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SHORT COMMUNICATION

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Behavioral correlates between daily activity and sociality in wild and captive origin African lions

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ABSTRACT

Study of behavioral correlations within and across populations has long been of interest to ethologists. An exploration of behavioral correlations between sociality and behavior of African lions (*Panthera leo*) was undertaken to examine if this approach is better able to reveal important aspects of lion behavior not easily discernible by looking at these behaviors separately. Resting behavior and received play interactions were correlated in 2 captive-origin prides and one wild pride, attributable to the involvement of cubs and sub-adults. Direct and exploratory movement was negatively correlated with groom centrality in 2 of the 3 prides, due to adults engaging in high levels of both of these activities. Exploration of these behavioral correlations highlighted the differences between age-groups in activity and sociality, facilitating the understanding of the complex behavior and interactions of lions. In addition, the finding of similar behavioral correlations between captive-origin and the wild prides provides confidence in the suitability of captive-origin candidates for ex-situ release. This is imperative to ensure the success of sub-groups and prides under an ex-situ reintroduction program.

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Behavioral correlates, which occur between 2 or more behaviors such as boldness, aggression and exploration, have been recognized to occur in various species.^{1,2} The presence of behavioral correlations can be used to provide a more complete account of animal behavior, forming the basis of identifying behavioral strategies and personality. Such correlations could potentially be used within pre-release assessment, providing an additional tool in identifying animals suitable for release, ultimately resulting in increased program success.

Activity budgets are an important assessment tool used to provide information on individual behavioral phenotypes and time animals dedicate to specific behaviors. Through assessing the daily activity of African lions (*Panthera leo*) in wild systems, it has been established that prides are largely crepuscular and nocturnal, with resting occurring largely during daylight hours.³⁻⁵ Activity budgets are a critical tool in the pre-release assessment of captive-origin prides within an ex-situ reintroduction program as they facilitate comparisons to wild prides. More recently, Social Network Analysis (SNA) has emerged as method that has proven effective in assessing and quantifying the social structure of a population.⁶⁻⁸ This analysis was first applied to a captive-origin pride by Abell et al. (2013),⁹ prior to use in

comparing captive-origin and wild prides by Dunston et al. (2016).¹⁰ SNA provides us with insight into the role of sub-groups and individuals within a pride.

While assessing daily activity and conducting SNA individually are useful in identifying individual and within-pride differences, the large number of metrics this provides can make it difficult to obtain a complete picture of lion behavior. Behavioral correlates provide a means of combining different metrics, and potentially facilitate the development of a clear understanding of the complexities of lion activity and social behavior. Behavioral correlations between SNA metrics and behavior may provide a more comprehensive account of lion phenotype and, since a clear understanding of the phenotype of captive-origin lions destined for ex-situ reintroduction is critical to determine their chances of survival, potentially provide further insights into the suitability of individuals for release.

Two captive-origin prides and a wild pride were observed (pride details outlined in Dunston et al.¹⁰), with an activity budget and social interactions collected simultaneously. For the activity budget, individual lions were identified and their behavior recorded every 5 minutes using a species specific ethogram. Captive-origin prides were observed for a total of 98 (Ngamo) and 67

(Dambwa) hours each, and 62 hours for the wild pride (Makhutswi). Activity budget behaviors were calculated to provide a percentage of total time seen performing a behavior (rest, alert, direct and exploratory movement, individual play and vocalisations). Social interactions were compiled into matrices for greet, groom, play, aggression and all social, and analyzed via SNA, detailed in Dunston et al. (2016).¹⁰ This analysis produced betweenness centrality, an indication of individual lion involvement in a social network,⁶ and degree, an indication of the frequency of interactions received and initiated by each lion,⁸⁻¹¹ values for each lion per pride. Through Spearman's correlations, the activity budget behaviors and SNA social metrics were correlated per pride, and associations found (Table 1). Mann-Whitney U tests were used to assess for differences between age groups, across all prides.

A negative correlation between resting behavior and received play interactions was found across the Ngamo and Dambwa prides, and a negative trend observed for the Makhutswi pride (Table 1). Correlations were also found across 2 of the prides; the Ngamo and Makhutswi pride had positive correlations between alertness and play centrality, and roaring and received interactions. A positive correlation between initiated and received social play, individual play and play centrality (positive trend for the Ngamo pride) and a negative correlation between direct and exploratory movement and groom centrality were found for the Ngamo and Dambwa prides. Correlations also occurred for individual prides, with alertness being positively correlated with received play and aggression interactions for the Ngamo pride. Individual play was negatively correlated with received all social and greet interactions (Dambwa), and positively correlated

with received aggression (Ngamo) and initiated greet, play and all social interactions (Dambwa).

All correlations were found to be influenced by age groups; adults and offspring (cubs and sub-adults). Correlations within all the 3 prides indicated that the pride members who rested more, adults, were less likely to receive play interactions. Adults were observed to not conduct individual play, while cubs and sub-adults performed this behavior at 0.18% of total time observed, resulting in this age group significantly influencing the correlations with this behavior with activity ($U = 80$, $p = 0.005$). All other correlations were due to age related differences where upon close examination, this would be expected as younger pride members were more active and central to play interactions, while being more likely to initiate greets and receive aggression. Adults rested at higher levels, were more involved in territorial vocalizations, and received more interactions. These age variations have been reported previously for pride daily activity^{3,4} and social behavior,^{3,4,9,10} but the existence of these correlations facilitates the formation of the complex activity and social behavior of lions of different ages.

The behavioral correlations reported here extend our understanding of lion behavior by revealing the differences that occur at an age level in sociality and behavior. Comparisons between prides indicate that these age associated behavioral phenotypes are unaffected by captivity. These comparisons are important in ensuring specific sub-groups have species and age appropriate behaviors. Long term, this will allow us to assess these and other captive-origin prides, ensuring that age groups perform behaviors at appropriate levels through the developmental stages of cub to adult. This is critical to ensuring that candidates for ex-situ reintroduction are behaviourally apt for survival.

Table 1. r_s and p-value of significant Spearman's correlations between activity budget behaviors and calculated SNA centrality and degree (received interactions) values, per pride.

Activity Budget	Social Network	Ngamo*		Dambwa*		Makhutswi	
		r_s	P-value	r_s	P-value	r_s	P-value
Rest	Play received	-0.671	0.024	-0.636	0.026	-0.602	0.050
	Aggression received	-0.676	0.022	0.077	0.812	-0.505	0.113
	Greet initiated	-0.309	0.355	-0.536	0.073	-0.645	0.032
Alert	Play centrality	0.705	0.015	0.032	0.922	0.668	0.025
	Play received	0.887	0.000	0.168	0.602	0.344	0.300
	Aggression received	0.723	0.012	0.191	0.553	0.305	0.361
M1	Groom centrality	-0.695	0.018	-0.625	0.030	0.056	0.870
Individual Play	Play centrality	0.604	0.049	0.697	0.012	0.384	0.244
	All social received	0.373	0.259	-0.639	0.025	-0.401	0.222
	Greet received	0.000	1.000	-0.850	0.000	-0.500	0.117
	Play received	0.641	0.034	0.819	0.001	0.000	1.000
	Aggression received	0.612	0.045	0.000	1.000	0.347	0.295
	All social initiated	-0.447	0.268	0.858	0.000	0.300	0.370
	Greet initiated	0.149	0.662	0.648	0.023	0.200	0.555
	Play initiated	0.539	0.087	0.828	0.001	0.524	0.098
Roar	Greet received	0.751	0.008	N/A	N/A	0.696	0.017

*Indicates a pride containing adult lions of captive-origin.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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