



Temporal dynamics of social hierarchy formation and maintenance in male mice



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Dominance hierarchies emerge when individuals must compete for access to resources such as food, territory or mates. Here, using traditional and network social hierarchy analysis, we show that 10 groups of 12 male laboratory CD1 mice living in large vivaria consistently form extremely linear dominance hierarchies. Within each hierarchy we determine that every individual mouse has a unique social rank and behaves with a high degree of consistency in their agonistic behaviour towards other individuals. Using temporal pairwise comparison Glicko ratings and social network triangle transitivity measures, we demonstrate that these hierarchies emerge rapidly, and that initial aggression is not predictive of later dominance. We also show that groups vary in how unequally power is distributed over time as social networks stabilize. Our results demonstrate that an ethologically relevant housing paradigm coupled with extensive behavioural observations provides a strong framework for investigating the temporal patterning of mouse dominance hierarchies and complex social dynamics. Furthermore, the statistical methods described establish a strong basis for the study of temporal dynamics of social hierarchies across species.

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Social dominance occurs when one individual repeatedly and consistently yields towards another individual's agonistic behaviour, leading to a de-escalation rather than escalation of future aggression within that relationship (Drews, 1993). A dominance hierarchy emerges when most relationships within a social group are organized such that more dominant individuals consistently induce yielding responses in more subordinate individuals (Chase, 1982b). Hierarchies form when there is competition for resources such as access to mates, food or territory. Recognizing and adhering to a social rank may be beneficial by preventing the need for constant conflict and risk of injury (Chase & Seitz, 2011). First described by Schjelderup-Ebbe (1922) based upon his observations of domestic fowl forming a 'pecking order', dominance hierarchies are now one of the most well-studied forms of social organization, occurring naturally in diverse species, including fish, reptiles, birds, mammals, primates and humans (Chase & Seitz, 2011). Dominance hierarchies also emerge readily in species studied in the laboratory such as cichlids (Fernald & Maruska, 2012; Oliveira & Almada,

1996), crayfish (Issa, Adamson, & Edwards, 1999) and chickens (Chase, 1982a).

Traditionally, the study of social behaviour in laboratory mice has been limited to brief dyadic interactions occurring in a context separate from the home-cage environment (Brodtkin, 2007; Crawley, 2007; Kas et al., 2014). Although these tests reveal behaviour characteristics of individual mice and the relationship between two individuals at a given point in time, they do not provide information about how relationships develop over time or how relationships are adjusted within a large social network. Dominance in pairs of mice is usually assessed with dyadic tube-tests (van den Berg, Lamballais, & Kushner, 2015; Curley, 2011; Wang et al., 2011), food, sex or other reward competition tests (Benner, Endo, Endo, Kakeyama, & Tohyama, 2014; Jupp et al., 2015; Nelson, Cunningham, Ruff, & Potts, 2015) and aggression tests (Branchi et al., 2013; Ginsburg & Allee, 1942). Problematically, results in these social contexts do not necessarily relate to overall social dominance within a larger group context where relationships are embedded (Chase, 1982b). Studies that have examined social dominance in groups of male laboratory mice have limited their scope to the emergence of an alpha male rather than determining finer details regarding the rank order of all individuals (Ely & Henry, 1978; Lewejohann et al., 2009). Moreover, previous studies of social

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dominance in the laboratory have limitations such as small group sizes, short duration of observations and few replicated groups (Arakawa, Blanchard, & Blanchard, 2007; Ely & Henry, 1978; Lewejohann et al., 2009; So, Franks, Lim, & Curley, 2015).

Our laboratory has developed a novel paradigm for the study of the social behaviour of group-living laboratory mice that addresses these shortcomings. We house groups of laboratory mice, *Mus musculus*, for several weeks in a large vivarium that mimics the natural burrow system of the ancestral species (Berry, 1970). The environment comprises a below-ground level of interconnected nestboxes and above-ground levels that contain food, water and environmental enrichment (So et al., 2015; Supplementary Fig. S1). Since *Mus musculus* are characterized by high male reproductive skew with high intermale competition (Crowcroft, 1973), we used all-male groups in the current study. We collected live observational data from 10 separate social groups and used advanced statistical techniques to investigate whether male outbred laboratory mice consistently form linear dominance hierarchies. We then examined the temporal dynamics of mouse social hierarchies, determining how hierarchies are established, how inequitable the distribution of power within the dominance network is, and how stable hierarchies are over time. We believe that this work provides a strong conceptual framework for the study of complex social dynamics within the laboratory that has implications for our understanding of behavioural parameters relevant to social relationships in natural contexts.

METHODS

Animals and Housing

A total of 120 male outbred CD1 mice aged 7 weeks were obtained from Charles River Laboratories (Wilmington, MA, U.S.A.) and housed in groups of three in standard sized cages (27 × 17 × 12 cm) with pine shaving bedding. All mice were assigned individual IDs and marked accordingly by uniquely dyeing their fur with a blue, nontoxic, nonhazardous marker (Stoelting Co., Wood Dale, IL, U.S.A.). These marks last for up to 12 weeks, so one application enabled unique individual identification throughout the 23-day study. At the age of 9 weeks, mice were randomly assigned to social groups (cohorts) consisting of 12 males. In each cohort, six males had no previous experience of any other male in the cohort and six males had previously been housed with only one other male that was in that cohort. Each individual was weighed and placed into a large custom-built mouse vivarium (150 × 80 cm and 80 cm high; Mid-Atlantic, Hagerstown, MD, U.S.A.; see Supplementary Fig. S1). Vivaria were constructed as described in So et al. (2015), consisting of multiple shelves, nestboxes and a metal backboard containing multiple holes for air circulation. Mice could explore and access each shelf and cage via ramps and tunnels. Standard chow and water were provided ad libitum at the top of the vivarium. Multiple enrichment objects such as plastic igloos and round tubes were also provided. Pine shaving bedding was used to cover the shelves and nestboxes in each vivarium. Animals were put into the vivarium just prior to the onset of the dark:light cycle on day 1 of the study and were not disturbed for the duration of their housing in the vivarium (21–23 days). All subjects were housed in the Department of Psychology at Columbia University, with constant temperature (21–24 °C) and humidity (30–50%), and a 12:12 h light:dark cycle with white light (light cycle) on at 2400 hours and red lights (dark cycle) on at 1200 hours. All procedures were conducted with approval from the Columbia University Institutional Animal Care and Use Committee (IACUC Protocol No. AC-AAAG0054) and are in concordance with ASAB/ABS guidelines. At the end of the experiment all animals were

euthanized via decapitation, with each individual's brain and blood being stored for future analyses.

Behavioural Observations

Live behavioural observations commenced on the first day of group housing in the vivarium and continued for 21–23 days per vivarium (see Table 1). Observations were conducted for 1–3 h per day during the dark cycle, with the majority of observations occurring in the first 4 h after the onset of the dark cycle. The mean ± SD total observations conducted per vivarium was 43.05 ± 6.29 h (range 34–52 h). Using all-occurrence sampling, trained observers recorded all occurrences of the behaviours listed in the ethogram in Supplementary Table S1 that occurred between two animals within each 1 h observation period. Often several behaviours co-occur within each aggressive contest. Each contest lasted 1–20 s (typically 5–10 s). Behaviours were recorded with the following priority: fighting, chasing, mounting, subordinate posture, induced-flee. For instance, if one animal fought another animal that responded by fleeing, this would be recorded as a fighting event only, as fighting takes priority over the co-occurring induced-flee. If an animal fled when approached but was not attacked by another animal, then this would be recorded as induced-flee. For each behavioural event, the subject directing the behaviour, the recipient of the behaviour, and the time and location within the vivarium was recorded. Individuals that directed fighting, chasing or mounting were considered winners of each interaction. Individuals that exhibited subordinate posture or induced-flee towards another subject were considered losers of each interaction. If there was no clear winner, then the event was recorded as a tie. Each subject would only receive one win (or one loss) per aggressive interaction even if several behaviours (e.g. chase, fight, subordinate posture) co-occurred during that interaction. This was done so as not to inflate the total number of wins and losses per individual. Aggressive interactions were considered to have ended when each individual separated and engaged in different behaviours such as self-grooming, social investigation of other animals, nest building, feeding, etc. All data were documented live via Google survey on Android devices. All observers were trained to >90% reliability.

Statistical Analysis

All statistical analyses were undertaken in R v.3.2.2 (R Core Team, 2015). The total frequency of wins and losses accrued by each individual was aggregated into separate frequency win/loss sociomatrices for each cohort, with winners in rows and losers in columns. A binarized 1/0 win/loss sociomatrix was derived from each frequency win/loss matrix. Following the methods of Appleby (1983), for each cell of the frequency win/loss matrix we assigned a 1 to individuals in rows that won absolutely more often against individuals in columns and a 0 to individuals in rows that lost absolutely more often to individuals in columns. If individuals were tied, both individuals received a 0.

Using the frequency win/loss sociomatrices, we calculated the following measures of the strength of the social hierarchy: (1) Landau's modified h' evaluates the extent to which individuals in a hierarchy can be linearly ordered (de Vries, 1995). It ranges from 0 (no linearity) to 1 (completely linear), with the significance of h' determined by performing 10 000 two-step randomizations of the win/loss frequency sociomatrix and comparing the observed h' against a simulated distribution of h' . (2) Directional consistency (DC) assesses the degree to which all agonistic interactions in a group occur in the direction from the more dominant individual to the more subordinate individual within each relationship. It is

Table 1
Group characteristics and hierarchy measurements

Cohort	Days	Unknown relationships	Number of observations	Landau's modified h'	Directional consistency	Triangle transitivity	Steepness D_{ij}
A	21	3	1093	0.83***	0.87***	0.93***	0.67***
B	22	7	1042	0.78***	0.94***	0.94***	0.61***
C	23	0	1345	0.93***	0.84***	0.93***	0.76***
D	21	8	911	0.72***	0.95***	0.86***	0.61***
E	23	11	933	0.71***	0.90***	0.92***	0.50***
F	21	2	1221	0.88***	0.87***	0.88***	0.75***
G	22	8	1050	0.87***	0.94***	0.95***	0.62***
H	23	16	584	0.74***	0.99***	0.91***	0.42***
I	22	0	790	0.91***	0.88***	0.90***	0.70***
J	22	6	892	0.85***	0.89***	0.93***	0.63***
Mean	22	6.1	986	0.82	0.91	0.91	0.63
SD	0.8	5.1	216	0.08	0.04	0.03	0.11

*** $P < 0.001$.

equal to $(H - L)/(H + L)$ where H is the frequency of behaviours occurring in the most frequent direction and L is the frequency of behaviours occurring in the least frequent direction within each relationship. We tested the significance of DC using the randomization test proposed by [Leiva, Solanas, and Salafranca \(2008\)](#). (3) Steepness measures the unevenness of relative individual dominance within the hierarchy. It ranges from 0 (differences in dominance ratings between adjacently ranked individuals are minimal) to 1 (differences in dominance ratings between adjacently ranked individuals are maximal). In brief, a cardinal score of the overall success of each individual at winning contests relative to the success of all other individuals is calculated (normalized David's scores, DS; see [de Vries, 1995](#)). This is derived from a dyadic dominance index (D_{ij}), which is the proportion of wins and losses of each individual corrected for the frequency of interactions. Steepness is then derived by regressing the normalized DS against the rank order of individuals. Ten thousand randomizations of the sociomatrix are then performed to calculate the significance of the observed steepness.

Using the binary win/loss sociomatrices, we calculated inconsistencies and strength of inconsistencies (I&SI) ranking, or the rank order of individuals in each social group ([Schmid & de Vries, 2013; de Vries, 1995](#)). This linear ordering algorithm determines the row and column order of each binarized sociomatrix such that as many 1s as possible appear above the diagonal (minimizing inconsistencies) and that those 1s that do appear beneath the diagonal are as close to the diagonal as possible (minimizing the strength of inconsistencies). A perfect linear hierarchy would possess all 1s above the matrix diagonal and all 0s beneath it. If more than one solution is found, then the matrix whose rank order correlates highest with the normalized DS is returned as the solution. We also calculated triangle transitivity (t_{tri}), which measures the proportion (P_t) of relations between all triads (subgroup of three individuals) in a network that are transitive (i.e. if individual A dominates individual B and individual B dominates individual C, then if individual A also dominates individual C, the triad is transitive; [Shizuka & McDonald, 2012](#)). Triangle transitivity is scaled between 0 (the number of transitive triadic relations are not higher than random expectation) and 1 (all triadic relations are transitive). The advantage of t_{tri} is its effectiveness in dealing with unknown relationships (i.e. structural zeros in the sociomatrix). We tested for the significance of t_{tri} using a Monte Carlo randomization of 1000 generated random graphs using the method outlined by [Shizuka and McDonald \(2012\)](#). To determine how t_{tri} changes over time, we repeated this analysis for each group using subsetting data from the beginning of observations up to the end of each successive day. We repeated this analysis but further subsetting the data to include only up to the last five interactions between any pair of individuals.

This was done to detect more rapidly any potential changes to t_{tri} that would not be picked up if the entire history of all relationships was used. Triangle transitivity was assessed using the R code provided by [Shizuka and McDonald \(2012\)](#).

We calculated the temporal changes in individual dominance ratings of each subject in each cohort using Glicko ratings ([Glickman, 1999; So et al., 2015](#)). Glicko ratings are an extension of the Elo dynamic paired comparison models ([Neumann et al., 2011](#)), whereby a cardinal dominance score for each individual is derived based on the temporal sequence of wins and losses. Briefly, all individuals begin with the same initial rating (2200) and rating deviation (300). Ratings points increase or decrease for each individual determined by a function accounting for the ratings difference between opponents as well as the measure of certainty of each opponent's rating (their ratings deviation) (see [Glickman, 1999; So et al., 2015](#)). The Glicko ratings formula uses a constant, c , that adjusts the rate at which ratings can be modified. Here $c = 3$ based on previous work, demonstrating that it is a theoretically sound value for mouse agonistic interactions ([So et al., 2015](#)).

We calculated the Gini coefficients for each cohort using the total number of wins and losses accrued by each individual within each group. The Gini coefficient is a commonly utilized method for assessing the inequality in a distribution and has previously been used to determine inequity in power within dominance networks ([McDonald & Shizuka, 2012](#)). It ranges from 0 (no inequity) to 1 (complete inequity). We compared Gini coefficients derived from wins and losses using Wilcoxon signed-ranks tests. Since the Gini coefficient does not detail whether more dominant or more subordinate individuals are responsible for any inequity, we also calculated the Lorenz asymmetry coefficient, LA ([Damgaard & Weiner, 2000](#)). Values of this coefficient that are <1 indicate that inequity is due to individuals with lower scores (e.g. fewer wins or fewer losses) and coefficients >1 indicate that inequity is due to individuals with higher scores (e.g. more wins or more losses). We tested whether the distribution of Lorenz asymmetry coefficients differed from 1 using a Wilcoxon signed-ranks test. We calculated both Gini and Lorenz asymmetry coefficients for the whole observation period of each cohort and repeated this analysis using subsetting data from the beginning of observations up to the end of each successive day to assess temporal changes. We further repeated this analysis using only data from the top four most dominant individuals per group to assess inequality even among more powerful individuals, which has previously been suggested to be an important feature of dominance networks ([McDonald & Shizuka, 2012](#)). We also calculated the proportion of all wins that each individual accrued within their social group. We then compared the total win proportion by the final alpha and beta males (i.e. those who finished in the first and second rank based on

their Glicko rating), as well as computing the absolute difference between these win proportions. This was done for the whole period as well as with data from the beginning of observations to the end of each day to assess temporal change. We then repeated this analysis but redefined alpha and beta males as those who were in first and second rank based on Glicko rating at the end of each successive day.

For each cohort, we also calculated the directional consistency of every relationship within a group. After ordering each directional consistency matrix in I&SI rank order, we derived the median directional consistency of each relationship across all cohorts. We also determined the interaction probability for every relationship in every cohort and likewise generated the matrix of median interaction probabilities by rank. To examine whether early dominance was predictive of final dominance, we correlated Glicko ratings and total wins accrued by each individual up to the end of each day with final scores using Spearman rank correlations.

Landau's modified h' , DC and I&SI were calculated using the R package 'compete' v.0.1 (Curley, Shen, & Huang, 2015). Steepness was calculated using the R package 'steepness' v.0.2.2 (Leiva & de Vries, 2014), Glicko ratings were calculated using the 'PlayerRatings' package v.1.0 in R (Stephenson & Sonas, 2012) and Gini coefficients and Lorenz asymmetry coefficients were calculated using the 'ineq' package (Zeileis, 2014).

RESULTS

The win/loss frequency and binarized sociomatrices are shown in [Supplementary Fig. S2](#).

Do Male Mice Form a Linear Social Dominance Hierarchy?

All 10 cohorts of vivaria-housed mice (labelled A through J) formed a significantly linear social dominance hierarchy (all $P = 0$). The average modified Landau's h' value \pm SD was 0.86 ± 0.08 (range 0.71–0.93). The mean directional consistency was 0.91 ± 0.04 (range 0.84–0.99) and was significantly above chance for all groups (all $P = 0$). The mean triangle transitivity was 0.91 ± 0.03 (range 0.86–0.95), with all being significantly higher than chance (all $P = 0$). All hierarchies were also significantly steep, with a mean \pm SD of 0.63 ± 0.11 (range 0.42–0.76). Out of the 66 unique relationships within each group, the average number of unknown relationships (no observations of any agonistic interaction occurring between two individuals) was only 6.1 ± 5.1 relationships. Landau's h' , steepness, directional consistency and total number of unknown relationships were all highly correlated with one another (Pearson correlation: all $r_8 > 0.7$, $N = 10$, all $P < 0.05$). These variables were not significantly correlated with triangle transitivity, a network measure which is much more robust to the presence of unknown relationships in frequency sociomatrices.

Do Individual Mice Occupy Unique Ranks within a Hierarchy?

The rank order of each cohort was calculated using the I&SI method. Eight out of 10 cohorts had one optimal solution that identified a unique rank of all 12 individuals. Two cohorts had two solutions that were equally optimal. For both of these cohorts, these solutions only differed with respect to which individuals were rank 11 and rank 12 in the hierarchy. Animals are ordered by I&SI rank order in the sociomatrices in [Supplementary Fig. S2](#). In all cohorts, body weight was not related to dominance rank (Spearman rank correlations: all $P = \text{NS}$). We then calculated the median directional consistency of agonistic interactions for every relationship within each cohort (i.e. the DCs for rank 1 versus rank 2, rank 1 versus rank 3, etc., through to rank 11 versus rank 12). We found that the

median directional consistency of relationships within cohorts was remarkably high ([Fig. 1a](#)). Seventy-one per cent of relationships had a median directional consistency of 0.99 or higher, and 86% of relationships had a median directional consistency of 0.9 or higher. Those relationships that were not characterized by a directional consistency of 0.9 or higher were almost exclusively individuals of rank 4 or lower that only differed by one, two or three ranks from the other individual ([Fig. 1b](#)). Such extraordinarily high directional consistency is indicative of a social system in which individuals have unique ranks and are showing social context-appropriate behaviour to animals of relatively higher or lower status.

We also examined the median interaction probabilities for each relationship across all cohorts ([Supplementary Fig. S3](#)). The most frequent interaction observed was that between alpha and beta males (7.7%), followed by interactions between the alpha male and all other males (all 3–6.1%). The most likely interaction between animals other than the alpha male occurred between the beta and gamma male (2.7%). The least common agonistic interactions occurred between animals of the lowest ranks, which likely explains the slightly more inconsistent directional consistencies among lower ranks.

How Quickly Formed and How Stable Are Dominance Hierarchies?

We examined changes over time in the overall degree of dominance hierarchy by calculating the triangle transitivity by day for each cohort. All cohorts rapidly formed dominance networks with high transitivity (see [Fig. 2](#)). Specifically, from the end of day 2 up to the end of observations, seven of the 10 cohorts had continuously significant transitive dominance networks. By the end of day 4, nine of the 10 had continuously significant transitive dominance networks. The final cohort (H) had a triangle transitivity of 1.0 from day 1 to day 19, but it was only significantly transitive from day 11 onwards, likely because this cohort had fewer agonistic interactions and more unknown relationships overall ([Table 1](#)). This consistency in dominance network structure was not due to the exaggerated influence of multiple early interactions, as the pattern of triangle transitivity by day was highly similar when we used only the most recent last five observations per relationship ([Supplementary Fig. S4](#)).

Temporal changes in the formation and maintenance of hierarchies were also assessed using Glicko ratings. The final Glicko ratings for each cohort are shown in [Fig. 3](#). Each group followed a similar pattern, with dominant individuals having disproportionately higher ratings than subdominant and subordinate individuals (median number of individuals that finished above their initial Glicko rating = 4 per cohort, minimum = 2, maximum = 7).

The change in individual Glicko rating over time is plotted in [Fig. 4](#). Each plot shows the individual Glicko rating of each individual after each observed agonistic interaction. Because the number of agonistic interactions varied between cohorts, vertical dotted lines in [Fig. 4](#) indicate the beginning of each new week of observations. In six of 10 cohorts (A, B, D, H, I, J), the individual that was the most dominant alpha male at the end of observations had already clearly emerged as the most dominant individual by the end of week 1. In two cohorts (C and E), the eventual most dominant alpha male did not reach alpha rank until halfway between week 1 and 2. In the remaining two cohorts (F and G), the eventual dominant alpha males took until near the end of observations (in the third week). Prior to their ascendancy, other individuals had been clear dominant males. Most notably, in cohort F, the initial alpha male lost a fight to the initial beta male on day 15 and did not win another fight in the remaining 6 days of observations. On day 16, the initial beta male then lost a fight to the original gamma male and he also then failed to win another fight in the remaining 5 days.

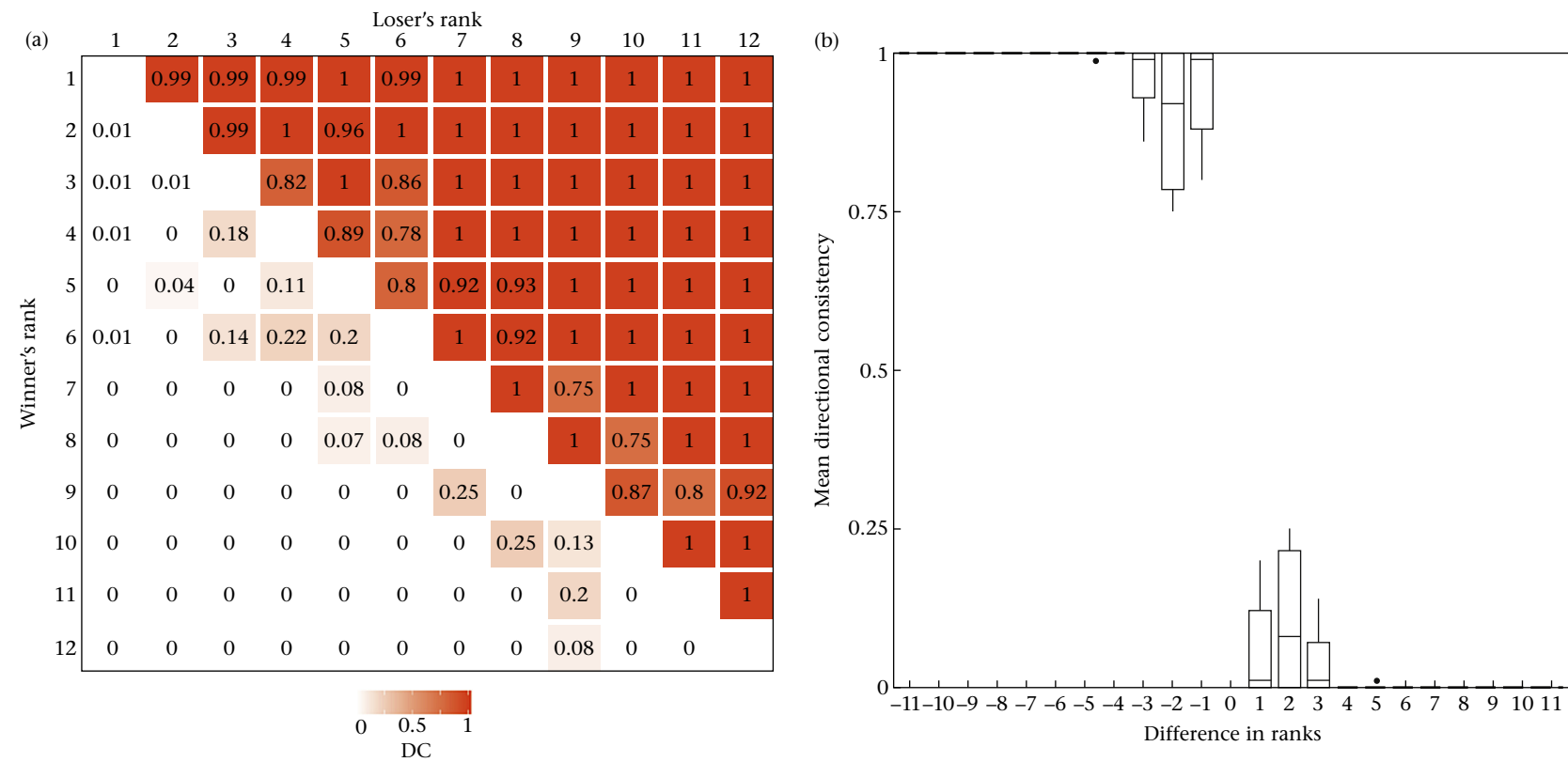


Figure 1. Median directional consistencies by relationship across cohorts. (a) The median directional consistency matrix for all relationships organized by winner and loser rank across cohorts (A–J). (b) Box plots showing the distribution of directional consistency values from the median directional consistency matrix ordered by absolute difference in winner versus loser ranks.

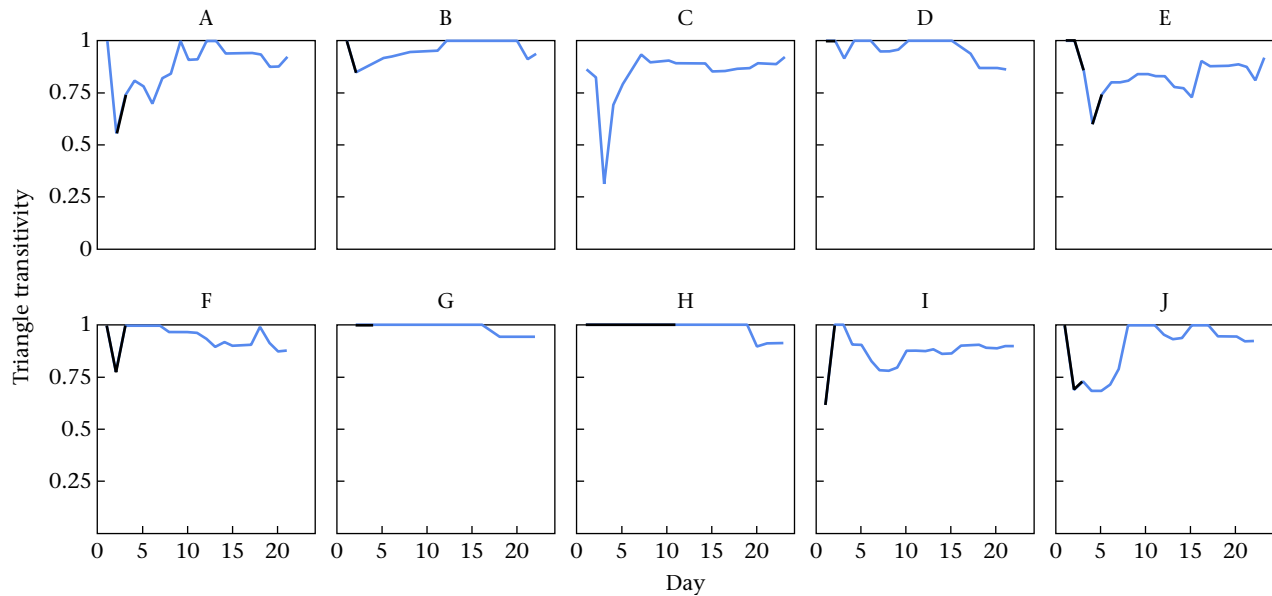


Figure 2. Triangle transitivity by day. Each line represents the triangle transitivity based upon the cumulative observations from the beginning of group formation to the end of each successive day for each cohort (A–J). Lighter lines indicate triangle transitivity values that were significantly above chance; darker lines indicate triangle transitivity values that were not significantly above chance.

The original gamma male thus took over as the alpha male. The rank reversal in cohort G was simply the result of the original beta male defeating the original alpha male 3 days prior to the end of observations and the directional consistency of this relationship being stable thereafter. Taken together, these results suggest that dominant alpha males readily and rapidly emerge in each hierarchy and are generally stable. However, in a minority of social groups, the original alpha males can lose this position if a challenger successfully defeats them.

Notably, among the most stable social hierarchies, the initial aggressive behaviour of males was not predictive of their final Glicko ratings and dominance ranks (see Fig. 5). Glicko ratings on day 1 were correlated with final Glicko ranks in only 2/10 cohorts, which increased to 4/10 cohorts using day 2 Glicko ratings. Total fights won on day 1 were correlated with final Glicko ranks in 4/10 cohorts, which increased to 5/10 groups using day 2 total fights won. By day 4, both the Glicko ratings and total fights won were significantly correlated with final Glicko ratings in 8/10 cohorts. This increased to 9/10 cohorts on day 7 and day 5 for Glicko ratings and total fights won, respectively, and to all groups on day 8 and day 6, respectively.

How Unequally Distributed Is Power within Hierarchies?

We analysed dominance inequality using the Gini coefficient and Lorenz asymmetry (Table 2). The Gini coefficients of total fights won were significantly larger than the Gini coefficients of total fights lost when including all animals (Wilcoxon signed-ranks test: $V = 55$, $N = 10$, $P = 0.006$) or just the top four most dominant individuals ($V = 52$, $N = 10$, $P = 0.010$). Total fights lost was therefore relatively evenly distributed among group members, whereas the total fights won was very unequally distributed even when considering differences just between the top four individuals of each cohort. Across groups, the Gini coefficients of winning and losing were not correlated with one another. When including all animals, the Lorenz asymmetries for both winning and losing did not differ significantly from 1, indicating that inequality in winning and losing was equally due to increased dominance of more

dominant individuals and decreased dominance of less dominant individuals. However, when considering only the top four individuals, the Lorenz asymmetry of winning was higher than 1 (Wilcoxon signed-ranks test: $V = 46$, $N = 10$, $P = 0.065$). It was absolutely greater than 1 in eight out of 10 cohorts, with a ninth group having an asymmetry of 0.996. The cohort with the lowest Lorenz asymmetry for total wins by the top four animals (0.78) was the one cohort (F) where the eventual dominant alpha male was the third-ranked gamma male for much of the observation period. The Lorenz asymmetry of losing among just the top four animals was significantly less than 1 (Wilcoxon signed-ranks test: $V = 7$, $N = 10$, $P = 0.037$). Thus, especially among the most dominant top four individuals, there was a very uneven distribution of power, with the most dominant animals having a disproportionately higher number of wins to losses compared to subordinate individuals. The change in Gini coefficients across days for total wins and losses by all animals is shown in Fig. 6.

The Gini coefficient of winning remained consistently high throughout the observation period, although there was some between-group variability in the overall patterning. The Gini coefficient of losing dropped dramatically from day 1 to day 2 (Wilcoxon signed-ranks test: $V = 45$, $N = 10$, $P = 0.004$) before asymptoting by day 5. Again, there was some intercohort variability, with some cohorts having a more precipitous and earlier decline. The changes in Gini coefficient for the top four most dominant animals are shown in Supplementary Fig. S5. Similar to when considering all individuals, there was a sharp decline in the Gini coefficient of losing fights from group formation onwards. Using a mixed-effects model, with each cohort having its own random slope, we found a significant effect of day on the Gini coefficient of winning fights ($\beta = 0.004 \pm 0.001$, $df = 209$, $t = 4.03$, $P < 0.001$), with Gini coefficients between the top four winners increasing over days. This indicates that the inequity in power between the most dominant individuals within each hierarchy gradually increased over time.

We also examined how despotic alpha males across groups were by evaluating how each alpha male monopolized agonistic interactions within their social group. Figure 7 shows the cumulative

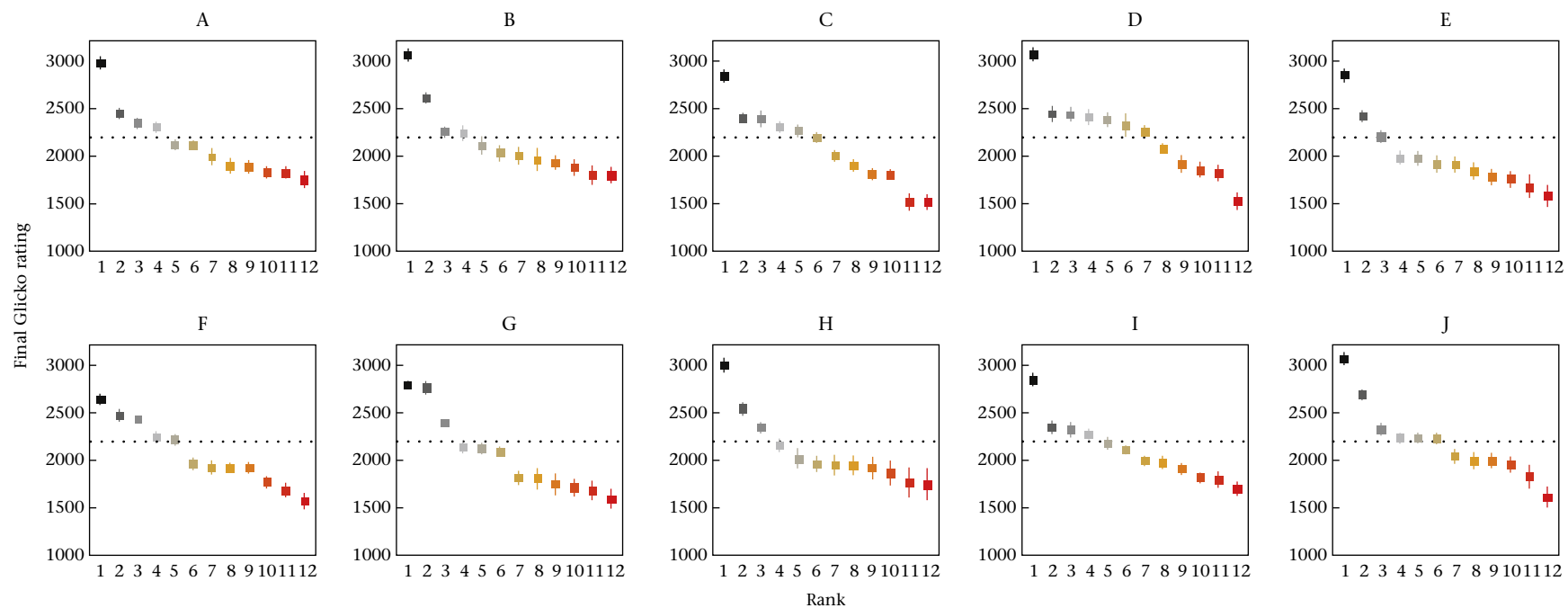


Figure 3. Final Glicko ratings by cohort. The distribution of final Glicko ratings \pm deviation in ratings by final rank order for all cohorts (A–J). Colours range from black (rank = 1, most dominant) to red (rank = 12, most subordinate). The horizontal dotted line represents the starting Glicko rating of all individuals.

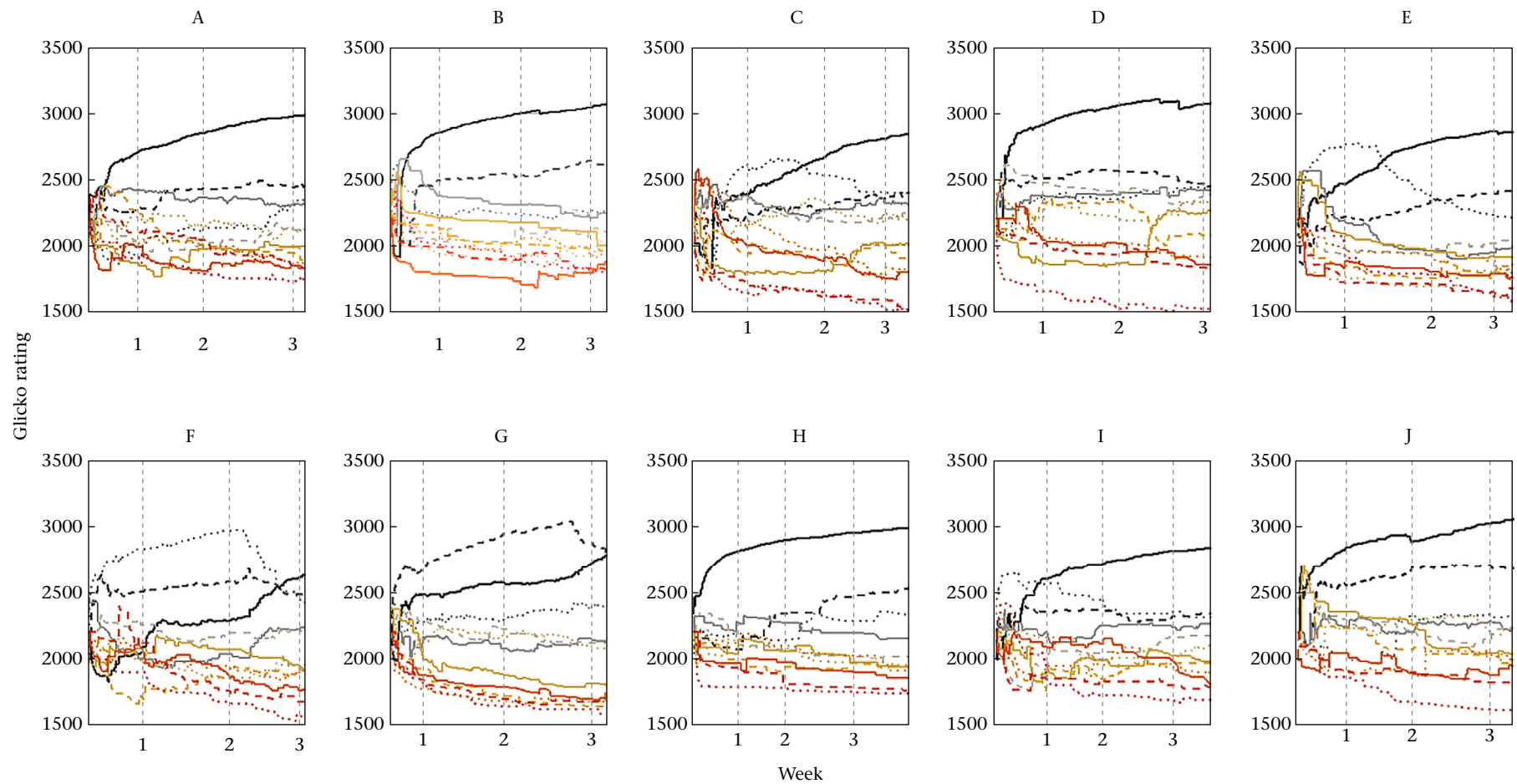


Figure 4. Temporal dynamics of individual Glicko ratings by cohort. The change in individual Glicko ratings over time for all cohorts (A–J). Each line represents the ratings of one individual with colours ranging from black (more dominant at end of observations) to red (more subordinate at end of observations). The solid black line represents the final alpha male and the dashed black line represents the final beta male. Ratings are recalculated for every individual after each agonistic interaction and are plotted on the Y axis against interaction number on the X axis. Because each cohort had a varying number of interactions, vertical dashed lines represent the end of each week of observations.

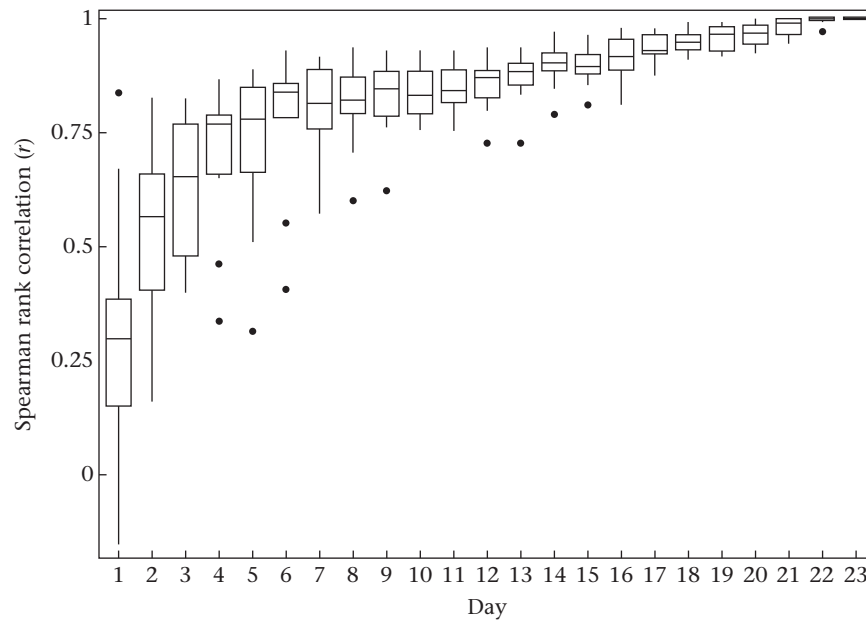


Figure 5. Correlation between Glicko ratings after each day and final Glicko ratings. Box plots representing the distribution of Spearman rank correlation (r) values across all cohorts calculated from correlating the Glicko rating of individuals up to the end of each day against final Glicko ratings.

win proportions of each alpha male as recorded at the end of observations. In four of 10 cohorts (B, D, E, H), the alpha male won over 50% of all agonistic interactions. Each of these interactions was characterized by a sharp increase in the win proportion of the alpha male shortly after group formation. In two further cohorts, the alpha male was the winner of over 50% of all interactions at least at some point during the observation period. In the remaining four cohorts, the win proportion of alpha males was always less than 50%.

We also assessed the despotism of alpha males by determining the absolute difference in win proportions between alpha and beta males (Supplementary Fig. S6). The final win proportions of the eventual alpha and beta male of each group are given in Table 3. The most despotic cohort was H, where the alpha male consistently won around 87% of all interactions and the beta male only 5–7% through the majority of the observation period, meaning that the absolute win proportion difference was consistently around 0.8 or 80%. The groups that had alpha and beta males with the closest win proportions were the two groups where the alpha male was displaced (F and G) and group J. The remaining six groups had alpha males that consistently exhibited win proportions that ranged between 0.23 and 0.55 higher than the win proportions of beta males.

Where Do Agonistic Interactions Occur?

The distribution of agonistic interactions by location across all cohorts is shown in Supplementary Fig. S7. The most common location for fights was in the top section of vivaria with 80.1% of

contests occurring there, which was significantly higher than the proportion of fights that occurred in nestboxes (Wilcoxon two-sample test: $W = 100$, $N = 10$, $P < 0.001$; Supplementary Table S2). We also found that the total frequency of contests significantly differed between locations within the top section of the vivaria (Friedman's rank-sum test: $\chi^2_2 = 8.6$, $N = 10$, $P = 0.014$). Post hoc t tests revealed that, across all cohorts, significantly more fights took place on the top shelf by the food hoppers than on the middle shelf ($P < 0.001$) or on the bottom shelf by the tube entrances ($P = 0.035$). Total fights did not differ in frequency between the middle and bottom shelves of the top part of the vivarium.

DISCUSSION

Our analyses of multiple cohorts of group-housed adult male mice reveal their ability to self-organize into highly linear, long-lasting and stable social hierarchies. The frequency and binary sociomatrixes of winners and losers for all 10 groups resulted in significant values for all three measures of hierarchical organization: Landau's h' value, directional consistency and triangle transitivity. Within each of these groups we were also able to identify the distinct rank order of all 12 individuals. Furthermore, by examining the temporal variation in both individual dominance ratings and overall dominance network measures, we found that each social group varied in overall stability, in the time taken to establish a linear hierarchy and in the degree of despotism of the alpha male.

Table 2
Gini coefficients and Lorenz asymmetries (LA) of total fights won and lost across groups

	Gini				LA			
	Win	Loss	Win (top 4)	Loss (top 4)	Win	Loss	Win (top 4)	Loss (top 4)
Mean	0.68	0.23	0.42	0.29	1.03	0.93	1.14	0.88
SD	0.10	0.03	0.13	0.05	0.10	0.16	0.17	0.17
Minimum	0.55	0.18	0.24	0.22	0.87	0.76	0.78	0.71
Maximum	0.84	0.28	0.61	0.36	1.25	1.17	1.32	1.15

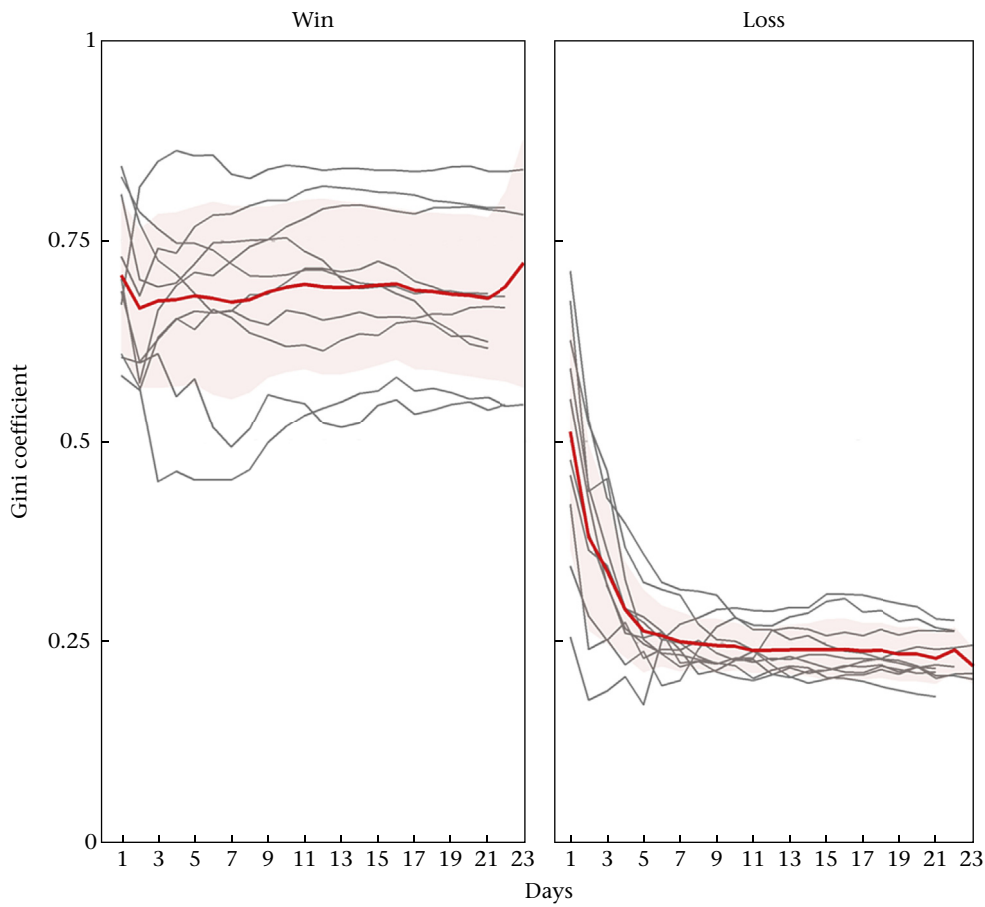


Figure 6. Changes in Gini coefficient in winning and losing by day. Each grey line represents the Gini coefficient of total wins or losses accrued against all other opponents based upon cumulative observations from the beginning of group formation to the end of each successive day for each cohort (A–J). The thick dark line indicates the mean value of all cohorts and the shaded area is ± 1 SD of the mean.

Formation and Maintenance of Social Hierarchies

Our results suggest that the rapid formation of highly organized linear social hierarchies in mice occurs within 48–96 h. Typically

an alpha male emerges within 2 days while the rank order of mid-ranking and lower-ranking individuals are resolved shortly thereafter, consistent with Chase's jigsaw model of hierarchy formation (Chase, 1982b, 1985). In some cohorts we found that the Gini

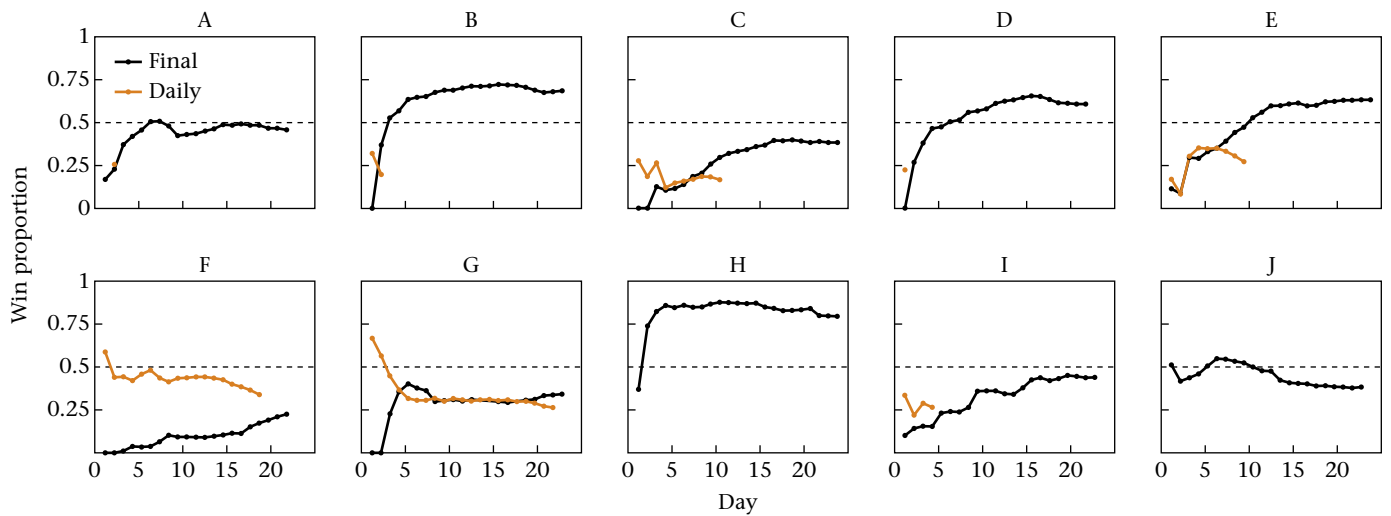


Figure 7. Win proportions by alpha males across cohorts. Each line represents the proportions of all wins accrued by alpha males based upon cumulative observations from the beginning of group formation to the end of each successive day for each cohort (A–J). Lines represent the win proportions by the individual who was the final alpha male (Final) and the alpha male at each successive day (Daily). If the final alpha and the daily alpha male were the same individual, then only the line for the final alpha male is shown for clarity.

Table 3
Win proportions of final alpha and beta males

Cohort	Alpha win proportion (%)	Beta win proportion (%)	Difference (%)
A	46	14	32
B	68	17	51
C	38	15	23
D	61	6	55
E	63	19	44
F	27	22	5
G	34	25	9
H	80	8	72
I	44	11	33
J	38	32	6
Mean	49.8	16.9	32.9
SD	17.2	8.0	22.7

coefficients of winning increased in the first few days post group formation, whereas in others, these coefficients decreased. This suggests that patterns of aggression used by more dominant individuals to achieve their rank order may differ depending on social context. Previous studies using male mice have focused on the social dominance within dyads or small groups of mice (3–5 animals) living in standard housing. These studies have found that one animal will rapidly (within 1–2 days) and reliably become the alpha dominant male and that subdominant males occasionally are also discernible (Mondragón, Mayagoitia, López-Luján, & Díaz, 1987; Poshivalov, 1980; Rodriguiz, Chu, Caron, & Wetsel, 2004; Ulrich, 1938). Studies of larger groups have also shown that dominant and subdominant alpha males will emerge if mice are given more space to establish relationships (Ely & Henry, 1978; Lewejohann et al., 2009; Poole & Morgan, 1975; Poshivalov, 1980; Weissbrod et al., 2013). Indeed, from our location data and behavioural observations, dominant alpha males typically appeared to patrol the top half of the vivarium, forming a territory surrounding the location of food. Access to this area appears to be the primary cause of the conflict leading to groups of mice organizing themselves into a linear hierarchy, with each subject being able to determine their own unique social rank.

Although linear hierarchies are established quickly, many individuals are willing to engage in agonistic interactions in the first few days and many mice that eventually become very subordinate may even win several contests (Fig. 4). Our finding that Glicko ratings and total wins in this time period immediately post group formation are not predictive of final ratings or wins raises two important issues. First, individual differences in aggression are not the sole mediator of social dominance in mouse hierarchies. Other individual characteristics that support fitness and health or promote social dominance (e.g. personality variables like risk taking or boldness, or social competence) may be just as important as or more important than aggression in determining social status in mice (David, Auclair, & Cézilly, 2011; Fox, Ladage, Roth, & IlPravosudov, 2009; Hsu, Earley, & Wolf, 2006; Taborsky & Oliveira, 2012). Second, this finding suggests that standard laboratory tests of social dominance using animals tested in pairs in tasks such as the tube-test (van den Berg et al., 2015; Wang et al., 2011), food competition (Benner et al., 2014; de Jong, Korosi, Harris, Perea-Rodriguez, & Saltzman, 2012; Timmer, Cordero, Sevelinges, & Sandi, 2011) or aggression (Bales & Carter, 2003; Branchi et al., 2013) tests, are not necessarily robust indicators of an individual's ability to ascend a social hierarchy when living within a large social group comprising a number of complex social relationships.

Another notable feature of our social hierarchies was the displacement of stable alpha males in two of the cohorts (F and G) during the third week of observations. Following the loss of alpha

status, displaced males were much less interactive with other mice, consistent with social withdrawal observed in deposed alpha males in many species (Price, Sloman, Gardner, Gilbert, & Rohde, 1994; Setchell, Wickings, & Knapp, 2006; Uehara, Hiraiwa-Hasegawa, Hosaka, & Hamai, 1994) as well as in chronically socially defeated males in rodent models of depression (Berton et al., 2006). Previous long-term observations of laboratory mouse social groups (3–5 per group) have anecdotally reported that males that had been the most dominant alpha for several weeks in groups may lose this ranking abruptly (Haemisch, Voss, & Gärtner, 1994; Ulrich, 1938). Studies of alpha male descent in natural populations of primates have found that it occurs for many possible reasons, including the alpha male being no longer physically capable of staving off challenger males, alpha males losing coalitionary support, the immigration of more dominant individuals into the social group, or the sexual maturation of younger, more dominant individuals (O'Shea, 1976; Perry, 1998; Uehara et al., 1994). It is highly metabolically costly for alpha males to consistently defend their dominance status and territory through physical fighting (Briffa & Sneddon, 2007; Castro, Ros, Becker, & Oliveira, 2006; Rohwer & Ewald, 1981) and other behaviours such as scent marking (Gosling, Roberts, Thornton, & Andrew, 2000). Dominant alpha males of many species also have higher levels of testosterone and cortisol that may be physiologically damaging (Gesquiere et al., 2011; Higham, Heistermann, & Maestripieri, 2012; Mendonça-Furtado et al., 2014; Sapolsky, 2005). There is some evidence that more dominant mice may have elevated testosterone and corticosterone, although these findings vary depending upon social context, how dominance is assessed and other paradigmatic features (Bronson, 1973; Ely & Henry, 1978; Haemisch et al., 1994; Hladlovská et al., 2015; Oyegbile & Marler, 2005; Selmanoff, Goldman, & Ginsburg, 1977; Zielinski & Vandenbergh, 1993). We propose that in our study, the mice that lost alpha status were physiologically no longer capable of maintaining their social position, although this hypothesis remains to be tested.

Variation in Dominance Inequality

In the current study, almost all animals exhibited willingness to contest agonistic interactions (only four out of the 120 males in 10 cohorts failed to win any fights, and only one male never lost any fight). Unsurprisingly, we found that there was a large discrepancy in the distribution of total wins and losses within each cohort, suggesting the formation of a variety of social structures within the hierarchical framework. Few previous studies have rigorously addressed the degree of despotism in male mice living in large groups (≥ 12 individuals). Two studies reported that alpha males were highly despotic, winning fights almost to the exclusion of all other individuals (Lewejohann et al., 2009; Poshivalov, 1980). One other study suggested that alpha males are unlikely to be despotic in large spaces (Poole & Morgan, 1975). By studying 10 separate cohorts of 12 male mice, our results suggest that none of the alpha males in this study could be considered truly despotic in the sense that they prevented any other individual from winning an agonistic interaction. Rather, there was a range of how unequally distributed power was within each social hierarchy. It remains to be determined what combination of characteristics of alpha males and other males within each group are associated with how despotic each alpha male becomes. It is possible that social groups characterized by an extremely dominant alpha male only occur when there is an individual of high aggression or fighting ability in conjunction with a lack of challenger subdominant males, or, it may be sufficient to only have one of these. In our study, there was no lack of challenger subdominant males in any of the social hierarchies; therefore, the high inequality in the distribution of

dominance power was most likely related to the hyperaggressive characteristics of individual alpha males.

Individuals Behave Consistently and Appropriately According to Their Social Rank

Dominance hierarchies are characterized by social relationships that show consistently high asymmetries in behaviour. Importantly, these asymmetrical relationships when considered together are ordered such that dominance networks have low levels of intransitivity. Theoretical and empirical work have shown that such orderliness may emerge given sufficient differences in prevailing attributes (e.g. fighting ability) or through individuals having the ability to infer relative rank via experiential effects such as winner, loser and bystander effects (Chase & Seitz, 2011). Across all of our cohorts, we found that individual animals showed extremely high directional consistency in their own individual relationships with each other (see Fig. 1). These results demonstrate that all individual mice in these social systems were able to recognize their relative status to all other animals in the group and behave appropriately to those ranked above and below them in the hierarchy. This high degree of social competence was not simply a function of every mouse responding appropriately to the alpha male, as even mid- and lower-ranking individuals responded correctly during agonistic interactions towards those ranked above them (i.e. showed subordinate behaviour) and below them (i.e. showed agonistic behaviour). Moreover, social competence can be achieved through even very limited social interaction. For example, although only 1.1% of fights occurred between ranks 3 and 4 and 0.1% of fights occurred between ranks 11 and 12, there were still a sufficient number of interactions to reliably generate a social hierarchy with high directional consistency within these relationships. Individuals also appeared to update this information rapidly as social status changed, as demonstrated by the fact that when there was a sudden change in the social hierarchy, such as the alpha male being displaced by a subdominant, the directional consistency continued to be remarkably high albeit in the opposite direction.

How mice are able to recognize their social status relative to other mice and how this recognition facilitates hierarchy formation and maintenance remain unanswered. It is well established that social recognition via olfactory cues is fundamental to mice being able to recognize their own social status. Compared to subordinate animals, dominant males have higher levels of major urinary proteins (MUPs) that bind to signalling volatile compounds (e.g. 2-sec-butyl-4,5-dihydrothiazole and 3,4-dehydro-exo-brevicomin) (Apps, Rasa, & Viljoen, 1988; Guo, Fang, Huo, Zhang, & Zhang, 2015; Harvey, Jemiolo, & Novotny, 1989; Humphries, Robertson, Beynon, & Hurst, 1999; Kaur et al., 2014; Nelson et al., 2015; Stowers & Kuo, 2015). Some of these urinary proteins (e.g. MUP3, MUP20) either promote or inhibit aggressive behaviour in males that receive these signals, depending on their own social status. Other volatiles such as α - and β -farnesene produced in the preputial gland are also excreted in urine and are higher in dominant males than in subordinate males (Harvey et al., 1989; Novotny, Harvey, & Jemiolo, 1990). Such olfactory cues may certainly be sufficient for learning about the most dominant alpha male in a social group, but it is not yet clear whether such markers allow mice to reliably discriminate between individuals of mid and lower rank and whether these cues could be utilized for discriminating subtle rank differences. A further issue is that these chemosensory differences appear to emerge over time and therefore may be used to identify social dominance in established groups but are not necessarily utilizable by individuals for learning about initial group formation (Harvey et al., 1989).

Another potential mechanism is individual recognition (Barnard & Burk, 1979). Mice are able to use a number of volatile and nonvolatile chemosignals (e.g. MHC class I peptides) to discriminate between and recognize individuals (Brennan, 2009; Hurst et al., 2001). Individual males may couple olfactory cues related to each opponent after initial agonistic contests and continue to update this information through repeated interaction. For instance, a mid-ranking individual must learn the individual odours of all animals that he has previously and recently lost to and beaten and then use that information to guide future interactions. In our vivarium, almost every agonistic interaction is preceded by direct chemosensory investigation, suggesting that individuals are using this information to update their relative social status to each other (So et al., 2015). Although the most likely sensory system is olfaction, we do not preclude the possibility that such learning may also occur through auditory or visual cues, both of which have previously been suggested to mediate some dominance interactions in rodents (Assini, Sirotin, & Laplagne, 2013; Wesson, 2013).

A limitation of individual recognition is that this is a very energetically costly method of forming a social hierarchy. It is also therefore likely that mice use sociocognitive mechanisms to guide their agonistic interactions. A number of species including cichlids, corvids and primates use third-party observational learning and transitive inference to learn about which animals in a social group are more dominant to which other animals (Bond, Kamil, & Balda, 2003; D'Amato & Colombo, 1988; Grosenick, Clement, & Fernald, 2007; Hogue, Beaugrand, & Laguë, 1996; Kumaran, Melo, & Duzel, 2012; Paz-y-Miño, Bond, Kamil, & Balda, 2004). Individuals may also determine their social status through winner and loser effects (Chase, Bartolomeo, & Dugatkin, 1994; Dugatkin, 1997). Winner effects are short-term boosts to the likelihood of winning future encounters that individuals gain after winning a conflict. Loser effects are the increased likelihood of losing subsequent encounters following a loss (Barnard & Burk, 1979; Frey & Miller, 1972). Both expedite social hierarchy formation (Chase, 1982a, 1982b). Empirical support for the presence of these experiential effects exist in numerous taxa including some mouse species (e.g. *Peromyscus californicus*; Oyegbile & Marler, 2005). In the present study, we did not find strong evidence for winner effects, as individuals that won contests on day 1 did not necessarily continue to win contests thereafter. However, we found some evidence of loser effects. Individuals that suffered a significant loss appeared to become much less likely to engage in future contests. This was true not only for individuals that lost fights early on in group formation, but also for displaced alpha males.

Conclusion

The organization of social groups into dominance hierarchies is a phenomenon that has been investigated thoroughly across taxa, both in the laboratory and the field. Here, we have shown that laboratory mice reliably form linear and stable dominance hierarchies after being put together within 48–96 h. Importantly, each mouse within a hierarchy had a unique and distinct social rank and responded consistently to more and less dominant members of their network with appropriate behaviour indicative of high sociocognitive competence (Branchi et al., 2013; Taborsky & Oliveira, 2012). There also was variability between groups in how unevenly power was distributed within the hierarchy. In the extreme, some despotic dominant alpha males monopolized up to 80% of all fights, but in other groups, there was much more extended competition as to which males became alpha or beta males. In some groups this competition led to the original alpha male being unable to maintain its position at the top of the hierarchy. We believe that studying the temporal dynamics of mouse social hierarchy

formation in such an ethologically relevant manner will provide an insightful basis for the future genetic and neurobiological investigation of complex social dynamics in mice and provide insights into the behavioural and biological dynamics critical for characterizing social groups in general. Finally, the statistical methods described here for identifying temporal stability and instability in dominance hierarchies provide a framework for the study of temporal dynamics of social hierarchies across species.

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Supplementary Material

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