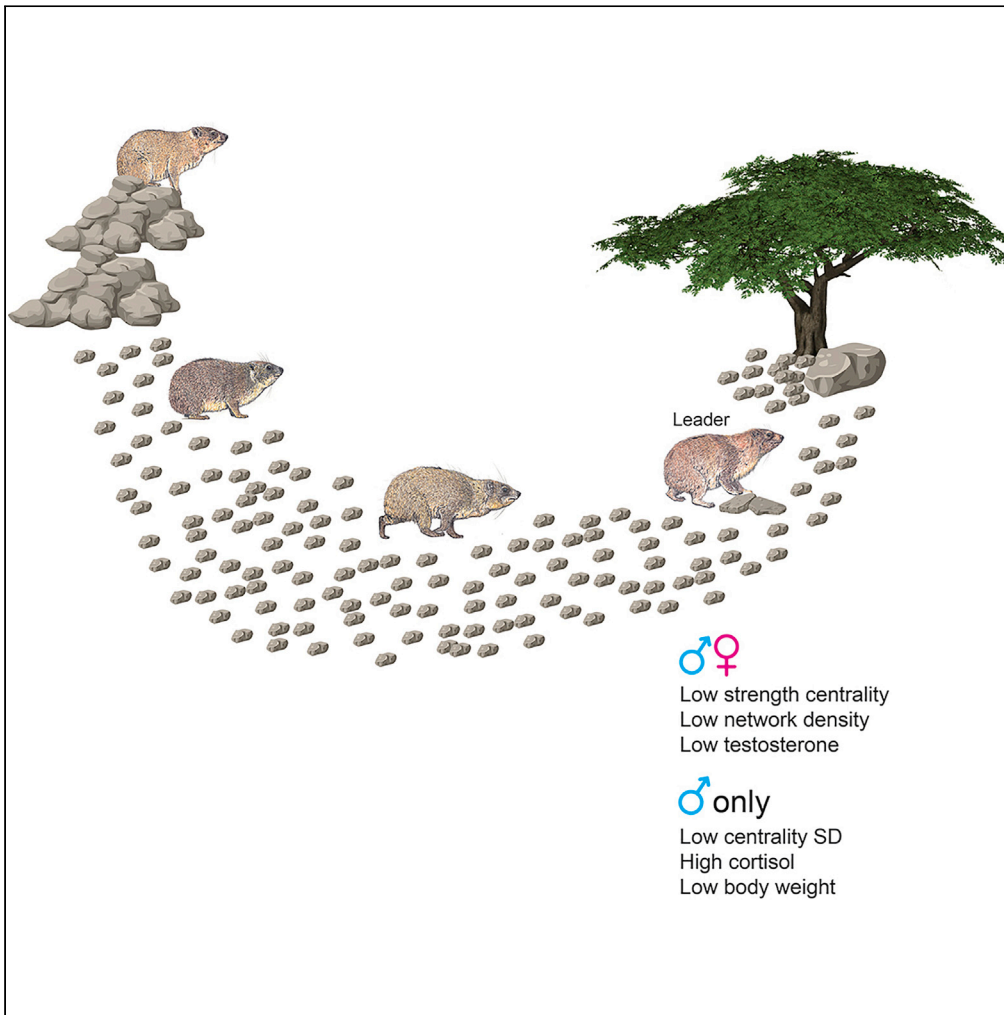


Article

Sex-associated and context-dependent leadership in the rock hyrax



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Highlights

Different traits play a role in hyrax male and female leaders, in different contexts

On moderate risk, younger resident males with high cortisol and low testosterone lead

During predation scenario, lower centrality status males lead

Among group females, leadership is more equally distributed

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Article

Sex-associated and context-dependent leadership in the rock hyrax

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SUMMARY

In many mammalian species, both sexes may take leadership role, but different traits may play a role in determining variation within species. Here we examine the effect of sex on leadership. We present three complementary datasets derived from a well-studied population of wild rock hyrax (*Procavia capensis*). The findings demonstrated that male and female rock hyraxes take on different leadership positions, depending on the context. When risk is moderate, more likely to lead are younger resident males, which experience high cortisol and lower testosterone levels. However, during acute predation scenarios, more likely to lead are males with lower centrality status. We suggest that hyrax males exhibit risky behaviors that may reflect their need for self-advertisement. In contrast, leadership among group females is more equally distributed. Females have little to gain from risky actions due to the lack of competition among them, but nonetheless take leadership positions.

INTRODUCTION

Animals make many decisions throughout the day on when and where to take risks related to foraging, resting, traveling, and socializing. In many social species, the members of a group coordinate their activities to maximize the benefits of group living, such as predator avoidance and enhanced foraging efficiency. Some members of a group might exert a greater influence than others, depending on the context and upon their specific needs or traits. Such differential social influence has also been defined as leadership (Smith et al., 2016). Although individuals naturally behave in response to external stimuli, such as time of day, the appearance of a food source, or a potential predator, a group may have one or several leaders that strongly contribute to the ability to coordinate collective actions efficiently (Brent et al., 2015; McComb et al., 2001, 2011).

The leadership among group members can range from the despotic control by one individual (also termed unshared leadership), to spontaneous, distributed leadership in which leadership roles are equally shared across all group members (shared leadership) (Smith et al., 2016). In unshared leadership, one or two dominant individuals lead the group, often by imposing power upon others (Smith et al., 2015). Dominant individuals usually possess a superior body size and/or better access to resources, operate more autonomously, and are in a better position than subordinates to attract followers. However, it is not always the high-ranked individuals that lead the group (Smith and van Vugt, 2020). Leadership and social rank should thus be assessed independently, as leadership status focuses on whether a particular individual imposes disproportional influence on group decisions. For instance, in an egalitarian society, group members show minor differences in social rank, but nonetheless show leadership in collective behaviors. The leadership roles in these groups are often fluid and can be context dependent and variable over time, even within a single species (Smith et al., 2015). Several individuals can occupy leadership roles at different times and context in a given social group, and leadership can arise from individual differences in motivation (Fischhoff et al., 2007; Rands et al., 2003), experience (Flack et al., 2012), knowledge (Brent et al., 2015), skills (Nagy et al., 2010; Pettit et al., 2015), age (Goldenberg et al., 2016; McComb et al., 2001, 2011), and personality (Harcourt et al., 2009).

In many species, both females and males may occupy leadership positions. Although the norm across the mammalian lineage appears to be male-biased leadership (males leading more often than females), a small number of mammalian species exhibit strong female-biased leadership, including killer whales (*Orcinus*

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orca), African lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*), and bonobos (*Pan paniscus*) (Smith et al., 2020). Female leaders are more likely to emerge within small egalitarian groups, when group females form strong social networks. A relevant question for mixed-sex groups is that of how sex differences relate to leadership emergence and traits.

The rock hyrax (*Procavia capensis*) is a social mammal that lives in stable mixed-sex groups for years, and maintains long-term affiliations (Barocas et al., 2011). In our study area (Ein Gedi, Israel), the hyrax group comprises several males (one mature immigrant resident and several young, local, late dispersers) and 3–20 females with their pups (1–3 pups/female; (Bar Ziv et al., 2016)). Male and female hyraxes have very different life strategies. A resident male arrives from outside the group and remains with the social group for an average of 3.1 years and a maximum of 5 years. Native males reach maturity at the age of 17–24 months, and soon after gradually leave their natal group or are occasionally forced to disperse by the resident male (Hoeck, 1989; Koren, 2000). These bachelor adult males live on the periphery of the social groups and associate with the groups in the area, mainly during the mating season (Ilany et al., 2013, Figure S1). All adult males produce long, complex songs (vocalizations), which reflect the caller's identity, age, social rank, and body condition (Koren and Geffen, 2011), and attempt to time their calls to periods of increased attention and an alert audience (Demartsev et al., 2014). Toward the mating season song frequency increases, and resident males are observed mate-guarding the older and experienced females (Bar Ziv et al., 2016). In contrast, hyrax group females invest a great amount of time in social relationships, forming strong ties with other group females, which play an important role in their daily lives. Most females remain in the group for life: an average of 5.9 years and a maximum of about 10 years (Barocas et al., 2011). Breeding is seasonal and synchronized (Mendelssohn, 1965), and females mate with multiple males, possibly to mask paternity (Bar Ziv et al., 2016; Koren and Geffen, 2009).

All hyrax group members regularly share sleeping dens and travel together to feeding locations and back to the sleeping dens in "tandem movement": each group member independently advances short distances and joins other group members in fixed stops. The time window between two consecutive individuals can range up to a few minutes. Through this movement pattern, although traveling in tandem with other group members, the first animals arrive individually at the destination alone and expose themselves to potential predation. Moreover, the predictable location of feeding sites makes such sites more dangerous. The Arabian leopard (*Panthera pardus nimr*) in Ein Gedi (now extinct in this area) used to ambush hyraxes in feeding bushes, or near sleeping dens, pouncing on the emerging hyraxes before they were able to react (Timna, 2000). Today, the common predators of hyraxes are wolves and foxes. Because position-related differential predation risk is predictable, with front positions being at the highest risk (Bumann et al., 1997; Hamilton, 1971), and successfully leading others is safer than becoming isolated from the group (Ioannou et al., 2019), hyraxes leadership is associated with the cost of predation.

Levels of the socially modulated hormones cortisol and testosterone can reflect on the relationship between the intrinsic response to the risk of predation and the social benefit from maintaining group cohesion in a leader. Testosterone influences the brain in archetypical situations, such as fight, flight, mating, and the search and struggle for social status, and has a well-established role in animal research as a social mediator. Although early studies suggested that testosterone facilitates physical aggression in social contexts, accumulating evidence indicates that it seems to drive a more general repertoire of motivated behaviors rather than aggression per se (Eisenegger et al., 2011). Cortisol is released in response to events and circumstances that involve acute stress, such as predation risk. Through the release of glucocorticoids, the hypothalamic–pituitary–adrenocortical (HPA) axis modulates a set of physiological, hormonal, and behavioral responses to enable adaptation to stressors (Monaghan and Spencer, 2014). However, cortisol is also released in response to social hierarchy challenges (Gesquiere et al., 2011), and the effects of glucocorticoid activity on cooperative behavior may have different consequences in males and females (Dantzer et al., 2017).

The expression of leadership (Smith et al., 2016) may vary across several contexts, so that leaders in one context can possess traits that differ from those of leaders in other contexts. In this study, in order to identify and characterize context-specific leaders, we analyzed three complementary datasets that represent different contexts: morning emergence, coordinated movement, and predator defense. Data were collected by means of direct behavioral observations, automated data collection using proximity loggers and base stations, and behavioral observations during live vocal playback trials. We suggest three models

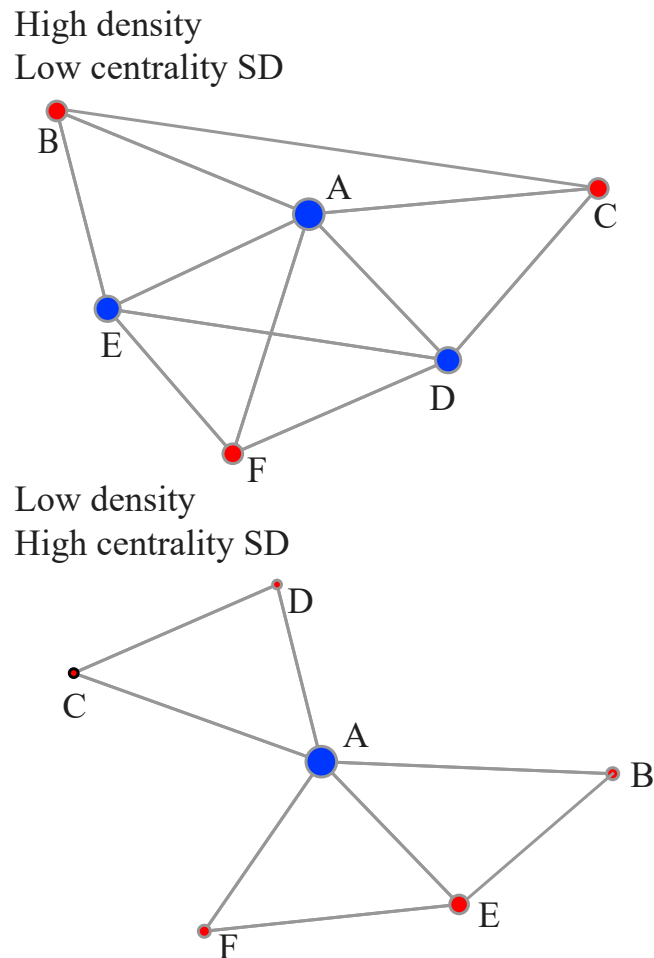


Figure 1. Hypothetical example of the association between network density and centrality SD with the expected numbers of leaders in a social group

We hypothesized that individuals with a lower strength centrality would tend to be leaders (blue circles), and single or specific leader-follower sequence was expected to emerge in groups with lower density (e.g. individual A) and in groups with less equal associations (i.e. high centrality SD). In the more egalitarian groups, where network density is high and strength centrality SD is low, we predicted reduced competition among members for leadership and therefore the presence of several equally likely leaders (e.g. individuals A, D, and E).

for each dataset by which to characterize a contextual leader: (1) the individual social features within a group; (2) the global group social network features; and (3) the hormonal profile (cortisol and testosterone) of a leader. Hyraxes' social groups differ greatly in their overall configuration of social relationship within a group: in groups with more equal associations, group members live longer, suggesting that the social tension may affect all group members (Barocas et al., 2011). Therefore, our first hypothesis, derived from the first model, was that group cohesion might be least important for less central group members, who follow their own intention of reaching particular destinations and attract other group members to follow. In groups with more equal associations (low strength centrality SD), where network density is high, we anticipated reduced competition among members for leadership and, therefore, the presence of several equally likely leaders (Figure 1) (shared leadership; (Smith et al., 2016)). Thus, our second hypothesis, derived from the second model, was that animals belonging to groups with more equal associations would each have a higher probability of becoming a leader (in other words, a higher proportion of the animals will lead in a given context), compared with those belonging to a group with less equal associations. Hyrax testosterone levels are associated with mating success, and males with higher testosterone levels were shown to mate-guard females with lower testosterone levels (Koren et al., 2019). Therefore, our third hypothesis, derived from the third model, was that lower-testosterone females and higher-testosterone

males might be more socially attractive and that this would be correlated with their tendency to lead. In addition, we posited that a front position leadership (Bumann et al., 1997), which involves predation risk, such as in everyday coordinated movement, should be related to higher cortisol levels in male leaders. We also hypothesized that female close social associations might mitigate the cortisol effect in female leaders. Finally, we expected that the absence of a strong status hierarchy in female hyraxes (Koren, 2000) would result in weak leadership generality (Smith et al., 2016), meaning that leadership in one context would not predict leadership in other contexts and that a leader's traits would vary across contexts. We also expected that the effect of female hyrax social associations would result in sex-associated leadership traits and would be related to testosterone and cortisol levels. Consequently, deduced from our above hypotheses, we predicted that (I) males and females would have distinctly different leadership traits and that (II) leaders in different contexts would have different traits. Specifically, we expected leadership in rock hyraxes to be influenced by social association parameters: males and females with a lower strength centrality will tend to be leaders, and a single or specific leader-follower sequence is expected to emerge in groups with lower density and in groups with less equal associations (Figure 1). Finally, male leaders are expected to possess high levels of cortisol and testosterone, whereas female leaders are expected to possess low testosterone levels.

RESULTS

Our results indicate that hyrax leadership can potentially be identified in two contexts: morning emergence and coordinated movement (Figure 2). Correspondence analysis showed a significant order in the movement of group members and the presence of a single individual that tends to move first while the others follow.

Below we outline the significant trends detected from the analyses.

Order of arrival at base stations (first dataset, Table 1, Figure 3A): sex and body mass were significant predictors, with significant interaction between the two. The arrival order of females was not related to body mass, but the probability of males being first in the order of arrival at a base-station decreased with the increase in male body mass (Figure 3A, blue and red indicate males and females, respectively). Males with higher levels of testosterone were also less likely to lead (i.e. to be first in order; Figure 3A). Furthermore, males that were in high-density networks or in a network with high centrality SD were less likely to be in the lead of order of movement (Figure 3A). Females with high levels of testosterone and those living in denser networks revealed a trend similar to that of the males and were less likely to lead. Centrality presented an inverse relationship with the order of first arrival: less central individuals were more likely to lead.

The order of arrival at the base station had a significant effect on the order of leaving (ordinal logistic mix model, Wald $\chi^2 = 27.0$, $p < 0.0001$). The probability that the individual that had arrived first at the base station would leave first was 0.369 or leave second was 0.355. Thus, the individual that arrived first is the most probable to be among the first to leave (>0.72).

Order of emergence from sleeping dens and order of movement toward a feeding tree (second dataset, Table 2, Figures 3B and 3C): the probability of being first in the emergence from sleeping dens decreased with the increase in body mass for males, but not for females. Moreover, males that were in a network with high centrality SD were less likely to emerge first from sleeping dens. Both high-density network and centrality showed an inverse relationship with leadership. Cortisol was the only predictor showing an opposite trend: males that led had higher cortisol levels, but this trend was not seen in females. Last, the probability of males being first in the order of movement toward a feeding tree decreased with the increase in body mass. This trend too was not seen in females.

Pup scream trials (third dataset, Table 3, Figure 3D): males that showed lower strength centrality were more likely to be the first to run toward the speaker during the trial. We did not detect any significant trend in females.

DISCUSSION

We found that different traits played a role in male and female leaders and in different contexts of coordinated activities. We defined the first animal to arrive at the destination as the leader, because the riskiest move for hyraxes displaying "tandem movement" is that of their arrival at a feeding location. The order of

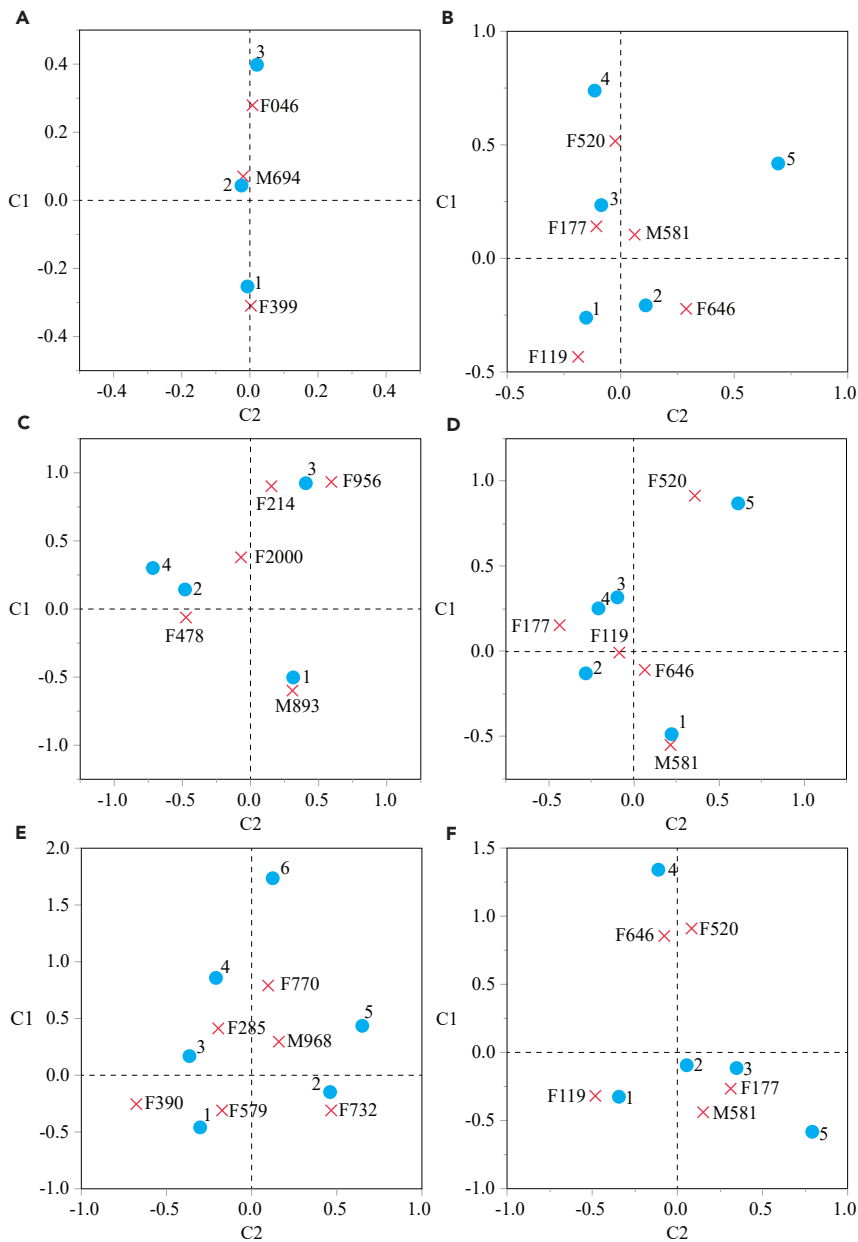


Figure 2. Examples of leadership in hyrax society

(A–F) Correspondence analysis showing the association between order of arrival at base stations (denoted by blue circle) and identity of individuals (denoted by red X) of the Cube social group during 2017 (A; $\chi^2_4 = 19.5$, $p = 0.0006$, $n = 293$) and the Isiim social group during 2018 (B; $\chi^2_5 = 26.8$, $p = 0.0023$, $n = 150$), order of emergence from dens during the morning of individuals of the Hill (C; $\chi^2_{12} = 37.1$, $p < 0.0001$, $n = 90$) and Isiim (D; $\chi^2_{16} = 56.8$, $p < 0.0001$, $n = 220$) social groups, and the order of arrival at a feeding tree of individuals of the Window (E; $\chi^2_{35} = 48.7$, $p = 0.038$, $n = 93$) and Isiim (F; $\chi^2_{16} = 46.1$, $p < 0.0001$, $n = 108$) social groups.

arrival does not allow classifying movements as leadership and followership events, as individuals may move independently of each other. To classify coordinated movement of leader and follower and distinguish it from independent movement of group members, the first animal to arrive at the destination was defined as the leader only when the follower group members were quicker to depart and arrived after the leader within the determined time window. We found that for a period of several months, all group members tended to follow one particular individual and not other group members that had arrived first

Table 1. The effect of sex, body mass, steroids (cortisol, testosterone), global network measures (i.e. density, strength centrality SD), and individual network measure (strength centrality) in the order of arrival at base stations (first dataset)

Model term	Order of arrival at base stations		
	Estimate	Wald χ^2	p
Steroids			
Sex	−16.76	147.3	<0.001
Body mass	−5.22	72.9	<0.001
Cortisol	0.09	3.5	0.061
Testosterone	−3.04	291.2	<0.001
Sex * Body mass	5.36	78.5	<0.001
Sex * Cortisol	0.15	0.8	0.376
Sex * Testosterone	2.74	271.5	<0.001
Global network measures			
Sex	−18.22	42.9	<0.001
Body mass	−3.33	6.0	0.015
Density	−7.91	76.3	<0.001
Centrality SD	−1.02	2.7	0.101
Sex * Body mass	5.30	86.5	<0.001
Sex * Density	3.40	5.9	0.015
Sex * Centrality SD	1.17	4.9	0.027
Individual network measure			
Sex	−2.90	8.0	0.005
Body mass	−0.30	2.9	0.088
Strength centrality	−0.70	20.6	<0.001
Sex * Body mass	1.20	12.9	<0.001
Sex * Strength centrality	0.09	0.1	0.769

The GEE results comprise model estimates and Wald χ^2 tests with $df = 1$ and their p-value. Individual identity was set as a random effect. The estimate for sex refers to the female level. N = 315.

at the destination. This particular individual thus influenced the movement of others and therefore had a stronger influence on the group and can be classified as a leader.

The use of three complementary datasets, which represent three different contexts, enabled us to examine the extent of generalized leadership in rock hyraxes. Particular traits defined male leaders: among resident males, the more central the male, the lower the likelihood of his leading in an acute predation scenario. In everyday coordinated activities, the younger (e.g. smaller) males are more likely to arrive or emerge first, and these also show higher levels of cortisol and lower levels of testosterone than the older males. Moreover, male leaders are more likely to emerge in networks with less equal associations than in networks with more equal associations and in networks with high density than in networks with low density. In contrast, rock hyrax female leadership was less influenced by the specific selected traits we examined, suggesting that any one of the group females may lead coordinated activities at different times. Thus, leadership among group females seems to be more equally distributed, with the exception of low-testosterone females (i.e. higher-ranked; [Koren and Geffen, 2009](#)), which were more likely to lead in coordinated movement to feeding trees, although the effect of testosterone on female leadership was much smaller than that on males. Similar to males, female leaders were less likely to emerge in networks with high density, but the effect was smaller than that on males.

The sex-based leadership qualities might be explained by hyrax females' egalitarian sociality ([Koren, 2000](#)). Similar to other female egalitarian societies ([Sterck et al., 1997](#)), at our study site feeding trees and vegetation patches are abundant and most hyrax females over two years of age breed synchronously and rear their pups

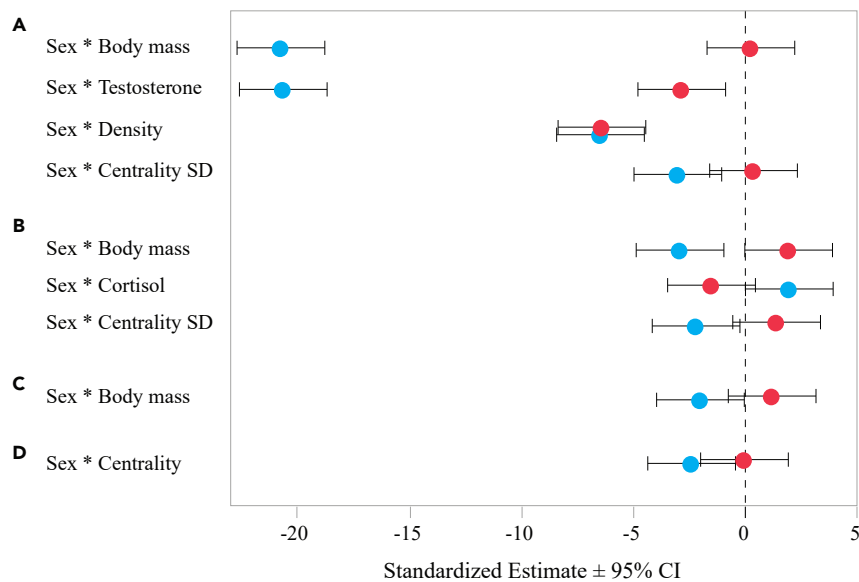


Figure 3. Sex-associated interactions

(A–D) Standardized estimates (\pm standardized 95% confidence intervals) in males and females for the significant interactions detected in the order of arrival at base stations (A; results in Table 1), order of emergence from sleeping dens (B; results in Table 2), order of movement toward feeding trees (C; results in Table 2), and running toward the speaker during pup scream trials (D; results in Table 3). Males and females are denoted as blue and red circles, respectively.

cooperatively. We suggest that each adult female group member similarly contributes to the overall hyrax communal organization; and, consequently, the social and hormonal parameters we tested revealed a smaller effect on leadership in females. Moreover, females may have little to gain from displaying risky actions due to the lack of competition among them, and therefore, most of the females in the group may share the leadership. We also did not observe any strong risk-involving trends in female leaders. Hyrax resident males, in contrast, may have greater motivation to intervene in a predator attack or to advertise their quality by exhibiting risky behavior. A hyrax male is more likely to lead in offspring predation scenarios if he is less socially central. A male defending his offspring from a predator also protects other females from injury and stress and is therefore likely to promote his social position by doing so. Female baboons, for example, often spend time near an adult male who protects them and their offspring from harassment (Buchan et al., 2003). In support of this concept, the “Handicap Principle” suggests that altruism can be interpreted as a handicap that signals high quality and that females prefer males that display these signals (e.g., bolder males; (Zahavi, 1995)). In the rock hyrax, body mass is an excellent predictor of age (Koren et al., 2008). Younger resident hyrax males are more likely to lead when the risk is moderate. These males also perform complex songs at their beginning of their residency tenure, but their songs’ complexity declines with age and is associated with increased competition pressure and increased tendency to be involved in fights (Demartsev et al., 2019). A possible explanation for the leadership of younger resident males is that these males may be calmer and tend to stop when the risk to the group is high compared with older resident males that tend to take greater risks. Another possible explanation may stem from the “pay-to-stay” hypothesis (Gaston, 1978), which suggests that younger males “pay” through their risk-involving leadership to secure their group membership and its associated benefits. Intuitively, we expected that older group members would lead, because experience accrues with age, and less experienced individuals usually follow their more experienced conspecifics (Flack et al., 2012). Experience may play an important role because hyrax leaders need to decide about where best to forage in order to minimize risk of predation. On the other hand, older resident males might be more experienced and thus tend to avoid the risky role of leader. In older African elephant (*Loxodonta africana*) leaders (McComb et al., 2011) and older resident killer whales (*Orcinus orca*) females (Brent et al., 2015) provide a vital source of social and ecological knowledge. Hyraxes, on the other hand, merely travel to nearby feeding trees and vegetation patches (up to several hundred meters away), which does not require exceptional navigation or ecological knowledge.

We found that hyrax global network features also correlate differently with male and female leadership: males and females living in high-density networks were less likely to lead in common coordinated movement scenarios.

Table 2. The effect of sex, body mass, steroids (cortisol, testosterone), global network measures (i.e. density, strength centrality SD), and individual network measure (strength centrality) in the order of emergence from sleeping dens and in the order of movement toward feeding trees (second dataset)

Model term	Order during emergence			Order during movement		
	Estimate	Wald χ^2	P	Estimate	Wald χ^2	p
Steroids						
Sex	−32.23	4.0	0.045	−6.49	4.9	0.027
Body mass	−10.87	5.1	0.024	−1.40	0.0	0.833
Cortisol	2.47	3.2	0.073	−0.12	0.6	0.443
Testosterone	−5.46	3.4	0.065	−0.15	0.7	0.408
Sex * Body mass	9.98	3.7	0.056	2.56	4.6	0.032
Sex * Cortisol	−2.69	4.5	0.033	−0.10	0.0	0.826
Sex * Testosterone	5.42	3.3	0.068	−0.10	0.0	0.839
Global network measures						
Sex	−65.54	5.7	0.017	−5.64	0.2	0.634
Body mass	−9.10	5.5	0.019	−1.42	0.0	0.974
Density	−34.35	4.3	0.038	0.33	0.1	0.737
Centrality SD	−8.04	3.8	0.052	−1.41	0.4	0.507
Sex * Body mass	10.71	10.7	0.001	2.76	1.8	0.186
Sex * Density	30.46	2.8	0.096	−2.52	0.2	0.649
Sex * Centrality SD	8.92	5.7	0.017	1.68	0.9	0.334
Individual network measure						
Sex	−1.13	0.1	0.819	−5.41	7.7	0.005
Body mass	0.10	0.1	0.822	−1.67	1.5	0.216
Strength centrality	−0.41	6.1	0.014	0.25	0.0	0.853
Sex * Body mass	0.23	0.0	0.904	2.41	10.9	0.001
Sex * Strength centrality	−0.29	0.4	0.523	−0.58	2.3	0.130

The GEE results comprise model estimates and Wald χ^2 tests with $df = 1$ and their p-value. The estimate for sex refers to the female level. Individual identity was set as a random effect. N = 315.

A possible explanation for this is that the differences in density may be a proxy of the strength of associations within a group. In a high-density network, or in a network with low centrality SD, individuals demonstrate similar social connections (Figure 1); this may also imply strong associations among all group members and, possibly, that in such groups the individual gain from a risk-involving act is very small, as everyone equally shares the group-living bonds and tasks. Thus, in such groups we expect individuals to equally share leadership roles, which will result in most individuals showing a modest frequency of leadership. In contrast, in groups in which network density is low and centrality SD is high, some individuals may have only a few connections with others (Figure 1). Such relatively isolated individuals can gain much by demonstrating superior qualities, by being bolder and taking on leadership roles (“Handicap Principle”; (Zahavi, 1995)).

Maintaining a risk-involving leadership position for several months is also expected to involve high levels of stress. In support of this, individuals that explore more novel environments demonstrate higher levels of corticosterone (Moyers et al., 2018). Male hyrax leaders demonstrate high levels of cortisol, which could be a result of frequent risk-taking behavior. Supporting this, cortisol levels are associated with social rank in hyrax males, reflecting the physiological cost of their frequent fighting and reassertion of their residency over new, competing, males (Koren et al., 2008). Interestingly, hyrax resident males live longer than solitary males (Barocas et al., 2011). A similar trend has been shown in alpha baboon males, which seem to escape the immunosuppressive costs of glucocorticoids (Archie et al., 2012). Close associations between group members have been shown to have beneficial physiological effects on the deleterious effects of stress (Silk et al., 2003), probably via the beneficial effects of oxytocin, which may be correlated with social support (Engh et al., 2006; Gust et al., 1991).

Table 3. The effect of sex, body mass, proximity to the speaker, steroids (cortisol), global network features (i.e. strength centrality SD), and individual network features (strength centrality, clustering coefficient) on two binary dependent variables: first to approach the speaker—whether an individual was the first to approach during pup scream playback trials, and run toward the speaker—whether an individual ran toward the speaker during the trial (third dataset)

	First to approach the speaker			Run toward the speaker		
	Estimate	Wald χ^2	p	Estimate	Wald χ^2	p
Steroid						
Sex	20.34	0.8	0.377	23.71	0.6	0.450
Proximity to speaker	0.57, 0.21	0.6	0.745	-1.39, -2.16	7.5	0.024
Body mass	7.65	1.5	0.214	8.10	0.8	0.363
Cortisol	1.08	0.1	0.748	1.36	0.1	0.711
Sex * Body mass	-6.73	0.9	0.332	-7.69	0.7	0.414
Sex * Cortisol	-1.29	0.2	0.635	-1.45	0.2	0.675
Global network measure						
Sex	22.28	1.3	0.263	14.76	1.5	0.216
Proximity to speaker	0.39, -0.15	1.1	0.577	-1.51, -2.03	6.2	0.045
Body mass	8.62	2.0	0.160	5.84	2.4	0.124
Centrality SD	-1.46	0.1	0.791	-2.24	0.1	0.822
Sex * Body mass	-7.81	1.4	0.242	-5.62	2.0	0.158
Sex * Centrality SD	2.04	0.4	0.549	3.81	1.8	0.185
Individual network measure						
Sex	40.02	1.4	0.238	42.96	2.3	0.130
Proximity to speaker	0.06, -0.58	1.2	0.561	-1.94, -2.55	11.4	0.003
Body mass	16.42	2.0	0.161	17.99	2.8	0.094
Centrality	-3.35	2.4	0.121	-5.21	6.0	0.014
Sex * Body mass	-15.81	1.7	0.197	-18.11	2.9	0.088
Sex * Centrality	3.56	3.0	0.082	5.58	8.4	0.004

The GEE results comprise model estimates and Wald χ^2 tests with $df = 1$ (except for proximity to speaker where $df = 2$) and their p-value. In these models, “Yes” is the response, and “No” is the reference category. The estimates for sex refer to the female level, and estimates for proximity to speaker refer to the near and far levels, respectively. N = 147.

When risk is moderate (i.e. daily activities), more likely to lead are younger resident males, which experience high cortisol and lower testosterone levels. However, during acute predation scenarios, more likely to lead are males with lower centrality status. Overall, centrality showed an inverse relationship with leadership under moderate predation risk situations as we predicted, meaning that the more central group members (males/females) are less likely to lead in everyday coordinated assignments. Interestingly, centrality turned out to be the only trait that significantly influenced the probability to lead in high-risk scenarios. One possible explanation is that leaving the group is easier for less central individuals, thereby marginally disrupting the group cohesion and generating a drive for the rest to follow and restore and maintain the cohesion.

Our results suggest that an individual’s strength centrality and its hormonal status are associated with leadership. However, we cannot attribute causality to these correlations. Hence, it is not clear whether (1) leadership is derived from social position, or (2) social position is derived from leadership, or (3) leadership contributes to hormonal status, or (4) hormonal status is derived from leadership behavior. These hypotheses concerning leadership-related social status and leadership-related hormonal profile are not mutually exclusive, and both sociality and hormones are expected to interact (Eisenegger et al., 2011; Raulo and Dantzer, 2018) in shaping the differences in hyrax leadership. Leadership has been shown to be correlated with additional variables (Fischhoff et al., 2007; King et al., 2008; Rands et al., 2003). In the future, longitudinal measurements may be useful to uncover whether changes in hormone or in position within the social network precede or follow changes in leadership patterns.

Conclusions

We found that males and females take on different leadership positions, depending on the context. Females demonstrate a more equally distributed leadership, whereas young (e.g. smaller) males demonstrate an emerging leadership in movement. Moreover, although younger leader males potentially take a moderate risk of going first and being attacked by a predator, it is the less central group members that take the lead when seeking to prevent an almost certain chance of losing a pup. Costly leadership is often associated with kin-directed benefits and may also signal personal qualities in order to motivate followers to reward leaders in terms of mating opportunities (Van Vugt and Smith, 2019). Contrary to the hypothesis that some reward is associated with being a leader, Heinsohn and Packer (Heinsohn and Packer, 1995) demonstrated that lionesses perform either as highly cooperative leaders at the front when approaching the recording of an intruder or as laggards that hang back timidly. They later argued that such leaders do not gain any “additional benefits” from leading, and although all the group females share a common resource, only a proportion of the females pay the full costs of territorial defense (Packer and Heinsohn, 1996). In contrast to the great diversity seen in lionesses’ leadership, hyrax leadership is equally distributed among females, even though they form stable egalitarian social groups that are similar to those of lionesses. Our results highlight the mutual influence of the different life strategies of male and female hyraxes in shaping how they acquire leadership positions in this species. Female leadership might be expected to be more equally distributed when it comes to coordinated movement, given the evolutionary benefits for females in maintaining group cohesion and protecting their offspring. In contrast, natural selection might favor males to exploit specific circumstances when group members are particularly alert, and the males can then benefit from advertising themselves and may attract more potential mates. Further research is needed to better understand whether leaders have a unique effect on other group members’ behavior or any generic individual can serve as a leader.

Limitations of the study

We studied collective behavior in social groups of rock hyraxes in the wild. Unlike laboratory experiments in which different configurations of social groups can be generated, in this study we were limited to the specific social composition of the groups in our study site. Moreover, most of the social groups in our study comprised only one mature male, a configuration that makes it hard to evaluate the leadership role of males. A larger number of social groups over more years are desired in order to confirm our current results and the role of network configuration on the probability to lead.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2022.104063>.

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AUTHOR CONTRIBUTIONS

Y.G. and E.G. conceived and designed the study; Y.G., C.B., I.S., and R.B. collected the data in the field; Y.G., I.S., and Y.W. conducted the hormonal assays in the lab; Y.G. and E.G. analyzed the data and drafted the figures; Y.G. wrote the paper. All authors reviewed the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interest.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Chemicals, peptides, and recombinant proteins		
Ketamine hydrochloride	Ketaset, Zoetis Inc.	www.zoetis.com/
Isopropyl alcohol	Sigma-Aldrich Israel Ltd, Rehovot, Israel	www.sigmaaldrich.com/
Methanol	Sigma-Aldrich Israel Ltd, Rehovot, Israel	www.sigmaaldrich.com/
Critical commercial assays		
ELISA for Testosterone	Testosterone: EIA-1559, DRG International Inc., Springfield Township, NJ, USA	drg-international.com/
ELISA for Cortisol	Cortisol: item no. 1-3002, Salimetrics, Ann Arbor, MI, USA	salimetrics.com/
Others		
Remote-controlled speaker	FoxPro Scorpion X1B speaker, FOXPRO Inc., Lewis-town, PA, USA	www.gofoxpro.com/
Proximity logger	E2C 162A; SIRTRACK, New Zealand	www.lotek.com/
Proximity base-stations	E2C 162A; SIRTRACK, New Zealand	www.lotek.com/
Software and algorithms		
R (version 4.1)		cran.r-project.org
JMP Pro (version 16)	SAS Inc.	www.jmp.com
SPSS (version 26)	IBM Inc.	www.ibm.com/analytics/products

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Eli Geffen (geffene@tauex.tau.ac.il).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Data is attached as supplementary excel tables
- No code was written for this study

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Ethical statement

Our study was conducted under annual permits from the Israeli Nature and Parks Authority (NPA) for capturing, handling, and tagging the hyraxes at the Ein Gedi Nature Reserve (2015/40768, 2016/41174, 2017/41507, 2018/41880). All procedures performed in this study involving animals were in accordance with the ethical standards of the NPA.

Field protocol

This research is part of our long-term study on hyrax sociality that has been conducted at the Ein Gedi Nature Reserve, Israel (31°28'N, 35°24'E) since 1999. Our study sites are located in two deep gorges, David and Arugot. Our trapping, handling, and observation procedures in the field follow the previously published protocols (Koren and Geffen, 2009; Koren et al., 2006, 2008). Our handling protocol has been practiced over 20 field seasons, extending annually from March to September. We observe rock hyraxes daily and

trap them whenever needed using live box traps (Tomahawk Live Trap Co, Tomahawk, WI, USA) baited with cabbage and kohlrabi. The traps are set before dawn and operate until late morning. The trapped animals are anesthetized by intramuscular injection of ketamine hydrochloride (10 mg/kg body weight) and each hyrax is individually marked with an electronic subcutaneous transponder (DataMars SA), as well as with either an ear tag (for pups and juveniles) or a light numbered collar (5 g), which assist in the visual identification of the individuals from a distance. During 2017–2018 adult members were fitted with a proximity logger (E2C 162A; SIRTRACK, New Zealand), on a collar (weight ca. 30 g). Captured hyraxes were sexed, weighed and measured for growth rate and body condition follow-up, and aged following [Barocas et al. \(2011\)](#). Following anesthesia recovery (at least 120 min), the animals were released in close proximity to the location of capture. Recaptured individuals were not anaesthetized and were released immediately after weighing and hair sampling. All animals were handled and marked in shaded places to prevent heat shock. No death, injuries, or other ill effects have been noted, and most individuals have been repeatedly captured within and between field sessions. Hyrax activities were observed using 10 × 42 binoculars (Monarch, Nikon) and a telescope with up to ×75 zoom magnification (Fieldscope ED82, Nikon). We initiated our observation sessions at first light, when hyraxes emerge from their sleeping sites, and continued till noon, when activity ceases. All activities, comprising movements, social interactions, feeding, and vocalizations, were recorded. In addition, proximity base-stations (E2B176A; SIRTRACK, New Zealand) were deployed in central shared locations (e.g., shared feeding areas, sleeping dens), and recorded the order of arrival at these areas of all adult individuals fitted with proximity logger (within a range of up to ~6 m from a base station).

METHOD DETAILS

Datasets

We used three different techniques to collect data: direct behavioral observations, automated data collection using proximity loggers and base stations, and behavioral observations during live playback trials. These datasets were collected at the same study site, but using different techniques, often from different individuals, and on different time scales, thus providing three complementary datasets.

The first dataset was collected in 2017–2018 and included the sequences of arrival of group members at base-stations located in feeding trees and sleeping sites (>40 m from one another) in the Arugot and David gorges ($n = 881$ leader/follower visits). Two groups (Isiim and Cube) visited base-stations located in six (in 2017) and three (in 2018) different locations in Arugot, and two groups (Window and Hill) visited base-stations located in three different locations (in 2017 and 2018) in David. Leaders/followers visits were noted for 50 ± 21 days in each location. Home ranges size of group members in Ein Gedi ranged $0.02\text{--}0.15 \text{ km}^2$, and average daily distances ranged 100–500 m. Base stations data for 2017–2018 is provided as [Data S1](#).

The second dataset was collected during 2017–2018, and comprised observations on the order of emergence from sleeping dens in the morning ($n = 472$ observations) and the order of movement towards a feeding tree ($n = 400$ observations) in Arugot and David gorges. Three groups were observed in Arugot (Isiim, Cube, and Sukkot) for 123 ± 30 days and two groups were observed in David (Hill and Window) for 106 ± 42 days. Coordinated movement data for 2017–2018 is provided as [Data S2](#).

The third dataset was compiled from the pup scream playback trials that were conducted in Arugot and David gorges during 2015–2018, and comprised 147 observations on the order of individuals approaching the speaker following the playback. Three groups were observed in Arugot (Isiim, Cube, and Entrance) and two groups were observed in David (Hill and Window).

Base station arrival sequence analysis

All hyrax group members travel together in ‘tandem movement’. The first animal arrives at the destination alone and exposes itself to potential predation. The predictable location of feeding sites makes such sites more dangerous, and so the riskiest move for hyraxes displaying tandem movement is their arrival at the feeding location ([Bumann et al., 1997](#); [Hamilton, 1971](#)). We therefore defined the first animal to arrive at the destination as the leader (only when followed by at least one group member). In order to identify those individuals with a stronger influence on the group, we defined a minimum time window (based on our empirical data) within which group members should follow one another. For base station data, we defined ‘coordinated movement events’ as those in which one or more group members had been tracked (using proximity loggers) following a leader, and in which the time window between two following individuals

did not exceed the upper 95% CI value of the time window in all base-station events (<18 min). Only in those events that included followers, was the first individual tracked by a base station defined as a leader. For example, every day the base station detected all animals that had arrived at the destination, and documented their arrival time. If the first hyrax to arrive was followed by another group member in less than 18 min, he was defined as the leader. If the following group member arrived at the destination in more than 18 min, this day did not include coordinated movement events for this group and the first hyrax to arrive did not classified as a leader. These sequences of group members moving together with a greater time interval between them were removed from the analysis. The analysis was conducted for adult group members only (>2.5 years) as social cohesion is more crucial for juveniles than for adults; and, as a result, juveniles had much less influence on group movement decisions (Conradt et al., 2009).

Morning emergence and coordinated movement analysis

We defined the observed 'coordinated movement events', or 'morning emergence events', as those in which the majority of the group (>75%) were observed engaged in the same activity (i.e. very few group members were participating in any other type of activity), and one or more group members were observed following a leader. Similarly to base station analysis, a leader was defined as the first animal to arrive at the destination, or the first adult animal to emerge from the sleeping den in the morning (only when followed by at least one group member). For both contexts, analysis was conducted for adult group members only (>2.5 years).

Playback trials

Pup scream playbacks in the field were conducted to simulate predation scenarios. We followed the protocol of (Ilany et al., 2011), who demonstrated that group females strongly react to the playback of pup screams (Figure S2; with a similar response to screams from their own group pups and those from stranger pups; (Ilany et al., 2011)) and were non-responsive to male songs (i.e. control). In each trial session, a remote-controlled speaker (FoxPro Scorpion X1B speaker, FOXPRO Inc., Lewis-town, PA, USA.) was placed before dawn in a location at which hyraxes frequently arrive. When a hyrax group was observed within a distance of 10–30 m from the speaker, pup scream playback was played via a FoxPro speaker using a TX200 remote control, and all hyrax activities were recorded. The order in which the hyraxes approached the speaker was recorded from first to last, with the first individual to approach defined as the leader. The distances of the hyraxes from the speaker before and during playback were estimated from direct observations (i.e. based on proximity to features like trees and boulders, where exact distance are known), and assigned to one of three categories: near (<20 m), far (>20 m), and not seen before playback. Pup screams used in the trials had been recorded by (Ilany et al., 2011) during the marking and measuring of captured pups. To minimize pseudo-replications, we used nine independent (i.e., from different individuals) recordings of pup screams. Pup scream playbacks were played for 30–60 s. As control playbacks, we used recordings of male songs (n = 9 different males), which had also previously been used by (Ilany et al., 2011). Male song playbacks were played for 1–2 min. No more than one experiment was performed in the same week on each group, to prevent habituation to the treatment.

Social network analysis

Social networks (Figure S1) were constructed based on the observation data (Table S1) following (Barocas et al., 2011). We used the SNA R package to generate an association matrix for each site in each season. A simple ratio association index was used (Cairns and Schwager, 1987), which is a ratio of the number of days in which two individuals were observed together within a distance of two meters, and in the same behavioral state, out of the total number of days that each was observed. Individuals that were observed fewer than five times (i.e. on fewer than five different days) were omitted. We concentrated on strength centrality (the number of direct association displayed by individual) for the individual network feature, and on density (the number of observed associations divided by the number of possible associations in the network), and centrality SD (standard deviation in strength centrality within the group) for the global network features (Wey et al., 2008).

Hormonal assay

Levels of cortisol and testosterone were measured following previously published protocols (Koren and Geffen, 2009; Koren et al., 2006, 2008). Steroids accumulate in hair, thus allowing a non-invasive and quick measurement procedure, as well as providing long-term profiles of integrated steroid levels. Hair samples

were collected once a year from the hind leg of a trapped hyrax. We analyzed a total of 136 hair samples from 87 individuals collected between 2015 and 2018.

Samples were washed twice in isopropyl alcohol while shaken (100 rpm; 3 min). Hair samples were dried and 20 mg or 30 mg (testosterone and cortisol, respectively) were weighed to the nearest 0.01 mg by an electronic balance; BJ610c, Precisa, Dietikon, Switzerland) were sonicated with methanol (4 mL, 30 min; Sigma-Aldrich Israel LTD, Rehovot, Israel) and then incubated with shaking (50°C, 130 rpm, 20 h). The methanol was evaporated with gaseous nitrogen (45°C), and the samples were run in duplicates on a commercial ELISA (enzyme-linked immunosorbent assay) kit for testosterone and cortisol quantification (Testosterone: EIA-1559, DRG International Inc., Springfield Township, NJ, U.S.A., Cortisol: item no. 1-3002, Salimetrics, Ann Arbor, MI, USA) following the kit protocol, following restoration with the zero standard provided. These kits had been previously validated for hyrax hair (Koren and Geffen, 2009; Koren et al., 2006, 2008).

QUANTIFICATION AND STATISTICAL ANALYSIS

Statistical analyses

Correspondence analysis is an ordination technique designed to project on two dimensions any hidden multivariate patterns in a count data table (Greenacre, 2017). The standard data for this analysis is a contingency table, and the association between columns and rows is tested using the chi-square statistics. In this study, we used correspondence analysis to associate between individual identity and position in coordinate movement or morning emergence within hyrax groups (Figures S3 and S4). Correspondence analysis was carried out in JMP Pro (version 16; SAS Inc.).

We analyzed three different complementary datasets. The first dataset was collected from the base-stations and comprised sequences of arrival of group members at base-stations (Table 1). The second dataset was compiled from observations on the order of emergence from sleeping dens in the morning and the order of movement towards a feeding site (Table 2). Tables 1 and 2 present the results of mixed ordinal logistic models, where order of arrival at base stations, order of emergence from sleeping dens, and order of arrival to a feeding tree were the dependent variables, and individual identity was set as the random effect. We used Generalized Estimating Equations (GEE) and ordinal logistic response as our mixed model framework as implemented in SPSS (version 26, IBM Inc). For each dataset, the tested models comprised: (I) the steroids (testosterone and cortisol); (II) two global network features (density and centrality SD); and (III) individual network feature (strength centrality). In these models we tested the main effects and the two-way interactions with sex.

The third dataset was compiled from the pup scream trials. The two dependent variables, *First to approach the speaker* (<80 cm from the speaker) and *Run towards the speaker* (any group member that approached the speaker) were both binary. Here we used Generalized Estimating Equations (GEE) and binary logistic response as our mixed model framework, and set individual identity as the random effect. These models tested the main effects, the two way interactions with sex, and the effect of distance from the speaker (categorical variable with three levels). This smaller dataset allowed us to construct only the minimal model for each of the predictors (Table 3). The models that included testosterone and density did not converge and are therefore not included.