years of age [24-27]. Lionesses have been known to breed up until 15 years of age with a decline in fertility beginning at 11 years. Lionesses can give birth at any time of the year with peak birthing times in free ranging populations generally coinciding with high prey abundance.

Depending on the complexity of the environment, the average litter size on emergence from the den varies from 2.3 to 3.1 cubs, with litter sizes ranging from one to six cubs [28]. Litter size is not correlated with a lionesses age or to the success of a previous litter with the mean time between surviving litter being 18-26 months [29]. Similarly, the sex ratio of litters is not correlated with a lionesses age or the density of lions in a given environment. The number of cubs in a pride can vary greatly and as a consequence high cub mortality is typically evident. In the Serengeti, for instance, only 37.5% of cubs reach the age of one with infanticide from incoming males, disease and starvation being the predominantly causes of mortality [30]. The reproductive success of lions in captivity is complex, influenced by a combination of biological and environmental factors. In general, however, this species has bred relatively well in captivity [31]. Lions are held in 473 institutions globally and in 14 zoos and parks within the Oceania region [32].

To help maintain an appropriate level of genetic diversity across each regional population, animals are strategically transferred between zoological institutions. Reproductive success can be determined by the level of infant survival, with this parameter influenced by patterns of maternal investment and behavior [33,34]. In captive carnivore species, maternal infanticide is a primary cause of infant mortality with some suggested links to factors such as dam origin, housing conditions and individual experience [35]. It has been noted in a number of studies that the breeding success of several felid species are sensitive to stressors associated with captivity [36,37]. Further to this, a prolonged stress response can occur when individuals are moved between facilities, which can be counterproductive to social bonding and future reproduction efforts [38,39]. Survival and lifetime reproductive success can strongly influence the dynamics of a population. Knowledge regarding reproduction is therefore crucial for managing successful breeding programs in captivity.

Despite this, very little research has been carried out on the factors that influence breeding and the effect of mimicking wild dispersal patterns of African lions within a captive setting. Mimicking the social structure from free-ranging conspecifics may have direct benefits when breeding threatened species in captivity. Studies of primate species, as well as cheetah have shown that breeding success can be increased by managing captive populations in a more naturalistic way [40,41]. In this study, a long-term data set is used [1988-2019] from the Zoo and Aquarium Association [ZAA] to describe the reproductive characteristics of the African lion population. The effect that transferring lions between facilities is examined, along with social grouping and the presence that littermates have on reproductive performance. It is predicted that reproductive success would be higher for lionesses that stayed with their natal pride animals that were transferred with littermates [or related females], and animals that were transferred before sexual maturity.

Materials and methods

Data collection and categorization

Data was sourced through the global database, Zoological Information Management System [ZIMS]. Data was constrained to living or deceased individuals that were born between the years 1988 and 2019 that were categorized as tawny lions, which have a direct conservation value [n = 147]. This contrasts with animals descending from a white lion pedigree that are bred purely for their phenotypic appearance. As tawny and white lions are treated independently within the regional studbook, white lions were removed from this dataset and from any further analysis. As the focus is on the breeding success of captive lions in the ZAA region, animals that died before sexual maturity [and hence never entered the breeding population], along with animals in which breeding was never attempted were removed from the dataset. Equally, if breeding attempts were not recorded or revealed in ZIMS, these animals were also removed from further analysis. This resulted in a dataset of 38 lions in which breeding had been attempted or occurred.

For each individual a series of parameters were recorded that included: the institution of birth; transfer history including the number of littermates transferred and the age of the animal at the time of transfer; the age of lion/lionesses when litters were produced; the number, sex ratio and survivorship of offspring; and the presence or absence of littermates during breeding events. From these variables, the age of first reproduction, lifetime offspring, inter-birth interval, mean litter size, cub mortality rate, fecundity, sex ratio of offspring, net reproductive rate, seasonality of births and the mean age at transfer were calculated. Similar or exact variables have been reported in [42-47]. All lions were categorized into social groups based on their transfer history. Here, animals defined as 'natal' were those that were never transferred from the facility in which they were born.

Individuals deemed 'singletons' were transferred to another institution as a single animal; while lions that were transferred with littermates or closely related individuals were categorized as 'cohort'. Sexual maturity in males was marked at 2.17 years [26 months] being the age in which spermatogenesis begins [48]. In females there is greater ambiguity on the age of sexual maturity, particularly between wild [~ 4 years in the Kruger NP] and captive populations. For instance, lionesses were considered sexually mature at a mean age of 2.67 Years [32 months] at Dublin Zoo [49] and at 3 years [36 months] at London Zoo [50]. In this study the age of sexual maturity was marked at 2.67 [32 months] for females. All lions were categorized as being either transferred before the age of sexual maturity, after the age of sexual maturity, or never transferred. A 'successful breeding' was one that resulted in the production of a litter for both males and females.

Statistical analysis

By examining this long-term dataset, it was possible to highlight some trends relevant to reproduction within the ZAA ex situ population. Breeding success was defined as the percentage of individuals, whether that be male or female, within a social group [i.e. natal, singleton or cohort] that had at least one successful breeding event recorded [51]. As with social grouping, breeding success relative to life stage [i.e., sexual maturity] at the time of transfer was similarly examined. Age of reproduction is a key demographic trait that can strongly influence evolutionary processes for individuals and populations. For both male and female lions, a one-way ANOVA with a Tukey post hoc test was conducted to compare the mean age of reproduction across each of the social groups and separate life stages. For multiparous individuals, reproductive lifespan was determined by the number of days from the first reproduction to the last reproduction. To provide an estimate of age-related reproductive success, fecundity tables were constructed for each sex separated into each social group with only offspring of the same sex as the parent group included.

Data was constrained to the reproductive lifespan with a two-way ANOVA performed on rates of fecundity to assess whether population means were identical across each social group and years. Litter size, relative to lionesses, were compared using a one-way ANOVA hypothesizing that each social group will have the same average size. To provide an additional insight into whether litter size was affected by a lionesses' age, or separately whether cub mortality was affected by litter size, a linear regression was performed. Using life history table parameters, fecundity and survivorship, the net reproductive rate for offspring [of the same parental sex] in each social group was calculated. The net reproductive rate can describe how population size can change in the next generation. This rate is defined as the average number of offspring produced per male/female over their lifetime. Here, generation time is defined as the mean age of each sex and social group based on the date of birth of their offspring [52]. This was calculated by multiplying the proportion of surviving individuals in that age class with the average number of offspring of the same age, up to the oldest age class. The values for each age class were then summed and divided by the net reproductive rate.

Calculating sex ratios for a population can be indicative to both the relative survival of each sex and the future breeding potential of the population. Sex ratios were calculated as a proportion of male to female births across the study period with each of the three decades examined for any temporal differences. A least squares regression analysis was performed plotting the sex of cubs against time. To assess whether there were any biases in sex allocation over the study period, a runs test was conducted to determine if there was a deviation in the trend of the residuals. For lionesses, a comparison was also made between sex ratios of cubs in each of the social groups using a one-way ANOVA. Cub mortality was calculated as the number of deaths divided by the total number of cubs born. A one-way ANOVA compared the rate of mortality against a lioness' social grouping and life stage. While a linear regression was utilized to assess whether there was a relationship between cub mortality and the age of a lioness, and separately a dam's experience [i.e., the number of litters born to a lioness].

Seasonality of births were examined relative to the dams' social grouping with the data arranged by date of litter to remove autocorrelation. The term 'seasonality' used here denotes any tendency toward temporal clustering of reproductive activity, whether discrete seasons or seasonal peaks. Data was pooled across all years with relative frequency of births calculated for each month. The mean vector length was estimated giving an indication of the degree of concentration of data in a circular distribution. Frequencies of births were grouped into 12 sections [months] of 30° each and overlaid on one another representing social grouping. To test for seasonality, the Rayleigh test for departures from a random distribution of the data across the entire year [360°] was calculated. Data was mined and statistically analyzed using Excel [53] and Graph Pad Prism [54] with statistical significance defined as P values < 0.05.

Results

Breeding Success

Across the 31-year study period [1988-2019] it was found that 23 females and 15 males bred producing 37 litters and a total of 102 offspring. The descriptive statistics associated with the social grouping of both male and female lions are reported in Table 1. Breeding had been attempted in another four females which had been transferred as cohort groups, but pregnancies did not eventuate. Of the 19 breeding females, 15 lionesses were transferred from their natal institution to another zoo as part of regional recommendations. Seven of these lionesses were transferred as singletons and eight were transferred as part of a cohort [excluding those that did not fall pregnant]. Thirteen lionesses were transferred before they reached sexual maturity, and three were transferred after maturity. Across the study period the proportion of lionesses that bred annually was 4.23% of females. Across all litters breeding success for lionesses was found to be 83%.

Breeding females who were transferred as part of a cohort were less successful [67%] when compared to those females staying in their natal pride or transferred as an individual, both respectively 100%. Females transferred to another zoo as a cohort after sexual maturity [n = 4] had reproductive success of 50%. No females were transferred without a littermate after reaching sexual maturity. Females transferred prior to sexual maturity had a breeding success of 87%, whereas those transferred after maturity had a 50% success rate. Females without female littermates present [n = 8], had a breeding success of 100% regardless of transfer history, compared with 73.3% breeding success for females with littermates present [n = 15]. For males, there was a 100% breeding success rate. From the 15 males in which breeding was attempted, all produced at least one litter. Thirteen of these animals were transferred from their natal institution, eight were transferred before sexual maturity, and five were transferred after maturity. Four were transferred as singletons and nine were transferred with littermates. Given that all males successfully bred, there were no impacts of social grouping, littermate presence or transfer life stage on breeding success.

Age at first reproduction

Lionesses were observed to breed from the age of 1.8 years to 11.3 years, with the mean age at first reproduction being 4.0 years [SE+0.46]. A one-way ANOVA was conducted to compare the age at which females produced their first litter relative to social grouping finding that they did not differ significantly, F [3,16] = 3.029, p = 0.0766. However, when performing a multiple comparison test it was found that lionesses that bred at their natal facility had their first litter at a much older age [M = 5.9 years, SE+1.4], with this being significantly different to lionesses that were transferred within a cohort group [p = 0.0283]. No significant differences were found between females that were transferred to another institution as a singleton or lionesses who were part of a cohort, with the mean age of first reproduction for each of these social groups respectively being 3.8 years [SE+0.56] and 3.1 years [SE+0.44].

The life stage at which females were transferred [i.e., before or after sexual maturity] had a significant effect on the age at first reproduction, F [2,16] = 7.624, p = 0.0047. As seen by Figure 1, females that were transferred before maturity bred much earlier [M = 3.1 years, SE+0.25] than those transferred after reaching maturity [M = 6.7 years, SE+1.3], or those never transferred [M = 5.1 years, SE+1.6]. For males, the mean age of first reproduction was 6.3 years [SE+0.12 days] from the 15 males that bred within the 31-year period. The earliest age a lion sired a litter was 1.7 years, with the oldest recorded sire being 14.6 years of age. Interestingly, it was also noted that the distribution of age for breeding males occurred bimodally with peaks observed in animals aged 5 and then again at 14, with 20% of lions siring their first litter when aged 12 years or older. Despite this, lions that were transferred as a cohort group [M = 4.8 years, SE+0.72] bred at a much younger age than those that were transferred as singletons [M = 7.6 years, SE+2.1] or the natal group [M = 12.7 years, n = 1], this difference was not significant, F [2,12] = 3.249, p = 0.0745 (Figure 2). This was also reflected in the age of first reproduction where lions that were transferred before sexual maturity [M = 3.9 years, SE+0.46] bred at much younger age when compared to those that were transferred after reaching maturity [M = 9.1 years, SE+1.6] or remained in their natal institution [M = 8.5 years, SE+0.42], F [2,12] = 5.374, p = 0.0215.

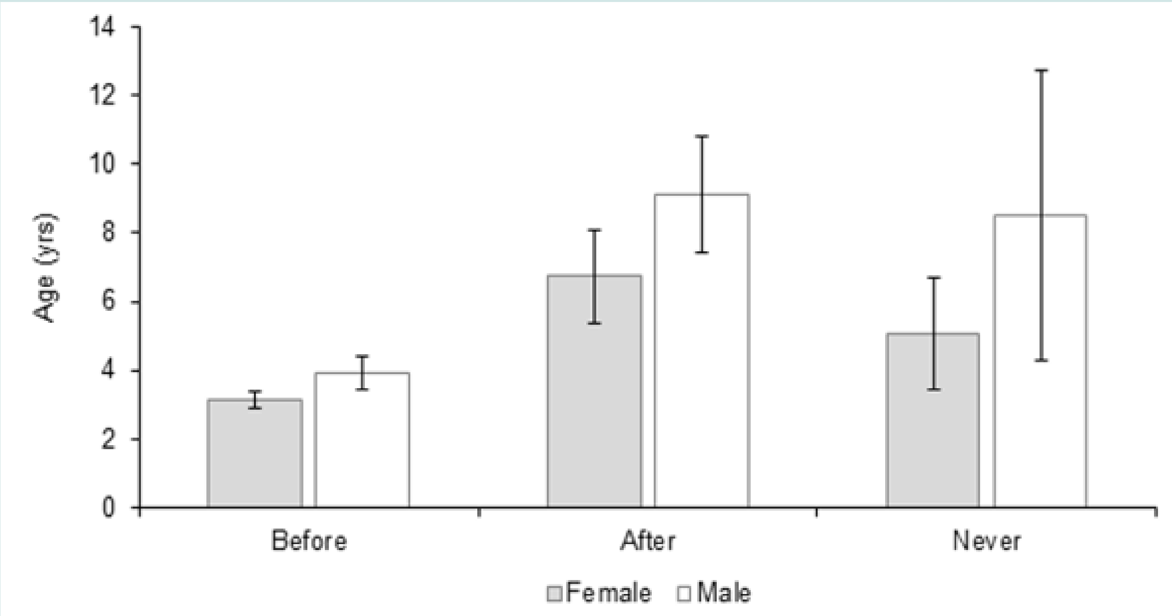

Figure 1: Mean Age (+ SE) at first reproduction for lions and lionesses as a function of whether they were transferred before maturity, after maturity, or if they were never transferred.

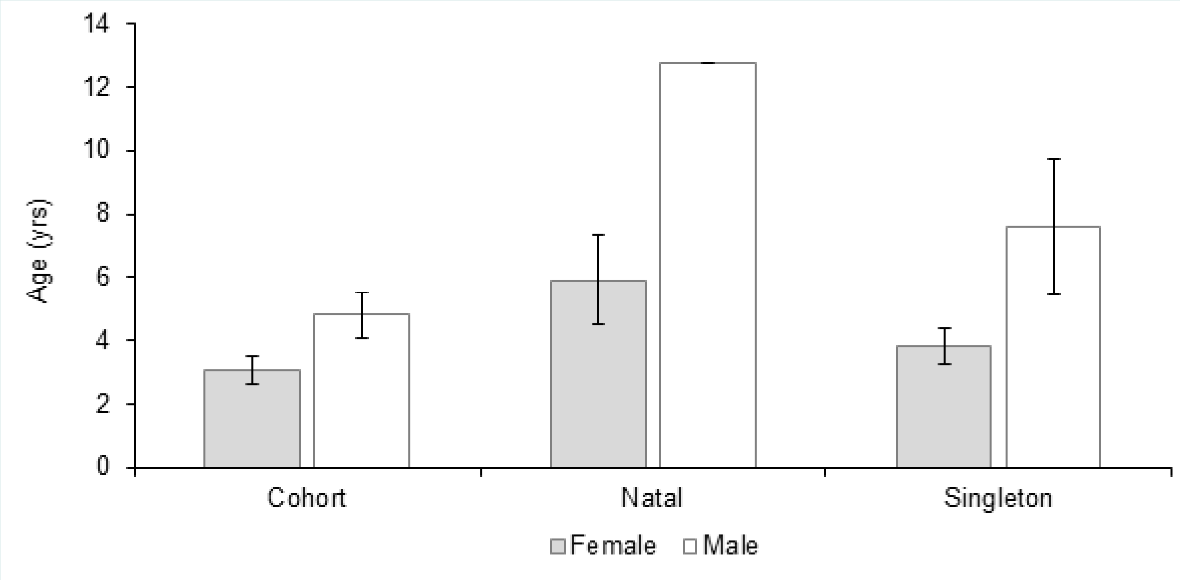

Figure 2: Mean age (+se) of first reproduction for lions and lionesses across each social group.

Fecundity

Between the sexes the reproductive lifespan was relatively consistent at 3.3 years [SE+1.18] for males and 3.3 years [SE+0.66] for females. A two-way ANOVA was run on the fecundity rates to examine the effect of social group and age class [year] for each sex. For male lions, there was no significant interaction found between age class and social group, F [2, 39] = 2.664, *p* = 0.0823. A simple main effects analysis showed that social group did, however, significantly influence fecundity rates with lions transferred as singletons being more fecund than lions that stayed at their natal facility [p = 0.0348]. There were no differences found between animals transferred as cohort groups or as singletons [*p* = 0.5924], or cohorts and those that stayed at their natal institution [*p* = 0.2371]. To contrast between the sexes, there was no significant effect of age class on fecundity for lionesses, but there was a difference amongst the social groups, F [2, 27] = 3.52, *p* = 0.0512. Lionesses that stayed in their natal pride had a significantly lower rate of fecundity compared to those females that were transferred as a singleton to other institutions [*p* = 0.0443]. No statistical difference was found between animals being transferred as a singleton versus as a cohort [*p* = 0.1596]; nor to females that were transferred as cohorts versus those that stayed in their natal pride [*p* = 0.7989]. Fecundity rates [mx] are presented for each sex in Figures 3 & 4.

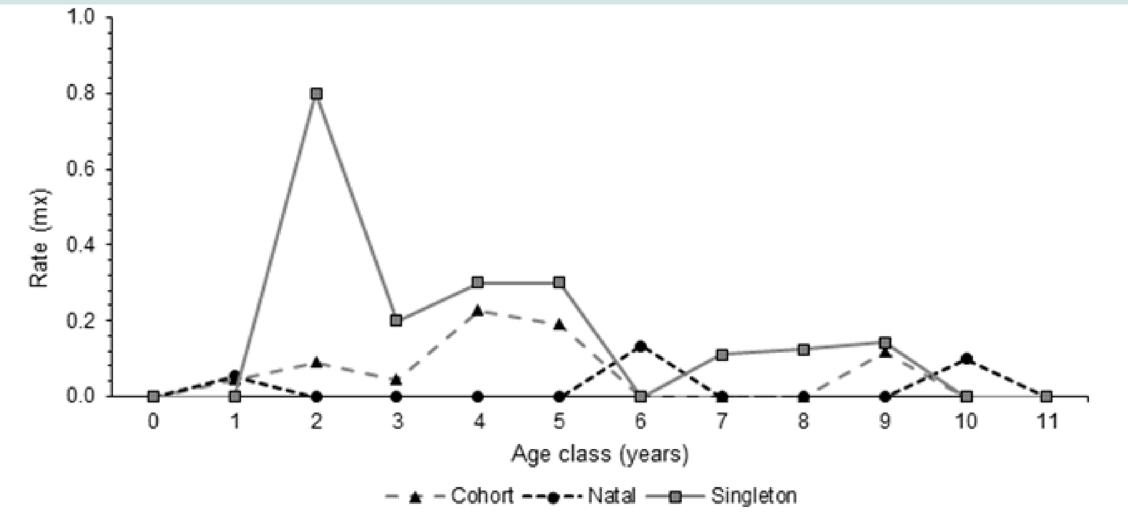

Figure 3: Fecundity rate of lionesses across age classes and social groups.

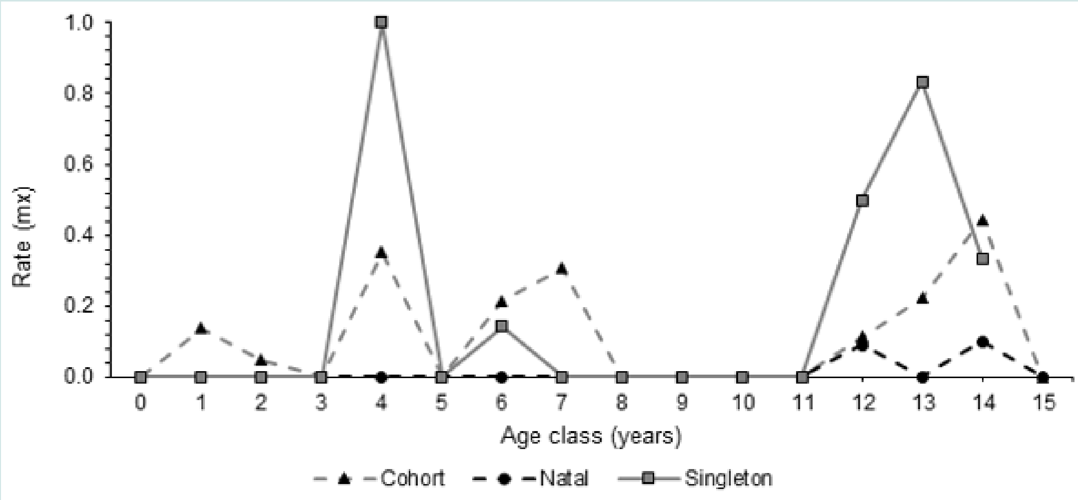

Figure 4: Fecundity rate of male lions across age classes and social groups.

Litter size

Litter size ranged from one to six cubs [n = 37], with an overall mean of 2.8 [SE+1.23] cubs per litter. The plurality of litters had either one or two cubs [40%], closely followed by litters comprised of three cubs [37%]. Only one lioness over the study period gave birth to a litter of six cubs, with this female staying at her natal institution (Figure 5). Most cubs were born to females that were transferred as singletons [21 litters, M = 2.5 cubs SE+1.1], followed by females that were transferred within cohort groups [10 litters, M = 3.2 cubs SE+1.3], and females that remained in their natal facility [6 litters, M = 2.8 cubs SE+1.7]. A one-way ANOVA comparing the differences between social groupings in relation to litter size showed no significant difference, $F [2,10] = 0.7692$, $p = 0.4889$. Furthermore, examining the effect of a lioness' age on litter size was not significant, $F [1, 35] = 1.504$, $p = 0.228$. A non-significant result was also observed when assessing litter size against cub mortality, $F [1,35] = 2.360$, $p = 0.133$, though this result may be influenced by the proportion of litter that had more than three cubs [23%, n = 9]. Synchronous breeding was found to occur six times throughout the 31 years with dual litters recorded once at Adelaide Zoo, Auckland Zoo, Orena Wildlife Park, Paradise Valley Springs Wildlife Park, and twice at Monarto Safari Park.

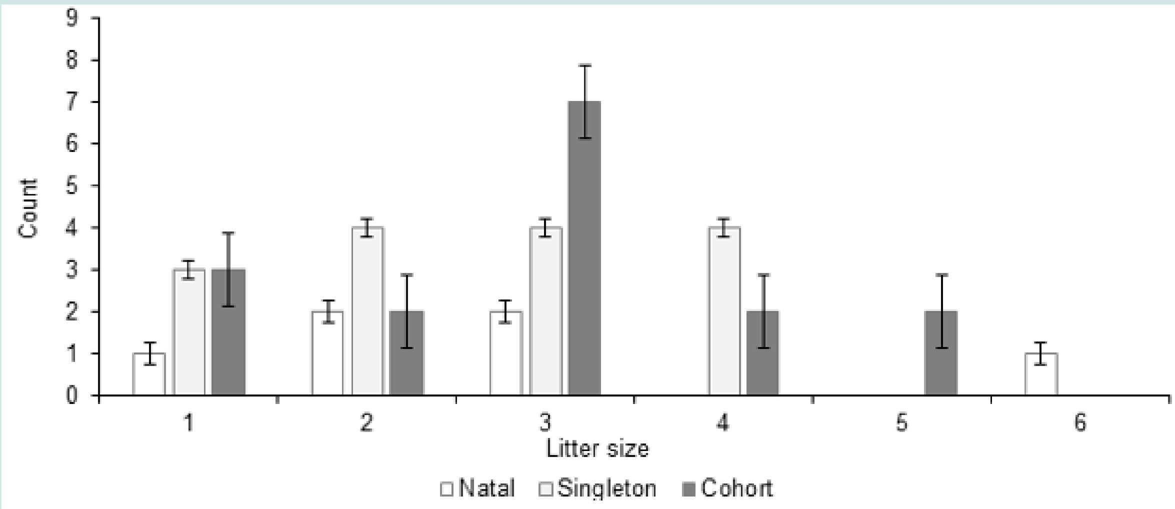

Figure 5: Litter Size Based On Social Grouping.

Net reproductive rate and sex ratio

Across the 37 litters born within the 31-year period, the sex ratio of cubs was 54 males to 38 females, with the sex of 10 other cubs being undetermined. Table 1 reports the reproductive growth rates and generation times for each sex and social grouping. Here, such rates are used to reflect on which social group can represent the greatest reproductive potential and the projected population change. It was established that, during the study period, lionesses that remained in their natal pride had a net reproductive rate of 0.2 over a generation time of 5.7 years; indicating that if breeding from just natal females occurred there would be an 80% decrease in the proportion of female cubs over a period of 5.7 years. Similarly, the proportion of female offspring born to lionesses that were transferred as part of a cohort group would also be expected to decline by 35% over a period of 4.4 years. This contrasts with females that are transferred as singletons, with it predicted that there will be an increase in the proportion of female cubs by 90% over a shorter period of 3.8 years. Males that were transferred within a cohort group had the greatest net reproductive rate for each social group with the proportion of male cubs expected to increase by 103% over 4.1 years.

Table 1: Descriptive Statistics (± SE) for Social Groupings.

Reproductive parameter	Females			Males		
	Natal	Singleton	Cohort	Natal	Singleton	Cohort
n	4	7	12	2	4	9
Number of litters	6	18	13	7	8	22
Number of offspring	17	53	32	18	22	60†
Breeding success rate	100%	100%	67%	100%	100%	100%
Mean age of transfer (yrs)	n/a	1.9 ± 0.6	1.3 ± 0.2	n/a	5.8 ± 2.4	1.8 ± 0.4
Mean age at first litter (yrs)	5.9 ± 1.4	3.6 ± 0.5	3.2 ± 0.5	8.5 ± 4.2	8.7 ± 2.4	4.7 ± 0.7
Mean number of offspring in first litter	2.0 ± 0.4	2.5 ± 0.4	3.0 ± 0.6	1.5 ± 0.5	2.5 ± 0.3	3.1 ± 0.3
Net reproduction rate	2.7	0.7	1.83	0.2	0.78	2.07
Generation time (yrs)	5.7	4.6	3.2	7.2	4.6	4.1
Mean overall litter size	2.8 ± 0.7	2.5 ± 0.2	3.2 ± 0.4	2.6 ± 0.3	3.1 ± 0.4	3.0 ± 0.3
Mean mortality of first litter	33.3% ± 23.6%	43.3% ± 15.8%	57.3% ± 20.5%	50.0% ± 50.0%	25.0% ± 25.0%	35.6% ± 14.2%
Mean overall cub mortality rate	20.8% ± 15.2%	25.6% ± 8.9%	43.5% ± 12.5%	42.9% ± 17.4%	17.1% ± 14.1%	30.0% ± 9.1%

In comparison, the number of male cubs from lions transferred as singletons or who remained in their natal pride are expected to decrease by 22% in 4.6 years, and 80% in 7.2 years respectively. Temporally, there was a large sex ratio bias in the population in the late 1980s and 1990s with more females born than males. This trend steadily decreased to equality by 2005. From 2008 to 2014 the sex ratio shifted to favor males in the regional population, with a shift back to females from 2014 to present. Overall, the mean sex-ratio at birth was 0.54 [Bm = 968, Bf = 1146], which suggests a small female bias. A linear regression runs test showed that the slopes of each sex was not significant, F [1, 36] = 0.3222, p = 0. 5724, indicating there was no observed biases in sex allocation at birth over the study period. This result supports [55] equal allocation theory, which states that selection should favor an unbiased sex ratio at a population level. Reviewing the observed sex ratio rates between social groups did show that cubs that were born to females that were transferred within a cohort group [M = 0.49, SE+0.07] or as singletons [M = 0.52, SE+0.08] were found to have a relatively even sex ratio. Interestingly, females that remained in their natal pride had a greater propensity to produce males [M = 0.31, SE+0.06], a trend that was statistically significant, F [2, 32] = 0.3014, p = 0.0186.

Cub mortality

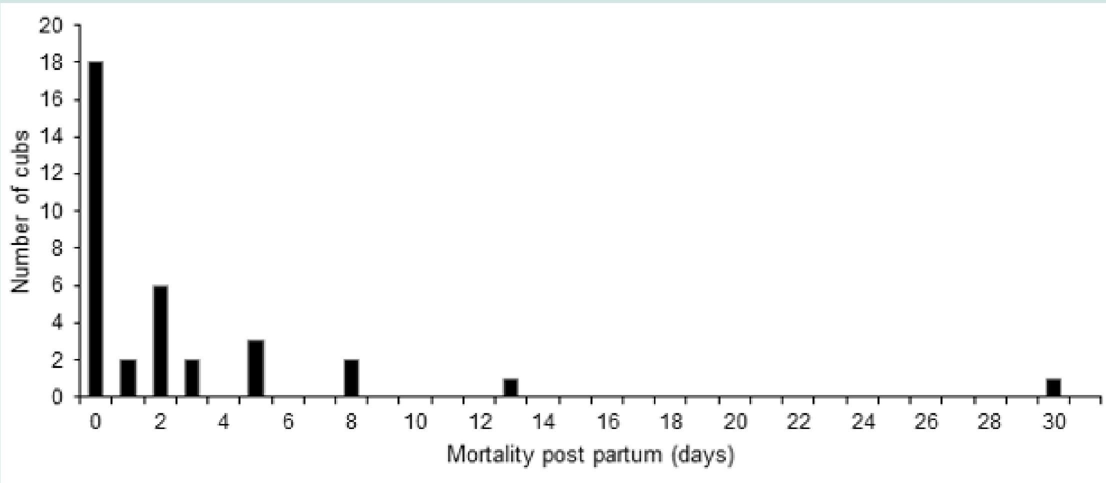

Figure 6: Mortality of cubs age less than one month old (n=32).

Of the 102 cubs born, 73 cubs survived to maturity [28.4% mortality rate]. From the cubs that died before maturity, 80% died within the first month of life with 70% within the first week. For cubs that died in the first month, 41% were either stillborn or died on the day of birth (Figure 6). Infant mortality was lowest for lionesses that stayed at their natal facility [20.5%] followed by females that were transferred as a singleton [22.6%], while lionesses that were transferred with a cohort group and bred had the highest cub mortality overall [38.7%]. Examining cub mortality across the social groups however, showed no significant differences, F [2, 34] = 1.454, p = 0.2478. In each of the social groups it was noted that at least one lioness lost an entire litter. For females that had littermates present [or related females] the mortality rate was lower [22.4%] than for lionesses where littermates or related females were absent [39.2%]. The life stage at which a lioness was transferred had no significant effect on cub mortality, F [2, 34] = 0.5712, *p* = 0.5702. Cub mortality was not found to be impacted by a dam's age, F [1, 35] = 0.5927, *p* = 0.4465; but rather by a dam's experience, F [1, 35] = 5.035, *p* = 0.0313, suggesting that cub survivorship significantly increased with the number of litters a lioness had over time. Of the eight litter that were lost entirely, seven were from first time mothers, with one being a second litter from a lioness that had previously lost a first litter.

Seasonality

Births were distributed throughout all months of the year with three specific months contributing to more than 30% of births. These included two months in summer and one in late winter, respectively January [10.7%], August [11.7%] and December [13.7%]. February [5.8%], March [4.9%] and July [5.8%] had the lowest number of cubs born with cub mortality also being lower in these periods, reflecting reduced neonatal deaths. In Figure 7 cub mortality [black dots] is represented on a 0 to 10 scale. Of all cubs born within the study period, September had the greatest number of deaths [77.8%] across the calendar year. This mortality rate is representative of a lag effect with most deaths occurring within 30 days. Lionesses that were maintained in their natal facility were found to have only bred in three months of the year, whereas females within cohort groups did not breed in February, March, and June only. This contrasted with females that were transferred as singletons which bred in all months. December 31st was calculated as the mean day in which cubs were born across all years. A Rayleigh test was performed showing that there was no seasonality in births [z =0.041, *p* = 0.001] with this finding supporting a birth-flow breeding system.

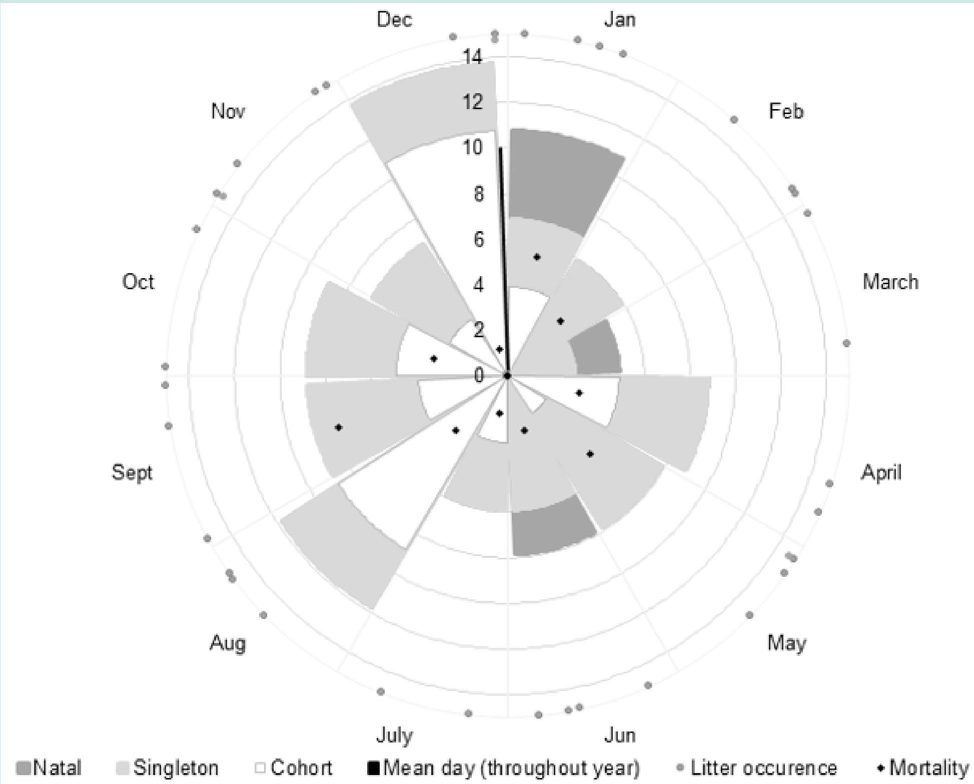

Figure 7: Relative Frequency of Cubs Born Per Month to Lionesses from Each Social Group and Mortality.
Note: mortality is represented on a 0 to 10 scale.

Discussion

Understanding the reproductive biology of captive species and the husbandry necessary to reliably produce offspring is essential for effective population management and future population viability. These results represent the first comprehensive analysis of African lion breeding success in the Australasian captive population. The social grouping and life stage at which animals were transferred did impact breeding success for females, but not for males. As expected, this study showed that the most successful female breeders, when considering breeding success and cub mortality combined, were those that remained at their natal facility. This is consistent with findings in a range of captive bred carnivore species, where females that are transferred between institutions exhibit lower breeding success. In free-ranging populations, females with natal philopatry and pride sizes of 3-10 animals experience higher per capita reproduction than dispersing females [56]. Up to one-third of subadult females disperse and establish new prides with these smaller groups being prone to reduced reproductive success, delayed first reproduction and higher mortality [57-59]. The cumulative effects of social separation and a transportation stressor have been noted to incur negative consequences both physiologically and behaviorally [60,61].

The deleterious effects of stress have been documented in a range of felid species including tigers, cheetahs and clouded leopards following transportation of captive individuals to other institutions for breeding purposes. High levels of stress can affect reproductive function, such as that pertaining to follicle and oocyte development [62], estrous cycle length [63] and egg fertilization [64]. The transfer of animals between zoological organizations may therefore reduce reproductive function, at least in the short term until a new equilibrium for that individual has been established. Unexpectedly, females that were transferred to another facility as a cohort had lower breeding success rates than transferred singletons. Dispersing females in wild populations generally remain together to form a new pride, facilitating increased cub survivorship through co-operative raising of multiple litters, crashing and allo-suckling [65]. In contrast reproductive success of solitary females is considerably lower. Therefore, it was expected that the presence of littermates might mimic the in situ social reproductive environment, and potentially increase the reproductive success when compared to singletons. This was not the case and may be related to the complex social structure of lion society.

Despite lionesses having a well-developed social network there is also a general belief that they do not form strict dominance hierarchies with the suggestion that each individual is equally affected by any factor that can raise or lower reproductive success [66]. Therefore, if one lioness bred within a cohort, she would not experience the full benefit that synchronous litters encounter. Poor success rates have also been noted in reintroduced lions with some failures attributed to a lack of social bonding, particularly in females with there being some tendency for females to associate only with direct kin rather than genetically distinct individuals. Lionesses transferred as a cohort may therefore be far less inclined than singletons to associate with unrelated animals once at a new institution. Equally, if there are weak dyadic relationships between related females a similar outcome could be expected. This has the capacity to make integration of the sexes to form new prides more challenging with the potential to lower overall breeding success rates. For males, none of the factors examined here impacted breeding success. The reproductive success of wild males depends solely on their ability to gain control of a territory and access to females. In captivity, there is no direct competition from rival males when being introduced to females, and hence it would be expected that there would be very few constraints on breeding success.

Based on life stage, lionesses that were transferred before maturity bred earlier than those transferred after maturity, or those that were never transferred. In free ranging populations, dispersal of females generally occurs just prior to the onset of maturity, with females forming new groups [or being recruited into the natal pride] likely to permanently remain in that pride. Age at the time of transfer may also have a significant effect on reproductive success as younger animals generally have a greater plasticity and resilience to change and therefore adaptability to new environments [67]. In free ranging populations, lionesses tend to copulate more frequently with males that either takeover or form a new pride, while also experiencing an initial period of infertility. The median time from such events until females fall pregnant was calculated as 102 days. Using a similar analogy, lionesses within the ZAA region that were transferred to new institutions prior to maturity fell pregnant after a median period of 1.6 years, while for mature female's pregnancy occurred one year after being transferred. Under both situations these time frames are considerably greater than free ranging lions.

When examining social grouping, the age at which natal lionesses bred was much older than those animals transferred as singletons or as cohort groups, likely due to the number of unrelated males at the natal facility and space requirements for additional litters. The median time for singleton females to produce the first litter after being transferred was 1.6 years and 1.3 years for females in a cohort group. Again, this is a notable difference in the timing of litters post transfer with it likely to be an artefact of management decisions and logistical delays in introducing groups, hence limiting the opportunities for animals to breed. In 2010 a regional *captive management* plan [CMP] was developed for lions outlining a strategic approach for managing the regional population to ensure that a genetically healthy lion population persists into the future, with consideration to the social and behavioral needs of the species [68]. This is accompanied by an annual report and recommendations for the program indicating which institutions are to breed, to transfer animals and those institutions that are to maintain non-breeding groups for that year. Across the study period the average age at which lionesses first bred was 3.59 years, being relatively consistent with both the North American population and that observed in free-ranging populations.

Of the 15 zoological organizations that held lions throughout the study period, 12 instituted contraceptive measures at some point in time, equating to 35% of all adult animals across the study period. The majority of these were female [n = 35] with hormonal implants being the primary contraceptive method, while 12 of the 16 males were permanently contracepted compared to just two females. Of these contracepted animals 34% [12F, 3M] did have the opportunity to breed having at least one litter of cubs thereby maintaining normal social behaviors. As the average age of contraception for male and females was 4.3 and 4.9 years respectively there was no influence of this population control method on the age of first reproduction. Lionesses in this study bred between the ages of 1.8-11.3 years with the reproductive lifespan of females being approximately 3.3 years, similar to that reported in the North American captive population. There are multiple factors that allow captive lionesses to breed successfully before three years of age, most importantly being opportunity and a consistent level of nutrition as described in [69]. Reviewing reproductive lifespan against contraceptive use did identify that lioness generally had two or three litters.

It would be fair to assume that contracepting animals did shorten the reproductive lifespan of these animals. In almost all instances where lions were contracepted after breeding it was done to minimize overrepresentation of that individual. Restricting the number of offspring per parent and managing those that breed [e.g. one individual in a cohort] is an effective measure in limiting inbreeding and genetic drift in small populations and one that is performed routinely in captive populations. What could not be discerned from the available data due to privacy reasons is the influence of housing; whether that be holding animals together or as individuals/single sexed groups, which occurs dynamically at an institutional level. Overall, the transfer history of lions in this study had no impact on litter size. The mean litter size of 2.8 is marginally higher than those reported in some free-ranging populations [70], but comparable to those of small, reintroduced populations where mean litter sizes range between 2.8 cubs and 3 cubs per litter [71]. It is also higher than the 1.6 cubs reported by Addis Ababa Zoo when similar reproductive parameters were investigated [72,73] highlights a range of social situations in captive lions that can be influential to larger litter sizes including, fewer males, the level of competition between adults, or the cohesiveness of females.

Interestingly in this study there was no impact of a lionesses age on litter size, which contrasts with other captive carnivore studies. For instance, older cheetah queens produce fewer cubs than younger females suggesting a decline in reproductive potential among older cats [74]. Mortality rates of free-ranging lions vary greatly from as low as 12% in Karangwa Game Reserve in South Africa where there is resident prey species, to >50% in the Serengeti Plains where prey is migratory. In such populations the main cause of neonatal mortality is starvation and infanticide from incoming males [75]. In captive populations higher survival rates are to be expected as the supply of food is consistent, and conspecific aggression from despots can be controlled by initially separating lionesses and then the slow introduction of cubs to the rest of the pride when they reach an appropriate age. The 28% cub mortality reported in this study is considerably lower than rates reported from other captive lion populations [50%]. Cub senescence within the first week [70%] and month [80%] however was found to be similar to other captive bred large felid species [76,77].

Cub mortality was not impacted by littermate presence, the life stage at which a dam was transferred, dam age or litter size. It is somewhat surprising that litter size had no impact on cub mortality. Other studies on big cats have found the main cause of cub mortality to be starvation resulting from maternal rejection, and lionesses being less likely to care for single cubs. It was expected that the general presence of littermates would increase cub survival as, in wild populations, birth synchrony, and subsequent communal rearing improves cub survival. The lack of any relationship found in this study may suggest that, despite their relatedness, consistent access to food resources and the protection afforded by greater management between the sexes may outweigh the advantages of synchronous births. The relationship between cub mortality and the reproductive experience of a lioness [i.e. number of litters] suggests that the more experience a female has, the more likely she is to successfully raise cubs to maturity compared to inexperienced lionesses. Increasing breeding success and offspring survivorship in relation to dam experience has been demonstrated in many species, including captive Asiatic lions [78].

Lions in the Australasian captive population were observed to breed all year round with a peak in early summer. Changes in photoperiod resulting from the additional day length is a proximate factor for gonadotropin-releasing hormone [GnRH] and gonadal maturation, which helps to stimulate and regulate breeding behavior in many species [79]. The lack of seasonality observed in this study is consistent with free ranging populations [80], as well as other captive institutions that have recorded similar year-round breeding behavior. Free ranging lions have similar peaks in reproduction, correlated to births of prey species, thereby maximizing the survival of offspring [81]. Ex situ populations have the advantage of a reliable supply of food, key to sustaining optimum body condition which in turn is important for conception. Age-specific fecundity rates for females that remained in their natal facility were found to be much lower than conspecifics of the same age that were transferred to other institutions. This finding was unexpected and could, in part, reflect the limited number of females in this study that remained at their natal facility. Despite there being no differences in sex allocation at a population level, further investigation revealed that natal lionesses produced a greater proportion of male offspring analogous to the male bias in wild prides described by.

This contrasts with lionesses that were transferred, which had an almost equal or greater proportion of female offspring. Sex-biased maternal investment has not been studied extensively in felids but has been recorded in canids [82,83], primates [84], ungulates [85] and rodents [86]. Sex ratio theory predicts that mothers can invest in one sex more than another, resulting in a bias in sex ratio at birth [87] and, as such, the sex that is invested in should provide a greater return for parental fitness. Sex ratios in monogamous grey wolves are skewed towards females in low-density populations and reach parity in high-density populations, as predicted by the advantaged daughter hypothesis [88]. However, for polygynous, dimorphic species such as the lion, mothers in good condition at the time of conception tend to have male-biased litters [88]. Lionesses that are either in poor condition or under some degree of stress are more likely to produce daughters, suggesting that sex ratio adjustments might occur around the time of implantation.

Singleton females did produce more female cubs which may suggest that there was added stress at the time of conception. Alternatively, it could reflect an adaptive evolutionary strategy to produce more females [89] for colonization post dispersal, which for wild lions would be an advantage for hunting and rearing young. However refutes a male bias in litters born to lionesses in good body condition at the Kgalagadi Trans frontier Park, indicating that there was an equal sex ratio in cubs that were first detected [i.e. within three months of birth]. The net reproductive rate for each social group also mirrored the sex ratio findings indicating that the proportion of females born into natal facilities and cohort groups are predicted to decline in respective generations, with the proportion of female cubs from singleton females expected to increase. As expected, males remaining in their natal facility have the lowest net reproductive rate with cohort males predicted to contribute the greatest proportion of male cubs in following generations. These findings mimic free ranging populations with subadult males dispersing to minimize competition with older males. Transferring males before the age of maturity to fulfil breeding recommendations may contribute to increasing breeding success.

Conclusion

Replicating natural behaviors is a proven strategy to increase reproductive success in other captive carnivores, such as cheetah. Results from this study can help facilitate scientifically based management decisions to increase breeding success and cub survival of captive lions. Lionesses that stayed in their natal institution or those transferred before maturity as singletons were more successful at breeding than females transferred with littermates. In converse, transferring males to another facility had no impact on breeding success. This highlights that population managers should consider these factors when compiling transfer recommendations to maximize potential and future breeding opportunities. Zoo-managed breeding programs may enjoy greater successes if the transfer of females away from their natal prides is minimized.

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Authorship

The author was responsible for collating and analyzing the dataset and writing the manuscript.

Conflicts of interest

The author declares that there are no competing interests.

Data availability statement

The data that supports this study cannot be publicly shared due to ethical or privacy reasons.

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