SOCIAL INHERITANCE

Rank-dependent social inheritance determines social network structure in spotted hyenas

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The structure of animal social networks influences survival and reproductive success, as well as pathogen and information transmission. However, the general mechanisms determining social structure remain unclear. Using data from 73,767 social interactions among wild spotted hyenas collected over 27 years, we show that the process of social inheritance determines how offspring relationships are formed and maintained. Relationships between offspring and other hyenas bear resemblance to those of their mothers for as long as 6 years, and the degree of similarity increases with maternal social rank. Mother-offspring relationship strength affects social inheritance and is positively correlated with offspring longevity. These results support the hypothesis that social inheritance of relationships can structure animal social networks and be subject to adaptive tradeoffs.

Social structure within animal populations plays an important role in all social processes, including pathogen and cultural transmission (*1*–*4*), as well as the evolution of social behaviors (*5*, *6*). For these reasons, social structure and an individual's position in it affect reproductive success and longevity (*7*–*9*). Social networks represent social structure by summarizing the varying associations between different individuals. Research in the past few decades has started to elucidate patterns in social networks across animal species. These studies have been mostly descriptive [with some prominent exceptions such as Seyfarth's model (*10*)], but a new generation of studies have employed generative models to explain observed patterns (*11*–*14*). In one such study, Ilany and Akçay proposed social inheritance, defined as a tendency for offspring social affiliations to resemble those of their parents, as a general process that can explain the structures of social networks across multiple species (*12*). They showed that the structure of model networks in which offspring tend to inherit (via passive or active copying) their parents' social affiliations resemble those of observed populations (*12*). Social inheritance of maternal associations leads to clustering, a key feature of social networks that distinguishes them from other types of networks (*15*). As such, social inheritance may be crucial to the maintenance of stability in social networks.

Social inheritance has already been empirically demonstrated for some aspects of social position. For example, individuals in many species socially inherit maternal dominance ranks, which determine priority of access to resources. These are calculated from observed agonistic interactions (*16*–*23*). Inheritance of rank is likely to be nongenetic because rank shows high plasticity in response to social and environmental factors (*19*–*21*, *24*). In rhesus macaques (*25*, *26*) and African elephants (*27*), social affiliations between offspring tend to resemble those of their mothers. More generally, evidence from primates suggests that mothers may influence the development of offspring social ties both passively and actively (*22*, *28*–*30*, *31*–*33*). In African elephants, the network position (betweenness) of mothers was the strongest predictor of their daughters' position a decade later, despite the population experiencing stress from poaching and drought (*27*). In rhesus macaques, betweenness and eigenvector centrality in grooming networks displayed significant heritability (*34*).

These findings provide strong indirect evidence that inheritance of social relationships plays an important role in many species. In this study we reveal social inheritance in the spotted hyena (*Crocuta crocuta*) using data from 27 years of continuous field observations. Spotted hyenas live in stable groups (clans) which resemble the societies of Old World primates such as baboons or macaques in terms of size and structure (*35*). Hyena clan size depends on local prey abundance and may vary from only a few individuals to more than a hundred (*36*). Hyena clans usually contain several matrilineal kin groups spanning multiple generations, with low average relatedness among clan members (*37*). Wild spotted hyenas live up to 26 years, can discriminate both maternal and paternal kin from unrelated hyenas (*38*, *39*), and prefer to socialize with their kin (*40*, *41*). Clan mates compete for access to killed prey, but high-ranking individuals maintain priority of access to food (*35*). Young hyenas live at a communal den with other members of their cohort until they are 9 to 10 months old. During this stage, their social interactions are restricted to members of their cohorts and other hyenas that may visit the den (*42*). The long-term social network dynamics of hyenas are determined by a complex set of factors, including environmental effects such as rainfall and prey availability, individual traits such as sex and social rank, and structural effects such as the tendency to close triads and form bonds with highly connected individuals (*41*).

Using this long-term dataset of spotted hyena social interactions, we ask whether offspring social associations with individuals in their social group resemble their mothers' associations with those same individuals. If associations of offspring with specific third parties strongly resemble those of the offspring's parent, this provides strong direct evidence for social inheritance of associations, rather than inheritance of general social tendencies.

We quantified social networks using yearly association indices, defined as the number of times two individuals were observed together in a given year divided by the total number of times either were observed. We then quantified the similarity between two individuals' social connections in a given year by looking at the correlation of their association indices with all other individuals (Fig. 1A). Social inheritance should result in a positive correlation between the association indices of mother and offspring with all other individuals in a population. Therefore, we first measured the mother-offspring correlation in association indices with others and compared that to correlations between all other pairs of individuals (Fig. 1, B and C). We found that the social associations of offspring were similar to those of their mothers, in contrast to a much weaker correlation within other pairs of hyenas (linear mixed model (LMM); pair combination was set as a random effect, $\beta = -0.32 \pm 0.02$, $P < 0.001$), and also within pairs of mothers and the offspring of different mothers (fig. S8). Associations between offspring and other hyenas were dependent upon those of their mothers with those same hyenas (table S1). Moreover, associations of mothers before their offspring left the den also predicted those of their offspring in the following year (fig. S9). This suggests that offspring indeed inherit their mothers' existing connections, rather than mothers acquiring offspring connections or mothers and offspring forming new social ties together. Although hyenas had stronger associations with their agemates than with non-agemates (fig. S3), the similarity in associations with agemates was less pronounced than with mothers (fig. S4).

To estimate social inheritance in our data using an alternative, model-based approach, we extended Ilany and Akçay's model to account for continuous variation in association indices. In this model, offspring social associations with any third-party individual are either inherited from their mother (with probability p_n) or are drawn from a "background"

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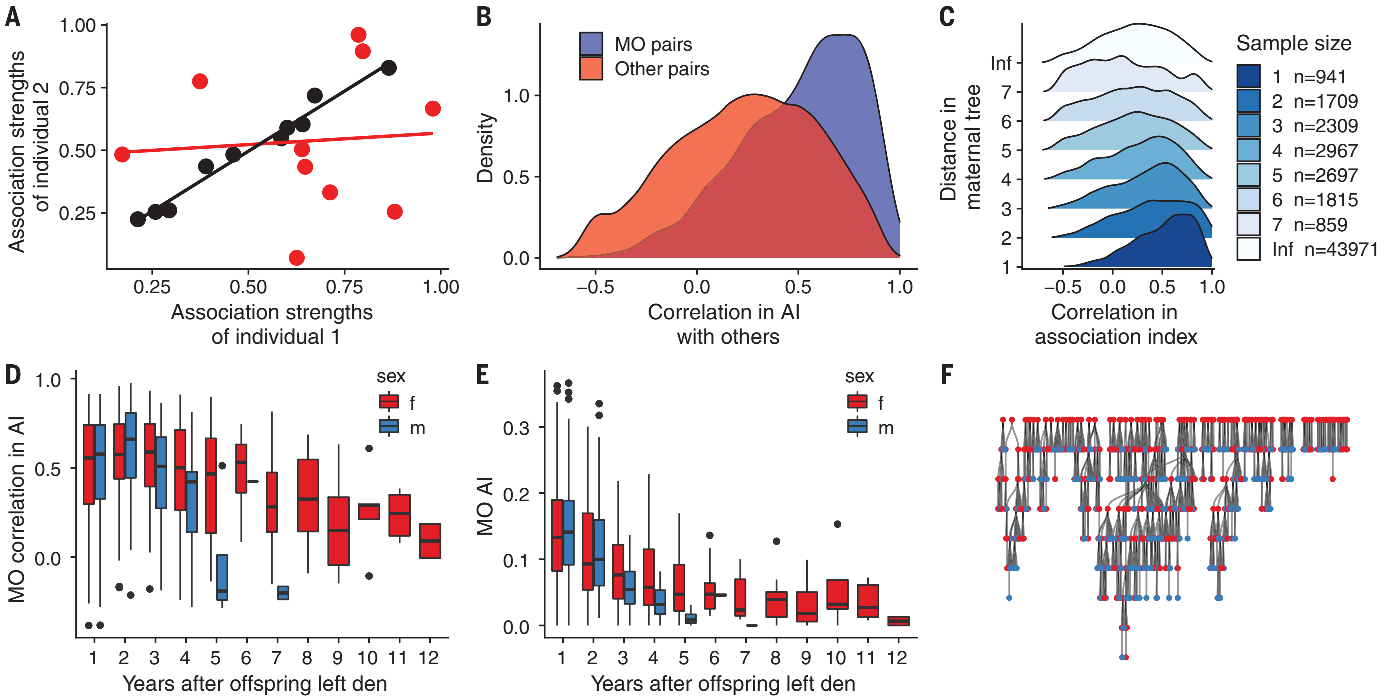

Fig. 1. Social inheritance and its ontogeny in spotted hyenas. (**A**) An illustration of correlation in association strengths, our measure of social inheritance. The association index measures the strength of association between two hyenas over one calendar year. The correlation in association index measures the similarity in association with others between two hyenas over one calendar year. In this illustration black points indicate a pair of individuals that are similar in their associations with others, whereas red points represent a pair whose associations with others are not similar. (**B**) Comparison of densities of correlations in AIs within pairs of hyenas. Mother-offspring pairs versus other pairs demonstrate that mother-offspring pairs have higher correlations than other pairs. (**C**) A comparison of densities of correlations in AIs within pairs of hyenas, as a function of their distance in the maternal pedigree. Sample size is the number of dyads for each distance on the tree. (**D**) Ontogeny of social inheritance. Boxplots depict the distribution of correlation between the AIs of mothers and those of their offspring, starting with the first year in which the offspring was observed at least 20 times away from the den. (**E**) Ontogeny of mother-offspring relationship. Boxplots depict the distribution of AIs of mothers and their offspring, starting with the first year the offspring was observed at least 20 times away from the den. (**F**) The hyena maternal pedigree. This tree shows all known maternal relationships within the Talek clan of spotted hyenas over 27 years. Red and blue circles depict females and males, respectively. Older generations are positioned higher. n = 1320 hyenas.

distribution (with probability $1 - p_n$; see Methods for details). Using a maximum likelihood approach, we inferred the probability p_n of offspring to inherit a given association strength from the full dataset including the association strengths of mothers and offspring in each year with all other hyenas (n = 65,597 associations). The inferred p_n was 0.403 ± 0.003 ($P < 0.001$). This probability is close to the mean difference in correlation coefficients between mother-offspring pairs and other pairs (Fig. 1B), suggesting that our social inheritance estimates are robust.

Our dataset also allows us to study the ontogeny of mother-offspring social inheritance. We found that in the first 4 (for males) or 6 (for females) years after the offspring left the den, social relationships remained similar to those of the mothers (Fig. 1D and Table 1). The median correlation coefficient of mother vs. offspring association indices with other hyenas varied between 0.44 and 0.67 in the first 6 years in which they overlapped. This similarity in social relationships remained high even when the strength of the relationship between offspring and mother decreased over the years (Fig. 1E and table S2), from a median of 0.14 in the first year after the offspring left the den to 0.05 in the sixth year. These results show that although social inheritance may initially depend on close association between mothers and offspring, it remains stable even after the mother-offspring association has subsided. The associations of male offspring decreased in similarity to those of their mothers faster than female offspring (Fig. 1D and Table 1), possibly reflecting their social disintegration before dispersal from the clan.

In spotted hyenas, social rank plays a major role in structuring the clan, with important consequences for fitness (*35*). Rank may affect social inheritance in at least three nonmutually exclusive ways. First, offspring of higher-ranked

Table 1. Ontogeny of social inheritance. Mixed-model outcome for the correlation between mother and offspring association with other hyenas as a function of offspring sex and years since leaving the den. Data include the first 6 years after offspring left the den. Mother-offspring pair ID was set as a random factor. n = 822 cases of 342 mother-offspring pairs.

	Estimate	SE	df	*t* value	*P*
Intercept	0.55	0.02	779.82	22.53	0.00
Years since leaving den	–0.02	0.01	717.22	–2.53	0.01
Offspring sex (ref:female)	0.07	0.04	814.95	1.72	0.09
Years since leaving den:Offspring sex	–0.04	0.02	740.59	–2.43	0.02

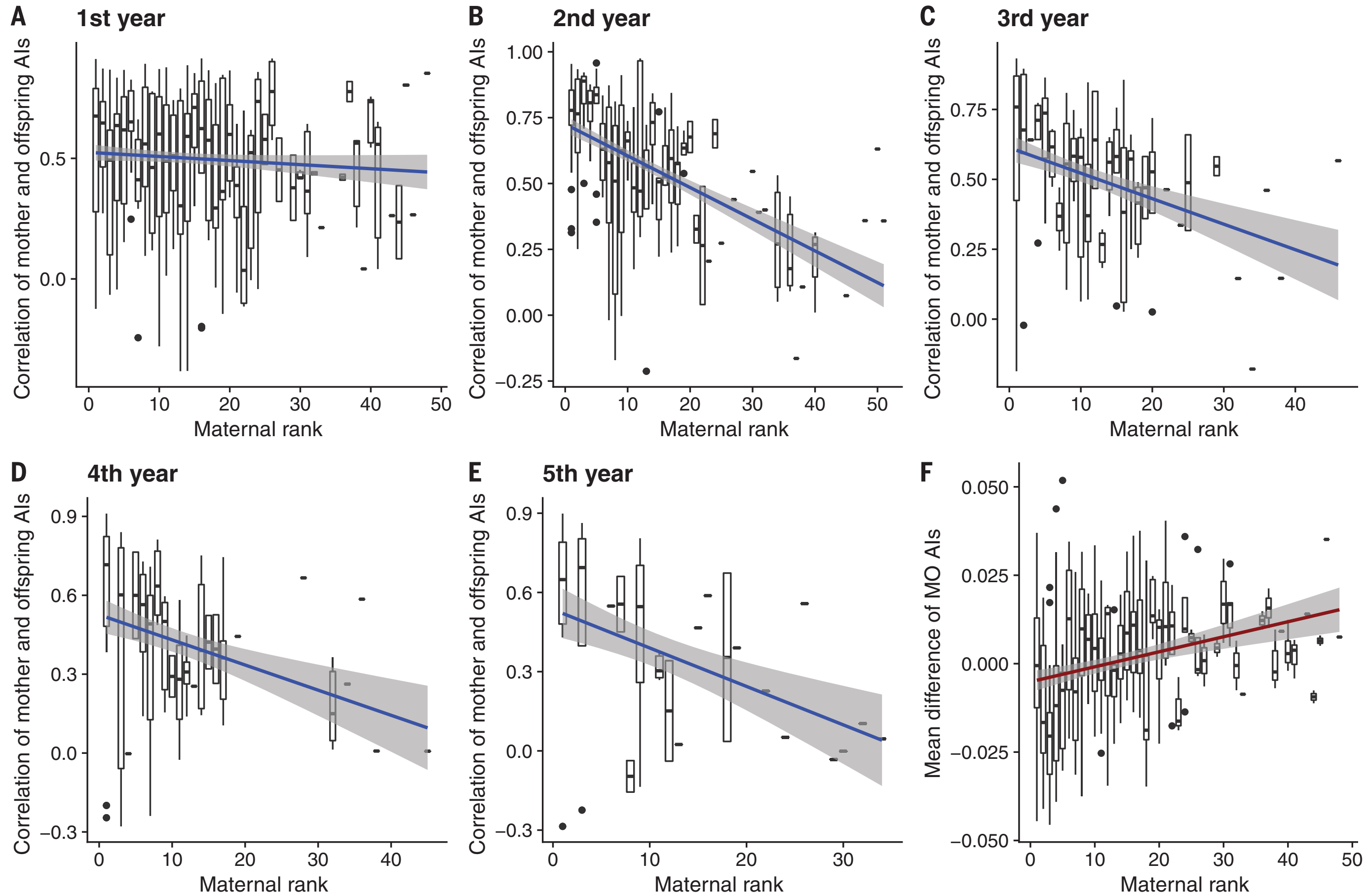

Fig. 2. The effect of maternal social rank on social inheritance. (**A** to **E**) Boxplots depict mother-offspring correlation in association indices (AIs) for each maternal rank. Year indicates time since offspring left the den. (**F**) The effect of maternal rank on deviation of offspring associations from those of their mothers. Boxplots depict the mean differences between the AIs of offspring and those of their mothers in the first year after leaving the den. By convention, smaller numbers represent higher ranks. *n* = 342 mother-offspring pairs.

individuals are expected to face fewer constraints in choosing social partners than lower-ranked offspring, due to having more time for socializing and also presumably having more willing partners (*41*). Second, offspring of lower-ranked individuals may benefit from forming different associations than their parents to compensate for their low rank. Third, offspring of high-ranked mothers may reinforce their high rank by utilizing the alliances of their mothers (*43*). All these hypotheses predict a weaker mother-offspring correlation in association indices for lower- than for higher-ranked mothers. As shown by Fig. 2, A to E, this prediction is confirmed by our data, but only after the offspring's first year out of the den (tables S6 and S7). In the first year of an offspring's life, most mother-offspring pairs have a high correlation of association indices, regardless of rank. Interestingly, although the mean mother-offspring correlation declines with lower rank, the variability of correlations increases, which means some parents and offspring maintain similar connections while others do not. This suggests that social constraints faced by lower-ranked individuals may play a role in the decline of mother-offspring correlation over time. On the other hand, the offspring of low-ranked mothers tended to form stronger associations overall with other hyenas than their mothers did (Fig. 2F; linear mixed model with mother ID and year set as random factors: $\beta = 0.0005 \pm 0.0001$, $P < 0.001$). This suggests that offspring may compensate for their low rank through increased socializing. We also found that after controlling for maternal rank, mother-offspring association strength, and offspring sex, offspring were not more likely to inherit maternal associations if there were more close relatives in the clan (table S3). This effect remained insignificant when more distant relatives were considered (table S4). However, offspring that formed stronger associations with close relatives than with distant relatives demonstrated stronger social inheritance (fig. S5; LMM with mother ID as a random effect, $\beta = 0.96 \pm 0.07$, $P < 0.001$)). This confirms Kummer's proposal that, as shown in primates, matrilineal group structure arises as an extension of the mother-offspring bond to other relatives (*29*).

Next, we documented that social inheritance is associated with longevity of both mothers and female offspring. There was a positive relationship between offspring survival and the similarity of social associations to mothers in their first year of overlap (Fig. 3A). For offspring of alpha females (highest ranked), no social inheritance (a mother-offspring correlation of zero) would translate to a predicted median life span shorter by 3070 days compared with offspring having maximum social inheritance (mother-offspring correlation of 1). In contrast, for an offspring of a mother ranked 30th in the clan, no social inheritance will translate to a predicted median life span longer by 867 days. The effect of social inheritance on offspring longevity held even when controlling for maternal rank, a known predictor of longevity in hyenas (*44*) and in other species (*45*). However, since social inheritance is also correlated with mother-offspring association strength in the first year (fig. S7; linear mixed model with mother and year as random effects: $\beta = 0.31 \pm 0.02$), it is possible that the association link between social inheritance and longevity is not causal, but instead both are caused by increased mother-offspring association. Indeed, structural equation modeling revealed

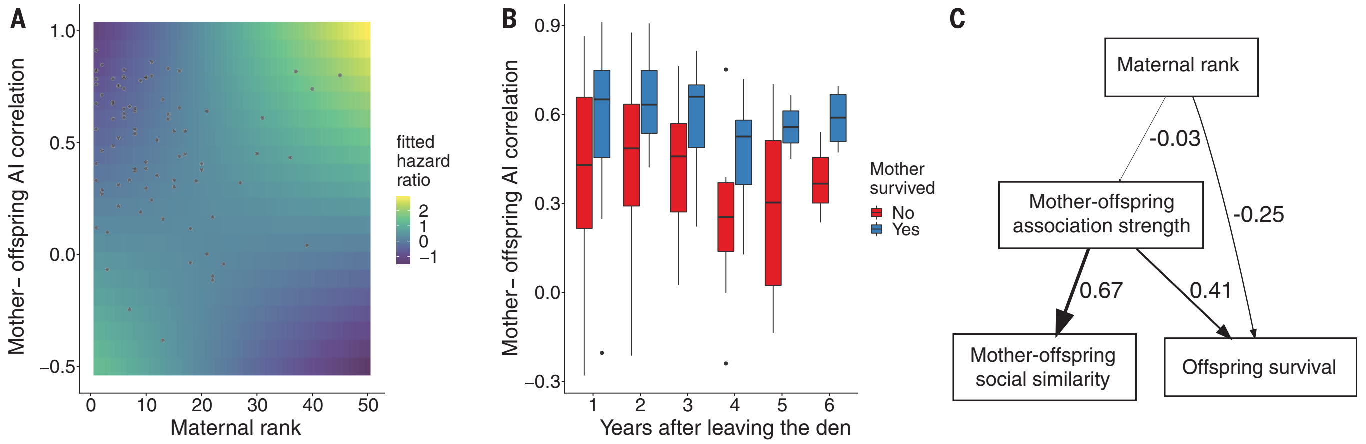

Fig. 3. Social inheritance is associated with both offspring and mother survival. (**A**) Fitted hazard ratios from a model of offspring survival depict dependence on maternal rank and mother-offspring AI correlation (higher hazard ratios reflect lower survival chances). Points indicate observed values (n = 88 offspring). (**B**) Social inheritance predicts maternal survival. The strength of social inheritance (correlation of mother and offspring association indices with other hyenas) was lower for mothers that did not survive to the following year (red boxplots), compared with those who did survive (blue). This trend was consistent across offspring ages. n = 206 mothers. (**C**) Mother-offspring association predicts both social inheritance and offspring survival. Path diagram showing correlations between maternal rank, mother-offspring association, social inheritance, and offspring survival. The partial regression coefficients for each arrow are given.

that the strength of mother-offspring association in the first year after leaving the den predicts both offspring longevity and social inheritance (standardized coefficients in the best-supported model: Mother-offspring correlation in association on association strength: $\beta = 0.67$; offspring's last age on association strength: $\beta = 0.41$; table S5).

Finally, our data suggest that social inheritance by offspring is associated with higher survivorship of mothers. Mothers of offspring who were more similar to them in social associations were more likely to survive to the following year (Fig. 3B; likelihood ratio test = 23.81, $d.f. = 1, P < 0.0001$; logistic regression of maternal survival with maternal rank and offspring age as fixed effects). Offspring that do not socialize with the associates of their mothers may thus provide a cue that those mothers are in physical decline.

Taken together, our results suggest that social inheritance plays an important role in structuring hyena social networks. This provides further support for Ilany and Akçay's hypothesis that in species with stable social groups, the inheritance of social connections from parents is the cornerstone of social structure. Furthermore, we show that in a gregarious carnivore, social relationships and the position within the social networks they represent are socially inherited similarly to how social rank is inherited in this species (*20*). This direct support for social inheritance is congruent with earlier, mostly indirect evidence in several species, including primates and elephants, as reviewed above. Taken together, this emerging body suggests that social inheritance may be a common force structuring social networks across group-living species. In several species, social integration is associated with higher survival and reproductive success, with the most central individual typically being the most successful (*45–49*). Our results show that social inheritance is also associated with both offspring and mother survival. The measures used to quantify social inheritance, the similarity of social connections of mothers and their offspring to third-party individuals, also add a new dimension to the analysis of animal societies. Whereas the strength of relationship among two individuals is widely used, the social similarity of two individuals in a network can provide additional information about a relationship, its origins, and its consequences. Overall, our results highlight the role social inheritance plays at the nexus of social network structure and life history.

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/373/6552/348/suppl/DC1
Materials and Methods
Figs. S1 to S13
Tables S1 to S7
References (*51*–*55*)

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Mother knows best
Inheritance of social status, and its associated costs and benefits, is well demonstrated in humans. Whether such an intergenerational system occurs in other species is harder to demonstrate. Ilany *et al.* looked at nearly 30 years of social interaction data in spotted hyenas, a female-dominated system with a highly structured society, and found that status inheritance is just as prominent (see the Perspective by Firth and Sheldon). Juvenile hyenas had social associations that were similar to their mothers, and the strength of the association was higher for higher-status mothers. Importantly, survival was associated with social inheritance, suggesting that these social roles are essential to hyena life.

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