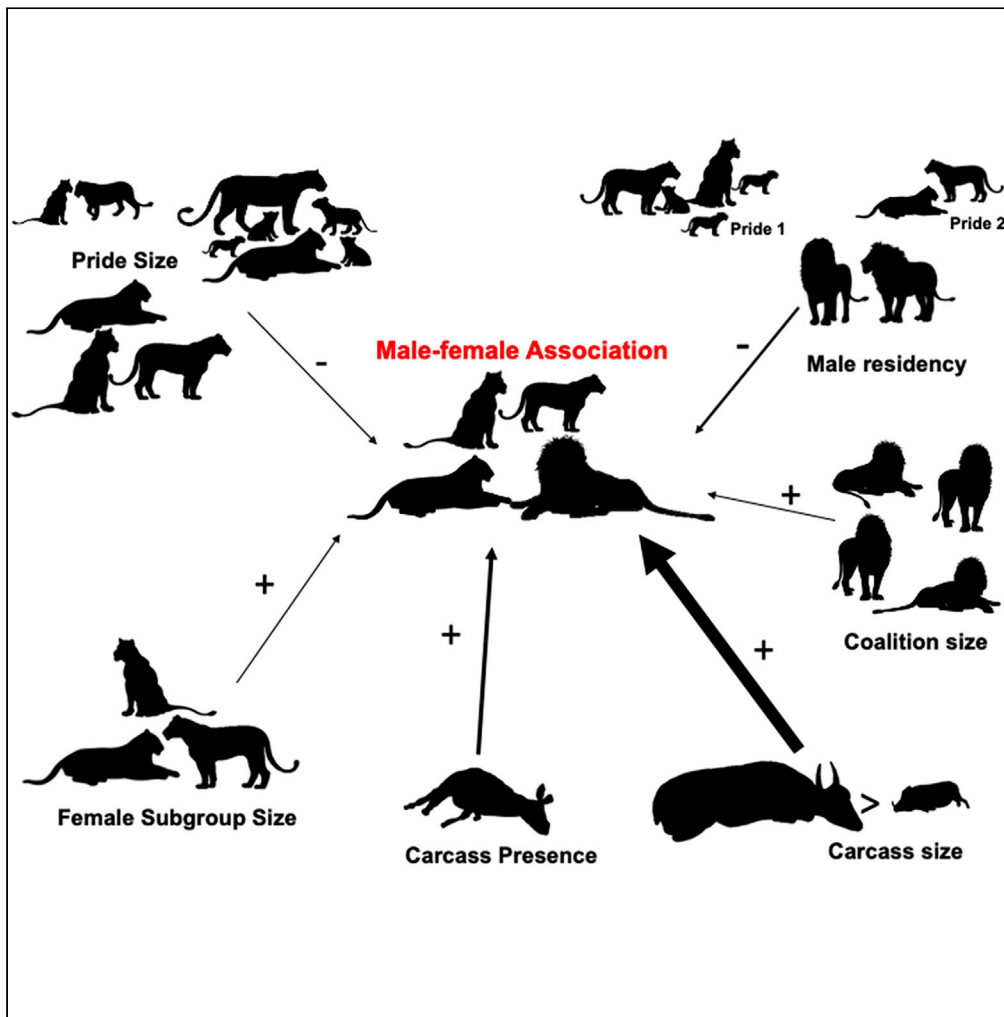


Article

# Contrasting levels of social distancing between the sexes in lions



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**Highlights**

Sexual segregation in lion populations is driven by resource availability

Females are responsible for segregating from males, except at large kills

When prey is scarce, females reduce detection by males by roaring less frequently

Contrasting proximity between the sexes has led to variation in mating strategies in these populations of African and Asian lions

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## Article

Contrasting levels of *social distancing* between the sexes in lionsStotra Chakrabarti,<sup>1,2,4,\*</sup> Joseph K. Bump,<sup>1</sup> Yadvendradev V. Jhala,<sup>2</sup> and Craig Packer<sup>3</sup>

## SUMMARY

**Understanding sexual segregation is crucial to comprehend sociality. A comparative analysis of long-term lion data from Serengeti and Ngorongoro in Tanzania, and Gir in India, reveals that male-female associations are contingent upon male and female group size, prey-size and availability, and the number of prides that each male coalition currently resides. Males maintain proximity with females, whereas females are responsible for segregation except at large kills. Lions feed on the largest prey in Ngorongoro and the smallest in Gir, and females spend the most time with males in Ngorongoro and the least in Gir. Females roar less often in prey-scarce circumstances in Serengeti and throughout the year in Gir possibly to prevent being tracked by males that parasitize on female kills. However, females readily associate with males when available prey is large and abundant. Contrasting availability of resources between Gir and Serengeti/Ngorongoro helps explain the varying degrees of sexual segregation and appears to drive differences in mating systems between these lion populations.**

## INTRODUCTION

The fundamental mechanisms underlying sexual segregation have been explored in a few systems (Conradt and Roper 2000; Ruckstuhl and Neuhaus, 2006) and are typically considered to result from disparate selection pressures operating on the two sexes (Conradt 1998). Sexual segregation in ungulates, fishes, elephants, and marine mammals have been shown to have originated from sex-specific differences in energetic demands, forage requirements, activity patterns, and vulnerability to predation (Clutton-Brock et al., 1987; Main et al., 1996; Ruckstuhl and Neuhaus, 2000; Croft et al., 2006; Shannon et al., 2006; Wearmouth and Sims, 2008). Here, we employ a comparative analysis of social behavior of a group living carnivore to investigate how the extent to which individuals associate with conspecifics is affected by intra-sexual grouping patterns, demography, and resources.

We present long-term data from African and Asian populations of lions (*Panthera leo*), a species with a fission-fusion social system, where members of the same “pride” may be separated for days or weeks at a time (Schaller, 1972; Packer et al., 1990). Individuals from both sexes interact remotely through long-distance vocal communications (/roars), which also help in territorial defense and gauging strength of opponents (McComb et al. 1993, 1994). Although male and female lions associate with each other outside of mating, the most stable subgroupings comprise females with dependent offspring that raise their cubs in a nursery group or crèche (Packer et al., 1990; Pusey and Packer 1994). Daughters are typically recruited into their mothers’ prides or disperse with members of their natal cohort to form new prides (Packer and Pusey, 1987). Adult males, on the other hand, enter the pride as a coalition from elsewhere and maintain residence for about two years and can sometimes maintain simultaneous residency in multiple prides (Bygott et al., 1979; Packer and Pusey, 1983a; Chakrabarti and Jhala, 2017). However, males are often found away from the females while patrolling and defending their pride ranges from rival coalitions (Grinnell et al., 1995; Chakrabarti and Jhala, 2017). Lions also exhibit sexually selected infanticide where newcomer males kill unrelated infants (Bertram, 1975; Packer and Pusey, 1983b; Chakrabarti and Jhala, 2019), thus resident males aggressively defend against invaders not only to maintain access to females but also to prevent the loss of progeny and fitness (Grinnell et al., 1995). Males occasionally capture prey large enough to feed the entire pride, but females perform the bulk of hunting, which mostly involves small- to medium-sized prey (Schaller, 1972; Funston et al., 2001), and, hence, males frequently scavenge and parasitize from kills made by the pride females (Schaller, 1972). Thus, within lion prides, males and females perform separate tasks—males: territorial defense and protection from infanticidal males, females: food, territorial defense,

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and rearing of cubs. Furthermore, male and female lions have subtly different grouping patterns that can limit the extent to which the sexes can associate with each other. Typically, males live in smaller groups/coalitions than females, with both sexes spending time in same-sex subgroups scattered across the pride territory. Prides are almost never found together but are instead found in subgroups of about three females, regardless of the pride size (see below). Consequently, larger prides will be more likely to be scattered in several subgroups that exceeds the number of males in the resident coalition, and male-female associations will inevitably decline with increasing pride size. Conversely, on occasions where females form larger (and hence fewer) subgroups, the males will have greater opportunities to associate with any given female in their pride(s). Similarly, because coalition partners also form subgroups, it is expected that at least one member of a large coalition would be available to associate with any given female, as would a male from a coalition that is only resident in a single pride rather than simultaneously resident in multiple prides. Such inter-sexual differences in tasks and grouping behavior are expected to determine the amount of time the two sexes spend together or apart.

To test this, we compare lions in three contrasting populations: Serengeti National Park and Ngorongoro Crater, Tanzania, and the Gir forest in India. Females live in a median pride size of five females in the Crater, six females in the Serengeti, and four females in Gir, whereas males are only found in a median coalition size of three males in the Crater, two males in the Serengeti, and two males in Gir. Furthermore, from the females' point of view, Gir represents a stable environment with low supply of resources, having a constant abundance of relatively small prey (e.g., chital *Axis axis* 35–65 kg and sambar *Rusa unicolor* 110–200 kg) that the females catch themselves (Chakrabarti and Jhala, 2019). The males do not aid females while hunting and generally do not help females during territorial confrontations with neighboring prides when their coalition is co-resident in adjacent prides (Chakrabarti and Jhala, 2019). Males dominate females at kills and may even exclude them altogether from smaller carcasses (Schaller, 1972; Jhala et al., 2019), thus females likely incur considerable immediate costs from associating with males. Among the Tanzanian sites, the Serengeti lions experience seasonal variations in the abundance of migratory wildebeest *Connochaetes taurinus* (160–200 kg) and zebra *Equus quagga* (220–250 kg), which are large enough for males and females to feed from the same carcass. However, in the absence of the migratory prey in the dry season, food is scarce, and the lions rely on smaller prey (Scheel and Packer, 1995), thus the system alternates between high- and low-supply prey regimes. The Ngorongoro Crater, on the other hand has a consistently high abundance of large ungulates (Cape buffalo *Syncerus caffer* ~ 450–750 kg, wildebeest and zebra) throughout the year (Estes and Small, 1981), which sustains a high density of lions (Hanby et al., 1995) with minimal competition between the sexes for food. In the Tanzanian sites, territorial confrontations with neighboring prides are more frequent in Ngorongoro than in Serengeti (Heinsohn, 1997; Mosser and Packer, 2009). The willingness of females to associate with males should depend on the extent to which males and females compete over the same resources, declining when resources are scanty because males can forcibly appropriate them from the smaller females. Consequently, we expect that sexual segregation would be most pronounced when the costs of associating with males are highest for females.

Based on this cross-habitat comparison, we identify the social and resource-mediated factors that affect sexual segregation in lions and gregarious mammals in general. Furthermore, from the frequency and contexts of mutual interactions between the sexes we discern which sex is responsible for maintaining proximity and separation. Our results provide mechanistic explanations why unlike in the African sites where each resident coalition maintains exclusive reproductive access to its pride(s) (Packer et al., 1991), male coalitions in India (that are typically small) are incapable of doing so. Pride females in Gir often mate with one "primary" coalition (that occupies most of the pride range) and multiple "peripheral" coalitions (that remain along the borders of the females' territory) (Chakrabarti and Jhala, 2019). We suggest that these differences in the lion's mating system have likely stemmed from differing abilities of males to monopolize the females in Gir versus Serengeti/Ngorongoro, which might have originated in turn from contrasting degrees of sexual segregation in these populations. Through this study we link sexual segregation with demography and food availability and, in so doing, relate the importance of sexual segregation to plasticity in mating strategies.

## RESULTS

### Factors governing male-female association

1. **Social factors:** Univariate models revealed that while all the chosen variables had significant effects on the odds of male presence, female subgroup size, male residency (number of prides where the

interacting male coalition was currently resident), and presence of kill/carcass had relatively stronger contributions (Table S2). The best multivariate model (Table S3) bearing significant variables indicated that the odds of male presence increased with an increase in female subgroup size, male coalition size, and the presence of a kill/carcass, whereas male presence declined with increasing pride size and an increase in the number of prides where the interacting male coalition was currently resident (Table S4, Figures 1A–1B and 2A–2E). However, the effect of coalition size differed between sites, exhibiting a stronger response per male in Gir; Serengeti and Ngorongoro showed similar trends (Figure 2E).

2. **Effects of prey resources:** Male presence was higher at carcasses weighing  $\geq 150$  kg than at smaller carcasses (Tables S5 and S6), and this contrast was most prominent in Gir (prob. =  $0.10_{\text{small}}, 0.45_{\text{large}}$ ) followed by Serengeti ( $0.23_{\text{small}}, 0.45_{\text{large}}$ ), and lowest in Ngorongoro Crater ( $0.36_{\text{small}}, 0.42_{\text{large}}$ ) (Table S5, Figure 2F). Edible biomass of prey carcasses differed between the three systems, with lions in Gir typically feeding on the smallest carcasses and the Ngorongoro lions feeding on the largest prey (Figure 3A). For Figure 3A, we used the *non-truncated* dataset from Serengeti/Ngorongoro (because this figure represents overall available biomass in the system) and all lion-prey carcass data corresponding to the study period from the entire landscape of Gir (beyond the groups that were intensively monitored for behavior data), observed as part of the long-term project (reviewed in Jhala et al., 2019). Please see transparent methods section and supplementary information for details regarding data and analysis.

The effect of site remained significant after controlling for social and resource-mediated factors (Table S3). Consequently, frequency of male-female association varied significantly between sites, with Gir having the lowest proportion ( $14\% \pm 1\%$ ), followed by Serengeti ( $18\% \pm 0.2\%$ ) and the highest in Ngorongoro ( $32\% \pm 1\%$ ) (Figure 3B).

#### Directionality of male-female association

Overall, males joined females significantly more frequently than vice versa ( $n = 199, 73\%$ ), whereas females were more likely to separate from the males ( $n = 153, 64\%$ ) at each site, except for the largest carcasses in each site ( $\geq 150$  kg in Gir and  $>350$  kg in Tanzania) (Figure 4).

#### Roaring rates

During the dry season when prey was scarce, Serengeti females roared at similarly low frequencies as females in Gir ( $p = 0.79$ , Figure 5A), whereas they roared less often than males in either Serengeti (dry season,  $p = 0.03$ ) or Gir ( $p < 0.001$ ) (Figure 5B). However, when prey was abundant during the wet season in Serengeti, females roared at similar rates as males ( $P = 0.77$ ) and more than the Gir females ( $P = 0.02$ , Figures 5A and 5B). The number of roaring bouts per session was similar across sexes and seasons, except that the Gir males roared more persistently than females in Gir ( $p = 0.002$ ) or Serengeti males during the dry season ( $p = 0.02$ ) (Figures 5C and 5D).

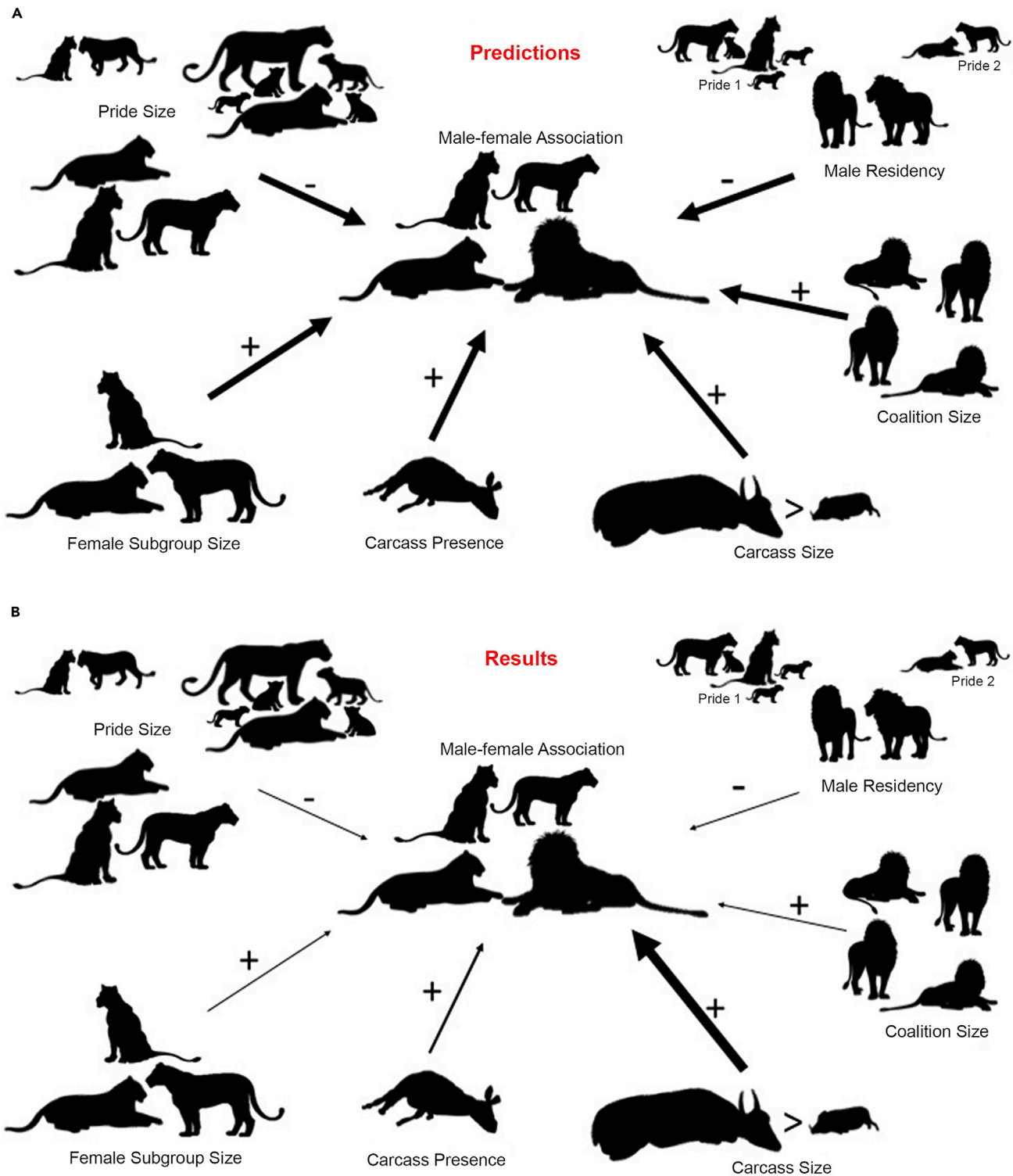
#### Spatial separation between male and female subgroups

Males remained significantly closer to females in Serengeti compared to Gir (difference in median distance: 834 m,  $p < 0.001$ , Figure 6A); however, the distance between male and female subgroups did not differ by seasons in the Serengeti (difference in median distance: 272 m,  $p = 0.12$ , Figure 6B).

## DISCUSSION

Sexual segregation has previously been considered to result from differences in ecological and social preferences between the two sexes (Ruckstuhl and Neuhaus, 2006). Our results suggest that these ecological and social preferences are also contingent upon intra-sexual grouping patterns that constrain physical proximity between the sexes, and more crucially that resource availability ultimately modulates the trade-offs between costs and benefits to females in affiliating with males. The costs to female lions from associating with males is potentially the highest in Gir and the lowest in Ngorongoro Crater, and females spend the least time with males in Gir and the most in Ngorongoro.

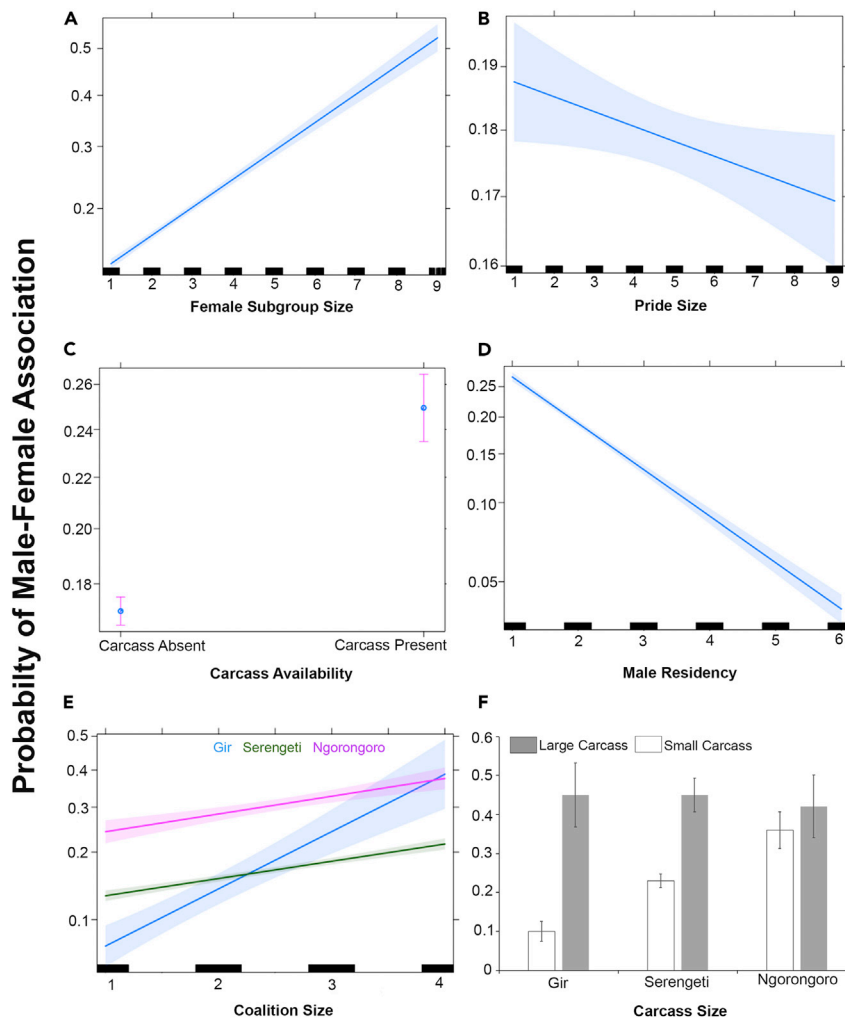
As expected, the fission-fusion nature of lion sociality significantly affects male-female associations. Females and males both spend considerable amounts of time in subgroups that are largely independent of pride or coalition size, thus it is physically impossible for males from small coalitions to associate with



**Figure 1. Infographic elucidating**

(A) Predictions relevant to social- and resource-mediated factors (variables) governing male-female association in lions across study sites.

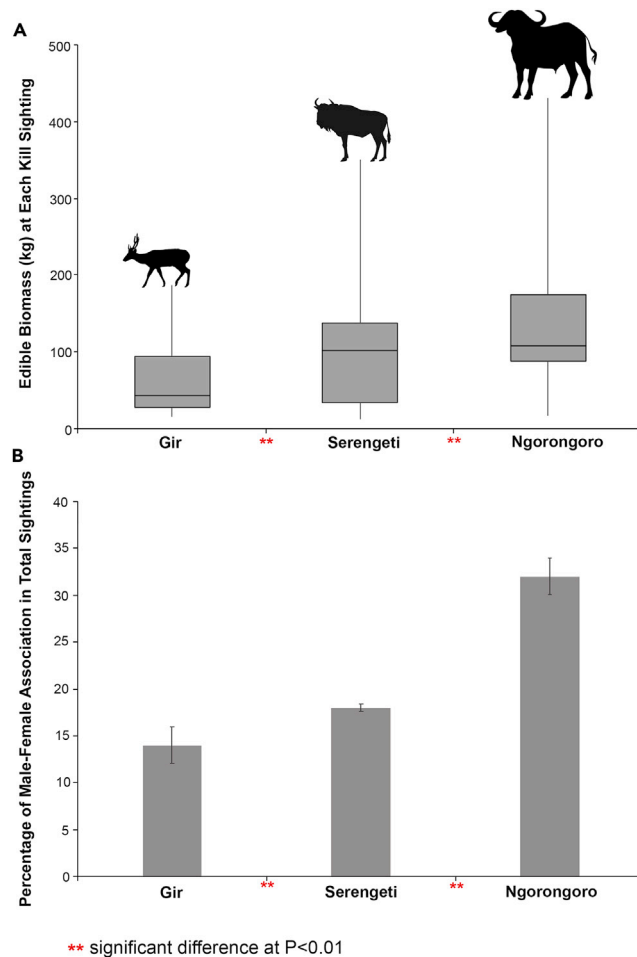
(B) Results of the predictions showing the effects of each variable on male-female association as per univariate relationships. For Figure 1B, width of the arrows represents the proportional contribution (coefficient strength) of each variable as per univariate models. For information on the variables, please see Table S1 in the supplemental document S1.



**Figure 2. Effect plots of the best multivariate model relating predictor variables and the odds of finding at least one adult male in proximity to female(s)**

(A–F) The probability of finding at least one male in relation to (A) female subgroup size; (B) pride size; (C) presence or absence of kill/carcass in the vicinity; (D) the number of prides the focal male coalition was simultaneously resident in or “male residency”; (E) the two-way interaction between coalition size and site, showing separate effects of coalition size in the three sites; and (F) large ( $\geq 150$  kg) versus small carcass ( $<150$  kg). For every relationship, the predicted probability of male presence was averaged across the other variables. Errors bars and bands are 95% confidence intervals (CIs). Predictors elucidated in transparent methods section in the supplemental information.

every female in their pride. The extent of male-female association is increasingly constrained in the largest prides as there are simply too many female subgroups for the males to associate with (Figure 2B). Similarly, coalitions that are simultaneously resident in multiple prides cannot possibly associate with all the females to the same extent as coalitions that reside in only a single pride (Figure 2D). However, males are more likely to overcome these constraints on occasions when the females form larger subgroups (Figure 2A), especially when an ecological factor (e.g., prey carcass) that has attracted the females to the same location has also attracted one or more of the resident males. A point to note here is that female subgroup size was similar across the three populations ( $2.5 \pm 0.05$ ; non-truncated dataset) with greatly differing pride sizes, and this lack of variability likely indicates that the proximate factors governing grouping tendencies in females posit an optimal subgroup size, below and beyond which the costs of appropriating, safeguarding, and sharing resources (primarily food) might outweigh the benefits. These results imply an upper limit to the number of female units/groups with which males can possibly associate at a given time, and similar constraints would likely apply to other species that exhibit “spatial defense by multi-male groups” (reviewed in Clutton-Brock, 1989). Species such as the banded mongoose *Mungos mungo*, ring-tailed lemur *Lemur catta*, sifaka



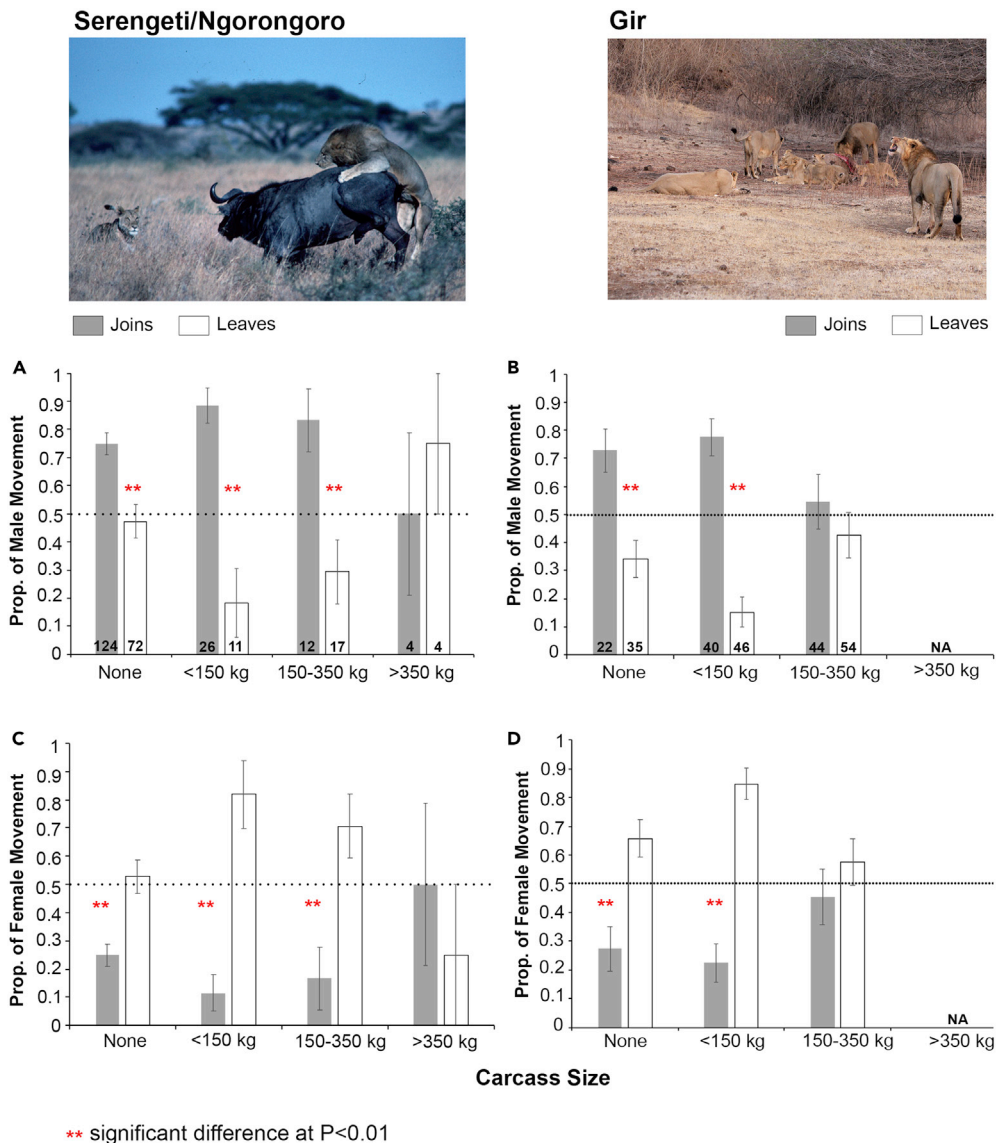
**Figure 3. Prey weight and male-female association in lions**

(A and B) (A) Boxplots (box: inter-quartile range, horizontal line within box: median, whiskers: 10–90 percentile) showing edible biomass (kg) from prey carcasses observed in Gir ( $n = 685$ ), Serengeti ( $n = 3,609$ ), and Ngorongoro ( $n = 794$ ). Edible biomass =  $5/8^{\text{th}}$  estimated carcass weight, and (B) sightings with adult male(s) and female(s) together as a percentage of the total number of observations compared across Gir ( $n = 1,092$ ), Serengeti (26,368), and Ngorongoro ( $n = 4,296$ ). Error bars are 95% CIs. \*\* denotes significant difference (at  $p < 0.01$ ) between comparisons tested using Mann-Whitney U and test of proportions, respectively

*Propithecus verreauxi*, chimpanzee *Pan troglodytes*, and bonobo *Pan paniscus* where multi-male units defend an area containing group(s) of females (reviewed in Clutton-Brock [1989]) would be ideal candidates for comparison with our findings. Such a limit to physical proximity between the sexes can also have an important bearing for species where males defend female groups particularly during the breeding season, such as red deer *Cervus elephas*, elephant seal *Mirounga angustirostris*, and sperm whale *Physeter catodon* (reviewed in Clutton-Brock [1989]). Intra-sexual grouping patterns have not traditionally been considered when testing whether a male's reproductive success increases with the number of females he can access (Bateman 1948), and our results suggest that the lack of physical proximity to "accessed/group" females may add to the reasons why the relationship (Bateman gradient) will not be always linear (Snyder and Gowaty, 2007; Tang-Martínez, 2016).

Availability of a prey carcass increased the chances of males associating with females by ~60% (Table S4). This suggests that outside of mating, males primarily associate with females to capitalize on feeding opportunities either by scavenging from the females' kills or by aiding them in prey capture. However, the latter is usually not applicable for Gir where females hunt on their own and typically capture small- to medium-sized prey (Chakrabarti and Jhala, 2019). Indeed, Gir females possibly time their hunting peaks when males are relatively less active to prevent losing their carcasses to males (Jhala et al., 2019). The general





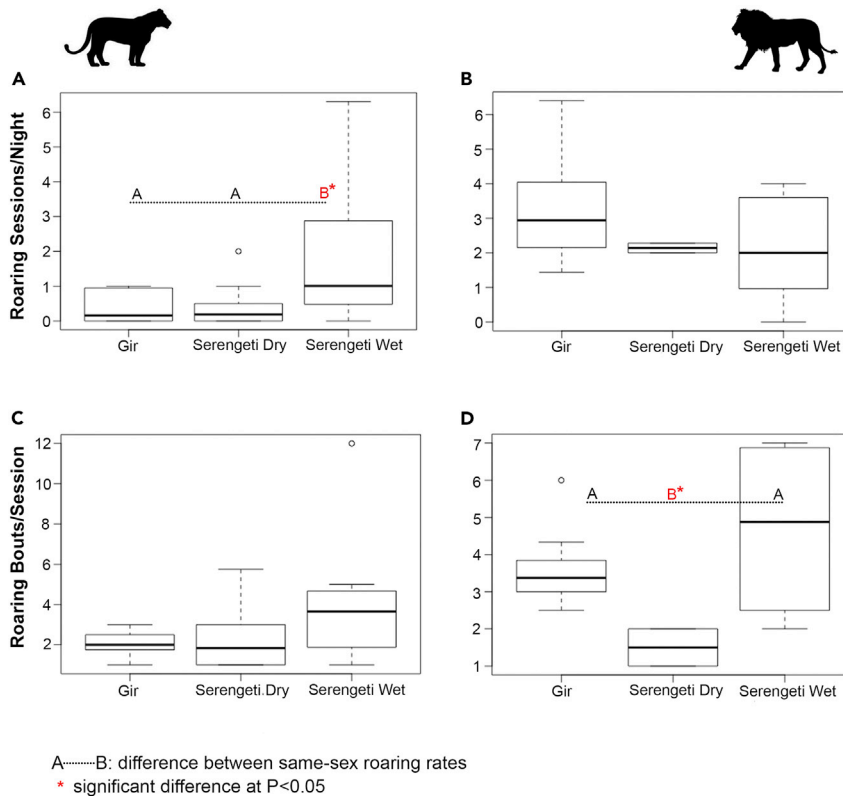
**Figure 4. Maintenance and avoidance of proximity between sexes**

(A–D) (A and C) Analysis of 166 joins and 104 leaves between male and female subgroups in Serengeti/Ngorongoro, and (B and D) analysis of 106 joins and 135 leaves between male and female subgroups in Gir. Patterns are represented across different scenarios of prey carcass availability. Error bars are SEs. Numbers at the base of the bars in (A and B) represent sample sizes that are symmetrical across both the sexes in their respective sites. \*\* denotes significant difference (at  $p < 0.01$ ) between comparisons tested using test of proportions.

reluctance of females to associate with males is demonstrated by our analysis of joins and leaves: males are more likely to join female subgroups, whereas females are more likely to separate from the males. However, this contrast disappeared at the largest carcasses where there was enough food to feed both sexes.

The influence of prey size on the reluctance of females to associate with males is also suggested by the differences in long-range vocalizations that provide opportunities for males to locate females. Females roared less frequently in prey-scarce environments such as Gir and the Serengeti during the dry season (Figure 5A), and this may help explain why females were more spatially separated from males in Gir (Figure 6A). However, we did not find significant seasonal trends in spatial separation between the sexes in Serengeti, which likely indicates additional processes affecting male-female associations. During the wet





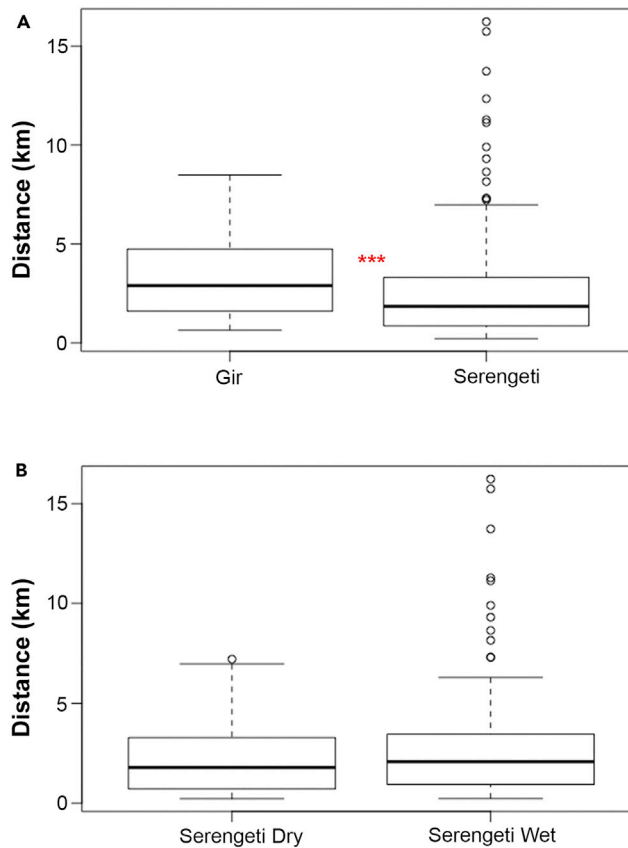
**Figure 5. Measures of roaring frequency and persistence of focal adult lions**

(A–D) Box-whisker plots representing (A and B) number of roaring sessions per night (roaring frequency) and (C and D) number of roaring bouts/session (roaring persistence) of female and male lion subgroups in Serengeti (dry and wet season separately) and Gir, measured from continuous night observations pertaining to at least 12 h for females and 6 h for males. The box in the box-whisker plots represents the inter-quartile range, the horizontal line inside the box denotes the median, the whiskers extend to  $\pm 1.5$  inter-quartile distribution, and unfilled circles are data points beyond that distribution. The left panel represents measures from female subgroups, and the right from males. \* denotes significant difference (at  $p < 0.05$ ) between comparisons tested using Mann-Whitney U tests.

season, Serengeti females roared frequently and could presumably be easily located by males throughout their pride range. However, even though Serengeti females were less communicative during the dry season, they predictably use a limited number of water sources to ambush prey (Hopcraft et al., 2005; Mosser et al., 2009), and can, nevertheless, be tracked by males. In contrast, Gir is characterized by thicker vegetation and more evenly distributed water sources with no relationship between lion distribution and water presence (Gogoi et al., 2020), possibly rendering non-communicative females more difficult to locate.

Carcass size is the smallest in Gir and the largest in Ngorongoro Crater, likely resulting in the overall reduction of male-female associations in Gir and the heightened associations in Ngorongoro (Figure 3B). However, the effect of carcass size was the highest in Gir followed by Serengeti and the lowest in Ngorongoro, which may again result from differences in vegetation structure. Being forested, Gir likely offers ample cover for lionesses to hunt and feed while remaining concealed from males. However, the comparably more open grasslands of Serengeti and Ngorongoro have high visibility as well as many sympatric carnivores. The Tanzanian lions frequently scavenge/kleptoparasitize from spotted hyenas (*Crocuta crocuta*), whose vocalizations may attract lions from considerable distances (Zuberbühler, 2008), as do vultures descending on a carcass (Schaller, 1972). In contrast, vultures are now rare in Gir and leopards (*Panthera pardus*) are the only other species of large carnivore, and they rarely attract lions to their kills.

Taken together, the results indicate that feeding ecology is likely the primary factor influencing the differences between the three study populations. Furthermore, the fact that the site differences remain after



\*\*\* significant difference at  $P < 0.001$

#### Figure 6. Spatial separation between male and female lions

(A and B) Box-whisker plots representing (A) straight line distance between concurrent locations (from the same day) of pride male and females belonging to different subgroups in Serengeti ( $n = 233$ ) and Gir ( $n = 97$ ), and (B) straight line distance between concurrent locations (from the same day) of pride male and females belonging to different subgroups during the dry ( $n = 107$ ) and wet season ( $n = 126$ ) in Serengeti. The box in the box-whisker plots represent the inter-quartile range, the horizontal line inside the box denotes the median, the whiskers extend to  $\pm 1.5$  inter-quartile distribution, and unfilled circles are data points beyond that distribution. \*\*\* denotes significant difference (at  $p < 0.001$ ) between comparisons tested using Mann-Whitney U tests.

controlling for social- and resource-mediated factors in the best statistical model of male-female associations suggests that the lions in each study site are not only reacting to prey size but also *anticipating* their next meal. Females in Gir tend to remain further apart from their resident males possibly because their next kill will not be sufficiently large to feed both sexes and males could exclude them altogether. Thus, the Gir females may anticipate that any association with males could be costly, whereas lionesses in the Crater do not have to take such pre-emptive/anticipatory actions because their kills are typically large.

The greater spatial separation between the sexes in Gir appears to explain why the smaller coalitions in Gir are unable to prevent females from associating with “peripheral” coalitions (Chakrabarti and Jhala, 2019), whereas resident coalitions in Serengeti and Ngorongoro successfully monopolize the pride females (Packer et al., 1991). In addition, all Gir males irrespective of coalition size reside in multiple prides (Chakrabarti and Jhala, 2019) unlike in Serengeti or Ngorongoro, where smaller coalitions are only able to reside in a single pride at a time (Bygott et al., 1979; Packer, *in press*). Being unable to “control” the relatively unaccommodating females, even the smallest Gir coalitions may compensate by simultaneously residing in multiple adjacent prides. This sort of feedback loop would further reduce the amount of time that males can spend with each female in Gir, as they must move/patrol over larger areas to cover multiple adjacent

territories (Chakrabarti and Jhala, 2019). However, it is noteworthy to mention that based on observations from the largest studied coalition of four males in Gir and its primary pride, there were no observations of the females mating outside of their primary coalition (Chakrabarti and Jhala, 2019). This might not necessarily confirm an absence of multi-coalition mating, but our data suggest that large coalitions might be able to monopolize pride females even in Gir.

Our results also highlight an interesting consequence of the “audience effect” on signaler behavior (reviewed in Zuberbühler [2008]) wherein lionesses were *quieter* in environments where food was in low supply and the costs of sharing meals were high. This is consistent with the possibility that a “non-targeted audience” shapes animal communication, where costs imposed by inadvertent information transfer to “eavesdroppers and bystanders” (in this case, males) can outweigh the benefits of roaring to distant female prides. These patterns would likely be similar in vocally communicative species (e.g., wolves *Canis lupus*, macaques *Macacca* spp., chimpanzees, baboons *Papio* spp.) where vocalization serves multiple purposes along with maintenance of group cohesion in fission-fusion societies (Hauser and Marler, 1993; Clark and Wrangham, 1994; Rendall et al., 2004; Faragó et al., 2014). Prior studies revealed that signalers modify their communication based on the potential impacts of non-targeted audience/bystanders, and our results provide evidence for the utility of comparative studies in systems where resources vary temporally and conflict of interest between group members can change accordingly. We also submit that changes in lion communication repertoire based on food availability can likely provide additional cues to the understanding of extra-auditory communication systems in an array of species (Hopkins and Cantero, 2003).

While our site-specific results are consistent with studies in other systems such as bottlenose dolphins *Tursiops* spp. where difference in activity budgets between the sexes coupled with allied male aggression drive sexual segregation (Fury et al., 2013; Galezo et al., 2018), we advance the field by quantifying how the contrasting levels of sexual segregation have possibly driven variations in the lion’s mating system. Resident coalitions in the Serengeti and Ngorongoro are better able to “track” and hence monopolize pride females, whereas small coalitions in Gir are unable to prevent the females from interacting with peripheral coalitions. By using a mechanistic and comparative approach, we identify the social and resource-mediated factors that govern sexual segregation. Our results also indicate how habitat structure and composition can affect group-cohesion and individual interactions, crucial for understanding social evolution.

### Limitations of the study

Although the three study populations experience a gradient of resources and intra-sexual grouping patterns, lions inhabit a wide range of eco-regions, and similar information from additional populations would help to confirm the robustness of our conclusions. Also, sample sizes for our behavioral data on joins/leaves and roaring are low when compared with the demographic parameters as we had to restrict our analysis to the behaviors of all-male and all-female subgroups.

### Resource availability

#### Lead contact

Further information, requests, and inquiries should be directed to and will be fulfilled by the lead contact, Stotra Chakrabarti ([stotra@umn.edu](mailto:stotra@umn.edu), [stotrachakrabarti@gmail.com](mailto:stotrachakrabarti@gmail.com)).

#### Materials availability

The study did not generate new materials.

#### Data and code availability

The original data will be made available by the lead contact on request.

## METHODS

All methods can be found in the accompanying [transparent methods supplemental file](#).

## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2021.102406>.

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## AUTHOR CONTRIBUTIONS

S.C. conceived the study with inputs from C.P. S.C., C.P., and Y.V.J. provided primary data. S.C. and C.P. curated the data and designed the analyses. S.C. and C.P. analyzed the datasets with inputs from J.K.B. and Y.V.J. S.C. wrote the first draft of the manuscript; C.P., J.K.B., and Y.V.J. edited manuscript drafts and contributed to writing relevant sections. All authors reviewed and edited subsequent drafts and gave final approval for submission.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

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**Supplemental information**

**Contrasting levels of *social distancing*  
between the sexes in lions**

**Stotra Chakrabarti, Joseph K. Bump, Yadvendradev V. Jhala, and Craig Packer**



1 Contrasting levels of *social distancing* between the sexes in lions

2 **Authors:** Stotra Chakrabarti, Joseph K. Bump, Yadvendradev V. Jhala , Craig Packer

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4 **Supplemental Document S1**

5 **Transparent Methods**

6 **Lion Monitoring**

7 Lions in the Serengeti National Park were studied continuously between 1966 and 2015  
8 (Schaller 1972; Bertram 1975; Hanby and Bygott 1979; Packer et al. 1991; Packer et al.  
9 2005) and in the Ngorongoro Crater, Tanzania, from 1963 onwards (Packer et al. 1991;  
10 Hanby et al. 1995). The 2,000 km<sup>2</sup> Serengeti study area typically included 21 study prides  
11 whereas the Crater floor typically holds six prides. Data in this paper come from a total of  
12 243 adult females in 29 prides and 116 males in 39 resident coalitions in the Crater and 862  
13 adult females in 74 prides and 440 males in 202 resident coalitions in the Serengeti. Crater  
14 lions were located opportunistically at least once every two weeks, sightings in the Serengeti  
15 were also opportunistic until 1984 when 1-2 individuals from each pride were fitted with  
16 radio collars, and subsequent sightings were either opportunistic or based on radio-telemetry.  
17 The Gir population represents the only extant population of Asian lions of ~600 animals and  
18 is located in the state of Gujarat, India. Scientific monitoring of this population was initiated  
19 in the early 1990s (reviewed in Jhala et al. 2019), and our data pertaining to interactions  
20 between individuals correspond to observations made on 21 males in 11 coalitions and 49  
21 females in 9 prides that were monitored through intensive directional searches and radio-  
22 telemetry between 2012 and 2019 (Chakrabarti and Jhala 2017, 2019; Chakrabarti et al.  
23 2020). Males were located once every two days and the mean interval between detection of  
24 the same adult female was five days (Chakrabarti and Jhala 2019). In addition to behavioural  
25 data on the intensively monitored ‘focal’ individuals, general information pertaining to

26 demography, predation, and space-use have continuously been generated from a larger subset  
27 of the population through on-going long-term efforts (reviewed in Jhala et al. 2019).

28 All observations on focal individuals across the three sites included date, time, spatial  
29 coordinates, pride and coalition membership, subgroup composition, prey species of any  
30 carcass present and reproductive status and behaviour. Individual recognition of all study  
31 animals was based on vibrissae spots and other permanent distinguishing body marks like  
32 scars and ear notches (Pennycuick and Rudnai 1970; Jhala et al. 1999).

### 33 **Ethics Statement**

34 All observations followed established protocols for studying wild animals as per the  
35 guidelines of the University of Minnesota and the Wildlife Institute of India, in accordance  
36 with the Park Management of Tanzania and India.

### 37 **Male-female association**

38 For each observation of a female or female subgroup, we noted the presence or absence of  
39 any resident male(s) within 200 m, excluding interactions that included mating pairs. We  
40 excluded observations of mating/consorting pairs because these necessarily involved male-  
41 female associations and were driven entirely by short-term mating strategies.

### 42 **Factors governing male-female association:**

43 **1. Social factors:** To quantify how intra-sexual grouping patterns affect male-female  
44 associations, we investigated the effects of the following social/demographic factors: pride  
45 size (all females  $\geq 2$  years of age), female subgroup size (all females  $\geq 2$  years of age within  
46 200 m of each other) at each sighting, male coalition size, and male residency or the number  
47 of female prides where the male's coalition was simultaneously resident (see **Figure 1a**).  
48 Subgroup size can include a minimum of a single individual.

49 **2. Effect of prey resources:**

50 **a) Carcass availability:** Males frequently scavenge from females (Schaller 1972). Thus, the  
51 presence of a prey carcass should increase associations between the two sexes.

52 **b) Size of carcass:** The detection of a kill by a scavenging individual/group is in large part a  
53 function of the persistence of the carcass. Large kills/carcasses are consumed over longer  
54 periods, attract more attention and should be easier to detect than smaller carcasses that are  
55 consumed rapidly. Further, males are more likely than females to catch very large prey such  
56 as Cape buffalo or giraffe (*Giraffa camelopardalis*, 700-1000 kg). Given both of these  
57 patterns, we would expect male-female association to be highest at large kills. We estimated  
58 the total edible biomass of carcasses present at each sighting and categorized the data into  
59 large ( $\geq 150$  kg) and small ( $< 150$  kg). The edible biomass of an intact carcass =  $5/8^{\text{th}}$  of the  
60 animal's live weight (Packer et al. 1990). Live weights corresponding to age-sex categories  
61 of prey were adopted from published literature (Sachs 1967; Chakrabarti et al. 2016), while  
62 the age-sex category of each prey carcass was estimated visually. The remaining biomass of a  
63 partial carcass scavenged from another predator was reduced accordingly (Packer et al.  
64 1990).

65 **Directionality of male-female association:** To determine which sex played the greatest role  
66 in maintaining proximity, we tabulated all cases where individuals “joined” or “left” a  
67 subgroup of the opposite sex. We restricted our analysis to cases where all-male subgroups  
68 joined/left all-female subgroups and vice versa.

69 **Roaring rates:** Lions typically roar during the hours of darkness to maintain social cohesion  
70 (McComb et al. 1993, 1994) and defend territories (Schaller 1972; Grinnell et al. 1995). If  
71 one sex seeks to avoid the other, those animals would be expected to roar less often because  
72 of the perceived constraints imposed by the listeners/eavesdroppers (Grinnell and McComb  
73 2001), particularly in circumstances when the presence of the opposite sex inflicts the highest  
74 costs. Each *roaring bout* consists of a continuous series of roars and grunts that persists for

75 about a minute. We defined “roaring frequency” as the number of *roaring sessions* per 12-hr  
76 night, where a single *session* included all *bouts* occurring <30 mins apart; “roaring  
77 persistence” is the number of *roaring bouts* per *session*. All measures pertain to group-level  
78 choruses because of the difficulty in discerning individual rates. All roaring data were  
79 collected between sunset and sunrise as part of our focal sampling/observations of same-  
80 sexed subgroups. In the Serengeti, roaring rates were averaged across 1-4 consecutive nights  
81 of observation on all-female subgroups (18 focal follows in the dry season and 13 in the wet  
82 season) and 6-hr observations of all-male subgroups (2 focal follows in the dry season and 5  
83 in the wet season) (Packer et al. 1990; Grinnell and McComb 2001). Data from Gir similarly  
84 come from overnight observations of female (12 follows) and 6-hour observations of male  
85 subgroups (16 follows) spanning 1-8 consecutive nights (Jhala et al. 2019). No roaring data  
86 was available from the Crater.

87 **Spatial separation between males and females:** To better characterize the ecological  
88 separation between the two sexes, we measured the straight-line distance between females  
89 and resident/primary males that were observed separately (i.e., >200 m apart) on the same  
90 day. Data from the Serengeti are restricted to cases where the male and female had both been  
91 fitted with radio collars; data from Gir include a combination of radio-telemetry and  
92 opportunistic sightings; comparable data were not available from the Crater.

### 93 **Statistical Analysis**

94 **Factors governing male-female association:** To minimize any differences in male-female  
95 associations that might have originated solely from the contrasting pride and coalition sizes in  
96 the different populations (Tanzania- pride  $size_{max}$ : 21, coalition  $size_{max}$ : 9; Gir- pride  $size_{max}$ :  
97 9, coalition  $size_{max}$ : 4) we truncated the Tanzanian dataset to match the maximum pride and  
98 coalition size as seen in Gir. Since pride and coalition sizes likely govern the magnitude of  
99 inter-sexual interactions, this truncation restricted the data to the same grouping potentials

100 across the three sites, allowing us to investigate similarities and differences between sites.  
101 With this truncated dataset (n= 31,756 observations; Serengeti: 26,368; Ngorongoro: 4296  
102 and Gir: 1092), we tested the effects of all the aforementioned variables (pertaining to both  
103 social and resource correlates, **Table S1**) to predict the odds of male presence using logistic  
104 GLMs after measuring correlations between the variables. We first used univariate  
105 relationships to determine the importance of each variable in predicting the odds of male  
106 presence. Since the chosen variables were not highly correlated with each other with the  
107 maximum correlation ( $r=0.28$ ) being between female pride size and subgroup size, we  
108 retained all significant variables (as is) in the final modelling. We explored the odds of  
109 observing male(s) together with female(s) using all the variables, while checking for disparity  
110 between populations by employing *site* as an interactive term with each of the variables.  
111 Models were first built by using all significant variables as additive effects to one another,  
112 and then with *site* interacting with each variable sequentially. We ranked models using  
113 Akaike Information Criterion (Akaike 1974) and explored model fit through significance  
114 levels and deviance tables.

115 **Directionality of male-female association:** We analyzed 272 joins (Tanzania: 166, Gir: 106)  
116 and 239 leave events (Tanzania: 104, Gir: 135) from male and female subgroups. Using test  
117 of proportions, we checked whether the proportion of joins was significantly different from  
118 the proportion of leaves for each sex in each comparison. We also checked if proportions  
119 significantly differed from 0.5, e.g. whether the estimated mean proportion encompassed a  
120 value of 0.5 within its 95% confidence limits, which would mean that both sexes joined or  
121 left subgroups at similar rates. To determine how prey size affects sexual segregation, we  
122 present proportions of joins and leaves for each sex across four categories: a) no prey carcass  
123 present, b) small carcass (<150 kg), c) large carcass (150-350 kg), d) super-large carcass (>  
124 350 kg).

125 **Roaring rates:** We used Mann-Whitney U tests to compare vocalization rates within and  
126 between sites. Within site comparisons pertain to differences between sexes in Gir and  
127 between sexes and seasons in Serengeti.

128 **Spatial separation between males and females:** To minimize any differences in spatial  
129 separation that might have originated from the contrasting territory sizes in the different  
130 populations, we further truncated the Tanzanian dataset to match the maximum 75% kernel  
131 female pride territory of ~120 km<sup>2</sup> observed in Gir (Chakrabarti and Jhala 2019). We used  
132 Mann-Whitney U tests to compare between (Serengeti: 233 locations, Gir: 97 locations) and  
133 within sites (Serengeti dry and wet seasons: 107 and 126 locations respectively).

134 All data processing was done using MS Excel (Microsoft Inc.) and analyses using program  
135 Rv4.0.3 (R Core Team 2020). Spatial data was analyzed in ARCGIS v9.3 (ESRI 2009).  
136 Errors are SEs if not specified otherwise.

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194 **Supplementary Tables**

195 **Table S1.** List and definition of social- and resource-mediated variables used to model the  
 196 frequency of male-female associations across the study sites. Related to Figures 1 and 2

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 198

Variable	Definition	Abbreviation
Pride Size	All females in a pride $\geq 2$ y of age	Prd_sz.
Female Subgroup Size	All females of a pride $\geq 2$ y which are within 200 m of each other	Sgr_sz
Coalition Size	Interacting adult male group size	Cln_sz
Male Residency	Number of prides that the focal coalition is simultaneously resident in	Resid.
Carcass Availability	Presence vs. absence of prey carcass	Carc_P1
Prey Carcass Size (Large/Small)	Large carcass (biomass $\geq 150$ kg), small carcass (biomass $\geq 150$ kg)	Carc_sz
Site	Site differences between populations (Ngorongoro, Serengeti, and Gir)	Site(SiteNgr, SiteSng and SiteGir)

199

200 **Table S2.** Exponentiated parameter estimates and their 95% distribution limits of univariate  
 201 models relating the odds of finding at least one adult male in proximity to female(s) and the  
 202 predictor variables. Related to Figure 2

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Variable	Exponentiated	2.5%	97.5%
Coefficients			
Prd_sz.	1.08	1.06	1.09
Sgr_sz	1.29	1.27	1.31
Cln_sz	1.08	1.05	1.11
Resid.	0.72	0.70	0.74
Carc_P1	1.61	1.48	1.74
SiteGir	0.17	0.14	0.20
SiteNgr	2.88	2.40	3.46
SiteSng	1.32	1.11	1.57

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231 **Table S3.** Model selection statistics of all models relating the odds of finding at least one  
 232 adult male in proximity to female(s) and the predictor variable. Related to Figures 1 and 2

233

Model	AIC	ΔAIC
Prd_sz+Sgr_sz+Carc_P+Resid+Cln_sz*Site	29284.93	0
Sgr_sz+Carc_P+Resid+Cln_sz*Site	29285.82	0.89
Sgr_sz+Carc_P+Resid+Cln_sz+Prd_sz*Site	29287.42	2.49
Prd_sz+Sgr_sz+Resid+Cln_sz+ Carc_P*Site	29297.14	12.21
Prd_sz+Sgr_sz+Carc_P+Cln_sz+Resid *Site	29304.17	19.24
Prd_sz+Sgr_sz+Carc_P+Resid+Cln_sz+Site	29307.14	22.21
Prd_sz+Sgr_sz+Carc_P+Resid+Cln_sz	29708.02	423.09
Sgr_sz	30570.68	1285.75
Resid	30953.55	1668.62
Site	31060.92	1775.99
Prd_sz	31378.06	2093.13
Carc_P	31380.42	2095.49
Cln_sz	31489.68	2204.75
Null	31512.20	2227.27

250

251 **Table S4.** Exponentiated parameter estimates, their 95% distribution limits and P-values of  
 252 the best multivariate model relating the odds of finding at least one adult male in proximity to  
 253 female(s) and the predictor variables. Related to Figure 2

254

Variable	Estimate	2.5%	97.5%	P-value
(Intercept)	0.06	0.04	0.09	<0.001
Sgr_sz	1.28	1.25	1.30	<0.001
Prd_sz	0.98	0.97	1.00	<0.01
Carc_P1	1.61	1.48	1.75	<0.001
SiteNgr	6.31	4.08	9.86	<0.001
SiteSng	2.95	1.99	4.42	<0.001
Cln_sz	1.98	1.66	2.37	<0.001
Resid	0.64	0.62	0.67	<0.001
SiteNgr:Cln_sz	0.62	0.51	0.76	<0.001
SiteSng:Cln_sz	0.62	0.51	0.74	<0.001

255

256 **Table S5.** Model selection statistics of all models relating the odds of finding at least one  
 257 adult male in proximity to female(s) to large versus small carcass present at the site. Related  
 258 to Figure 2.

259

Model	AIC	ΔAIC
Site*Carc_sz	4126.11	0
Site+Carc_sz	4154.96	28.85
Carc_sz	4209.03	82.92
Null	4360.04	233.93

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270 **Table S6.** Exponentiated parameter estimates and their 95% distribution limits of the best  
 271 model relating odds of finding at least one adult male in proximity to female(s) to large  
 272 versus small carcass present at the site. Related to Figure 2  
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 274

275	Variable	Exponentiated Coefficients	2.5%	97.5%	P-Value
276	SiteGir	0.11	0.08	0.15	<0.001
277	SiteNgr	4.97	3.51	7.12	<0.001
278	SiteSng	2.65	1.98	3.62	<0.001
279	Carcsz_Lg	7.25	4.68	11.28	<0.001
280	SiteNgr:Carcsz_Lg	0.18	0.10	0.32	<0.001
281	SiteSng:Carcsz_Lg	0.39	0.24	0.63	<0.001