CARE FOR THE RARE
Innovation at the Nexus Between Conservation, Animal Welfare & Public Engagement

Animal Welfare Priority Assessment: Summary Results and Interim Descriptive Analysis for African Lion (*Panthera leo*)

Sponsored by:

LIONSROCK Big Cat Sanctuary

FOUR PAWS

IUCN SSC Species Survival Commission
CONSERVATION PLANNING SPECIALIST GROUP Changing the Future for Wildlife
commercial member ASSOCIATION OF ZOOS & AQUARIUMS

ww.carefortherare.com
Design & Management Services
Care for the Rare Ltd is a registered company in England and Wales. Company Number: 10308418 VAT Reg. GB 446416784

CARE FOR THE RARE
Innovation at the Nexus Between Conservation, Animal Welfare & Public Engagement

Contents

Preamble

The following report contains a provisional review of the data harvested from the African lion (*Panthera leo*) welfare priority assessment, together with some initial commentary on the data. This assessment took place during October and November 2023 and was generously sponsored by Four Paws International and launched from the home of the EEP (breeding program) for African lion; Givskud Zoo, Denmark.

Twenty-six experts from 9 countries assessed 35 behaviours and cognitive processes against 16 criteria yielding 14,560 data points, from which a ranked welfare priority (AWPIS score) has been established for the species.

The notes and analysis here are intentionally provisional; a more comprehensive review, including more in-depth interpretation and species-appropriate recommendations will follow, incorporating the input of additional expert contributors.

For ease of review, key points are underlined in the main text, and summarised at the end.

Participant Background

In total, 26 panellists from nine countries participated in the African lion welfare priority assessment. Panellists were aggregated into three cohorts based on their self-reported experience as ex-situ, in-situ, or welfare experts. 65% of experts were classified as ex-situ specialists, with 19% and 25% made up of in-situ and welfare science specialists respectively. The composition of the panel and its constituent cohorts is summarised in Table 1 and Figure 1. Ideally, the assessment would have had more contributors, particularly those with experience of the species in the wild. However, in previous assessments, results have been consistent between different cohorts, despite the number of constituent members of each cohort being relatively small. And so, whilst larger numbers of participants adds further credence to the results, evidence from previous assessments suggests, additional participants would be unlikely to change the overall findings.

Cohort	*Total Participants*	*Proportion*	*Average years of experience by cohort*				
			In-situ management	*In-situ research*	*Ex-situ management*	*Ex-situ research*	*Welfare research*
Ex-situ	17	65%	0.24	0.18	14.94	3.12	5.94
In-situ	5	19%	11.20	22.00	5.40	5.20	6.00
Welfare science	4	15%	1.25	1.75	9.50	3.75	15.50

Table 1. Average years of experience in each area, including overlapping years of experience.

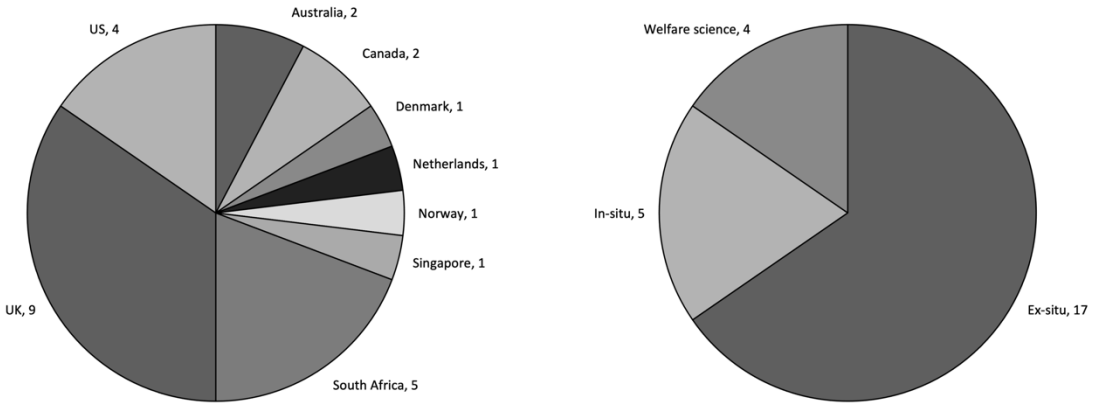


Figure 1. Panel composition by expert location and cohort

Cohort Effect on AWPIS Values

It is possible to test whether the results might be negatively impacted by the absolute number of panellists together with the relative proportions of experts from differing backgrounds by comparing the results of the different cohort groups. The mean assessment values for behaviours and cognitive processes provided by each cohort are presented in Figure 2. Visually, there appears to be good overall agreement amongst the cohorts, however, the welfare cohort appear to rank several behaviours lower than the in-situ and ex-situ cohorts, notably foraging, hunting alone, and grooming. To investigate the potential impact of both panellist cohort and the specific behaviour and cognitive process on welfare significance (AWPIS value), a two-way ANOVA followed by an

Intraclass Correlation Coefficient (ICC) was conducted following standard procedures, the results of which are summarised in Table 2. The two-way ANOVA revealed a highly significant effect of behaviour / cognitive process type on AWPIS values (F(34,68) = 27.21, p = 4.16E-28), indicating that not all naturally occurring behaviours and cognitive processes are equally important to the welfare of captive African lions. Whereas, whilst there was a marginally significant effect of the expert panel cohort (F(2,68) = 4.30, p = 0.018) according to the two-way ANOVA, the ICC confirmed good to excellent inter-cohort reliability giving confidence to the conclusion that despite differences in expert background compounded by a wide variation in the numbers of participants in each cohort, the relative AWPIS assessments for each behaviour and cognitive process were not systematically influenced by cohort. This finding provides additional assurances as to the validity of the dataset and enables us to safely combine data from all cohorts into a single AWPIS assessment value for each behaviour and cognitive process - summarised in Figure 3.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Behaviours / cognitive processes	0.96283544	34	0.02831869	27.2145122	4.1589E-28	1.60115933
Cohorts	0.00893996	2	0.00446998	4.2956903	0.01750598	3.13167197
Error	0.07075897	68	0.00104057			
Total	1.04253437	104				
Intraclass Correlation Coefficient			*0.88871791*			

Table 2. Two-Way ANOVA and Intraclass Correlation Coefficient (ICC) reviewing the impact of behaviour / cognitive process type and cohort on AWPIS values

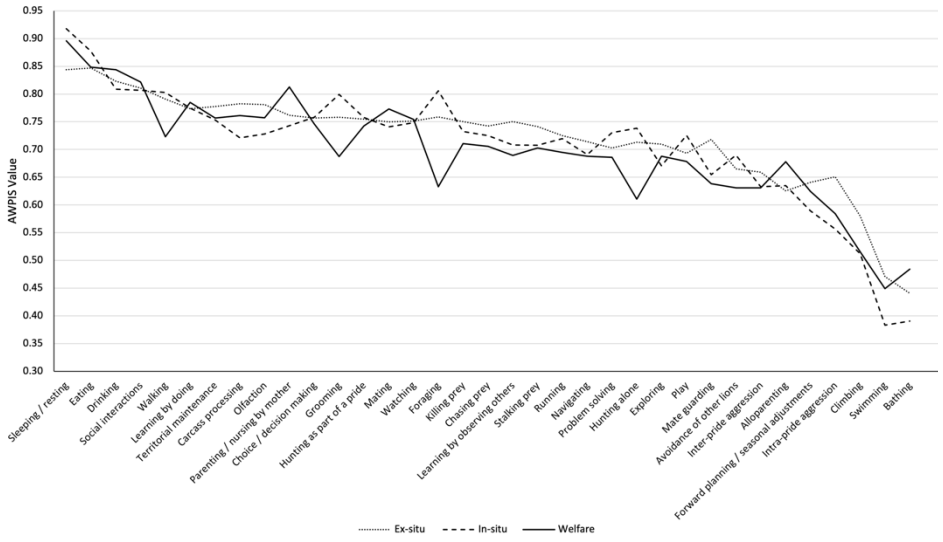


Figure 2. Mean AWPIS values provided by the three expert panel cohorts for each behaviour / cognitive process.

The apparent inconsistency between the results of the ICC and the two-way ANOVA on the effect of cohort on AWPIS scores is a function of their relative sensitivities to systematic and random variations, with ICC being better suited to detect agreement in rankings even where there are variations in absolute scores. ICC is therefore more appropriate a tool in determining differences in AWPIS values between cohorts than a two-way ANOVA since AWPIS works by considering relative rankings / AWPIS values of specific behaviours and cognitive process within individual panel assessments, or within groups in which data has already been pooled, rather than absolute AWPIS values compared between panellists and groups. And so, whilst one panellist or a cohort

may produce consistently higher AWPIS values than an another, it is their relative rankings / AWPIS value of each behaviour / cognitive process that is key in determining welfare priorities using AWPIS data.

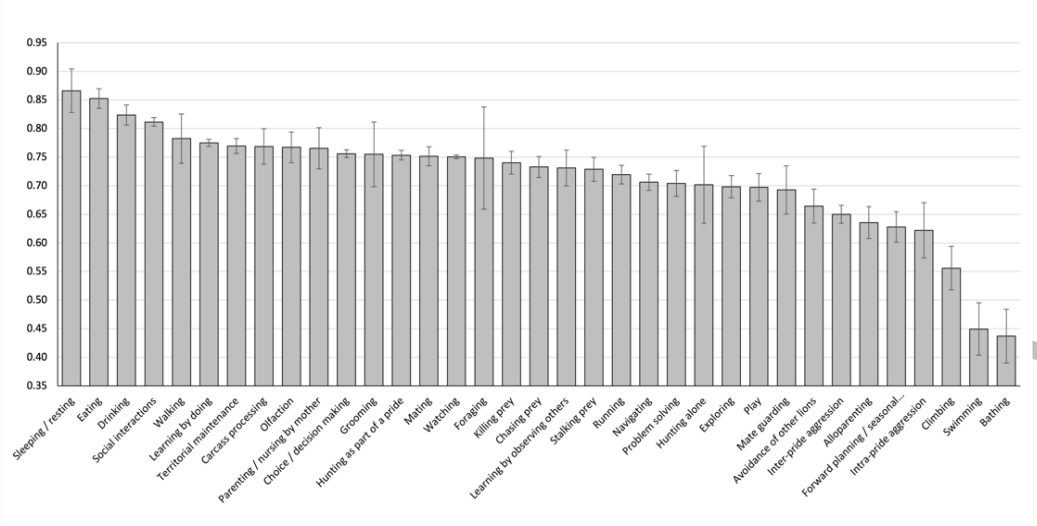


Figure 3. Mean AWPIS values provided by all panellists for each behaviour / cognitive process.

Welfare significance / AWPIS values

The consolidated AWPIS values for each behaviour / cognitive process are set out in Figure 3. A one-way ANOVA revealed a significant impact of behaviour category on AWPIS values ($F(1,68) = 94.65$, $p < 0.0001$), with a substantial difference observed between categories of behaviour and cognitive process, underscoring the influence of behaviour types on mean AWPIS values / welfare significance (see Figure 4). As with previous assessments, behaviours associated with physiological necessities (eating, resting, and drinking) scored most highly, underlining the importance of addressing the psychological aspects of those behaviours in captivity rather than merely addressing the physiological needs, which will be discussed in more detail later.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	80.5074122	1	80.5074122	94.6539961	<0.0001	3.98189626
Within Groups	57.837009	68	0.85054425			
Total	138.344421	69				

Table 3. One-Way ANOVA reviewing the impact of behaviour / cognitive process type on AWPIS values.

Captive Curtailment and Welfare Risk Factors

While, accurately and comprehensively assessing the extent to which behaviours and cognitive process are curtailed in captivity in terms of both comparability and prevalence of expression would preferably involve a more in-depth analysis than was possible within the scope of the AWPIS assessment, the data incorporated into the AWPIS model, is nonetheless informative.

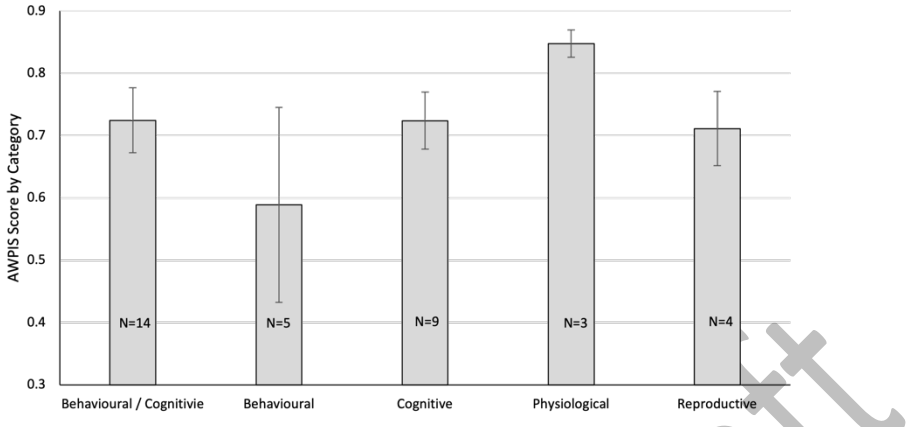


Figure 4. Mean AWPIS values of behaviours and cognitive processes aggregated by type.

To assess whether there is an interaction between the comparability of captive behavioural and cognitive expression with expression in the wild, and the prevalence of expression amongst captive populations, a Pearson's correlation coefficient was calculated. The results revealed an extremely significant positive correlation between captive comparability and captive prevalence of behaviours and cognitive processes ($r(35) = 0.821$, $p = <0.00001$), see Figure 5. In other words, the more comparable the expression of behaviours and cognitive processes in captivity were considered to expression in the wild, the more likely they were believed to be expressed amongst captive lions.

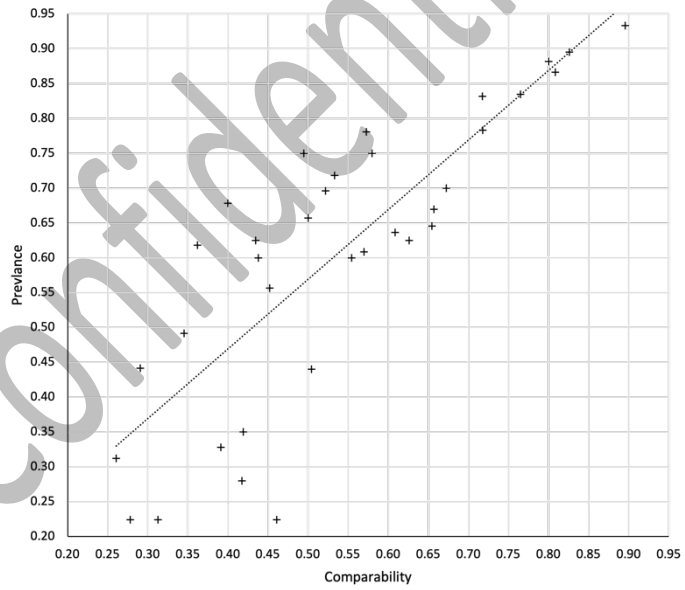


Figure 5. The relationship between the extent to which captive expression of behaviours / cognitive processes are comparable to expression in the wild and their prevalence in captive population.

A multiple regression analysis was undertaken to explore the relationships between comparability, prevalence, and AWPIS value. The model was statistically significant ($F(2, 32) = 7.82$, $p = 0.0017$),

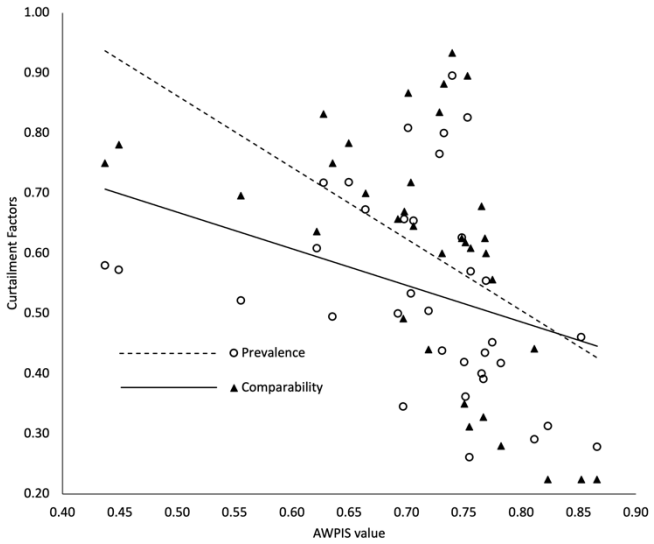


Figure 6. The relationship between the extent to which captive expression of behaviours / cognitive processes are comparable to expression in the wild and their prevalence in captive population with their respective AWPIS value.

explaining 32.82% of the variance in AWPIS scores ($R^2 = 0.3283$). While comparability of expression was not found to be statistically significant in effecting AWPIS scores ($\beta = 0.182$, $p = 0.204$), there was a highly significant negative association between AWPIS scores and prevalence of captive expression ($\beta = -0.369$, $p = 0.003$), suggesting that in this analysis, prevalence plays a more influential role in predicting AWPIS values than comparability (see Figure 6).

Whilst acknowledging the limitations of the existing dataset to adequately quantify the true extent of captive curtailment, a Captive Curtailment Index (CCI) was created to consider its overall relationship with welfare significance / AWPIS values. While multiple regression analysis suggests prevalence has a stronger relationship with AWPIS values than comparability, the extent which expression is comparable to the wild will be more influential to welfare at the individual animal level, with prevalence better reflecting a population level risk dimension. Subsequently, CCI is ostensibly calculated using the following formula which places a greater emphasis on comparability due to its greater direct impact on the welfare of individuals:

CCI = (Comparability x 66.66…%) + (Prevalence x 33.33…%)

A Pearson's correlation analysis demonstrated a highly significant negative relationship between Captive Curtailment Index (CCI) and AWPIS values / welfare index, with behaviours and cognitive processes of higher welfare significance seemingly being less curtailed across captive lion populations in terms of both comparability and prevalence ($r(35) = -0.433$, $p = 0.009$), see Figure 7.

While the AWPIS ranking set out in Figure 3 establishes the relative welfare significance of behaviours and cognitive processes for African lion which should inform both facility design and management planning, by plotting the relationship between AWPIS values against CCI it is possible to establish a welfare risk matrix which identifies those behaviours and cognitive processes that are most likely to have the biggest impact across captive lion populations (see Figure 7). Behaviours

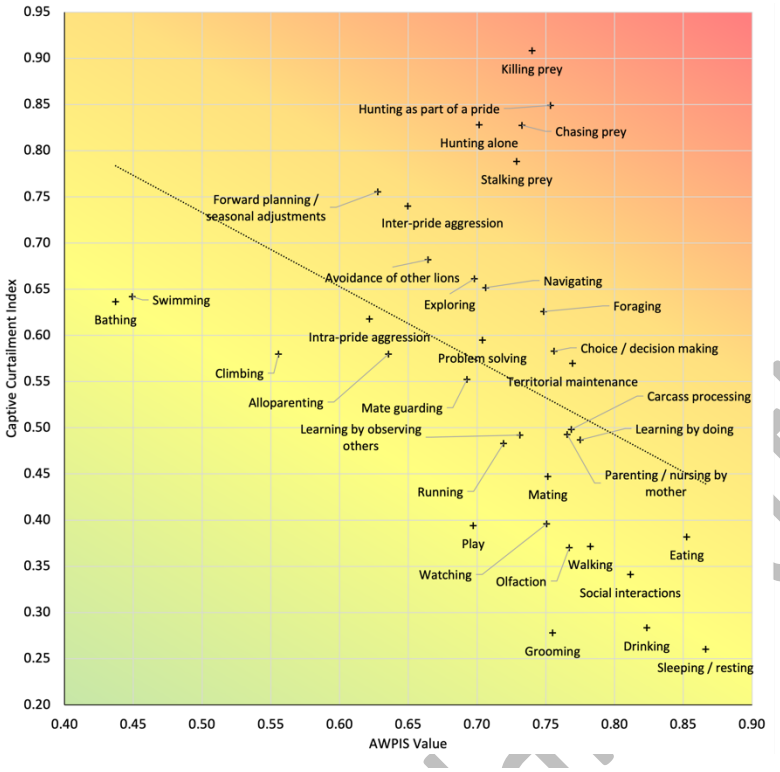


Figure 7. The relationship between captive curtailment and AWPIS value of each behaviour and cognitive process

and cognitive processes which rank highly from a welfare perspective but also are the most widely and functionally curtailed across captive lion populations, likely pose the greater risk to captive African lion population welfare and are located in the orange and red zones of Figure 7, whereas those which pose a lesser risk tend toward the greener zones.

It's important to acknowledge the potential bidirectional nature of this relationship and subsequently, the range of different and not necessarily mutually exclusive interpretations of these results. The first explanation is that captive management accurately reflects welfare needs, whether by accident or design, with greater effort afforded behaviours and cognitive process that are of greater welfare significance. Alternatively, it's possible that those behaviours and cognitive process that are of higher welfare significance, tend to be easier to cater for. This explanation might to apply to physiological necessities (rest, eating, and drinking) which could influence this result given their high ranking. Finally, it is also possible that welfare significance influences perceptions of curtailment amongst panellists, with behaviours and cognitive process perceived to be of high welfare significance being perceived to be better catered for. However, with the possible exception of physiological necessities, this explanation appears less likely as in previous assessments, surveyed expert perceptions of the welfare significance of behaviours and cognitive processes do not necessarily align with AWPIS results, and the data is founded on insights from panellists with experience outside captive management.

In addition to the risk matrix, it is also possible to consolidate AWPIS values with the extent to which behaviours and cognitive processes are quantitively and qualitatively curtailed in captivity (prevalence and comparability), to establish a welfare risk factor (WRF). Given that the AWPIS

value determines the overall welfare significance, this forms the bulk of the risk factor, followed by the extent to which expression is comparable to the wild, together with prevalence of expression in captivity, in the same relative ratio used to establish the CCI. The formula by which the welfare risk factor (WRF) is calculated is as follows:

WRF = (AWPIS x 0.7)+(Comparability x 0.2) + (Prevalence x 0.1)

Ranks based on WRF values will differ from ranks based on AWPIS values by virtue of the interaction between welfare significance and extent to which captivity caters for behaviours and cognitive processes; behaviours and cognitive processes of high welfare significance that are more effectively catered for in captivity in terms of population prevalence and comparability may for example pose a lesser welfare risk at a population level than lower ranking behaviours and cognitive opportunities that are highly constrained amongst captive populations. This appears to be the case with African lions, where hunting related behaviours rank highly in terms of WRF, despite their "middling" AWPIS ranking with hunting related behaviours ranging from 13th to 24th out of 35, with a mean AWPIS rank of 18.4 (see Figure 8).

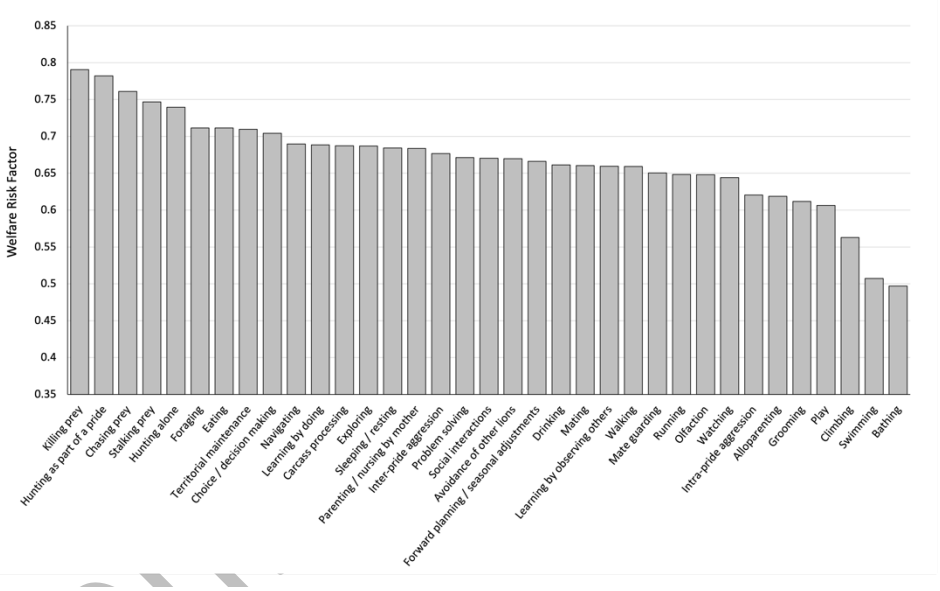


Figure 8. Welfare Risk Factors (WRF) of captive African lions by behaviour and cognitive process

It's important to reiterate that the formulae / algorithms employed to determine the CCI, WRF and indeed AWPIS are not rooted in mathematical proofs, rather, they are based on logical and defendable, evidence based a priori assumptions regarding the relative influence of specific component of welfare risks and impacts. As of now, these assumptions remain untested and, to some extent are potentially unprovable. However, despite lacking mathematical validation, these formulae provide a conceptual basis and mechanism by which welfare risks, impacts and priorities for captive African lion can be considered, and explored further in a real-world context.

Comparisons with other Species.

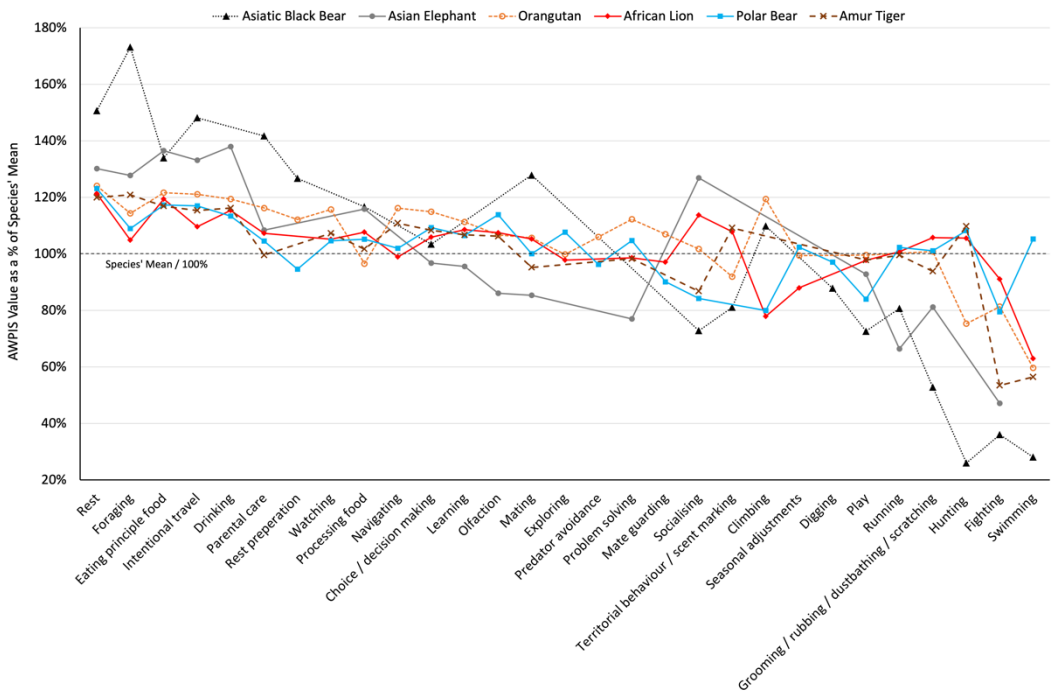


Figure 9. AWPIS values for comparable behaviours and cognitive processes across a selection of species

Whilst AWPIS is intended to allow the relative welfare significance of behaviours and cognitive processes to be compared within rather than between species, and because the methodology continues to evolve, direct inter-species comparisons of AWPIS values are less reliable than intra-species comparisons. However, valid comparisons can be made by comparing the relative AWPIS ranks of behaviours and cognitive processes between species together with AWPIS values as a % of each species' AWPIS means. Further adjustments also need to be made to consolidate behavioural and cognitive categories to enable inter-specific comparison, as well as eliminating some categories for which comparators are not present in other species – such as for example, hunting on sea-ice for polar bears.

Despite the taxonomic variability and differences in behavioural ecology between the range of species for which AWPIS assessments have been completed, the results set out in Figure 9 demonstrate some clear trends and a consistently high welfare ranking of physiological necessities (rest, eating and drinking). Behaviours linked to intentional travel, including foraging, ranked highest amongst those behaviours that aren't physiological necessities in all species except African lions, for which walking / intentional travel ranks immediately below sociality. The high ranking of sociality in African lions, places it on a par in terms of relative welfare significance with Asian elephants. There is a value in recognising that sociality is likely as important to African lions as it is to Asian elephants for two reasons; first it is more widely accepted that keeping elephants in isolation is unacceptable than it is for lions, and secondly, it supports the case that sociality must be considered the lens through which all lion welfare priorities are viewed.

Given the close taxonomic relatedness of African lion and Amur tiger combined with specific differences in behavioural ecology, comparing their respective AWPIS results as percentage of species' mean in more detail will be useful in providing some insights into how behavioural ecology influences welfare risks. Additionally, because of the behavioural overlap between the two species, it is possible to consider more shared behaviours than is possible across the six species for which full AWPIS assessments have been completed. Figure 10 compares AWPIS values as a % of each species' mean for the comparable behaviour and cognitive processes categories for Amur tiger and African lion. Foraging / intentional travel is markedly more important for tigers than it is lions, as are exploring / navigating, and behaviours related to hunting, whereas socialising and "fighting" (inter-pride aggression) are relatively more important to lions than tigers.

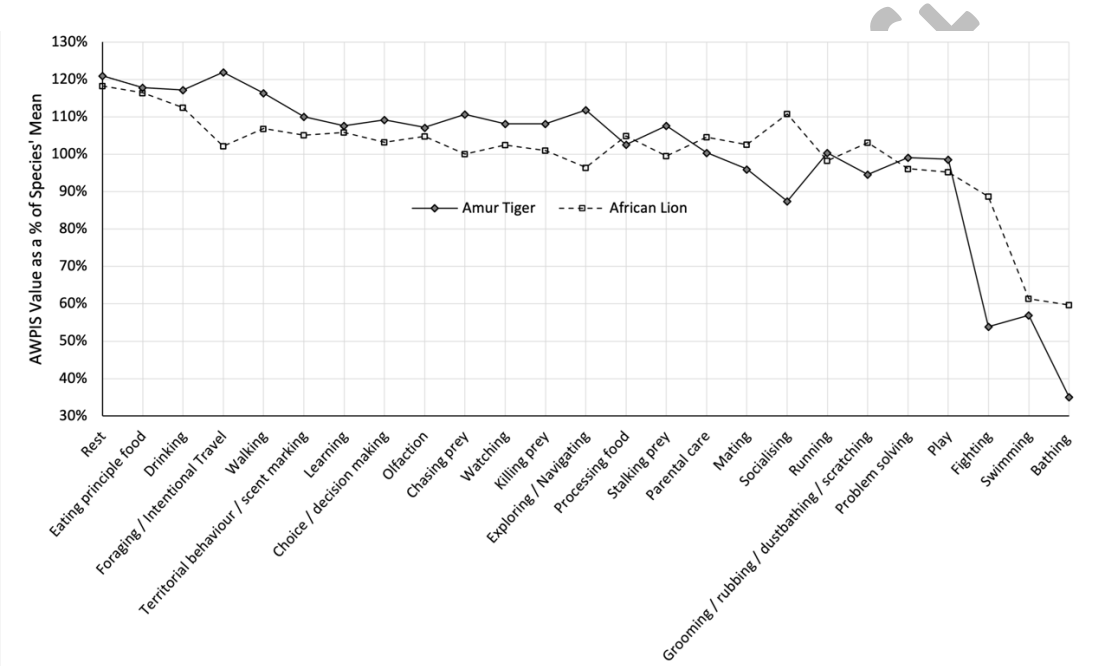


Figure 10. Comparison of AWPIS values as a % of species means of comparable behaviours between African lions and Amur tigers.

A Wilcoxon Signed-Rank Test revealed no significant difference in AWPIS ranks of behaviours between the species ($W = 137.5$, $p > 0.05$) and a Spearman's Rank Correlation revealed there was a significant correlation between the relative ranks of shared behaviours and cognitive processes ($r_s = 0.54231$, $n = 25$, p (2-tailed) = 0.0051). The similarity in ranks between most of the two species' shared behaviours and cognitive processes underlines their ecological, evolutionary, and taxonomic similarities and also provides further reassurance into the consistency of the AWPIS methodology between different assessments. However, while these results suggest overall agreement in AWPIS ranks, the scatter plot in Figure 11 reveals the subtle yet crucial differences that do exist between the two species in terms of their relative ranks in behaviours and cognitive processes. Those behaviours and cognitive processes in the red areas of Figure 11 are relatively more important to lions than tigers, whereas those thar are relatively more important to tigers occupy the bluer areas. The difference in ranks of behaviours and cognitive processes between African lion and Amur tigers are also compared in Figure 12 which plots numerical rank difference between the two species. Collectively, this reinforces the impacts of differences in behavioural and cognitive ecology linked to sociality and travel between these closely related species and reinforce

the need for far more targeted, species-specific management and facility design. That behaviours linked to sociality, including grooming, mating, and fighting, are more important to lions than tigers is self-explanatory, but that travel, foraging, navigation, and to a lesser degree hunting related behaviours are less important to African lions than tigers is perhaps less obvious at first and worthy of consideration.

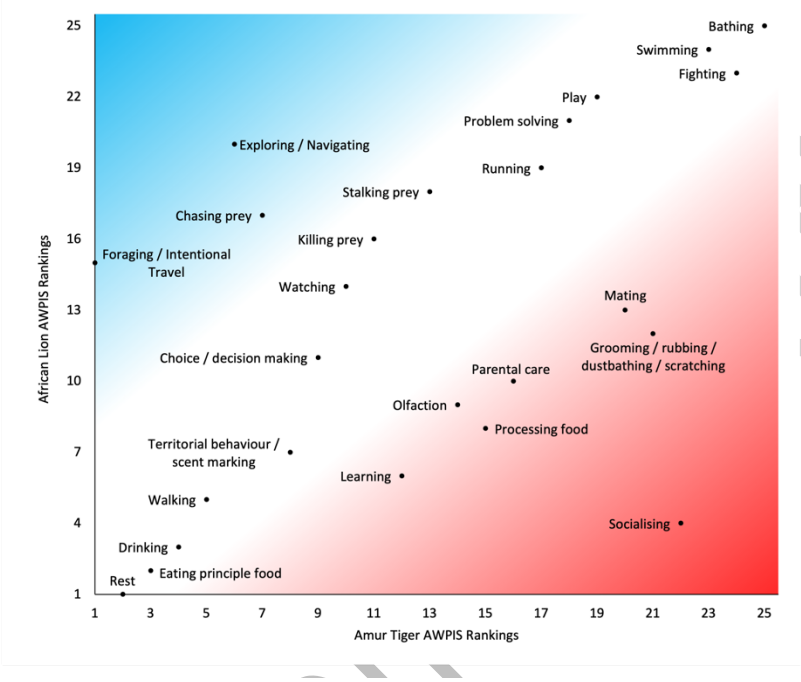


Figure 11. The correlation of AWPIS ranks for comparable behaviours and cognitive processes between African lions and Amur tigers; the red zone represents behaviours and cognitive processes that are relatively more important to lions than tigers, whereas those in the blue zone are relatively more important to tigers than lions.

As a solitary species, in a less productive habitat with markedly lower prey density, and in which prey also tend to live in smaller groups, Amur tigers typically range more widely than African lions, and subsequently, foraging / intentional travel, navigating, and exploring likely represents a greater behavioural and cognitive burden on individual Amur tigers, than it does on individual lions living as part of a pride in a smaller home-range. This is supported by the marked difference in activity levels of wild tigers (42.75%) compared to wild lions (13%) (Kroshko et al 2016), a home range that can reach 2,500km^2 for tigers (Hernandez-Blanco et al 2015) compared to a median for lions of 103km^2 (Kroshko et al 2016) which collectively may explain why tigers tend to stereotype 36% more in captive environments compared to lions (see Kroshko et al 2016).

Differences in welfare priorities linked to hunting are more nuanced than those linked to sociality and travel. While prey density, maximum prey size, and prey herd size will be lower for Amur tigers than African lions due to the influence of latitude on ecosystem productivity and the tendency for grazing ungulates to exist in larger herds than forest-dwelling, browsing, or rooting species (Szemán et al. 2020), combined with the greater capacity of a pride of lions to kill bigger prey than a single tiger, the modal prey size for African lions may be significantly smaller than it is for Amur

tigers. In the Kruger for example, impala weighing approximately 40kg make up over 50% of kills for lions (Owen-Smith & Mills 2008), whereas wild boar weighing around 100kg make up over half of the diet of Amur tigers across the Sino-Russian border (Dou et al. 2019). Add to this, the average pride size of African lions being ~15 (Schaller 1972), their average meal size is likely much smaller than it is for Amur tigers who not only have larger modal prey, but do not have to share kills. Subsequently, individual kills will typically sate adult Amur tigers, potentially for days at a time, a scenario that appears far less common for lions, particularly when living in a pride context. This is borne out in the relative kill frequency, with lions on average completing 0.22 kills from 1.18 hunts in a 24hr period compared to a tiger's kill frequency of 0.13 (Kroshko et al 2016). And so, whilst hunting is a daily necessity for a pride of African lions as a consequence of their sociality, it's a rarer event for solitary Amur tigers. However, unlike Amur tigers, not all lions in a pride necessarily have to hunt to eat, with males routinely not hunting (Funston 1998 cf Borrego & Gaines 2016), and not all females participating in all hunts (Borrego & Gaines 2016). And so, whilst individual tigers might hunt less frequently than a pride of lions, outside of opportunities to scavenge or steal prey from conspecifics or other predators, all Amur tigers are required to hunt, whereas, due to greater productivity levels creating even more opportunities for scavenging and kleptoparasitism, combined with their sociality, lions likely have an even more flexible relationship with hunting than Amur tigers.

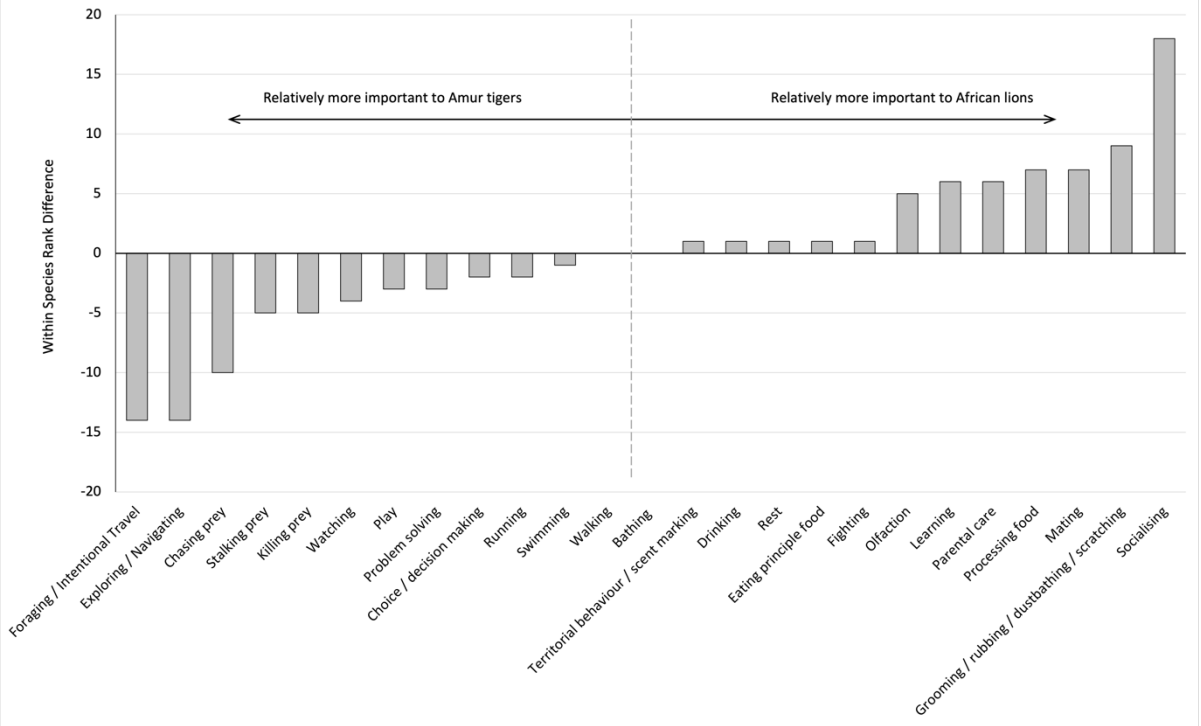


Figure 12. A comparison of AWPIS ranks of comparable behaviours and cognitive processes between African lions and Amur tigers.

Provisional Synopsis

When it was first posited that tigers had a flexible relationship with hunting from a motivational and captive welfare perspective, it contradicted received wisdom about large carnivore welfare prioritisation as it is manifest in prevailing enrichment paradigms. It now seems the same is also true of lions. Our understanding of what matters to tiger welfare in captivity has shifted from hunting related behaviours towards behaviours and cognitive processes linked to travel and territory maintenance; foraging, travel, and navigation / exploration (Veasey 2020). Whilst, hunting related behaviours are likely similarly, or even marginally less critical to lion welfare than they are to the welfare of captive tigers, behaviours linked to travel have not emerged as an elevated priority in the same way for African lions as they did for Amur tigers. Walking and territory maintenance are more or less comparable between the two species (see Figures 10-12), but foraging, exploring and navigating, rank markedly lower for lions than tigers. Instead for lions, sociality, emerges as the preeminent welfare focus, and it is reasonable to assume that all important behaviours and cognitive processes need to be seen through the context of sociality.

Lions are unique amongst the Felidae in being social, and it is widely recognised that sociality in any species evolves when the fitness benefits of group-living, outweigh the risks and costs, most notably in relation to predation, disease, and competition for resources or reproductive opportunities. Sociality in lions is a product of ecological, environmental, and evolutionary factors, centred around resource distribution, and in particular, it's believed the pride structure offers advantages in resource defence, particularly when resources are unevenly distributed in time and space (see Johnson et al., 2002; Macdonald & Johnson, 2015). Across much of Africa outside of closed canopy forest, lion density correlates with ecosystem productivity and prey density, meaning there are geographic and temporal variation in pride sizes, with smaller prides and even singletons being more common in arid areas, and larger prides in resource-rich, more competitive environments where the defence of carcasses becomes a critical factor (Kissui et al., 2009; Kotze et al., 2018; Mosser et al., 2009).

This "resource dispersion hypothesis" proposes that when resources are dispersed and yet abundant, individuals can aggregate into groups that share the same space at little cost to each other. For lions in circumstance where abundant yet dispersed prey mean social groups cease to be a disadvantage, smaller prides will be exposed to an increased risk of kleptoparasitism (stealing food) from bigger prides, further accelerating this effect. Kleptoprasitism results in more frequent hunting, requiring lions to expend additional energy, and take greater risks for comparable food intake were no competition present. Subsequently, in situations where competition is greater due to an abundance of prey increasing predator densities, group size may be larger to counter interference and competition from other lions, as well as other social predators such as hyena (Höner et al., 2002).

Furthermore, the risky nature of hunting, where lions regularly pursue prey larger than themselves, means group hunting can be an important risk mitigation strategy. This collaborative approach can also improve capture success, improve the ability to kill larger, more diverse prey species, and facilitate a division of labour within the pride. However, the relationship between per capita food intake is complex; while some research supports the case that lions achieve higher capture rates when hunting in groups compared to solitary efforts (Van Valkenburgh & White, 2021; Schaller & Lowther, 1969; Schaller, 1972), other research suggests that larger hunting groups do not necessarily make more captures per hunting attempt than smaller groups or singletons,

with group hunting potentially limiting search efficiency, reducing overall prey encounter rates (Gittleman, 1986; Packer & Ruttan, 1988). Furthermore, sociality requires kills to be shared meaning whilst solitary hunters may take smaller prey, they can still enjoy larger overall meals because there is no need to share it, a situation that becomes more acute when food is scarce (Packer et al., 1990). However, despite these effects, as previously alluded to, group size may still be selected for if it mitigates the net impacts effects kleptoparasitism.

While the reasons behind pride development and evolution are multifaceted and include a wider range of interconnected factors ranging from prey density and distribution, the probability of encountering other lions, competition for food and territories, the cost / benefits of group hunting, optimal outbreeding, and the division of labour, the unique sociality of lions is ultimately a mechanism to optimise per capita rates of food intake that has evolved over countless generations, but is nonetheless, highly context specific. And there are two important points to consider here in respect of the implications of sociality on captive African lion welfare in light of the results of this assessment, which at first might seem to counteract each other. The first is that sociality in African lions is of high evolutionary significance and therefore highly motivated for, and consequently, it is also of high welfare significance, as this assessment confirms. The second is that sociality / pride size is flexible, suggesting lions may have a flexible relationship with their social circumstances / group size and how it might influence captive welfare.

However, whilst sociality may be flexible, being solitary, whether for males or females, in nature arises as a consequence of sub-optimal and typically transitory circumstances. Such situations might occur when food is in extremely short supply or when social circumstance are in a state of flux. This might occur when incumbent males are usurped from a pride which can result in overthrown males becoming solitary or part of a dyad, an event that may also drive individual females from prides to avoid infanticide of their offspring by new resident males. And so, whilst recognising sociality can flex according to external forces, where they do sufficient to create solitary situations for lions, those circumstances are invariably highly challenging for the effected individuals. This means that social flexibility will not insulate lions from welfare challenges associated with a solitary or sub-optimal social situation in captivity. The apparent flexibility in relation to sociality for lions is therefore entirely different from the flexibility lions and tigers appear to have in relation to hunting, which arise out of positive circumstances in nature – a "free meal" in which food can be consumed without the need to hunt such as might arise due to scavenging or kleptoparasitism.

Consequently, sociality must be viewed as a fundamental need for African lions. However, intuitive these findings are, they have implications far beyond whether lions are maintained in isolation or not. Firstly, captive lion welfare needs to be viewed in part as a function of the cohesiveness of social groups, not simply whether lions are in social groups or not. Secondly, all behaviours and cognitive opportunities need to be viewed through the lens of sociality. If this is achieved through strategies that might for example include social feeding and other motivated social activities, with all other relevant factors such as relatedness being equal, this is likely to feed back to support social cohesion. Opportunities for captive lions to be empowered to act together or independently as they choose, to achieve shared, motivated goals, replicating the fission-fusion dynamic seen in the wild, are likely improve social cohesion. And so, whilst hunting related behaviours may not be as important to the welfare of lions as might have been believed to be the case prior to this assessment, the value hunting related behaviours represent, may stem from the social opportunities they create / require. The fact that uniquely amongst species assessed so far, that

socialising was the most important welfare priority after physiological necessities, ahead of walking / foraging / intentional travel, underlines just how uniquely important sociality is to captive lion welfare.

Whilst captive management invariably caters for physiological necessities, their high AWPIS scores underline the importance of adequately catering for the psychological components of those necessities, and for African lions, it is essential to consider how these necessities are catered for within the context of a highly social species. Subsequently, whilst all captive management allows African lions to feed, drink, and rest, few come close to truly enabling all of these behaviours to occur socially, or in a species appropriate manner (see Graphic 1).

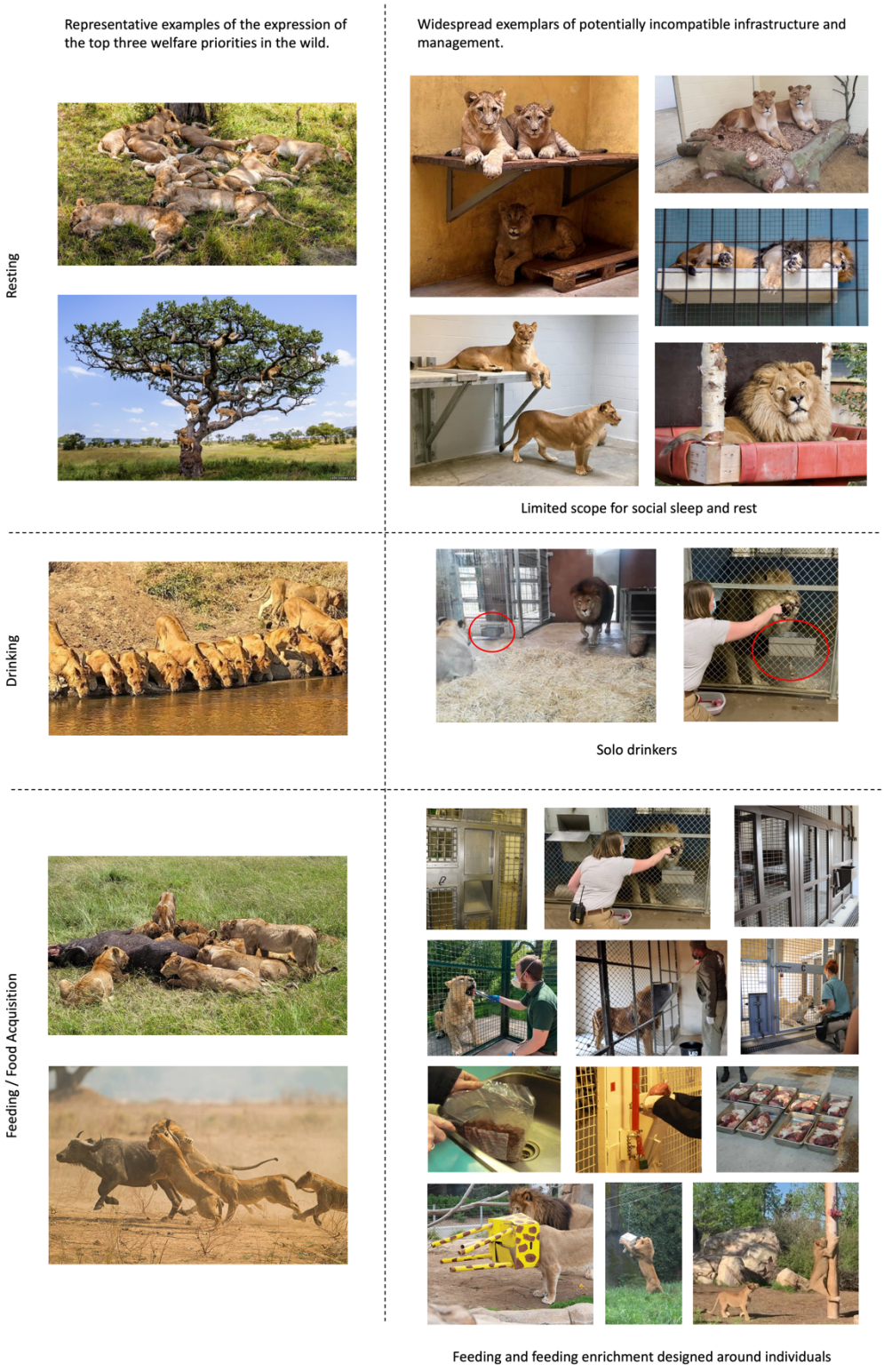
As previously noted, the welfare significance of lion sociality necessitates all other priorities to be viewed through the lens of sociality. Thus, for example, feeding lions individual portions of meat dispersed throughout paddocks to minimise competition, or even feeding lions separately in dens, may have unforeseen welfare consequences. While it is commonly stated that lion society is egalitarian, lacking a rigid hierarchy, intragroup competition is a recognised phenomenon within lion prides (VanderWaal et al., 2009), and will be particularly heightened when feeding. Consequently, the absence of opportunities for active competition over a single carcass in captivity, could potentially erode the 'pecking order', or other as yet unobserved social constructs within the pride, which, in turn, could contribute to heightened social stress over the long term, even if a hierarchy is only outwardly discernible during instances of food competition. The collapse in captive pride structures over time will likely arise primarily due to a lack of species-typical reproduction and mortality, but a lack of appropriate social opportunities to reinforce the function of the pride, may also play a crucial part in this. Similarly, feeding related enrichments need to focus on establish social / cooperative activities rather than solitary ones, in particular ones where lions are required to cooperate to achieve outcomes as they do when hunting.

Whilst the importance of sociality is to some degree self-evident, there are no mandatory standards pertaining to sociality, and the majority of prevailing management practices do not adequately account for the profoundly social nature of African lions. Maintaining African lions in species appropriate social groups wherever possible, should be considered as a welfare priority, but one that it is acknowledged, needs to be balanced against the requirement to stringently manage reproduction in captive populations.

Next Steps

Continue to work on the full-report and pending discussions with the Four Paws team, agree the format of the report, and reach out to additional contributors.

Start work on developing design and management solutions to address the welfare priorities identified in this report, for deployment at Lions Rock and across the Four Paws sanctuary network.



Graphic 1: Images illustrating how captive management, enrichment and facility design norms bear little resemblance to wild social norms, and subsequently, likely compromise welfare.

Summary

- The Animal Welfare Priority Identification System (AWPIS) is a process which seeks to establish the relative welfare significance of behaviours and cognitive processes for a given species. The process hinges on the relationship between evolution and captive animal welfare. The greater the evolutionary significance of a behaviour or cognitive process, the more strongly and / or more frequently it will be motivated. Consequently, if the expression of behaviours and cognitive processes are frustrated by the captive state, the negative welfare impact of that will be broadly proportional to their evolutionary significance. This is modulated by the origin of the stimulus; externally motivated behaviours and cognitive processes (such as predator evasion) pose a lesser welfare risk if the motivating stimulus is removed compared to internally motivated behaviours and cognitive processes (such as rest) which arise regardless of the environment an animal finds itself in.
- Using species-experts from a range of backgrounds, behaviours and cognitive processes are ranked against 16 criteria that provide insights into their evolutionary significance, motivational characteristics, and welfare impacts, from which an AWPIS value is created representing the relative welfare significance of that behaviour or cognitive process to that species.
- Twenty-six experts from nine countries participated in the African lion welfare priority assessment. 65% of these participants were ex-situ specialists, while 19% and 25% were specialists in in-situ and welfare science respectively.
- The AWPIS values for each behaviour and cognitive process were not systematically influenced by cohort size, or expert background, reinforcing the validity of the combined dataset using data from all participants.
- Behaviour or cognitive process type was shown to significantly effect AWPIS values underscoring the point that not all naturally occurring behaviours and cognitive opportunities are equally important to captive lion welfare. This in turn reinforces the necessity to understand the actual welfare significance of each behaviour and cognitive process to optimise captive care and facility design.
- Behaviours associated with physiological necessities such as eating, resting, and drinking were identified as being of the greatest welfare significance. This underscores the importance of addressing not only the physiological outcomes of these behaviours, but their associated psychological and cognitive aspects as well.
- There was found to be a negative association between AWPIS scores / welfare significance and the extent to which expression in captivity was curtailed. This suggest that overall, the more important a behaviour and cognitive processes is to captive lion welfare, the less it is curtailed across captive lion populations in terms of both comparability and prevalence. There are three possible explanations for this; firstly, captive management is accurately targeted to attempt to address welfare needs (by accident or design) prioritising behaviours and cognitive processes of greater welfare significance. Secondly, behaviours and cognitive processes of higher welfare significance might be easier to provide for, and finally, welfare significance may influence panellists' perceptions of curtailment in captivity.
- Unique amongst species for which AWPIS assessments have been completed, sociality emerged as a being the greatest welfare priority to lions after physiological necessities, followed by walking, learning and territorial maintenance.
- Sociality for lions appears to be of comparable importance to their captive welfare as it is to captive Asian elephants, a species for which the importance of sociality to captive welfare is more widely recognised and enshrined in regulatory standards.

- Lions are unique amongst large felids in having evolved to be social. Sociality confers evolutionary benefits to lions, making it a highly motivated component of their lives, and therefore highly pertinent to captive welfare. The inherent flexibility of lion pride size in response to prevailing ecological circumstances might suggest lions have some innate insulation from the welfare challenges associated with varied captive social circumstances, however, while wild pride sizes may vary, wild lions in solitary situations occur only in very challenging, short-term situations that impact individual wellbeing significantly. Social flexibility in the wild is therefore unlikely to insulate lions from welfare challenges associated with solitary, unstable or imperfect social situations in captivity.
- Lion sociality must therefore be viewed as a fundamental need and welfare priority, and the cohesiveness of social groups will play a crucial role in captive lion welfare. Opportunities for lions to act together, or independently as they chose to achieve shared goals will likely enhance social cohesion and in doing so improve welfare.
- The capacity of captive environments to mirror opportunities for the fission-fusion dynamics seen in the wild are also likely to be critical to optimising welfare beyond prevailing baselines. Technologies under development to facilitate travel to discrete motivated destinations for captive tigers could be adapted to facilitate self-selected fission-fusion opportunities for captive lions.
- Additionally, sociality must be a principal consideration when evaluating the provisioning of all behavioural, cognitive, and physiological opportunities – and so for example whilst captive environments will invariably satisfy the physiological needs associated with rest, eating and drinking to keep animals alive (and identified here as paramount welfare priorities), few will do so in a way that is conducive to the needs of a highly social animal such as a lion.
- Intragroup competition within wild lion prides during feeding times challenges the notion of a truly egalitarian lion society, and subsequently, the absence of opportunities for active competition over a single carcass in captivity could potentially erode subtle or situation specific social constructs within the pride that could in turn contribute to heightened social stress over the long term.
- While AWPIS values represent welfare significance, a Welfare Risk Factor (WRF) was also created combining AWPIS values with the limited data collected relating to curtailment in captivity. Behaviours relating to hunting which ranked around the midpoint of in terms of welfare significance, emerged as amongst the highest welfare risks due to their near complete elimination in captive environments.
- Comparison of AWPIS values between lions and Amur tigers demonstrated travel and exploring / navigation to be more important to tigers than lions, with sociality being more important to lions than tigers.
- These differences between these two related behaviours are rooted in the species' respective behavioural ecology, shaped by prey density, distribution, and habitat type. Amur tigers are required to be more mobile in search of more widely dispersed prey in a less productive landscape and to maintain territorial integrity of a markedly larger home range than lions. For lions, sociality has evolved because the benefits of living in a group to combat kleptoparasitism in a more productive, competitive landscape, outweighs any costs linked to competition for food within prides or reduced hunting efficiency.
- Hunting related behaviours, whilst potentially representing some of the biggest welfare risk to African lions, were less important to lions than they were to Amur tigers. While social living requires lions to hunt more often than Amur tigers because of the need to share food, in comparison to Amur tigers, lions have a greater probability of feeding without having hunted. This is a result of lion sociality creating opportunities for a division of labour meaning those not

involved in hunts are still permitted to access carcasses, and the higher levels of ecosystem productivity / prey biomass ensuring opportunities for scavenging and kleptoparisitism are greater for African lions than they are for Amur tigers.

- Despite their close genetic relationship, these important, yet nuanced differences underscore the need for highly species-specific management strategies – whilst all motivated outcomes should ideally be connected to travel in tigers, all motivated outcomes need to be considered through a social lens for lions. Currently, this understanding does not underpin prevailing management practices or facility design for either species.

Summary Data

	AWPIS	Comparability	Prevalence	CCI	WRF
Sleeping / resting	0.8662	0.2783	0.2240	0.2602	0.62560959
Eating	0.8526	0.4609	0.2240	0.3819	0.67219581
Drinking	0.8235	0.3130	0.2240	0.2834	0.61039582
Social interactions	0.8116	0.2909	0.4417	0.3412	0.61840511
Walking	0.7825	0.4174	0.2800	0.3716	0.62269537
Learning by doing	0.7750	0.4522	0.5565	0.4870	0.65631327
Territorial maintenance	0.7695	0.5545	0.6000	0.5697	0.68805697
Carcass processing	0.7685	0.4348	0.6250	0.4982	0.65404928
Olfaction	0.7672	0.3913	0.3280	0.3702	0.61048336
Parenting / nursing by mother	0.7656	0.4000	0.6783	0.4928	0.64719101
Choice / decision making	0.7561	0.5700	0.6087	0.5829	0.68549977
Grooming	0.7549	0.2609	0.3120	0.2779	0.56241962
Hunting as part of a pride	0.7534	0.8261	0.8952	0.8491	0.78940276
Mating	0.7515	0.3619	0.6182	0.4473	0.6213167
Watching	0.7505	0.4190	0.3500	0.3960	0.61103786
Foraging	0.7484	0.6261	0.6250	0.6257	0.6993695
Killing prey	0.7400	0.8957	0.9333	0.9082	0.80603248
Chasing prey	0.7328	0.8000	0.8818	0.8273	0.76786014
Learning by observing others	0.7312	0.4381	0.6000	0.4921	0.63011917
Stalking prey	0.7289	0.7652	0.8348	0.7884	0.75035647
Running	0.7194	0.5043	0.4400	0.4829	0.62693896
Navigating	0.7062	0.6545	0.6455	0.6515	0.68465224
Problem solving	0.7039	0.5333	0.7182	0.5949	0.65418609
Hunting alone	0.7016	0.8087	0.8667	0.8280	0.75024807
Exploring	0.6982	0.6571	0.6696	0.6613	0.68300684
Play	0.6973	0.3455	0.4917	0.3942	0.57115927
Mate guarding	0.6927	0.5000	0.6571	0.5524	0.63131985
Avoidance of other lions	0.6644	0.6727	0.7000	0.6818	0.67047167
Inter-pride aggression	0.6498	0.7182	0.7833	0.7399	0.68365123
Alloparenting	0.6356	0.4947	0.7500	0.5798	0.60478808
Forward planning / seasonal adjustments	0.6278	0.7176	0.8316	0.7556	0.67514757
Intra-pride aggression	0.6219	0.6087	0.6364	0.6179	0.61936629
Climbing	0.5557	0.5217	0.6960	0.5798	0.55952018
Swimming	0.4493	0.5727	0.7810	0.6421	0.51948389
Bathing	0.4371	0.5800	0.7500	0.6367	0.51128122

Table 4. Key metrics for each behaviour and cognitive process with red indicating high values / priorities and green low. (AWPIS =Animal Welfare Priority Identification System value, CCI = Captive Curtailment Index, WRF = Welfare Risk Factor).