Report

Current Biology

# Sex-specific social aging in wild African lions

## Highlights

- Evidence of sex-modulated social aging in a wild lion population over 30 years
- Female connectivity declines with age, while average group size increases
- Male connectivity peaks in mid-life to males but dips in mid-life to females
- Connectivity is key to female longevity but associate numbers are key for males

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## In brief

Rudd et al. report sex-modulated social aging in wild lions. Female intra-sex connectivity declines with age, while male intra-sex connectivity dips in mid-life. Average group size increases with age in both sexes. Moreover, the quality of social associations is key to female longevity, while the quantity of associates is important for males.

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Report

# Sex-specific social aging in wild African lions

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## SUMMARY

There is a growing interest in social behavior change with age,[1–5] and the impacts of sociality on longevity,[6–8] but current knowledge is broadly limited to primates, societies structured by dominance hierarchies, or single-sex studies. It is less clear how social aging patterns emerge in carnivores. The African lion (*Panthera leo*), a species that lives in egalitarian fission-fusion societies, presents an exceptional opportunity to examine social aging. Across felids, lions are unique in their dependence on conspecifics for many essential processes,[9–11] and there is vast knowledge of lion behavioral ecology,[10–14] including documented reproductive senescence in both sexes.[14,15] Applying spatial-social network analyses across 30 years of data on the wild Serengeti lion population, we show that sex strongly modulates patterns of social aging and longevity. Group size increased with age for both sexes, but only males experienced significant changes in associate numbers (degree), specifically to females, which peaked in mid-life before declining. While aging females experienced declines in intra-sex connectivity (strength) and bond strength (mean strength), they peaked in both to males during mid-life. Male inter-sex strength also peaked in mid-life, while conversely their intra-sex strength and mean strength significantly dipped in mid-life. Although social associations were important for survival in both sexes, the investment diverged significantly: females' overall network connectivity was key for longevity, while the number of associates was important for males. These findings illustrate important potential effects of social aging in a wild carnivore and demonstrate how these diverge strongly between the sexes.

## RESULTS

Understanding how individuals' social behavior changes with age (referred to as "social aging") can help illuminate the role of aging individuals in structuring societies[1–5] and in processes such as disease transmission and information spread.[2,16,17] Multiple social aging hypotheses have been proposed, including within-individual changes (e.g., competition avoidance and alteration of spatial behavior) and population-level changes (e.g., selective disappearance and demographic shifts).[3] Throughout adulthood, inter-individual variation in social behavior is common and often emerges between the sexes.[18] As such, important between-sex differences in social aging are likely but remain understudied. Understanding sex-based variation could provide insights into drivers of social aging in wild populations and highlight the underlying evolutionary and ecological mechanisms.

Additionally, inter-individual variation in social behavior across the lifespan has been found to impact longevity variably across species.[6,8,19] Such phenomena are increasingly well documented, particularly in primates,[4–7] but are often restricted to a single sex.[3] Owing to the often-divergent social strategies of males and females,[20–23] lifetime sociality is likely to differentially impact fitness and longevity between the sexes.[24] As such, drawing broad inferences concerning the impact of sociality on longevity remains difficult, with findings often limited to particular taxa and single-sex examinations.[25] Particularly lacking are considerations of such processes in social carnivores. Owing to the unique ecological and evolutionary dynamics of such species, they may provide insights into the drivers and mechanisms of social aging that remain poorly understood.

The African lion (*Panthera leo*) is unique amongst felids: lions are highly social, with individuals living in egalitarian fission-fusion social groups.[11,14] Dispersal is highly sex skewed; most females remain with their natal pride (though some disperse to form new prides),[13] but all males disperse aged 2–4 and spend time in nomadic coalitions before taking residence in their first pride.[14,26] Coalitions can be resident within multiple prides at once, with larger coalitions more successful in retaining residencies and enjoying greater reproductive success.[27] Aging males exhibit reproductive senescence, likely due to their increasing vulnerability to intruding infanticidal males.[14] All female pride-mates breed at similar rates until reproductive senescence begins around ~10 years old,[15] with cubs raised in creche groups where caring and nursing responsibilities are shared.[14,28,29] While individuals of both sexes spend significant time alone, essential behaviors (e.g., territorial defense, cub rearing, and hunting) are regularly executed in groups,[10,29] meaning singletons struggle to successfully reproduce and survive.[14,27] Despite the vast body of lion behavior research, little is known about intra-pride social associations, how sociality changes across a lifetime, and the role of sex-specific aging in mediating patterns of sociality. Given the variation in (and timing of) behaviors such as dispersal and reproduction between the sexes, we predict sex-based divergence in investment in the number of associates and strength of associations across the lifetime.

Using 30 years of data from 665 adult lions of the wild Serengeti population, we employed spatial and social network analyses to investigate sex-specific social aging and the association between fine-scale sociality and longevity. We compared individuals' (1) average group size, (2) number of associates (degree), (3) total sum amount of weighted social associations to others (strength), (4) social bond strength to associates (mean strength), and (5) the connectivity of their associates to one another (clustering) across their lifetimes within the population. Using an integrated nested Laplace approximation (INLA) model, we directly considered spatial autocorrelation in social network positions, accounting for each individual's average location at each timepoint. In addition, to decipher the effects of fine-scale, intra-pride social associations, we controlled for average annual group size as well as observation frequency, natal vs. foreign birth status, individual GPS collar status, year, current pride, natal pride, and individual identity. We analyzed male and female data separately to allow the comparison of sex-specific social aging and the impacts of sociality on longevity between sexes.

All models were substantially improved by considering spatial autocorrelation, indicating that social connectedness was spatially autocorrelated, so we report those models throughout. All response variables except male clustering showed at least a slight model improvement (DeltaDIC > 2), and the majority showed marked improvements (DeltaDIC > 100; Figure S1). However, accounting for these had little impact on other effect estimates, showing that spatial behavioral changes were unlikely to be driving the observed social aging trends.

## Female social aging and longevity

While average group size (average number of other individuals the focal lion was observed with per sighting) provides a simple measure of grouping behavior within a fission-fusion society, degree (number of unique individuals the focal lion was observed with over that year) provides an indication of overall gregariousness. Female lion networks were characterized by a substantial increase in group size with age (estimate 0.081; 95% CI 0.034, 0.127; $p < 0.001$; Figures 1 and 2). Once an individual's average group size was controlled for, we found no additional relationship between age and the unique number of associates females had (Figures 1 and 2).

The females' total sum of weighted social associations to other females (strength—a measure of an individual's overall social connectivity) decreased significantly with age (estimate −0.072; 95% CI −0.097, −0.048; $p < 0.001$; Figures 1 and 2). Aging studies commonly test for quadratic effects due to the possibility of non-linear relationships between response variables. A negative quadratic relationship with age was evident for females' strength to males, with a peak in connectivity during mid-life (estimate −0.067; 95% CI −0.091, −0.043; $p < 0.001$; Figures 1 and 2).

Female-female mean strength (a measure of the tightness of an individual's social bonds to its associates) declined with age (estimate −0.118; 95% CI −0.159, −0.078; $p < 0.001$), while female-male mean strength peaked significantly in mid-life (estimate −0.086; 95% CI −0.118, −0.054; $p < 0.001$; Figure 2).

The observed social aging trends contrasted strongly with the relationship between sociality and female longevity. Despite decreasing with age, female intra-sex strength was associated with greater longevity (estimate 0.039; 95% CI 0.012, 0.066; $p = 0.004$; Figures 1 and 3), confirming that the longevity effects cannot be attributed to selective disappearance. This was similarly true for the relationship between female-male strength and longevity (estimate 0.035, 95% CI 0.003, 0.068; $p = 0.030$; Figures 1 and 3). These results suggest that females benefit from investing in their social associations across their lifetime.

There was a small negative association between female-female clustering and longevity (estimate −0.063, CI −0.126, −0.001; $p = 0.047$). As such, there is potentially a survival cost to existing within tightly connected social cliques with female pride-mates, compared with groups with more fluid membership. Notably, there was no significant relationship between the number of associates females had (degree) and longevity (Figure 1).

## Male social aging and longevity

Similarly to females, there was a positive relationship between age and male average group size (estimate 0.172; 95% CI 0.064, 0.279; $p = 0.002$; Figures 1 and 2). Even when controlling for individuals' average group size, males also showed a strong and significant increase in their unique female associate numbers (degree) with age (estimate 0.172; 95% CI 0.087, 0.258; $p < 0.001$; Figures 1 and 2). There was a further negative quadratic effect of age, meaning the number of unique female associates peaked in mid-life (estimate −0.137, 95% CI −0.199, −0.075; $p < 0.001$; Figures 1 and 2). There was no significant change in the number of male-male associates with age (Figures 1 and 2).

Additionally, males showed decreasing strength with age when considering their intra-sex connections (estimate −0.321; 95% CI −0.399, −0.243; $p < 0.001$; Figure 1), but the quadratic relationship showed peaks in early and late-life (estimate 0.131; 95% CI 0.074, 0.187; $p < 0.001$; Figure 2). Male-female strength showed the opposite pattern, with a peak in mid-life (estimate −0.075; 95% CI −0.127, −0.024; $p = 0.004$; Figures 1 and 2).

As was true for females, male intra-sex mean strength decreased significantly with age (estimate −0.283; 95% CI −0.381, −0.184; $p < 0.001$; Figures 1 and 2). However, when considering the quadratic relationship, and in contrast to females, male-male mean strength peaked in early and late life (estimate 0.141; 95% CI 0.071, 0.211; $p < 0.001$; Figures 1 and 2).

Male longevity was significantly positively related to the number of male associates (estimate 0.087; 95% CI 0.002, 0.173; $p = 0.045$), and the number of female associates (estimate 0.134; 95% CI 0.046, 0.222; $p = 0.003$; Figures 1 and 3).

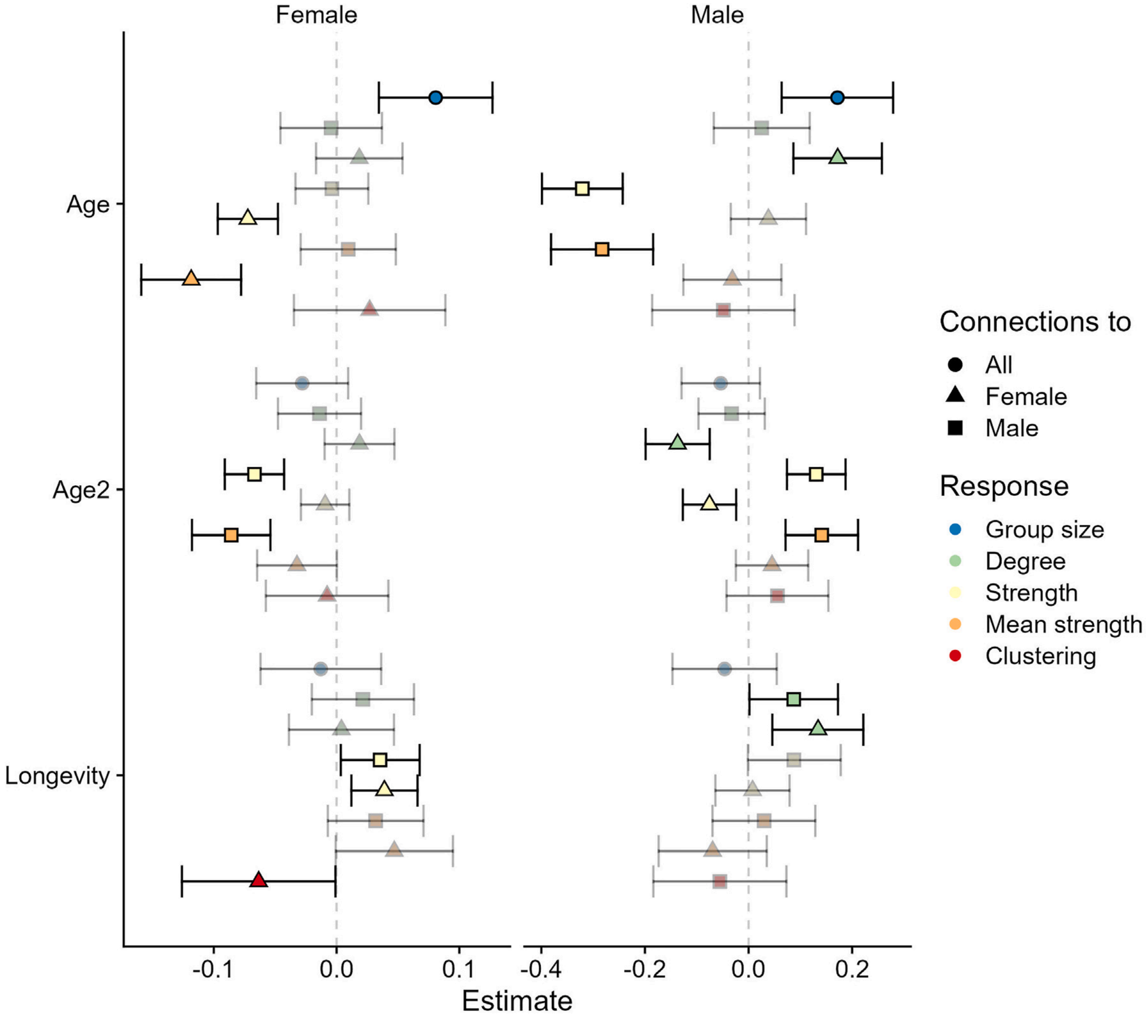

**Figure 1. Associations between age, longevity, and social metrics**

Estimates taken from the SPDE single-sex model for females (left) and males (right) showing the age and longevity effects for each social metric tested. Points represent the model estimate with error bars showing the 95% credibility intervals (estimated according to the 95% upper and lower quantiles of the posterior density distribution for each effect). Bold points indicate a significant relationship; faded points indicate a non-significant relationship. See also Figure S1 and Table S1.

## DISCUSSION

Our findings demonstrate strong, sex-dependent, and often-nonlinear changes in social behavior with age in a wild carnivore, the African lion. These relationships existed even after accounting for individuals' group size changes, and the metrics of fine-scale social behavior were also related to longevity. It is plausible that the strongly divergent patterns of sex-based social aging relate to the profound differences in reproductive biology and social behavior between males and females. Similar to the orthodoxy from studies of other mammals (e.g., primates and ungulates[2,3]), aging females appeared to broadly lose social connectivity while retaining a similar absolute number of associates. In contrast, males' connectivity was highly nonlinear and peaked in early and late life, showing that there are strongly divergent drivers governing the expression of social behavior. This illustrates social aging patterns should be considered more broadly in social animals, potentially uncovering a range of further processes governing the underlying causes and consequences of ecological and behavioral processes.[1,2] As theorized in primates specifically,[5] animals with highly divergent sex roles in their society may exhibit similar divergence in social aging patterns due to shifts in motivation and power; further comparative work may help to elucidate the wider drivers and consequences.

### Group size and number of associates

Due to the fission-fusion structure of lion society, individuals' group size and the total number of unique associates they are observed with (degree) provide two informative yet relatively simple social measures. There was a significant increase in female sub-group size with age but a lack of change in associate numbers (when controlling for group size changes). This could partly be explained by reproductive senescence,[15] as mothers

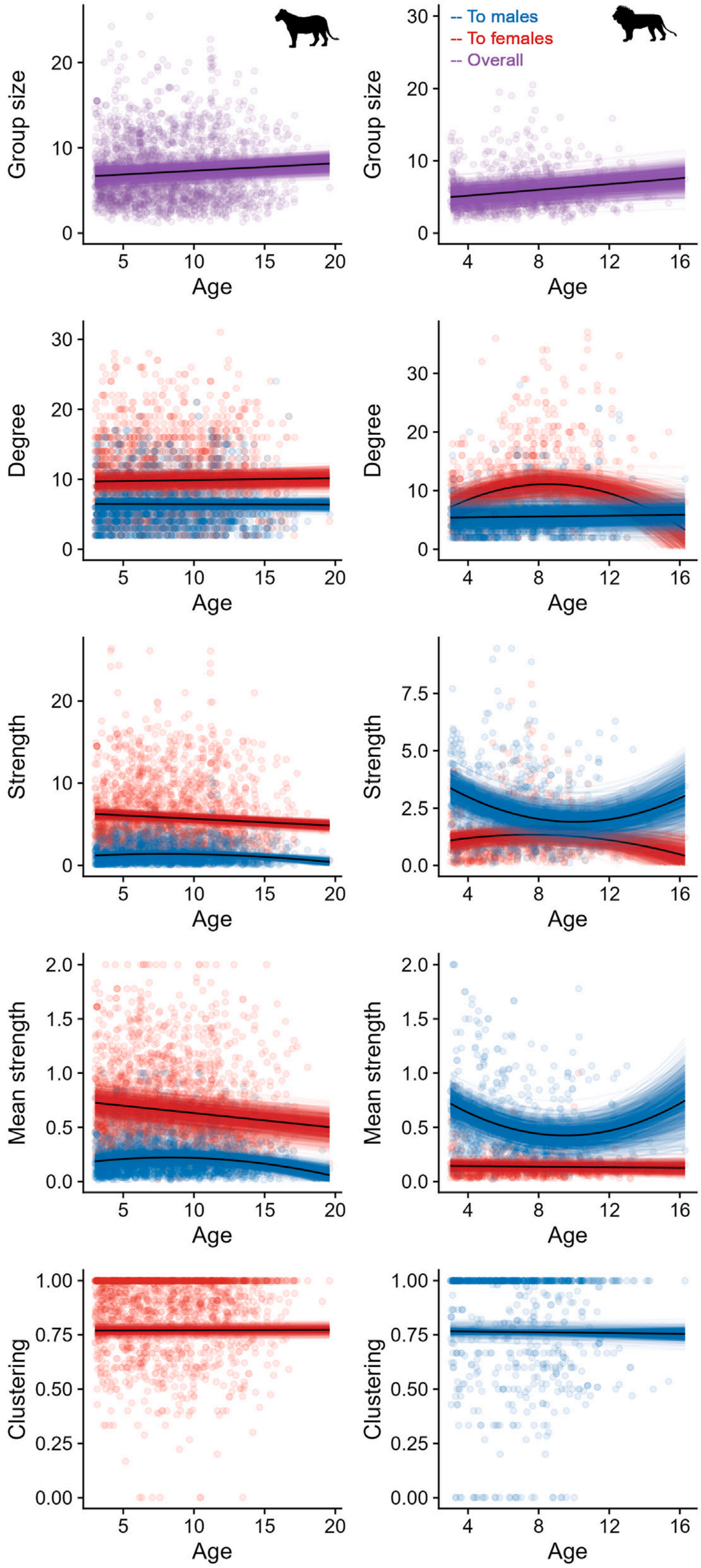

**Figure 2. Social aging patterns vary between the sexes**

Age related changes in (from top to bottom) group size, degree, strength, mean strength, and clustering for females (left column) and males (right column). Red points and lines indicate associations to females, blue points and lines indicate associations with males, and purple points and lines indicate associations to both sexes combined. Where significant, quadratic age effects are included in the plot, generating n- or u-shaped curves. The black lines represent the mean of the posterior distribution for the age effect estimate; the colored lines are 100 random draws from the posterior to represent uncertainty. The points represent individual-by-year replicates, with transparency to allow for visualization of overplotting. For females, group size, strength, and mean strength plots show significant relationships. For males, group size, degree (to females only), strength, and mean strength (to males only) plots show significant relationships. See also Figure S1 and Table S1.

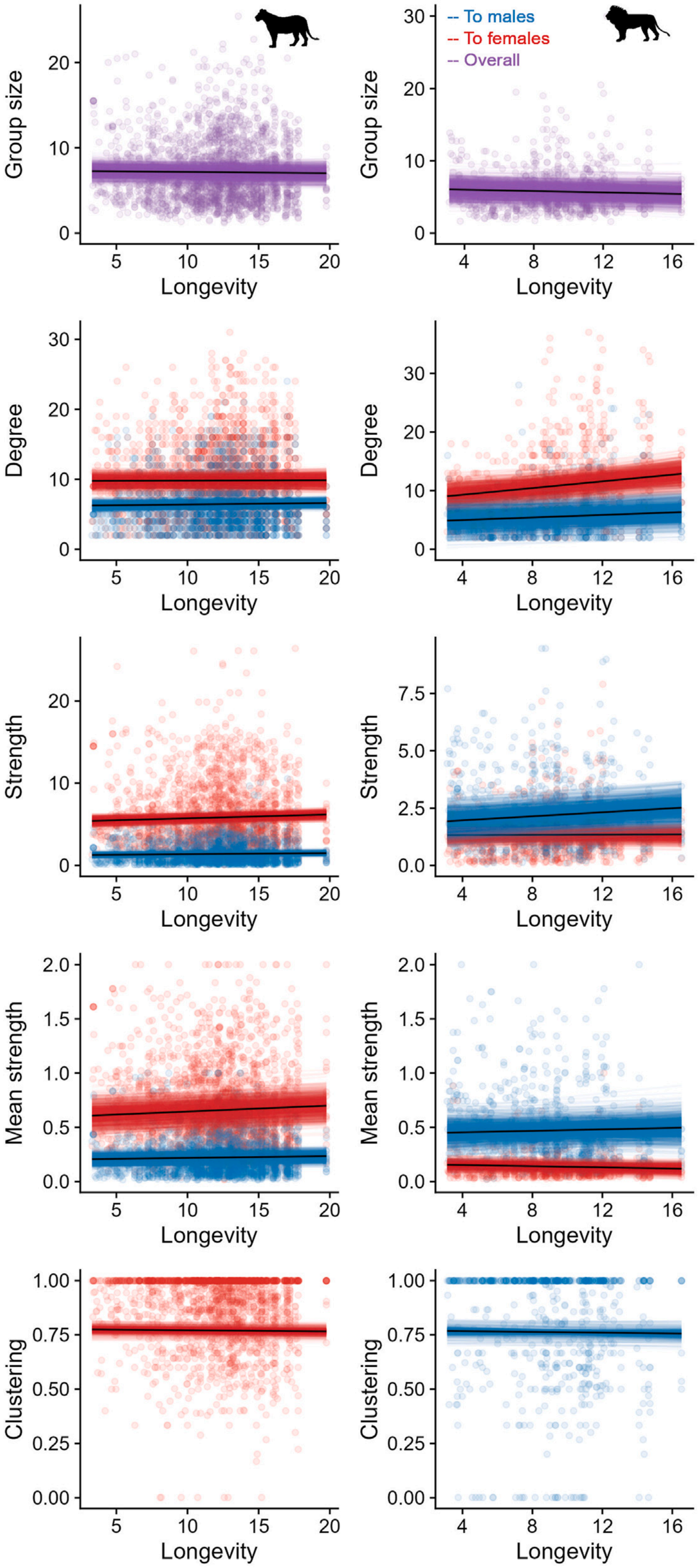

**Figure 3. Sociality correlates with longevity differentially between the sexes**

Longevity effects of (from top to bottom) group size, degree, mean strength, and clustering for females (left column) and males (right column). Red points indicate associations to females only, while blue points indicate associations with males only, and purple points and lines indicate associations to both sexes combined. The black lines represent the mean of the posterior distribution for the age effect estimate; the colored lines are 100 random draws from the posterior to represent uncertainty. The points represent individual-by-year replicates, with transparency to allow for visualization of overplotting. For females, strength and clustering plots show significant relationships. For males, the degree plot shows a significant relationship. See also Figure S1 and Table S1.

are highly dependent on small creche groups while cub rearing.[28,29] Furthermore, females frequently hunt alone or in substantially smaller groups than the maximum pride size.[14,29] In other social apex predators, declines in hunting success with age have been observed,[30] and aging female lions do show signs of deteriorating physicality that could impair their hunting ability. It is plausible that aging females become increasingly dependent on the pride for food, rather than hunting themselves, and so are observed more frequently in bigger group sizes. Understanding female hunting behavior across the lifespan could elucidate this further.

Similarly, male sub-group size increased with age, which could reflect the increasing likelihood of a male's pride being taken over by intruding males.[14] Further research into whether aging males spend an increasing proportion of their time with the bulk of the pride, in recognition of their physical vulnerability, would be useful. While female associate numbers did not change with age, males exhibited an increase in female associate numbers to a mid-life peak even when controlling for group size changes. This is likely because, in the Serengeti, many coalitions are resident within multiple prides simultaneously. These prides grow in size to a tipping point; however, pride residencies can also be surrendered by coalitions as they age, particularly if their non-dispersing daughters have reached reproductive maturity.[14]

Across the lifetime, neither yearly average group size nor yearly number of associates held statistically significant relationships with female longevity, suggesting that the extent of grouping behavior individuals display does not directly relate to survival. However, male longevity increased when their associate numbers were higher, and this was true when only considering their associations to females, or to other males. This could be partly indicative of selective disappearance[3] in that larger coalitions are more successful in maintaining pride residence, and therefore persisting in the study area, when compared to smaller coalitions.[14] Further, males resident within larger prides (or multiple prides) may simultaneously have access to better quality territory,[10] which would positively contribute to their survival.

## Connectivity and bond strength

Lions demonstrated significant reductions in their overall connectivity to same-sex individuals (intra-sex strength) and average bond strength to their associates (mean strength) with age. Sex-specific differences were again found: female lions exhibited a peak in both metrics in mid-life to males only. Males exhibited early- and late-life peaks in strength and mean strength when considering their male associates only. This contrasted with the evident mid-life peak in strength to females.

These findings may reflect the differing influence of reproductive behavior on social aging between the sexes. Females are reliant on the creche for cub rearing and protection from infanticidal males during their prime adult years.[31] As reproductive senescence progresses, investment in creche-mate associations may decrease. Additionally, the early-life peak in mean strength mirrors the time of highest vulnerability for females that do disperse,[14] so this could be when they are most dependent on their cohort for survival. For resident males, the biggest threat to their reproductive output is intruding male competitors. Counteracting this threat requires early-life investment in coalition bonds during the natal pride and nomadic life stages. These within-coalition bonds may once again become important as males age and become more vulnerable to intruding males.[13] Conversely, aging males' drop off in overall connectivity to females (male inter-sex strength) could reflect reproductive senescence and perhaps even post-pride residence social behavior when intra-sex associations will dominate.[14]

Across their lifetime, lionesses that invested more in their social associations (with greater intra- and inter-sex strength) appeared to live longer. The direct causal mechanisms underpinning this remain unclear; however, where similar patterns exist in primates, it has been hypothesized that females experience fitness benefits from their associates through increased buffering against stressful events[6] and improved cooperation in shared behaviors.[7] Both could tangibly impact female lion longevity given the threat frequently posed by infanticidal males, and the extensive cooperation required during territorial defense, hunting and cub rearing. Another possibility is that females are more likely to emigrate from the study area if they are less strongly connected to others, generating the perception that increased connectivity improves longevity.

## Cliquishness

For females, there was a slight but significant negative relationship between longevity and their embeddedness in highly clustered intra-sex groups (as opposed to groups with relatively frequently shifting membership). This may reflect the higher rate of fission-fusion in larger prides, which hold better quality territories.[10] Similarly, this suggests that a tendency for individuals to be overly cliquish (and less integrated in the wider population) holds relative costs, compared with being more socially transient and having connections outside of their immediate clique.

## Ecological consequences

These findings will have a range of ecological and evolutionary implications for age-structured lion societies. For example, lionesses' decrease in social connectedness could drive reduced exposure to pathogens, while males' tendency to gain extra unique associates might disproportionately predispose them to acquiring novel parasites.[16,32] Such changes in exposure rates could interact with their reproductive investment and resulting changes in immune resistance,[33] as well as with immunosenescence.[16] Given that this population has previously experienced high-mortality disease outbreaks,[34,35] understanding these phenomena could be important for predicting the resilience of the Serengeti lion population in the future. Similarly, there could be important consequences for social learning, as knowledge about the environment is likely to improve with age.[36] As such older lionesses are likely to be key resources for prides, but their tendency to become less connected could reduce the ability for information to spread. Yet more research into how behaviors spread socially in wild social networks with diverse structures is now needed.[37]

## Conclusion

We found evidence of sex-differentiated patterns of social aging, and links between lifetime sociality and longevity, in African lions. The individual-based and long-term nature of our data, as well as our incorporation of both age and longevity effects, confirm that age-related patterns of sociality likely emerge through a combination of within-individual aging and selective disappearance. Females lived longer when they were more strongly connected to their associates but existed in less tightly interconnected groups. This was true despite decreases in strength and mean strength with age. Additionally, we found that, despite interacting with the same number of individuals as they age, females are on average found in larger groups. These social aging patterns may mirror declines in reproductive output and so creche attendance,[11,15,28] as well as increasing reliance on pride hunts due to physical senescence. As males aged, their number and strength of connections to female associates increased to a mid-life peak. However, the strength and mean strength of their intra-sex connections to other males were highest in early and late life. Further, males with more associates appeared to live longer. These findings likely reflect changes in pride size and residency patterns with age, as prides grow but coalitions surrender secondary prides containing mature daughters.[14] Additionally, as males in larger coalitions are more likely to be resident in multiple prides, they may concurrently have access to better quality territories that will contribute positively to their fitness and survival.[10] Our results demonstrate social aging in wild lions, how this can shape individual longevity, and the role of sex in modulating this relationship. Such insights add to existing knowledge of the species' sociality and further our understanding of social aging across diverse mammalian systems.

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
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## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2024.07.040.

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## AUTHOR CONTRIBUTIONS

Conceptualization, L.F.R., D.B., C.P., J.A.F., and G.F.A.; methodology, L.F.R., G.F.A., and J.A.F.; formal analysis, L.F.R. and G.F.A.; writing – original draft, L.F.R.; writing – review and editing, L.F.R., G.F.A., D.B., C.P., and J.A.F.; visualization, L.F.R. and G.F.A.; supervision, D.B., C.P., J.A.F., and G.F.A.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

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# STAR★METHODS

## KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| Deposited data | | |
| Data | Github | https://github.com/gfalbery/Old_Lion. |
| Software and algorithms | | |
| R code | Github | https://github.com/gfalbery/Old_Lion. |

## RESOURCE AVAILABILITY

### Lead contact

Further information and requests for resources relating to this manuscript should be directed to and will be fulfilled by Lauren Rudd (lauren.rudd@gtc.ox.ac.uk).

### Materials availability

This study did not generate new unique reagents.

### Data and code availability

- Data have been deposited (see key resources table) and are available as of the date of publication.
- All original code has been deposited (see key resources table) and is available as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

## EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

This study did not use experimental model animals, experimental *in vivo* animals, human participants, plants, microbe strains, cell lines, or primary cell cultures.

### Study system

The research was carried out using data from the long-term study of African lions in the Serengeti National Park, Tanzania. The study area comprised 2700km$^2$ of the national park, including both the grassland plains and acacia woodlands habitats. Two seasons can be identified, with the wet season spanning November-May and the dry season spanning June-October. Year-round prey densities are higher in the woodlands habitat (which is more heterogeneous), while in the plains habitat prey density fluctuates with seasonal migrations (and is considerably lower in the dry season).[12]

Throughout the study area, female lions generally live in fission-fusion prides composed of related female adults and their offspring. Pride size ranges from 2 to 20 individuals, and 75% of female offspring cohorts are recruited back into the mothers' pride, while 25% disperse to form new prides (often in adjacent territories).[14] Conversely, male offspring disperse from the natal pride and form coalitions of up to 9 individuals, composed of kin and non-kin. These coalitions live a nomadic life following dispersal until they are able to take over a pride of their own, usually between age 2-4.[14,27] There is no clear dominance hierarchy among female pride-mates[10] or male coalition-mates.[14]

### Data collection

The observational data used in this study was collected between 1984 and 2013. During this time, 1 female per pride was fitted with a GPS collar and was tracked at least once every 2 weeks. Once located, individuals within 200m of each other were considered co-occurring, so recorded as part of the same group sighting event (GPS location, date and time). Opportunistic sightings of non-collared individuals and groups were recorded in the same way. For each known individual (recognized by facial markings), age (estimated from date of first sighting as a cub or adult, accurate to within 2-3 weeks and 1 year respectively), sex, natal pride (if born in the study site) and current pride data was available.

Method details

### Social metrics and networks

Only data on individuals aged 3 and above were included, giving a total of 150842 observations of 665 individuals (mean per individual [SD] = 48.1 [85.2]) from 60 prides over 30 years. We created social networks at yearly intervals commencing in June 1984, following the seasonal calendar, running from the start of the dry season to the end of the wet season. Following the "gambit of the group" approach,[38] individuals observed in the same group according to the date and GPS location recorded (as described in the "Data collection" section above) were classed as associating at that time-point. This process generated a "group-by-individual" matrix, and the Simple Ratio Index (SRI) was used for deriving dyadic association matrices (i.e., social networks) between individuals, where the proportion of overall sightings in which two individuals were observed together was calculated rather than the absolute count (see Farine and Whitehead[39] for more details). All SRI values range between 0 (individuals never seen together) and 1 (individuals always seen together).

Using the annual networks, we derived 5 commonly used metrics to characterize lion social behavior.

(1) Group size: the average number of other individuals the focal lion was observed with per sighting
(2) Degree: the number of unique individuals the focal lion was observed with over the course of the year (i.e., number of the node's network edges)
(3) Strength: the total weighted sum of the focal lion's associations within the network over the course of the year (i.e., sum of the node's weighted edges, thereby quantifying overall connectivity)
(4) Mean strength: the average value of the focal lion's weighted associations to its non-zero associates over the course of the year (i.e., mean of the node's weighted edges, thereby quantifying bond strength)
(5) Clustering: the propensity for a focal individual's associates to also be associated with one another (with higher values indicating greater "cliquishness")

## Statistical analysis

We fitted linear models using the Integrated Nested Laplace Approximation (INLA), which is a deterministic Bayesian modelling framework. We fitted three broad classes of models: those examining the population as a whole, only females, or only males. We only included individuals aged 3 and above. This analytical setup is based on an established method for differentiating within- and between-individual age effects[40] which we have used in social aging models before[3] : by fitting age, longevity, and individual identity, the model controls for selective disappearance of certain individuals (i.e., of the more or less social) through mortality. This allows us to identify whether age-related changes in social network position are resulting from within-individual behavioural aging, or whether such patterns might emerge through population-level structural changes.

As such, each model included the following fixed explanatory variables: age (continuous, in years); Age[2] to detect quadratic shapes (continuous, centred around the mean value for age); Longevity (continuous, calculated as age at disappearance from study site in years; Observations (continuous, calculated as the number of times an individual was seen that year); Group size (continuous, calculated as an annual mean from the observation data); Foreign (binary variable, representing whether or not the individual was born in the study area); and Collared (binary variable, representing whether or not they had a GPS collar). We also included a suite of random effect factors: Natal pride (the pride in which an individual was born); Pride (the pride in which an individual was most often seen each year); Year; and Individual identity. We did not fit a Maximum Pride Size factor in addition to the Group Size and Pride based on the comparable results of prior analyses (see Figure S2 for SPDE model including Max Pride Size; Figure S3 for correlation between Max Pride Size and Group Size). In the overall models, we also fitted some effects to examine differences between sexes: first a main sex effect, and then interactions between sex and our continuous variables (Age, $Age^2$, Longevity, Observations, and Group size).

INLA models allow the fitting of a stochastic partial differentiation equation (SPDE) effect to account for spatiotemporal autocorrelation. Controlling for spatial autocorrelation is potentially important because in this and other wildlife populations, older individuals could exhibit changes in spatial behaviour that drive changes in social behaviour.[3,16] Further, spatial patterns of environmental structure or demography could drive social changes across the study area in a way that confounds with age structuring.[1] As such, isolating the spatial and social components of behavioural aging patterns is therefore likely to be important for ecological understanding.

To investigate spatial dependence in this way, we used each individual's average X and Y coordinate in each year (i.e., their annual spatial centroid); the effect modelled the expectation that individuals will have more similar response values (i.e., social network positions) when their locations were closer in space. To assess whether the models were significantly spatially autocorrelated, we first fitted the base model, and then added the SPDE effect and compared the model fit using deviance information criterion (DIC). We took 5 DIC to differentiate between competitive models, such that if the SPDE effect reduced DIC by more than 5 it was taken to be significantly autocorrelated. The base model + SPDE effect estimates for each of the single sex models can be found in Table S1, and the spatial DIC changes can be seen in Figure S1.