Social manipulations trigger shifts in group-level dominance patterns

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Abstract

Recent computational approaches discovered group-level patterns within dominance hierarchies which are based on relative rank differences between individuals. Within species, groups could follow different dominance patterns, indicating these patterns could be group- rather than species-specific traits. Moreover, these patterns differ in complexity, with some requiring an individual to access more social information than others. However, we know little about how and why a particular dominance pattern emerges within a group. To address what social dynamics inform a group's pattern use, we performed social perturbation experiments in four captive groups of monk parakeets (*Myiopsitta monachus*) via removals and reintroductions of differently ranked birds creating social instability. We found that 1) dominance patterns can shift over time within a group after removal of top-ranked birds, 2) the perturbed individual's rank resulted in different group-level responses, 3) patterns remained stable within a group when we did not experimentally perturb the system, and 4) groups did not shift to less informative patterns after perturbations. When we removed top-ranked birds, groups were more likely to bully that bird, piling aggression onto it upon its reintroduction, whereas the removal of a middle/low-ranking bird was associated with a downward heuristic pattern, where individuals aggress indiscriminately against others ranked below themselves. Dominance patterns shifted upon reintroductions more consistently than after removals of top-ranked birds. This work shows group-level plasticity in social dominance patterns as groups vary in their patterns over time and shows that social instability is one mechanism for a group to shift patterns.

Significance statement

Social structures are dynamic over time due to changes in group membership and/or relationship strengths. However, the consequences of social change on social dynamics are difficult to predict. Determining what factors influence social dynamics can help us understand how animals cope with changing environments, which is particularly relevant due to rapid environmental change in the face of urbanisation and climate change. Using perturbation experiments causing social instability, we show that the removal and reintroduction of top-ranked birds has group-level consequences on hierarchical organization and dominance patterns and has the potential to destabilize social structure. Predicting the effect of perturbation events and identifying network resilience, may allow us to prevent future instability from emerging and reduce potential costs upon system collapses.

Introduction

Dominance hierarchies direct and structure aggression in many species (1, 2). In some of these societies, individuals make decisions about how to direct aggression based on their own rank in the hierarchy, as well as the rank of potential opponents. When most group members use the same decisions about aggression and rank, it can be described as a *social dominance pattern* (1) and categorized by the type of dominance pattern the group uses.

Recent work has categorized rank-based aggression into three categories: 1) the downward heuristic, where individuals indiscriminately aggress against others ranked below themselves, 2) close competitors, where individuals preferentially aggress against those ranked slightly below themselves, and 3) bullying, where individuals preferentially aggress against those ranked far below themselves (1). Of the three patterns, the close competitors and bullying patterns have been described as more complex than the downward heuristic (1, 3). This is because both patterns require individuals to use more detailed information about the relative rank differences between themselves and potential opponents. For example, aggressors would need to know which individuals were ranked just below (close competitors) versus far below (bullying) themselves, a distinction which requires greater social information assessment. In contrast, to use the downward heuristic pattern, individuals only need to know which opponents are ranked lower than themselves, requiring less social information to determine opponents.

Despite differences in the underlying information needed to use the patterns, all three patterns are found across myriad species in the animal kingdom, with no evidence that any of the three dominance patterns are phylogenetically restricted (1). Within species, different social groups can follow different dominance patterns, indicating that these patterns should not be considered a species-specific characteristic, but as group-specific characteristics (1). However, we do not know how flexible groups are, whether a group can switch from following one pattern to following another pattern over time, and what factors induce shifts in dominance patterns. Thus, an open question is how and why particular dominance patterns emerge within groups. A better understanding of the conditions under which a group might change to a different dominance pattern would provide insight into the flexibility of group-level consensus about structured aggression.

One potential driver of dominance pattern changes is a change to group composition causing social instability. Social networks, including the aggression networks that underlie rank, can be strongly affected by changes in group membership due to natural demographic processes. These changes can be permanent, for example when individuals leave groups through death or dispersal, or new individuals join groups through birth or immigration (4). In contrast, these changes can be temporary, as individuals join or depart groups through temporary movement decisions (5, 6). Demographic processes have been documented to affect rank and sociality. For example, demographic turnover influenced hierarchy dynamics at the individual-level in spotted hyenas (*Crocuta crocuta*) (7). The joining or departure of key individuals, i.e., individuals that have a disproportionately large effect on group dynamics, may be particularly impactful (8). In groups with dominance hierarchies, animals with higher ranks are often considered to be key individuals because of their influence on group dynamics and network resilience, particularly in species that show the potential for cognitive and/or social complexity (9–12).

To disentangle the mechanism driving dominance patterns within groups, we performed a series of social perturbation experiments and tested whether the removal and reintroduction of single individuals could be sufficient to trigger a shift in the group-level dominance pattern. We investigated dominance patterns in four captive groups of monk parakeets (*Myiopsitta monachus*). This species is particularly well-suited to study these questions as it is a highly social parrot that readily forms dominance hierarchies in captivity (13–16), can develop and follow different dominance patterns (1, 15), and exhibits high fission-fusion dynamics in both wild and captive populations (13). Monk parakeets nest colonially and use their nests year-round, often leaving the colony area during the day to forage but returning to the colony area at night (17, 18). While most studies have focused on within-day fission-fusion dynamics, parakeets can move longer distances (19, 20) and may visit or settle in other colony areas, although long-distance natal dispersal (>10km) is not common (21).

To address how and why social dominance patterns shift within parakeet groups, we determined the propensity of groups to shift between dominance patterns using a series of social perturbation experiments. We tested how groups responded to the removal and subsequent reintroduction of a key individual, who was top-ranked in the group at the time of removal. We compared this reaction to how groups responded when we removed a middle/low ranked individual and when we did not experimentally perturb the social structure, serving as our controls. Finally, we analyzed the effects of perturbation type (removals vs reintroductions) on dominance pattern dynamics, focusing on the top-ranked perturbations, and analyzed how perturbations affect the complexity of dominance pattern shifts.

We used these perturbation experiments to test hypotheses about the plasticity and complexity of the dominance patterns demonstrated by the groups. First, we hypothesized that if dominance patterns are plastic and can respond to changes in group membership or the environment, that our experimental perturbations would result in the group shifting between dominance patterns, rather than the pattern remaining stable and consistent. We predicted that different groups would show different dominance patterns, even in the absence of perturbations. This prediction is based on previous evidence that monk parakeet groups can develop and follow distinct dominance patterns (1, 15). We also predicted that the perturbation of a key individual would lead to a shift in the group-level aggression pattern in the group and that groups subjected to a top-ranked perturbation would have a higher occurrence of shifts in patterns than perturbations of a middle/low-ranked bird. In contrast, groups may be resilient to this kind of disruption and show no shifts in dominance patterns if another individual immediately assumes the social role, or if they are accustomed to frequent group membership changes, as would be experienced with high fission-fusion dynamics. Both wild and captive populations of monk parakeets show high levels of fission-fusion dynamics (13), in which case they may not respond to perturbations.

Second, we hypothesized that removals and reintroductions would differentially affect the dominance pattern shifts. We predicted that the removals would cause the dominance pattern to shift, as the sudden absence of an individual could break the group's information and force remaining members to update their rank. In contrast, we predicted that reintroductions would not result in pattern shifts, because the whole group would have updated information about the interactions of the last removal period, except for the reintroduced bird. Finally, we hypothesized that if close competitors and bullying are both more complex dominance patterns than the downward heuristic pattern, we should see groups shifting to a less-complex pattern following a perturbation as the perturbations would cause social disruptions that would decrease the amount of information birds had about each other and their relative ranks in the hierarchy, forcing them to default to a dominance pattern based on less-detailed social information. We predicted that the pattern would transition to the less-complex downward heuristic pattern after a top-ranked perturbation.

Results

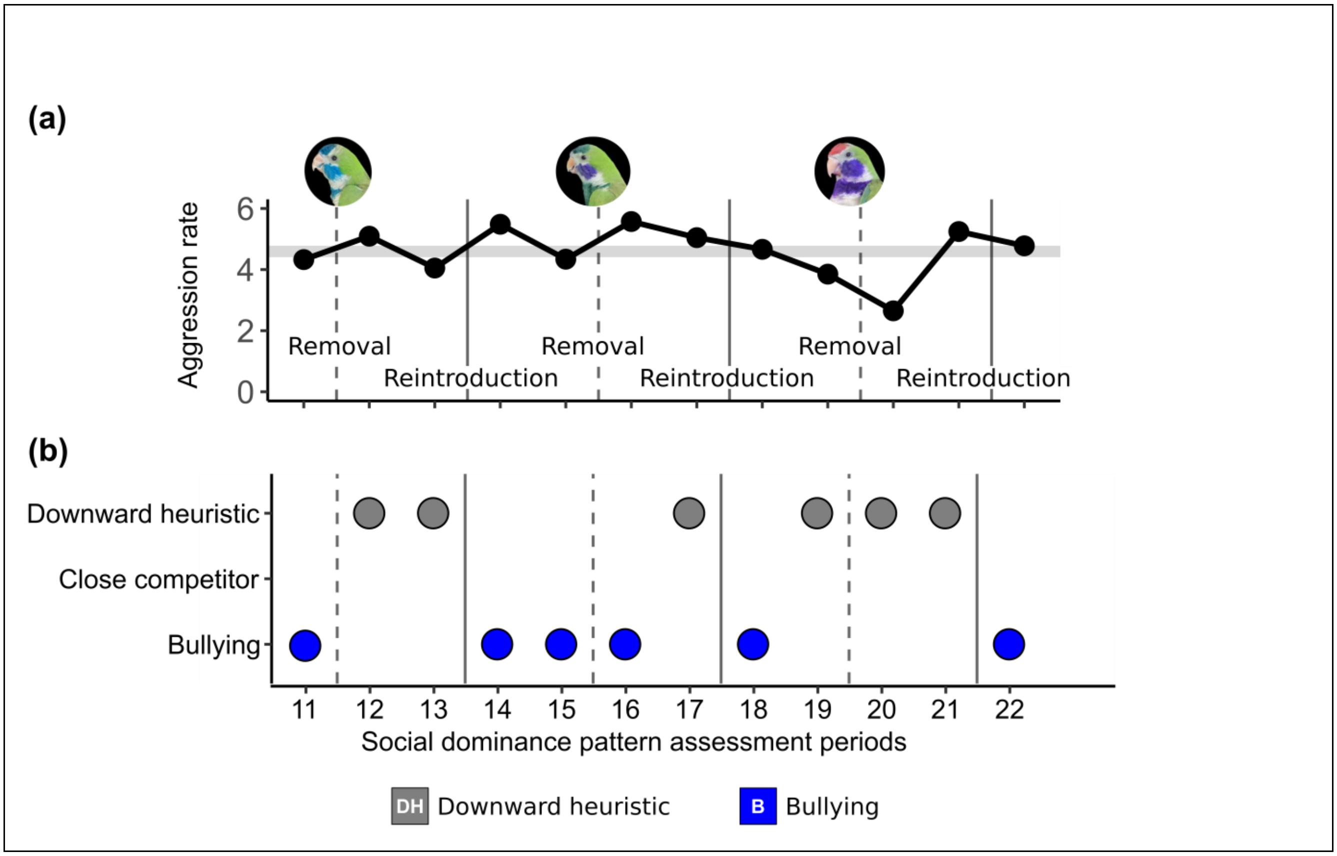
We experimented with 51 unique individual monk parakeets housed in four captive groups across three years of study (2020-2022), resulting in 1,461 hours and 3,530 person hours of social observations and a total of 118,219 observed aggressive events (SI1). We binned these aggressive events into 3-day periods. For each 3-day period, we used observations of directional aggression where there were clear winners and losers and determined each individual's continuous power score within the group using a network-based ranking algorithm and categorized the social dominance pattern of the group using a rank-based reference model (1). We determined the group's dominance patterns at 77 assessment periods. Across the studied groups, we detected all three patterns. The most common pattern was the downward heuristic which we found in 45.4% of the 77 assessment periods, followed by the bullying pattern which we found in 32.5%, and the close competitors pattern in 22.1% of assessment periods.

Dominance pattern dynamics following perturbation of a key individual

To test whether the perturbation of a key individual could elicit a transition in the dominance patterns of a social group, we targeted top-ranked birds as the focal individuals in removal/reintroduction experiments. We performed three 17-day trials of this experiment in the 2021 social group following a 31-day observation period, which was used as a control where we did not experimentally perturb the social structure (Fig. SI1). Following this period, we began perturbations in which we removed and reintroduced the focal bird over the span of 17 days. We identified the top-ranked bird using three days of aggression observation prior to removal days. On removal days, we trapped the whole group, removed the top-ranked focal bird, released the rest of the group members back into the flight pen, and observed the group interact for eight days. After eight days, the focal bird was reintroduced, and we observed the group interact for another eight days. In total, we observed 23,076 agonistic interactions recorded over 255.5 hours.

We detected a total of six dominance pattern shifts in our 2021 experiment. Four of the six shifts occurred directly following a perturbation (Fig. 1b). Although the dominance patterns shifted, the removals and reintroductions of the key individuals did not markedly affect overall aggression in the group. The group's aggression level remained relatively stable following each top-ranked perturbation (mean ± SE = 4.59 ± 0.24 rate of aggression; Fig. 1a). These results showed that a single group could change their dominance pattern use over time, and that the propensity to shift appeared to be mainly, but not exclusively, associated with changes in group membership.

Figure 1. Dominance patterns shifted when the group was experimentally perturbed by removing and reintroducing a top-ranked monk parakeet. Panel a shows the periods where the top-ranked individuals (3 different birds) were removed and reintroduced, the rate of directed aggression (n = 23,076 agonistic interactions) controlled for hours observed and group size (removal: n = 19; reintroduction: n = 20), and the overall mean aggression rate (in grey). Panel b shows the dominance patterns for each assessment period. Vertical lines indicate the timing of experimental perturbations for removals (dashed) and reintroductions (solid). Pictures show the focal birds who were perturbed in the three trials.



Rank-related effects on social dominance patterns

In 2022, we conducted another series of perturbation trials to determine whether the observed dominance pattern shifts were a consequence of a general effect of social perturbations or a specific effect of the perturbation of top-ranked individuals. In these experiments, we tested how the social dynamics resulting from the perturbation of a top-ranked bird compared to the perturbation of a middle/low-ranked bird. To test for the rank effect on dominance pattern shifts, we removed and reintroduced three top-ranked and three middle/low-ranked individuals per group, totaling 12 perturbations. We performed this experiment in two groups of 11 birds each. In total, we observed 42,280 agonistic interactions across 458.5 hours in Group 2022-1 and 42,403 agonistic interactions across 464.4 hours in Group 2022-2. The two groups exhibited different propensities to follow each dominance pattern. Overall, Group 2022-1 followed a downward heuristic pattern in 34.6%, close competitors pattern in 42.3%, and a bullying pattern in 23.1% of assessment periods, compared to Group 2022-2 which followed a downward heuristic pattern in 38.5%, a close competitors pattern in 23.0% and a bullying pattern in 38.5% of assessment periods (Fig. 2aii and bii). The rate of aggression was higher in these two smaller groups (mean ± SE = 8.83 ± 0.58 in Group 2022-1, Fig. 2ai; and 9.01 ± 0.67 in Group 2022-2, Fig. 2bi) compared to the larger group we observed in 2021 (Fig. 1).

Consistent with our 2021 results, we found that dominance patterns in our two 2022 groups changed over time. Both 2022 groups switched between all three possible dominance patterns. We detected a total of ten dominance pattern shifts in Group 2022-1 and five of those occurred directly following a perturbation. Top-ranked perturbations resulted in 3 out of 6 shifts compared to shifts in 2 out of 6 middle/low-ranked perturbations in Group 2022-1. In Group 2022-2, we detected 13 shifts of which seven occurred directly following a perturbation. In this group, we detected 5 out of 6 shifts after top-ranked perturbations and 2 out of 6 shifts after middle/low-ranked perturbations.

We then compared how the rank of the perturbed bird affected the number of dominance pattern shifts across both groups combined. We found that top-ranked perturbations resulted in dominance pattern shifts in 66.7% of a total of 12 perturbations compared to shifts in 33.3% middle/low-ranked perturbations (Fig. 3).

When we analyzed how directed aggression changed with the perturbations by rank, we found that the groups switched to or kept a bullying pattern in 8 out of 12 (66.7%) top-ranked perturbations (Fig. 3a). These results contrasted with those from middle/low-ranked perturbations, in which birds did not markedly shift the targets of their aggression. Instead, group members directed their aggression toward anyone ranked lower than themselves (shift to or kept a downward heuristic pattern in also 66.7% of trials; Fig. 3b). Despite these changes in dominance patterns, the level of aggression in both groups remained relatively stable regardless of the rank of the perturbed birds (Fig. 1a and 2). We included the results by rank and perturbation type in Supplemental Information 3 (Fig. SI3) and summarized the dominance pattern transitions across all trials and social groups (Fig. SI4).

Figure 2. Dominance patterns changed over time when group composition was experimentally perturbed. The results of Group 2022-1 are shown in panel a and Group 2022-2 in panel b. Panel (i) shows the rate of directed aggression (n = 42,280 agonistic interactions in Group 1 and 42,403 in Group 2) controlled for both hours observed and group size, where we highlighted the overall mean aggression rate in grey, and panel (ii) the dominance patterns for each assessment period. Perturbation trials consisted of removal (dashed line) and reintroduction (solid line) of a top-ranked (orange highlight) or middle/low-ranked (grey highlight) focal bird.

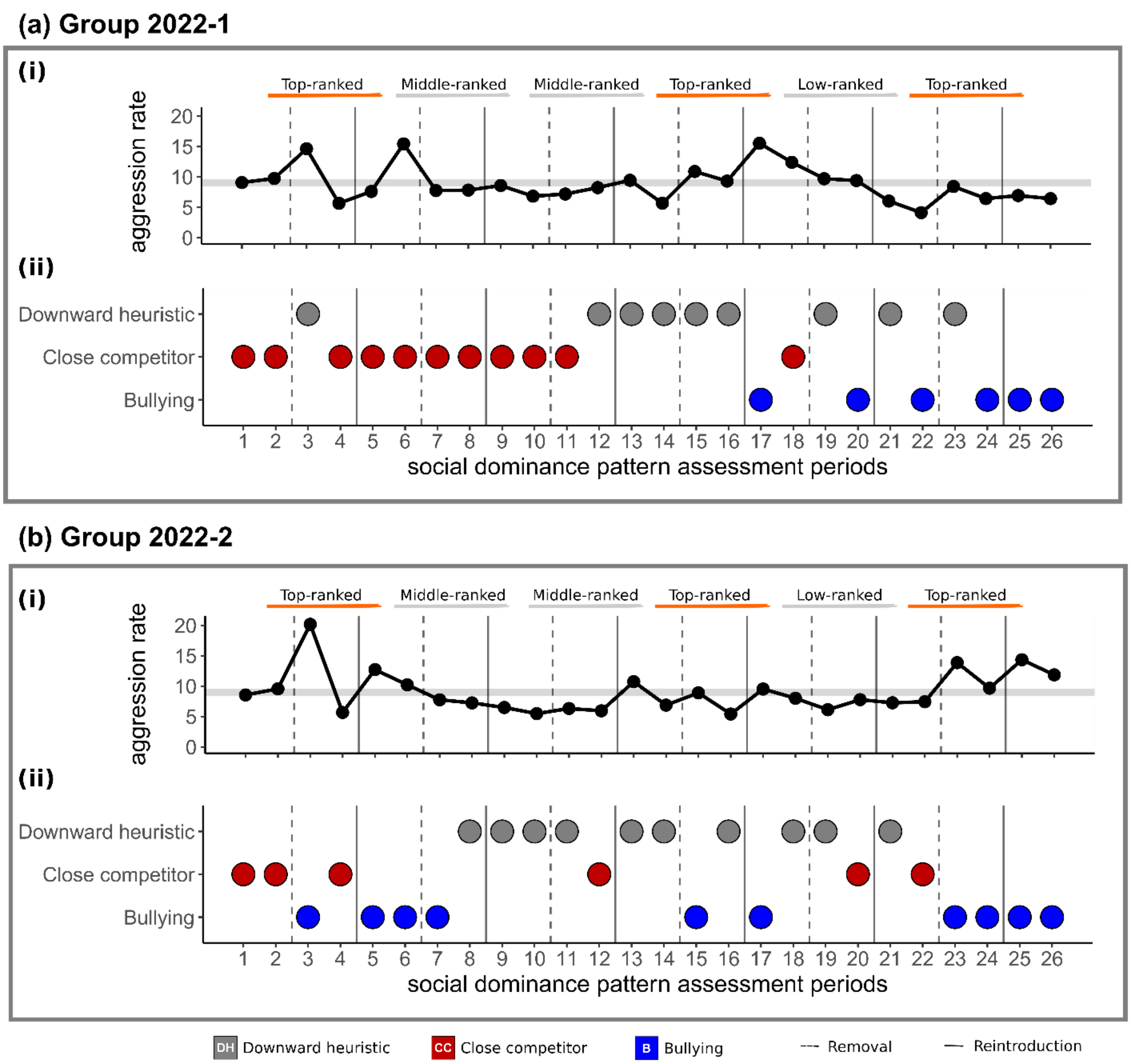
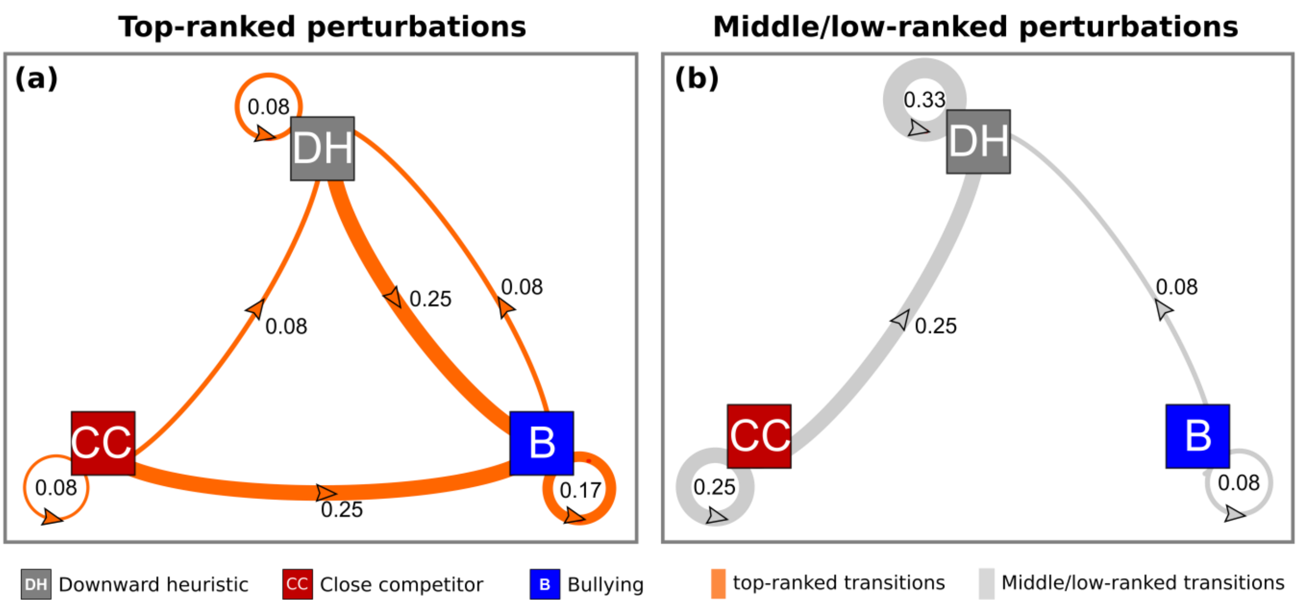


Figure 3. Perturbations of top-ranked monk parakeets resulted in more shifts than perturbations of middle/low-ranked birds. Using transition diagrams, we summarized dominance pattern transitions for both 2022 groups after perturbations (removals and reintroductions combined) of (a) top-ranked and (b) middle/low-ranked focal birds. The proportions represent the number of shifts out of the total perturbations.



Dominance pattern dynamics in the absence of experimental manipulation

To differentiate whether social dominance pattern shifts could be attributed to a general effect of the perturbations themselves, we studied the extent to which dominance patterns changed without experimentally perturbing the social structure. We found that two large captive groups (Group 2020: n = 20 and Group 2021: n = 22 birds) did not shift their dominance patterns during the observation period (SI1). The two groups differed in the dominance patterns they followed: one consistently followed a bullying pattern (Fig. SI1c) and the other a downward heuristic pattern (Fig. SI1d). Although the groups differed in dominance pattern used, neither of these social groups changed their pattern during the observation period.

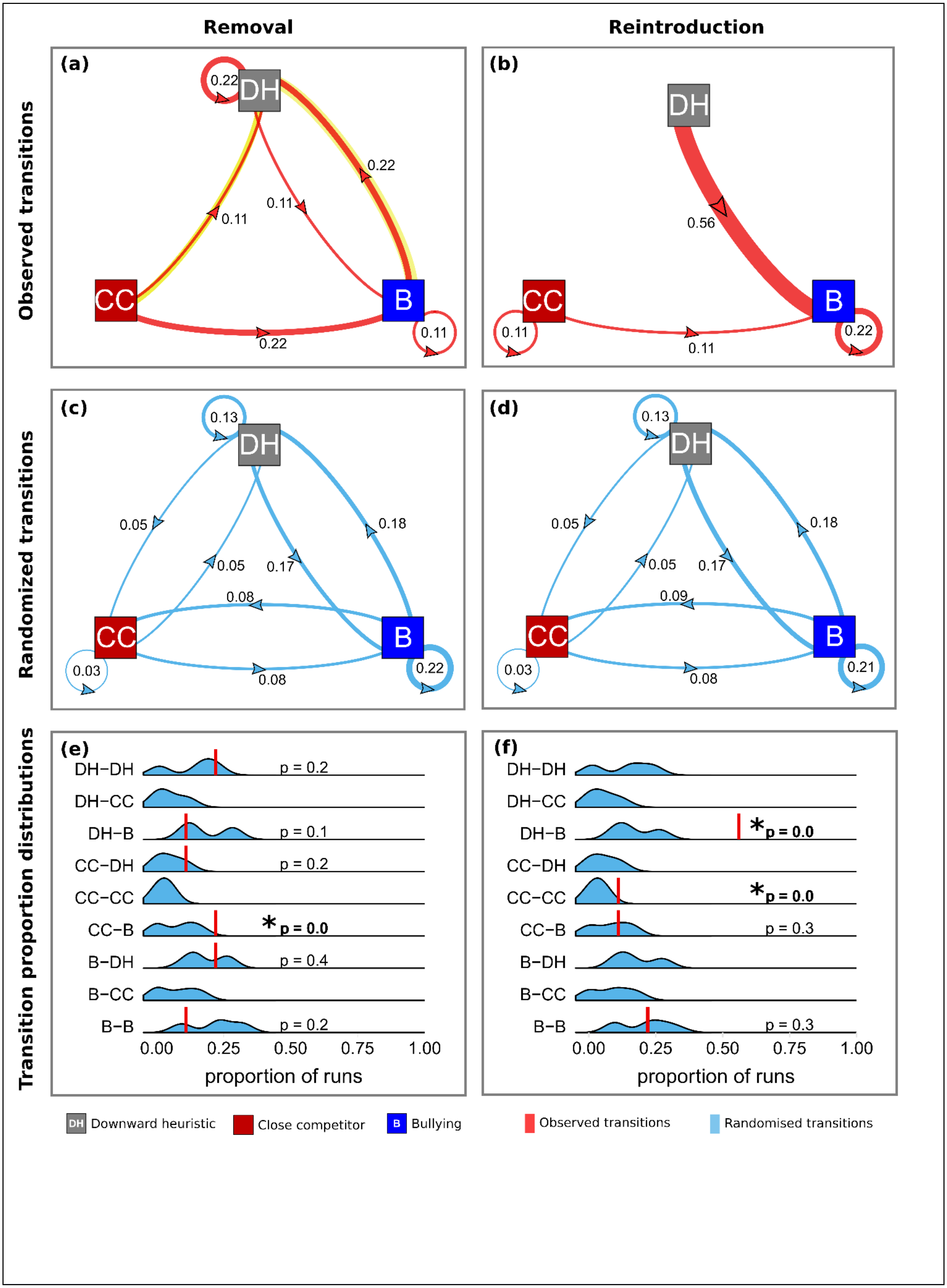
Effects of top-ranked perturbations on social dominance dynamics and shifts in patterns according to complexity

The perturbations of key individuals influence the number of dominance pattern shifts in monk parakeets (Fig. SI4). Here, we study how perturbation type, i.e., removals or reintroductions, affect dominance pattern shifts and how perturbations affect the complexity of the dominance patterns for only the top-ranked perturbations across three social groups (n = 9 trials including 9 removals and 9 reintroductions). To test whether removals and reintroductions differentially affected pattern dynamics, we compared the observed pattern transitions to a reference model where we randomized the patterns over 1000 iterations for each study group (see SI5). If the observed patterns fall outside the distribution of changes produced by the reference model which did not account for the perturbation type, then our observed results would provide evidence that the type of perturbation could be important in describing the observed shifts. In contrast, if the observed patterns fall within the reference model distribution, the observed pattern shifts could be due to random processes and not the perturbation type. Finally, we summarized the number of pattern shifts from more complex patterns to less complex patterns.

Across all top-ranked trials, we observed a similar number of shifts prior to and after removals and reintroductions (Fig. SI4). In both cases, we observed shifts in a total of 6 out of 9 trials (66.7%). However, the use of dominance patterns after removals and reintroductions differed (Fig. 4a, b). After removal, we found that in 5 out of 9 trials, the dominance pattern shifted to or remained a downward heuristic pattern (Fig. 4a). While after reintroduction, the dominance pattern shifted to or remained a bullying pattern in 8 out of 9 trials (Fig. 4b). When we compared the shifts to expectations if dominance pattern changes were randomly ordered (Fig. 4c, d), we found evidence that the shift from a close competitor to a bullying pattern happened more often than expected by chance after removal and the difference between the observed and randomized transition proportions was 0.14 (Fig. 4e). After reintroductions, we found evidence that the shift from a downward heuristic to a bullying pattern and that the pattern remained a close competitors pattern happened more often than expected by chance (Fig. 4f). The difference between the observed and randomized transition proportions for the shift from downward heuristic to bullying and from close competitors to close competitors after reintroduction, was 0.39 and 0.08, respectively. Perturbation type did not affect the number of pattern shifts but did affect what dominance pattern was used by the group after each perturbation of a top-ranked bird, where, particularly, the shift from downward heuristic to bullying upon reintroduction was significantly different from a random distribution.

Across all the 18 top-ranked perturbations, ten perturbations had a more complex pattern (close competitors and bullying) prior to the perturbation and three of those went from a more complex pattern to a less complex pattern (downward heuristic). The three predicted shifts were only observed after removals (highlights in Fig. 4a), and these were not different from a random distribution of pattern shifts (Fig. 4e). None of the shifts from complex to less complex patterns were observed after reintroductions of top-ranked individuals (Fig. 4b).

Figure 4. Effect of perturbation type on dominance pattern dynamics across all nine top-ranked perturbations. The transition proportions of the observed dominance patterns (a) after removal and (b) upon reintroduction. The yellow highlighted transitions in (a) represent where the pattern shifted from a more complex pattern (close competitor or bullying) to a less complex pattern (downward heuristic). The average transition proportions of the randomized dominance patterns across all nine trials (c) after removal and (d) upon reintroduction. The bottom panels (e and f) show the distributions of the proportion pattern changes, which is the sum of the iterations that shows a specific pattern transition divided by the 1000 reference model runs by group and by trial (e) after removal and (f) after reintroduction. The y-axis represents the number of runs out of a 1000 runs that shows the specific pattern transition in at least one of the trials. We included the proportion of reference values that was less than the observed values in bold and the proportion of reference values that were more than the observed values in black.



Removal
Reintroduction
Observed transitions
Randomized transitions
Transition proportion distributions
(a)
DH
CC
B
0.22
0.22
0.11
0.11
0.22
0.11
(b)
DH
CC
B
0.56
0.11
0.11
0.22
(c)
DH
CC
B
0.13
0.05
0.18
0.05
0.17
0.08
0.03
0.08
0.22
(d)
DH
CC
B
0.13
0.05
0.18
0.05
0.17
0.09
0.03
0.08
0.21
(e)
DH−DH p = 0.2
DH−CC
DH−B p = 0.1
CC−DH p = 0.2
CC−CC
CC−B * p = 0.0
B−DH p = 0.4
B−CC
B−B p = 0.2
0.00 0.25 0.50 0.75 1.00
proportion of runs
(f)
DH−DH
DH−CC
DH−B * p = 0.0
CC−DH
CC−CC * p = 0.0
CC−B p = 0.3
B−DH
B−CC
B−B p = 0.3
0.00 0.25 0.50 0.75 1.00
proportion of runs
DH Downward heuristic
Close competitor
B Bullying
Observed transitions
Randomised transitions

Discussion

We assessed social plasticity in captive parakeet groups by determining if groups could shift from one social dominance pattern to another, whether we could induce this shift by perturbing the group, whether the rank of the perturbed individual affected the group's responses, and whether groups shifted from information-rich to dominance patterns based on less information following a perturbation. We found that groups did shift in their use of dominance patterns, that some experimental perturbations appeared to induce these shifts, and that the rank of the perturbed bird affected both the propensity of the group to shift and which dominance pattern the group shifted to. We found no evidence that groups shifted from a more to less informationally-rich pattern following perturbations. Overall, we measured social plasticity in groups by investigating the dynamics in shifting dominance patterns. The causes of differences in social characteristics could be inferred if groups subject to experimental manipulations of environmental, ecological, or social conditions reliably induced predictable changes in social characteristics.

Existence of dominance pattern shifts within groups

Our results across multiple replicate groups provide evidence that groups of captive monk parakeets shifted between dominance patterns over time. Previous work has shown that within species, independent groups could follow different dominance patterns (1, 15). However, it was unknown whether independent groups could shift to a different dominance pattern. In our study, we documented 29 shifts in dominance patterns, with evidence for shifts within the same group from multiple groups. These results confirm that dominance patterns should not be treated as static features of a particular group. Instead, our results illustrate that social groups can change which dominance pattern they use over time.

Treating social traits as inherent to a species is based on the idea that sociality depends mostly on the phylogenetic history of a species, rather than representing an adaptive response to changing socioecological conditions (22). However, if a group can adaptively respond to changes in environmental, ecological, or social conditions, we would expect to observe variability not only across social groups of a given species, but within social groups over time. Groups that can respond to changes in conditions by altering their behavior and switching to a different dominance pattern may be more resilient to short term disruptions. This study found that monk parakeets show plasticity in social dominance pattern use. This ability may be one of the factors that have helped these parakeets become such successful invaders (23–25). For a group to transition to a different dominance pattern, the group must have a consensus as to who to direct aggression towards. For example, to switch from a downward heuristic to a bullying pattern, the bulk of individuals must switch from a target set that includes all individuals ranked below themselves to a targeting set that includes only the individuals ranked far below themselves. The ability to cohesively switch to a different pattern may require individuals to either all have a consistent switching response to changes in conditions, or for individuals to observe and conform to switching aggression exhibited by others in their group. More research is needed to determine the connections between individual aggression choices and the emerging group level social dominance patterns.

Potential drivers of dominance pattern shifts

We found that many of the group membership shifts were observed directly following an experimental perturbation. While most shifts followed perturbations, they did not exclusively occur just after a perturbation, and not all perturbations resulted in shifts. Even though not all perturbation events triggered a dominance pattern shift, the removal of top-ranked birds (key individuals) made up the majority of perturbations that triggered a shift. Although monk parakeets can be subjected to frequent changes in group compositions via fission-fusion dynamics (13), and thus expected to be robust to changes in group membership, our results suggest that perturbing just one individual in the group could drive the group to shift to a different dominance pattern. Shifts in aggression patterns and social interactions may be caused by changes in the social environment or the physical environment (26, 27). Overall, a group's response to the perturbation of a group member may be species- and context-dependent (10, 12, 28–34), where the social system and environment (e.g., resource availability (35)) may influence whether a species is resilient to a perturbation.

Different aspects of our study could have affected the results. Social networks in general represent a single time shot of dynamic social environments, where it is difficult to account for fission-fusion dynamics (but see (36)). Our experiments allowed for a 3-day snapshot of the agonistic social network but did not allow for large-scale group fission-fusion dynamics within the flight pen nor changes in the duration of the removal and reintroduction period of the focal birds. Furthermore, our experiments were all done with feral birds captured from four relatively closely located non-endemic populations in southern Florida, potentially representing genetically similar populations. More research is needed to determine whether other feral populations, stemming from independent invasion processes, or native range populations exhibit similar patterns. Non-endemic populations also tend to be smaller than wild colonies of monk parakeets in their native ranges (37). Our social groups of 20 and 11 birds may be less or more resilient than their wild counterparts that can forage in flocks of up to several hundred birds (17). Currently, we do not know how invasion status or how the size of the group affects the hierarchy structure or social dynamics, but studies of wild-caught native-range parakeets would provide an interesting comparison.

Rank effects on dominance pattern shifts

Our experiments provide insight into how the ranks of the perturbed individuals affected group responses in addition to documenting shifts in dominance patterns over time within social groups. Our groups showed a striking difference between responses to perturbations of top-ranked birds compared to middle/low-ranked birds, even though general levels of aggression remained largely stable. Rank affected both the propensity of a group to shift as well as which dominance pattern the group shifted towards. Perturbations of key (top-ranked) individuals led to more shifts in dominance patterns than perturbations of middle/low-ranked individuals, where groups were more likely to maintain their dominance pattern. This difference in propensity was strongest when we compared the rank treatment for the removal perturbations. High-ranked removals resulted in many more dominance pattern shifts than middle/low-ranked removals. The propensity to shift patterns was similar in the two rank treatments for the reintroduction phase, but the types of patterns the groups shifted to were different. Top-ranked reintroductions were significantly associated with shifts towards bullying patterns while middle/low-ranked perturbations rarely resulted in a shift to a bullying pattern.

While we found consistent evidence that the rank of the removed/reintroduced bird affected the group's responses to the perturbations, the current suite of experiments cannot determine why these differences in responses might exist. Neither does it explain how different responses might be beneficial for the functioning of the group. One potential explanation for rank effects on dominance pattern shifts is when individuals obtain benefits by maintaining or gaining rank. Interestingly, we did not observe a consistent shift towards a close competitors pattern, even though in some cases using this pattern may help individuals preserve their own ranks. For example, it might be beneficial for individuals to switch to using a close competitors pattern if the perturbation leads to conditions that are conducive to rank overthrow because a close competitors pattern could reduce the chances of rank challenges from close-ranked opponents. On the other hand, individuals may benefit from shifting to a downward heuristic pattern in times of social upheaval if aggression across all lower-ranked individuals helps re-stabilize the structure of the hierarchy, or if individuals are susceptible to rank overthrows from any lower-ranked challenger. Finally, the shift towards bullying a previously top-ranked reintroduced individual, which occurred the most in this study, may be beneficial for group members as it may be one way that members of the group could preserve their new rank status. Upon reintroduction, the remaining birds in the group could work together to suppress the ability of the formerly top-ranked bird to re-take the top rank.

Other factors might also explain the switch to bullying, such as copying other group member's behavior (38). While the birds may switch to bullying if they simply copy the target choices of their group members, we would not expect to see a strong difference between the reintroductions of top and middle/low-ranked birds. In these cases, if the reintroduced bird happened to suffer initial aggression from one or a few group members on its return, and then these targeting decisions were copied by group members, we would expect to see a switch to bullying in both rank-based perturbations. Our observed results contradict simple copying of aggressive targets because we did see a difference between how top and middle/low-ranked birds were targeted following their reintroductions.

A switch to bullying can also occur if individuals use aggression to signal dominance to potential opponents observing aggression (39) or to deter potential opponents from aggressing (40). Previous work with the parakeets has provided strong evidence that the parakeets remember the identities of opponents, outcomes of their own fights, and the opponents and outcomes of others (41) and that rank in these groups appears to be an outcome of social history in the groups (16). Thus, there is a potential basis for thinking of aggression and bullying in these parakeets as a signaling system rather than being solely an outcome of competition for resources. Other work also found evidence that bullying may be involved in information transfer. For example, captive common waxbills (*Estrilda astrild*) show a bullying pattern particularly when the audience consists of waxbills that were not close associates of the aggressors (39). Also, in paper wasps (*Polistes dominulus*) aggression functions as a deterrent signal, where wasps can use short term social history and memory for aggressive decision-making (40). Thus, bullying may be a method for individuals to signal their rank to uninformed individuals or potential opponents.

Social information complexity and dominance pattern shifts

Although we predicted that perturbations would lead to a switch to a less informationally-rich dominance pattern, we did not observe this pattern. What we saw instead was that the groups most strongly affected by perturbations, where we removed and reintroduced top-ranked birds, frequently shifted to a bullying pattern.

One reason our information complexity results did not match our predictions is that the perturbations may not have destroyed the existing information in the group, allowing the group to use a more complex pattern. Alternatively, the patterns that we described as more informationally rich may not actually be more cognitively complex for the parakeets to use. For example, parakeets could use a much simpler heuristic of "attack the most-attacked bird", rather than disentangling their own ranks and the ranks of others in their hierarchy. Whether the birds used a cognitive shortcut or the more cognitively complex process, these could both lead to the expression of a bullying dominance pattern. Our results highlight the need for further research into the connections between information and cognition in social species.

Conclusions

Using social perturbation experiments, we characterized the ways monk parakeets used aggression within hierarchies and identified how, and potentially why, these dominance patterns change over time. Our approach has shed light on how resilient social networks may be as well as how animals use social information in aggressive decision-making to cope with dynamic social environments. Many animals are faced with an increasing number of threats, such as those associated with urbanization and climate change, which can change their socioecological environment (26, 27). Social plasticity may be one way to cope with changing environments. Evidence for social plasticity across taxa includes intraspecific variability in social organization (42–46), alternative reproductive strategies (47), or behavioral variation within groups, for instance, due to habitat complexity (48, 49) or group composition (50). We now also described social plasticity in social dominance patterns.

Methods

We observed four captive groups of monk parakeets at the United States Department of Agriculture, Wildlife Services, National Wildlife Research Center (USDA WS NWRC), in Gainesville, Florida. The four groups differed in group size, size of the flight pen, tenure in captivity, the time of year we observed the groups, and the experimental conditions. We first provide the methods that are the same across the study and then we provide the methods that differ from one another for each research question. We performed all analyses in R version 4.1.2 (51) and created the figures using ggplot2 (52), diagram (53), and ggridges (54).

Social interaction data collection

Multiple observers (3-4 observers) performed daily observations approximately between 08:00 and 19:00 from different blinds. The observers recorded agonistic dyadic interactions using all-occurrence sampling (55) using the Animal Observer application (Diane Fossey Gorilla Fund v1.0, (56)). Observers identified the birds using a unique body color combination made with nontoxic permanent markers (Sharpie, Inc.®) (57). The recorded agonistic interactions included crowds (the aggressor approaches a target, but the target moves away before the aggressor is in striking range) and displacements (the aggressor aggressively approached another bird within striking range and supplanted it from its location). We used a previously described framework to ascertain that crowds and displacements were functionally similar and thus part of the same behavioral context (15). We combined crowds and displacements for further analyses, removed duplicate observations, and retained the interactions were both the actor and the receiver were identified (see for details (16)).

Social dominance pattern analysis

We used agonistic interaction events binned across three days of observations to assess the dominance patterns. We used the function *domstruc* from the 'Domstruc' package (58) to calculate the global dominance patterns (1). We calculated 1) focus, which measures the distribution of the relative rank difference between the aggressor and the receiver, and 2) position, which reflects where aggression is most focused relative to the aggressor's rank to derive dominance patterns using a reference model. This reference model is created using the observed aggression data frame and the outcome of this reference model is always a downward heuristic pattern, where higher-ranking individuals aggress against any lower-ranking individuals. If the group follows a downward heuristic pattern, the observed pattern will be the same as the pattern from the reference model.

The group directs aggression differently if the observed dominance pattern deviates from the reference model, where the group could either follow a bullying or close competitor pattern.

Do dominance patterns shift due to the perturbation of a top-ranked bird?

To answer whether the removal and reintroduction of a top-ranked bird could change the dominance patterns, we observed the same social group of 20 birds that was already present in the large flight pen for 31 days (see above, Table SI1.2). We performed the perturbation experiment from May until July 2021. In total, we observed 23,076 agonistic interactions recorded over 255.5 hours and 940.3 person hours in 37 days, with an average of 21.3 ± 2.3 (SD) hours of observation per three-day bin (n = 12 bins). We started the perturbation experiment after the birds interacted for 31 days in the flight pen. To start our experiment, we calculated the dominance rank of all group members using agonistic interaction events where there were clear winners and losers binned across three days of observations prior to removals and a modified version of PageRank, called power, using the 'Domstruc' package (1, 16, 58). Only one of the observers (AM) performed the dominance rank analyses, the other observers were blind to the standing of the remaining group members in the dominance hierarchy.

We performed removal/reintroduction trials of three top-ranked birds. To remove the top-ranked bird, we caught all birds in the morning using mist nets and removed the top-ranked bird (the focal). We placed the focal back in its standard housing cage (2 x 2m wire cage). The focal bird was by itself in the housing cage but this cage was positioned in larger housing with other parakeets away from the experimental group in the flight pen. We then released the remaining birds back into the flight pen. We allowed the birds (n = 19) to interact undisturbed for eight days which is sufficient time for the social structure to restabilize (57). We reintroduced the removed bird at the same time (8:30) and location each time after the 8-day removal period. We then allowed the birds (n = 20) to interact for another eight days and used the agonistic interactions binned across the three days of observations prior to the next removal to identify the top-ranked individual for the next trial (Table SI1.2).

What is the response to perturbations of differently ranked birds?

Prior to the start of the field season in 2022, we randomized the top-ranked and middle/low-ranked trials. From January through May 2022, we performed the perturbation experiments in two groups of eleven monk parakeets that were caught from feral populations in 2021 (see above, Table SI1.3) and consisted of birds previously (n = 14 birds) and not previously (n = 8 birds) used in our 2021 experiment. Four observers monitored the groups from different blinds in two 10 x 4.5 x 3m flight pens. Two observers focused on one social group each day and the observers were randomly assigned to one of the four blinds. In total, we observed 42,280 agonistic interactions in group 1 across 458.5 hours and 793.9 person hours in 77 days, with an average of 17.6 ± 3.2 (SD) hours of observation per three-day bin (n = 26 bins). In group 2, we observed a total of 42,403 agonistic interactions across 464.4 hours and 771 person hours in 78 days, with an average of 17.9 ± 3.7 (SD) hours of observation per three-day bin (n = 26 bins). We allowed the birds to interact for 8 days prior to first removal for the dominance hierarchy to stabilize (57). We followed the same experimental methods and timeline as in 2021 for our 8-day removal and 8-day reintroduction trials.

We described the most dominant pattern shift as we were not able to perform mantel correlations on our observed dataset to test whether the pattern transitions were the same for top-ranked and middle/low-ranked trials because of small sample size. We included the results by removal and reintroduction in SI2. We then summarized the dominance pattern transitions across all trials and social groups to show the general patterns of the social manipulation experiment (for results see SI3).

Do dominance patterns shift without experimental manipulation?

To answer whether dominance patterns shift when group composition was not perturbed, we performed behavioral observations of one captive social group from March until April 2020 and another captive group from March until April 2021 (Table SI1.1). Both groups were introduced into a large 45 x 45 m flight pen. This analysis does not involve the 2022 groups as we only performed experimental perturbations with the 2022 groups.

In 2020, we observed a group of 20 monk parakeets that were long-term captives. USDA personnel captured these birds from four different feral populations in Southern Florida in 2003, 2007, and 2012. Three of the 20 parakeets were hatched in captivity in 2006 and 2007 at the USDA WS NWRC facility. We observed a total of 3,148 agonistic interactions across 61.4 hours and 191.3 person hours across 12 days, with an average of 20.5 ± 3.6 (SD) hours of observation per three-day bin (n = 3 bins). The observation period was much shorter than planned due to disruptions from the COVID-19 pandemic, which required us to drastically truncate our field season.

In 2021, we observed a group of 22 monk parakeets captured from four feral populations in Southern Florida in February 2021 just prior the experiment. We observed a total of 18,858 observations across 220.9 hours and 832.8 person hours across 31 days, with an average of 22.1 ± 2.4 (SD) hours of observation per three-day bin (n = 10 bins). We allowed the group to interact to stabilize their dominance hierarchy prior to our perturbation experiment. This initial stabilization period lasted 31 days as we incurred unplanned perturbations. First, there was a thunderstorm that resulted in some injured birds. During our first capture event, we had to remove two injured birds (both lower-ranked) so that they could receive professional care. The third perturbation was a partner switch of the most dominant bird which caused the dominance hierarchy to destabilize. We considered that these events occurred during periods of unchanging group composition as these were not part of our planned perturbation experiment.

What are the perturbation type effects on social dominance pattern dynamics and pattern complexity?

To study the general patterns of how the groups respond to perturbation type (removals and reintroductions), we combined the top-ranked trials across three social groups (2021-group and the two 2022-groups), resulting in 9 removals and 9 reintroductions. We analyzed whether the observed pattern transitions prior and after the perturbations were different from random (see SI4 for the conceptual figure). First, we randomized the order of the observed dominance patterns 1000 times (Fig. SI4 *step 1*). We then quantified the number of times the pattern remained the same or transitioned to another pattern across all 1000 reference models comparing the 3-day periods before and after for both removal and reintroduction for each perturbation separately (Fig. SI4 *step 2a*). We calculated the proportion of randomized pattern transitions and averaged these across the perturbations, which we then visualized. Next, per reference model run, we summarized the number of perturbations that showed a particular dominance pattern change. We included all nine possible pattern changes per run and calculated the proportion of pattern changes per run across all perturbations. We visualized this reference distribution and included the observed pattern changes (Fig. SI4 *step 2b*). If the observed value falls outside the reference model distribution, this tells us that the observed change is unusual and is due to the perturbation. We determined whether observed values significantly differ from random values in the reference models using the proportion of random values that are less than the observed values. We used 2-tailed tests: observed values needed to be <0.025 or >0.975 of values produced by the reference model to be considered significantly different.

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Data accessibility

All data have been deposited at https://github.com/annemarievdmarel/Monk_dompattern, van der Marel & Hobson, 2022).

Ethics

The University of Cincinnati IACUC protocol (#AM02-19-11-19-01) and the National Wildlife Research Center Quality Assurance (#3203) approved all animal-related activities.

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