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

Chakrabarti et al., iScience 24, 102406
May 21, 2021
https://doi.org/10.1016/j.isci.2021.102406
Contrasting levels of social distancing between the sexes in lions

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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,
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 ≥150 kg than at smaller carcasses (Tables S5 and S6), and this contrast was most prominent in Gir (prob. = 0.10small, 0.45large) followed by Serengeti (0.23small, 0.45large), and lowest in Ngorongoro Crater (0.36small, 0.42large) (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% ± 1%), followed by Serengeti (18% ± 0.2%) and the highest in Ngorongoro (32% ± 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 (≥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.
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 ± 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 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 (≥ 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.

![Figure 2](image-url)
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 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 = 5/8th 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.
The 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
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 (Zuberbuhler, 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

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 ±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.
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 un-accommodating 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 prides.

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 ± 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.

*** significant difference at P<0.001
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 pridemates. These patterns would likely be similar in vocally communicative species (e.g., wolves Canis lupus, macaques Macaca 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, 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.
ACKNOWLEDGMENTS

We thank the Ministry of Environment Forests & Climate Change, India; Gujarat Forest Department; Tanzanian Wildlife Research Institute; and Tanzanian National Parks for granting permissions and facilitation of the study. We thank all the researchers and field assistants working in the Gir Lion Project and Serengeti Lion Project for their hard work and perseverance in the field. S.C. would like to personally thank Ninad Mungi for his help with spatial data, Mayank Kohli, Aamod Zambre, and Manjari Roy for providing inputs on an earlier version of the manuscript, and Aarush De for his help with Figure 1. Also, as this paper was drafted during the “unprecedented” times of a pandemic, S.C. acknowledges the mental support provided by Rupa Chakraborty, Stabak Chakrabarti, Anika Chakraborty, Debalina De, Subhadeep De, Nancy Gibson, Ron Sternal, Amy Schrank, and Sreyashi Ray. The research was supported by grants from the NSF programs in Psychobiology, Population Biology, and Long-Term Research in Environmental Biology (LTREB) to C.P., and Department of Science and Technology, India grant (SERB/F/0601/2013-2016) and funds provided by the Wildlife Institute of India to Y.V.J.

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. 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, Yadavendra V. Jhala, and Craig Packer
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Supplemental Document S1

Transparent Methods

Lion Monitoring

Lions in the Serengeti National Park were studied continuously between 1966 and 2015 (Schaller 1972; Bertram 1975; Hanby and Bygott 1979; Packer et al. 1991; Packer et al. 2005) and in the Ngorongoro Crater, Tanzania, from 1963 onwards (Packer et al. 1991; Hanby et al. 1995). The 2,000 km² Serengeti study area typically included 21 study prides whereas the Crater floor typically holds six prides. Data in this paper come from a total of 243 adult females in 29 prides and 116 males in 39 resident coalitions in the Crater and 862 adult females in 74 prides and 440 males in 202 resident coalitions in the Serengeti. Crater lions were located opportunistically at least once every two weeks, sightings in the Serengeti were also opportunistic until 1984 when 1-2 individuals from each pride were fitted with radio collars, and subsequent sightings were either opportunistic or based on radio-telemetry.

The Gir population represents the only extant population of Asian lions of ~600 animals and is located in the state of Gujarat, India. Scientific monitoring of this population was initiated in the early 1990s (reviewed in Jhala et al. 2019), and our data pertaining to interactions between individuals correspond to observations made on 21 males in 11 coalitions and 49 females in 9 prides that were monitored through intensive directional searches and radio-telemetry between 2012 and 2019 (Chakrabarti and Jhala 2017, 2019; Chakrabarti et al. 2020). Males were located once every two days and the mean interval between detection of the same adult female was five days (Chakrabarti and Jhala 2019). In addition to behavioural data on the intensively monitored ‘focal’ individuals, general information pertaining to
demography, predation, and space-use have continuously been generated from a larger subset of the population through on-going long-term efforts (reviewed in Jhala et al. 2019).

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

Ethics Statement

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

Male-female association

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

Factors governing male-female association:

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

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

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

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

Roaring rates: Lions typically roar during the hours of darkness to maintain social cohesion (McComb et al. 1993, 1994) and defend territories (Schaller 1972; Grinnell et al. 1995). If one sex seeks to avoid the other, those animals would be expected to roar less often because of the perceived constraints imposed by the listeners/eavesdroppers (Grinnell and McComb 2001), particularly in circumstances when the presence of the opposite sex inflicts the highest costs. Each roaring bout consists of a continuous series of roars and grunts that persists for
about a minute. We defined “roaring frequency” as the number of *roaring sessions* per 12-hr night, where a single *session* included all *bouts* occurring <30 mins apart; “roaring persistence” is the number of *roaring bouts per session*. All measures pertained to group-level choruses because of the difficulty in discerning individual rates. All roaring data were collected between sunset and sunrise as part of our focal sampling/observations of same-sexed subgroups. In the Serengeti, roaring rates were averaged across 1-4 consecutive nights of observation on all-female subgroups (18 focal follows in the dry season and 13 in the wet season) and 6-hr observations of all-male subgroups (2 focal follows in the dry season and 5 in the wet season) (Packer et al. 1990; Grinnell and McComb 2001). Data from Gir similarly come from overnight observations of female (12 follows) and 6-hour observations of male subgroups (16 follows) spanning 1-8 consecutive nights (Jhala et al. 2019). No roaring data was available from the Crater.

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

**Statistical Analysis**

**Factors governing male-female association:** To minimize any differences in male-female associations that might have originated solely from the contrasting pride and coalition sizes in the different populations (Tanzania- pride size$_{\text{max}}$: 21, coalition size$_{\text{max}}$: 9; Gir- pride size$_{\text{max}}$: 9, coalition size$_{\text{max}}$: 4) we truncated the Tanzanian dataset to match the maximum pride and coalition size as seen in Gir. Since pride and coalition sizes likely govern the magnitude of inter-sexual interactions, this truncation restricted the data to the same grouping potentials.
across the three sites, allowing us to investigate similarities and differences between sites. With this truncated dataset (n= 31,756 observations; Serengeti: 26,368; Ngorongoro: 4296 and Gir: 1092), we tested the effects of all the aforementioned variables (pertaining to both social and resource correlates, Table S1) to predict the odds of male presence using logistic GLMs after measuring correlations between the variables. We first used univariate relationships to determine the importance of each variable in predicting the odds of male presence. Since the chosen variables were not highly correlated with each other with the maximum correlation (r=0.28) being between female pride size and subgroup size, we retained all significant variables (as is) in the final modelling. We explored the odds of observing male(s) together with female(s) using all the variables, while checking for disparity between populations by employing site as an interactive term with each of the variables. Models were first built by using all significant variables as additive effects to one another, and then with site interacting with each variable sequentially. We ranked models using Akaike Information Criterion (Akaike 1974) and explored model fit through significance levels and deviance tables.

**Directionality of male-female association:** We analyzed 272 joins (Tanzania: 166, Gir: 106) and 239 leave events (Tanzania: 104, Gir: 135) from male and female subgroups. Using test of proportions, we checked whether the proportion of joins was significantly different from the proportion of leaves for each sex in each comparison. We also checked if proportions significantly differed from 0.5, e.g. whether the estimated mean proportion encompassed a value of 0.5 within its 95% confidence limits, which would mean that both sexes joined or left subgroups at similar rates. To determine how prey size affects sexual segregation, we present proportions of joins and leaves for each sex across four categories: a) no prey carcass present, b) small carcass (<150 kg), c) large carcass (150-350 kg), d) super-large carcass (>350 kg).
Roaring rates: We used Mann-Whitney U tests to compare vocalization rates within and between sites. Within site comparisons pertain to differences between sexes in Gir and between sexes and seasons in Serengeti.

Spatial separation between males and females: To minimize any differences in spatial separation that might have originated from the contrasting territory sizes in the different populations, we further truncated the Tanzanian dataset to match the maximum 75% kernel female pride territory of ~120 km² observed in Gir (Chakrabarti and Jhala 2019). We used Mann-Whitney U tests to compare between (Serengeti: 233 locations, Gir: 97 locations) and within sites (Serengeti dry and wet seasons: 107 and 126 locations respectively).

All data processing was done using MS Excel (Microsoft Inc.) and analyses using program R v4.0.3 (R Core Team 2020). Spatial data was analyzed in ARCGIS v9.3 (ESRI 2009).

Errors are SEs if not specified otherwise.

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Supplementary Tables

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

| Variable                  | Definition                                                                 | Abbreviation |
|---------------------------|---------------------------------------------------------------------------|--------------|
| Pride Size                | All females in a pride ≥2 y of age                                        | Prd_sz.      |
| Female Subgroup Size      | All females of a pride ≥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 ≥ 150 kg), small carcass (biomass ≥ 150 kg) | Carc_sz      |
| Site                      | Site differences between populations (Ngorongoro, Serengeti, and Gir)     | Site(SiteNgr, SiteSng and SiteGir) |

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

| Variable | Exponentiated Coefficients | 2.5%  | 97.5% |
|----------|----------------------------|-------|-------|
| 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  |
Table S3. Model selection statistics of all models relating the odds of finding at least one adult male in proximity to female(s) and the predictor variable. Related to Figures 1 and 2

| 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 |

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

| 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_P | 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 |

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

| Model | AIC  | ΔAIC  |
|-------|------|-------|
| Site*Care_sz | 4126.11 | 0 |
| Site+Carc_sz | 4154.96 | 28.85 |
| Care_sz | 4209.03 | 82.92 |
| Null | 4360.04 | 233.93 |
**Table S6.** Exponentiated parameter estimates and their 95% distribution limits of the best model relating odds of finding at least one adult male in proximity to female(s) to large versus small carcass present at the site. Related to Figure 2

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