Modeling Leadership Hierarchy in Multilevel Animal Societies

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A typical feature of many natural and social networks is the presence of communities giving rise to multiple levels of organization. We investigate the decision-making process of a group combining self-organization and social dynamics, and reproduce the simultaneous emergence of a hierarchical and modular leadership network. All individuals in the model try, with varying degrees of ability, to find a direction of movement, with the result that leader-follower relationships evolve between them, since they tend to follow the more successful ones. The harem-forming ambitions of male individuals inspired by an observed Przewalski horse herd (Hortobágy, Hungary) leads to modular structure. In this approach we find that the harem-leader to harem-member ratio observed in horses corresponds to an optimal network regarding common success, and that modularly structured hierarchy is more beneficial than a non-modular one, in the sense that common success is higher, and the underlying network is more hierarchical. We also find that the experimental and model harem size distributions are close to a lognormal.

Keywords Collective animal behaviour · Leadership hierarchy · Multilevel societies · Collective decision making · Modular hierarchy

1 Introduction

Like in human communities, several unique species of gregarious animals have developed social structures based on multiple levels of hierarchical organization 10 11. Small groups of closely related individuals can unite in clans which can form bands or loose aggregations. This phenomenon appears through several different taxonomical orders, but since a complex multilevel society requires high social and cognitive skills, common examples are mainly from primates 16 1, elephants 29, whales 28 3 and equids 25 7. The smallest stable sub-unit where strong bonds exist between members can be a family group based on kinship. One basic unit form is a matrilineal family group consisting of one matriarch and her descendants (african elephant 29, sperm whale 28, killer whale 3). Another basic form is a one-male reproductive unit, a harem that consists of several breeding females, their subadult descendants, and is dominated and guarded by only one male (Przewalski horses 5, plains zebras 25), it sometimes includes several non-dominant males as well (hamadryas baboons 16, geladas 6). These highly social animals build stable, sometimes lifetime long communities, usually characterized by a strong hierarchical order. The ordering between group members is usually complex and context dependent 20. The dominance hierarchy serves for the effective division of natural resources, while the leadership hierarchy for the facile flow of information in making a collective decision. This was demonstrated in flocks of pigeons, where lower ranking individuals copy the directional choices of the higher ranking ones 19. It would be an evidence that the whole group gains if led by the one with the best knowledge about the good direction to food resources, but this type of leadership was observed

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only in few cases, e.g. in bottlenose dolphins [17]. Many other traits are empirically shown to affect the individual’s chance of becoming a leader, such as dominance [14], central position in the social network [26], increased nutrient requirements [8, 27] and age [30].

The group dynamics of a complex society can be well described in terms of hierarchical networks, where the social bonds between group members are associated with directed connections. This approach is very useful in understanding collective behaviour. A collective decision making process is often based on imitation of groupmates [23], and in the network view the spreading of the imitated behaviour can be interpreted as an information flow through the directed edges of the network. In principle a network can have a modular structure in addition to being hierarchical. In the past a few models have been proposed to display these features, however, in those cases the edges between the units were not directed [24, 9], thus, did not correspond to leader-follower relationships. Our aim is to build a model which reproduces the above introduced phenomenon of the “group of groups” in a decision making process. What are the simplest rules which can cause the emergence of smaller sub-units in a group? It is a natural assumption that every individual has his own upper limit for the number of bonds he is able to maintain due to the cost of sociality, and this introduces a typical sub-unit size. Besides the limitation in bond number, there is also a need for intra-unit cohesive forces that give rise to higher connectivity inside the sub-units. In large animal groups (flocks of birds, fish schools, insect swarms), where individuals can communicate only locally and individual identification is costly, self organizing can be the main driving mechanism of collective decision-making processes. In small stable groups, where global communication is possible and complex social relationships can evolve between members, sociality is more important in leadership [15, 13]. In the case of social animals living in big groups, a good modeling approach combines both of the above mechanisms.

Here we present a model which combines self organization and sociality in simulating a collective decision-making process, and leads to the spontaneous emergence of a modular hierarchical network underlying a group composed of sub-units. An observation of a cohesive herd of Przewalski horses (Equus ferus przewalskii, Fig. 1) helps us in defining the rules of the algorithm. This herd consists of clearly distinguishable harems, each of them is dominated by one stallion. During movements they show an astonishing collective motion pattern (see Fig. 2). We aim to reproduce first of all the special case of leadership hierarchy of a wild horse herd. We can thus use equid behaviour to help us formulate social rules and integrate them into the agent based model of [21].

Figure 1: The motivation of our model is the understanding of the leadership hierarchy in Przewalski horses.
Figure 2: Przewalski horse herd during movement ($n \approx 150$). The spatial distribution of the herd roughly shows us the border-lines of the sub-groups. Colored areas emphasize the harems and bachelor groups identified based on positions and cohesive movements. White edges point from the leader to the follower group, and are defined between the neighbouring harems within a given range. As the herd takes on a V formation, from two groups connected by an edge, the one closer to the tip of the V is identified as leader. If both are a similar distance from the tip then the more centered one is the leader. We base this leadership definition on the observation that in plains zebras the individuals in the front are more likely to lead [8]. The black arrow shows the direction of moving. The bachelor groups in the bottom left corner and on the right, and the oxen in the top right corner are not considered.

2 Observation

We use small flying robots to capture aerial records of a herd of Przewalski horses living under semi-reserve conditions in the Hortobágy National Park, Hungary. The herd has around 240 individuals, and consists of stable harems and bachelor groups, with sizes ranging from 2 to 18, including the harem leader stallion. The spatial distribution of the horses shows their social organization, since harem members keep closer to each other than the typical distance between the harems. During collective movements harems remain as cohesive units inside the herd, thus a leadership hierarchy between them can be established. In order to get an insight into the leadership of the harems we make an estimation based on positions and orientations in a still image captured while the horses are on the move. It was shown in plains zebras that movement initiations inside the harems are determined by a consistent hierarchy of the individuals, and the position during travelling correlates with the initiation order [8]. We propose here that consistent hierarchy can exist on the level of groups as well, and the position occupied in the herd can be an appropriate indicator of the rank. This assumption is also supported by the observation that larger harems can be seen in the central frontal area of the herd, and a larger harem can be associated with a more successful stallion. The estimated leadership network is shown in Fig. 2 and the reaching centrality layout of it in Fig. 3(a). Our definitions of the nodes and edges are the following:
**Definition of nodes**: a node represents a harem. Individuals who are within one horse length of each other, and/or individuals who keep together during moving, belong to the same group. As a verification of the group definition the number of adults and infants was compared with the catalogue of groups established by ethological observations.

**Definition of edges**: groups which are within a given interaction range of each other, and are seen directly (i.e. not covered by another group) by at least one of the pair, are linked with an edge. The envelope of the herd is a V formation, pointed in the direction of movement. Thus from two harems we define as leader the one which is closer to the tip of the V. In the case when both of them are roughly the same distance from the tip, then the more central one is defined as leader. The direction of an edge points from the leader to the follower. Note that this is an estimation of the precise leadership hierarchy, which is to be determined through a deliberate analysis of individual tracks.

3 Model description

The starting point of our model is the agent-based model of [21], which leads to spontaneous emergence of a leadership hierarchy. It consists of individuals facing a problem solving situation iteratively in each time step. Their environment evolves slowly in time over several discrete states. The individuals attempt to guess the actual state of the environment using their own diverse abilities, and the ones that guess correctly gain benefit. In the context of collective motion the environment can represent the seasonally changing habitat of the group, including the actually accessible drinking or feeding places, and the good answer represents a good direction towards it. More generally, the environment can be any decision making situation, where the good answer is the adequate behavioural adaptation. In order to keep the herd’s cohesiveness, the individuals should synchronize their behaviour, which can be achieved by imitation. Every individual in the model is likely to consider the decision of several other groupmates and ponders over them, taking into account his own estimation as well. Finally he copies a decision based on trust to groupmates or decides on his own. The extent of trust in someone else is determined by earlier experiences. The leadership hierarchy is defined through imitation: we assign an edge between two individuals if one copied the other, with the arrow directed from the source of information to the target.

In order to arrive at a herd consisting of harems that are led by only one male, we introduce two types of individuals (genders) to the model. Basically both genders tend to follow others, but males have some extra role in herding their harems. The different behaviour of genders comes from the different roles and interests. The aim of the females is to follow the best performing individual, from whom a probably right answer can be copied. The aim of the males, beside copying a good answer, is to collect as many females as possible and monopolize them, in the sense that the males try to prevent relationships between their females and other males. The term male denotes here only the harem leader stallion, while female denotes all the non-dominant harem members regardless of gender, as they behave similarly from the point of view of group dynamics. More generally male can denote a leader-type individual, while female a follower-type one. Hence, the ratio of genders (the leader to follower ratio) is preferably unequal. The male individuals realize their leading role with the following three herding behaviours:

1. Herding a harem member: harem stallions herd their harem by not allowing the harem members to follow outsiders and thus leave their harem. This serves as a cohesive force inside the harem. The target individual is a female from his harem, who follows an outsider female (a female belonging to a different harem) as well. The herding male tries to cut this undesired edge by resetting the respective trust value.

2. Fight for a harem member: if a female has a relationship with two stallions, they fight for her. The target individual is a female from the herding male’s harem who has an outgoing edge with another male. The trust between the female and the losing male will be reset.

3. Herding a lonely female: every stallion tries to maximize his harem size by herding lonely mares. The target is a female not belonging to any harem. The herding male tries to build an edge with her by increasing her trust in him.

Males and females differ in their typical ability in guessing the right state of the environment. The largest ability values are matched to males enabling them to assume higher positions within the hierarchy. It can be argued that the harem leaders typically have higher abilities, since only the best ones from all males can end up
as harem leader males. Every individual has a link capacity, which is the maximum number of outgoing edges they are able to establish. The two genders do not differ in the typical link capacities, but in the case of the males, its value also determines the aggression and strength of the individual. On the one hand it determines the maximum harem size of a given male, and on the other hand the frequency that a male shows herding behaviour and the probability that he succeeds in herding is proportional to his link capacity. Further details of the implementation of the above model are given in Appendix.

4 Results

As the model evolves iteratively, a network of leadership emerges. The individual leadership graph consists of nodes representing the individuals, and the directed edges between them show who led whom in previous rounds. Since as a consequence of herding sub-groups are expected to emerge led by a single male, we define a harem leadership graph in the simplest way, by considering only the subgraph of males. In the harem leadership graph the male individuals are the nodes, and the male-male connections the edges. Note that the edges in the empirical network of Fig. 2 denote the possible leader-follower relationships, and not the realized ones, by definition. A given harem \( i \) has an incoming edge pointing from harem \( j \), if \( j \) can be seen from and thus followed by \( i \), but it does not necessarily mean that \( i \) followed \( j \). The situation is the same in the model, an individual (or a harem) \( i \) has an incoming edge from \( j \) if his estimation is considered by \( i \). But in making his decision \( i \) weights all the considered estimates, and may finally choose a different estimation than \( j \).

One outcome of our model is that the leadership graph, both on the level of individuals and on the level of harems, converges to a stable state. Convergence is reached after several hundred time steps and it is indicated by the convergence of the values of the underlying trust matrix, and by the fact that the fraction of changed edges in a time step goes to zero. The structure of the converged network is qualitatively similar to a herd consisting of harems. Examining it with CFinder [22, 2], which uses the clique percolation method, communities can be revealed that are associated with more highly inter-connected subgraphs, typically made of \( k = 3 \) and \( k = 4 \) cliques. The communities are typically of two types: one-male-multifemale units, and all-male units. Obviously a male is participating in both community types. On the one hand he has one or more one-male-multifemale communities, thus a harem from this point of view is the union of these communities. On the other hand he is communicating through an all-male community with several males that are usually also harem leaders. Most of the communities are connected with each other via a male node, and thus the all-male communities serve as male alliances and connect different harems. The communities inside a big harem are often overlapping with many shared nodes, most commonly one or two 4-clique communities are embedded in a 3-clique community. Overlaps between different harems, led by different males, are very rare, but they are connected through some female-female edges, beside the male alliances. If the summarized link capacity of the males is abundant, all-female communities do not survive. Females tend to follow only one male, despite the fact that their followings are basically spontaneous. Therefore in the model we define a harem as the list of female followers of a given male. With this definition a harem contains some females as well who do not belong to the harem forming communities. As the network converges, the difference between the two harem definitions (the list of female followers and the union of one-male-multifemale communities of a male) decreases. However, after 1000 time steps some differences remain, and there are some females who are not participating in any community. The network inside a harem is very hierarchical, with a male leader on the top, but strong hierarchy exists between female followers as well. There is also a tree-like hierarchy between harems typically with one single leader harem on the top. It is identified as the hierarchy of harem-leaders and represents the next level of organization. The whole herd keeps cohesive, since the network of individuals forms one connected cluster. The network of harems in most of the cases also remains cohesive, but if the number of males is relatively low, it can break up into smaller networks, as discussed later.

In analysing the model, we identified some input parameters, such as the ratio of males to the number of all individuals and the typical value of link capacities which influence the results more sensitively. Other parameters, like group size, frequency of herding behaviour in a round and the number of considered decisions by an individual have less considerable effect. The frequency of herding behaviour affects first of all the rate of convergence to the stable state, but not the resulting network. The higher the frequency, the faster the convergence is.
Figure 3: Harem leadership hierarchy (a) in the experiment of the wild horses based on Fig. 2 and (b) in our model. The blue nodes with names starting with M denote harems, and the directed edges point from the leader to the follower harem, showing thus the flow of information. The global reaching centrality values are close for the two networks, 0.65 and 0.67 for the experimental, and for the model, respectively, which indicates a similar extent of hierarchy. Visualization is performed by the reaching centrality layout with \( z = 0.1 \). The enlargements of the blue square areas reveal the internal connections of individuals inside some harems. The pink nodes with names starting with F denote the females, and orange emphasizes the males whose harem is enlarged. Light blue areas denote the females participating in one-male-multifemale communities identified with CFinder \([2]\). Female-female relationships between two different harems are indicated in gray. The number of harems in the simulation is \( m = 17 \), and the number of all individuals is \( n = 150 \), as it is in the experiment, the number of edges between the harems is 26 and 36 in the model and in the experiment, respectively.
Figure 4: Heatmaps of relative performance improvement (2) and global reaching centrality (GRC) [18] of model networks, as a function of time and ratio of males to the number of all individuals. An optimal male to all ratio can be observed, where performance and hierarchy is maximized. The location of the optimum is robust to changes in the shape of the link capacity distribution (LCD) if its average is fixed: (a)-(b) is for a Poisson LCD with $\lambda = 20$, and (c)-(d) for a lognormal LCD with $\mu = 20$ mean and $\sigma = 20$ standard deviation. For lower average LC values the optimal range is shifted: (e)-(f) is for a Poisson LCD with $\lambda = 10$, and (g)-(h) for a $\left(3, 17\right)$ uniform LCD. The number of all individuals in the simulations is $n = 200$, their ability distribution is bounded Pareto with 0.25 expected value and $1/\sqrt{48}$ standard deviation, each data point is averaged over 1000 runs.
4.1 Experiment and model

Carrying out simulations with similar input parameters as those observed in wild horses, a very similar network can result both qualitatively and quantitatively. Based on Fig. 2 and the network definition in Sect. 2, the hierarchy of harems in the experiment can be established (see Fig. 3(a) for a hierarchical layout). The number of identified harems in Fig. 2 and thus the number of nodes is 17, the harems contain roughly a total number of 150 horses. A typical harem network of the model is shown on Fig. 3(b). The number of all individuals is $n = 150$ in the simulation, and the number of harem leader males is $m = 17$ in order to fit the experimental parameters. Both the experimental and model networks are visualized with reaching centrality method [18].

At first glance one can see the similar pyramid-like layout of the networks and the common features, such as the presence of one single leader, several nodes in higher layers, and many at the bottom layer. There are many layers that indicate the varying roles, and the edges can connect distant layers. The global reaching centralities (GRC) are very close, quantifying the similar level of hierarchy in the two graphs, taking the values 0.67 for the experimental and model networks, respectively. However, the number of edges is less in the model ($e = 26$) than in the experiment ($e = 36$). The enlarged areas in the right display the internal structure in some harems.

4.2 Optimal male to female ratio

An investigation of the model shows that the presence of leader-type individuals results in an increment in relative performance improvement from about 135% to as high as 170%. In addition, the resulting network is more hierarchical according to all the three measures studied (fraction of noncyclic edges, global reaching centrality and fraction of forward arcs). For example GRC, can increase from 0.25 up to 0.9 in particular cases. The despotic approach of our model removes many of the non-efficient cycles. As a consequence, the decisions of top ranking individuals spread more effectively to lower ranking individuals, thereby improving overall success.

The proportion of leader-type individuals plays an important role in determining the quality of the resulting network. The simulations indicate that there is an optimum in the value of this parameter (Fig. 4), where performance and hierarchy is maximized. For example, for Poisson link capacity distribution (LCD) with $\lambda = 20$ the optimal proportion of males lies around 1 : 10, where the relative performance improvement reaches 180% after several hundred steps, and networks producing performance above 170% lie in the range from 1 : 20 to 1 : 5 leader ratio, while outside this region performance does not exceed 160% (Fig. 4(a)). The GRC has an optimal region as well, where its value reaches 0.9, in contrast to 0.4 outside this region (Fig. 4(b)). However, the optimal region of the GRC is narrower than the one of the performance, it lies between 1 : 20 and 1 : 10. The overlap between them, and thus the optimum from the point of view of performance and degree of hierarchy together, is between 1 : 20 and 1 : 10.

The location of the optimal range is robust to changes in the shape of the link capacity distribution, if its average value is fixed. We examine uniform, delta, Poisson and lognormal link capacity distributions with averages ranging from 5 to 20. Fig. 4(c)-(d) shows results for lognormal LCD with $\mu = 20$ expected value and $\sigma = 20$ standard deviation. In comparison with Fig. 4(a)-(b), the optimal range remains the same, and the performance is maximized around 1 : 10 male to all ratio, similarly as for the underlying Poisson LCD with $\mu = 20$ average. For lower average link capacity values a minimum of performance appears below the optimal area, see Fig. 4(e) and (g) for a Poisson and uniform LCD with $\mu = 10$ mean. If the number of males is decreased to the extent that $m (c_i) < n - m$, i.e. the sum of all link capacities becomes less than the number of all females, then link capacities start to limit the free formation of harems. If this threshold is reached the network of communities starts to break apart, since the male alliances split up, giving rise to separated one-male-multifemale communities, and this can cause a decrease in performance. Decreasing $m$ still further can slightly increase performance, this can occur because the size of the separated communities increases. The optimal range is shifted upwards, probably because the optimal network structure can evolve when the total number of link capacities is abundant. For an underlying LCD with $\mu = 10$ average, the optimal leader to harem-member ratio is around 1 : 8. Comparison of simulations with different average link capacities leads to the conclusion that the optimal region lies around $m \approx 1.5n / (c_i)$.

The observed maximal harem size in wild horses is 18 and the average size is 9. It is reasonable to assume that in the absence of male competition every horse may be able to have the maximal harem size. Therefore the theoretical average link capacity can be between 10 and 20, giving rise to an optimal harem-leader to harem-
member ratio of roughly between 1:8 and 1:10, from the point of view of the common success. It is very interesting that the 1:9 empirical ratio observed in wild horses is close to the model result.

Figure 5: Harem size distribution. (a) Model distributions tend to follow a lognormal distribution, provided the total number of link capacities is large enough, and it does not limitate the harem formation. It does not depend on the shape of the link capacity distribution: harem size distributions with underlying delta(25), uniform(15,35) and Poisson(λ = 25) LCD are shown on the plot. A lognormal distribution is fitted to the case of Poisson LCD with μ = 9.61 mean and σ = 6.65 standard deviation. (b) The experimental harem size distribution is plotted together with the model distribution (with an underlying Poisson LCD with λ = 25) and the lognormal fitted to the model. Using the Kolmogorov-Smirnov test the fitted lognormal is accepted as the theoretical distribution of the experimental sample at p = 0.97 significance level. The experimental distribution is based on data from m = 21 wild horse harems including n = 188 individuals. The number of all individuals in the simulation is n = 200, m = 25 of which are males. Each data point is averaged over 1000 runs with harem sizes measured at the t = 1000 time step. Semilog plots are shown in the top right corner.

4.3 Harem size distribution

Since our model aims to simulate a group of groups, it is natural to ask what kind of cluster size distributions (in our case, harem size distributions) characterize the resulting network. The harem sizes are defined through the number of female followers of a given male, and the male is also counted in the size. When the network, and thus the harem sizes, can be considered as converged, we build a histogram and investigate it for different LC distributions. In order to have a roughly optimal performing network in all cases, when simulating with LC distributions with average values ranging from 10 to 25, the ratio of males to all individuals is set to 1:8. The distribution of harem sizes is an asymmetric heavy-tailed distribution, and can be fitted by a lognormal (Fig. 5(a)). Like the optimal proportion of males, it seems to be independent of the shape of the link capacity distribution. It is very similar for uniform, delta and Poisson distributed link capacities (Fig. 5(a)). However, this only holds if the predefined LCD of the individuals does not limitate the harem formation. Again, if m ⟨c_i⟩ < n − m, males fill up all their links and a trivial harem size distribution emerges, with a shape determined by the link capacity distribution. As the total number of links is increased, the harem size distribution approaches a lognormal.

The comparison of the model with the experiment also shows encouraging agreement. The experimental harem size distribution is based on data from m = 21 wild horse harems including n = 188 individuals, and its histogram is shown in Fig. 5(b). Despite the considerable error due to the small sample size, an accordance can be proposed with the lognormal harem size distribution coming from the model. We assume the null hypothesis, that the theoretical distribution of the observed harem sizes is the lognormal fitted to the model results for a Poisson (λ = 25) LCD, with fitting parameters μ = 9.61 mean and σ = 6.65 standard deviation. Using the Kolmogorov-Smirnov test it can be accepted at p = 0.97 significance level that the experimental sample comes from this theoretical distribution.
5 Discussion

The endangered status of the Przewalski horse calls for more profound studies of the overall behavioural patterns of this species [12], and indeed, their collective movements have attracted interest as well [4]. Our model on the social bonds of the wild horses is based on the horses copying the behaviour of some of the herd mates when making individual decisions. Collective decision emerges from these individual ones. The specific feature of our present approach is its simultaneous accounting for the two basic hierarchical levels of a herd consisting of individual harems. We find that a modularly structured hierarchy is more beneficial than a non-modular one regarding the success rate of the herd in properly guessing the environmental clues. This observation suggests that multilevel societies or social structures are not only by-products of family relations, but may be the results of alternative optimization factors. Modeling shows that the harem-leader to harem-member ratio observed in herds of wild horses corresponds to an optimal network in the sense that the performance is maximized. In addition, hierarchy is maximized with this ratio as well, suggesting that the degree of hierarchy in a group correlates with common performance. The experimental distribution of harem sizes is in a good agreement with the lognormal distribution obtained when applying our model. The mechanism leading to modules is based on the ambition of males to build exclusive harems, thus, this model may be applicable to other harem-forming species.

Appendix: Formal model description and input parameters

Individuals and their environment. The model consists of $n$ individuals, of which $m$ are assigned as male and $n-m$ female. The individuals are embedded in an environment, which, at every time step, changes randomly its state with probability $p = 0.1$ to one of $l = 5$ discrete states. All individuals have a predefined ability $a_i$, which is the probability that an individual can guess the right state of the environment. They have a $c_i$ link capacity (LC), that is an upper bound of outgoing edges. Both of them are random variables chosen from a given distribution. The abilities are drawn from a bounded Pareto distribution with 0.25 expected value and $1/\sqrt{48}$ standard deviation, since fat-tailed distributions maximize group performance [31] and promote the emergence of hierarchy [21]. From the ordered abilities the $k$ largest values are assigned to males. The higher ability values enable the males to assume higher ranking positions in the hierarchy. If the abilities of males and females would be drawn from different distributions, then when changing the ratio of genders, the overall ability distribution of the group would change. The results would not be comparable to each other, because the ability distribution has a notable effect on the common performance [21]. The link capacities are drawn from different distributions to test their effect on harem formation, namely uniform, Poisson, delta and lognormal distributions. Link capacity determines in the case of the females the maximum number of all outgoing links an individual can have. In the case of the males it determines an upper bound of female followers and it is also their strength parameter.

Trust in groupmates. The individuals have information about the gender, but not about the ability of others, though they can estimate the ability of those whom they have already copied. The estimation of another’s ability is the basis of trust in him. Followings occur spontaneously, and individuals consider copying those they trust the most. Trusts are stored in a trust matrix, where the element $t_{ij}$ denotes how much individual $i$ trusts an individual $j$, and is calculated by using the rule of succession

$$ t_{ij} = \frac{s_{ij} + 1}{n_{ij} + l}, $$

where $s_{ij}$ is the number of good responses copied by $i$ from $j$ and $n_{ij}$ is the number of all attempts when $i$ copied $j$.

Different behaviour of the males. The genders behave differently during the process, since males have an extra role. Before clarifying it, some terms should be defined. Each individual receives a feedback about the harems he belongs to after each round, where the feedback consists of an array of the harem leaders’ indices. A male belongs automatically to his own harem, and a female belongs to a male if she considered his decision in the previous round, in other words she followed him. With this definition a female can belong to one, more or zero harems at the same time. In this latter case she is called a lonely female. The female followers of a male
Table 1: Default values of the input parameters in the simulations.

| Parameter                              | Default value |
|----------------------------------------|---------------|
| number of environmental states         | $l = 5$       |
| probability of changing the env. state  | $p = 0.1$     |
| noise                                  | $\eta = 0$   |
| maximal number of considered groupmates| $3$           |
| aggression level                       | $r = 0.5$     |
| number of all individuals              | $n = 200$     |
| number of males                        | $m = 25$      |
| ability distribution                   | bounded Pareto|
| average ability                        | $\mu = 0.25$ |
| standard deviation of abilities         | $\sigma = 1/\sqrt{48}$ |
| upper limit of abilities               | $1$           |
| link capacity distribution             | uniform(3,20) |

are all the females, who followed him in the previous round, and his harem size is the number of his female followers plus one. In each round, before the individuals make a decision, $q = r n$ herding attempts takes place, where $r$ is an input parameter called the aggression level, which ranges from 0 to 1 and $n$ is the number of all individuals. A herding attempt consists of three steps:

1. First, a herding male is chosen with probability proportional to his link capacity.

2. For a given herding male, the possible females are identified for herding. This includes lonely females if the herding male has free links, and his female followers who follow an individual from a different harem as well (either a male or a female), or are followed by another male. More precisely, all the possible edge operations are identified, including the adding of new edges and the deleting of undesired edges.

3. A possible edge operation is chosen with uniform probability. If an edge is chosen for adding, directed towards a lonely female, the herding male reinforces her trust in him. In the algorithm it means that the $s_{ij}$ and $n_{ij}$ values in (1) are increased by one in the corresponding trust value. This action has equivalent effect to the male giving the lonely female the right answer. Since her trust in him increases after this attempt, she is more probable to follow him in the next round. If an edge is chosen for deletion, three cases can occur. In the first case the undesired edge links two females, and the herding male succeeds in unlinking it with probability $c_i/c_{\text{max}}$, where $c_i$ is his LC, and $c_{\text{max}}$ the maximal LC. Unlinking a trustor $i$ and a trusted $j$ means to reset the trust value $t_{ij}$ to its initial value. In the second case the female follows two males, this time the males fight for her, and the male $i$ wins over $j$ with probability $c_i/(c_i + c_j)$. The winner reinforces the female’s trust in him and unlinks the edge between the female and the losing male. In the third case the female is followed by another male, thus the males fight for her as above.

**Decision making.** After herding the individuals make their decisions. Each individual in each time step makes an estimation about the actual state of the environment and nominates $1 - 3$ individuals for imitation, independently of gender, whom he trusts the most. The number of nominated individuals decreases linearly with the nominator’s ability. Nominated individuals consider their nominators and propagate their decision of the last round to $c_i$ individuals, with a preference to the followers of previous rounds. Individuals make their final decisions by averaging the propagated answers and weighting them with trust values. They also always take into account their own estimation with the weight of their own ability. They maintain taboo list, and do not ask again the ones who cannot propagate the answer to them. After the decisions the state of the environment is revealed and trust values are updated. The simulations were performed without noise. More details on the model can be found in [21], default input parameters used in the simulations are listed in Table 1.

**Measured quantities of the networks.** To characterize the effectivity of the information flow through the edges, we quantified the common performance of the society through the ratio of right responses of individuals. Each individual in each time step scores 1 if successfully guessing the environmental state and 0 if not.
The individual performance $p_i$ is the time average of his scores, with an exponential moving average with a half life of 50 steps. The performance of the whole society is the average performance of the individuals. Performance improvement is defined as the common performance minus the average ability, which would be the performance without imitation. Relative performance improvement is the performance improvement divided by the average ability expressed in percentages

$$\frac{\langle p_i \rangle - \langle a_i \rangle}{\langle a_i \rangle},$$  \hspace{1cm} (2)

where $a_i$ are the abilities, $\langle \rangle$ denote averaging over individuals and overline denotes averaging over time. In order to get a qualitative insight of the network layout, we visualize the individual and harem network with the reaching centrality method [18], and characterize the extent of hierarchy with three measures, the fraction of noncyclic edges, global reaching centrality [18] and fraction of forward arcs. The reaching centrality method is based on the assumption that the rank of the nodes is related to their impact on the whole network. A node's impact can be quantified with its local reaching centrality, which is the proportion of all nodes reachable from it via outgoing edges. The global reaching centrality (GRC) of a network is related to the heterogeneity of the local reaching centrality distribution of its nodes which is wider for hierarchical structures. Thus, the quantity GRC measures the level of hierarchy of a network, with a value close to zero corresponding to no hierarchy, while GRC being about 1 signaling a highly hierarchical network. The visualization of the graph is based on the local reaching centralities of the nodes, where nodes with similar values lie in the same layer and the highest value is on the top. To reveal modular structure and find communities we use the clique percolation method (CPM) and program CFinder for visualization [2,22]. The indicator of convergence is the fraction of changed edges in a time step going to zero, and the harem sizes, which converge to stable values.

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