Social manipulations trigger shifts in group-level dominance patterns

Annemarie van der Marel[1,2,3], Xavier Francis[1], Claire L. O'Connell[1], Cesar O. Estien[1,4,5], Chelsea Carminito[1], V. Darby Moore[1], Elizabeth A. Hobson[1]

corresponding author: Annemarie van der Marel, email: avdmarel@outlook.com

[1] Department of Biological Sciences, University of Cincinnati, Cincinnati, OH, USA

[2] Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

[3] Instituto de Ecología y Biodiversidad (IEB), Santiago, Chile

[4] Department of Environmental Science, Policy, and Management, University of California–Berkeley, Berkeley, CA, USA

[5] Second Nature Ecology & Design LLC

Author Contributions:

- Conceptualization: EAH, AM
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Abstract

Within dynamic social systems, individuals are expected to change how they interact with each other over time. This social plasticity is critical to understand in groups with dominance hierarchies, where changes in aggression patterns could alter the characteristics of the hierarchy. However, whether changes in individual aggression decisions can alter characteristics of group-level dominance structures, and what factors might lead to these changes, are not well understood. To investigate factors affecting dominance patterns, we experimentally manipulated captive groups of monk parakeets (*Myiopsitta monachus*) using targeted perturbations to cause social instability through rank-based removals and reintroductions of group members. We found that 1) dominance patterns remained stable when no experimental perturbations occurred, 2) dominance patterns often shifted after experimental perturbations, and 3) the rank of the perturbed individual affected the propensity and types of group-level aggression changes. We showed that removals and especially reintroductions of top-ranked birds had group-level consequences on hierarchical organization. Determining what factors influence social dynamics, such as group-level dominance patterns, can help us understand how animals respond to changing social environments. Predicting the effects of disturbances and identifying network resilience may allow us to prevent future instability from emerging and reduce potential costs upon system collapses.

Introduction

Social systems are inherently dynamic: individuals join or leave groups, relationships between individuals form or weaken, and social networks re-wire (1–5). This shifting social landscape requires individuals to be socially plastic and able to modify their behavior in response to changing social dynamics (6). The ability to respond to changes in socioecological environments, or social plasticity, is likely crucial for navigating complex sociality, especially in groups structured by aggression and dominance hierarchies (7, 8).

Within a group's dominance hierarchy, an individual's decisions about how to direct aggression can be based on their own rank and the rank of potential opponents, especially in cases where rank in the hierarchy is based on the social history of interactions (9, 10), rather than simpler systems structured mainly by individual characteristics (11–13). When there is consensus among group members on who to aggress, a within-group aggression pattern (social dominance pattern) can emerge. Recent work identified three such patterns: 1) *downward heuristic* (aggress towards any ranked lower than self), 2) *close competitors* (preferentially attack those ranked slightly lower than self), and 3) *bullying* (preferentially attack those ranked much lower than self) (7). These patterns were found across myriad animal species, with no evidence that any of these patterns were phylogenetically restricted (7). However, this work also showed that dominance patterns could differ within species (7). Because this work focused on stable hierarchies and did not measure the dynamics of aggression over time, it could not determine whether a particular group could change its dominance pattern over time, or what factors might alter aggression preferences and induce shifts in the emergent group-level dominance patterns. Understanding the conditions under which groups might change dominance patterns would provide insight into the social plasticity of structured aggression.

We performed social perturbation experiments in which an individual was removed from a stable social group, the group was allowed to restabilize, and the removed individual was reintroduced after the re-stabilization period. Within four captive groups of monk parakeets (*Myiopsitta monachus*), we tested whether the perturbations of single individuals that differed in their social role (dominance rank) would 1) change individual aggression decision-making and 2) trigger dominance pattern shifts. Monk parakeets are well-suited for studying social dynamics as they are a highly social parrot that readily forms dominance hierarchies in captivity (10, 14–16), can develop and follow different dominance patterns (7, 16), and exhibits high fission-fusion dynamics in both wild and captive populations (14).

First, we hypothesized that if aggression dynamics and dominance patterns are plastic, our perturbations would result in individuals shifting their aggression to different subjects and social groups changing dominance patterns. Second, we hypothesized that social role (top-ranked or middle/low-ranked) and perturbation type (removals or reintroductions) are possible drivers inducing changes in aggression dynamics and dominance patterns. We predicted that the perturbation of top-ranked individuals would lead to more changes in aggression, dominance patterns and number of pattern shifts compared to middle/low-ranked perturbations. We predicted that perturbation of top-ranked individuals would have a greater impact because we considered these individuals as ‘key’ individuals, which have significant impact on social dynamics (17). We also predicted that top-ranked removals would cause dominance pattern shifts, as the sudden absence of a key individual allows or force remaining members to update their rank. In contrast, we predicted that reintroductions would not result in pattern shifts, because the whole group would update their ranks, except for the reintroduced bird, and would not change their aggression decisions.

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, Figure 1). We binned these aggressive events into 3-day assessment periods. For each 3-day period, we used observations of directional aggression where there were clear winners and losers, determined each individual’s continuous power score within the group using a network-based ranking algorithm, summarized individual aggression decisions, and categorized the social dominance pattern of the group using a rank-based reference model (7).

Aggression summary

We observed many agonistic interactions in all four social groups (Fig. 1). Across group 2020 (Fig. 1a) and group 2021 non-experimental phase (Fig. 1b), where we did not experimentally perturb the social groups, the rate of aggression controlled for hours observed and group size remained relatively stable. In 2021, we also performed three 17-day trials of top-ranked birds (from period 11 onward). The removals and reintroductions of these individuals did not markedly affect overall aggression in the 2021 experimental phase (Fig. 1b). In 2022, we performed six 17-day trials, replicated in two groups, where we removed and reintroduced three top-ranked and three middle/low-ranked individuals (i.e., focal birds). The group’s aggression level in the 2022 groups remained relatively stable following perturbations of both top-ranked and middle/low-ranked birds (Fig. 1c, 1d). The aggression rate was higher in the two smaller groups in 2022 compared to the larger groups we observed in 2020 and 2021 (Likelihood ratio (LR) test: $\lambda = 10.62$, $p = 0.001$; Fig. 1).

Changes in aggression dynamics and dominance pattern shifts

We highlighted the change in the direction of aggression toward focal birds and remaining group members using aggression networks (SI2, Fig. 2a) and individual aggression balance (i.e., aggression given/aggression given + received, SI3). The aggression networks showed that the identity of the target of aggression changed during our perturbation experiment and that focal birds went from an aggression balance value closer to 1 (only aggress) before removal to a value closer to 0 (only receive aggression) upon reintroduction (SI2, SI3). We then analyzed the absolute change in aggression balance between the periods before removal and upon reintroduction across the experimental groups. We found that focal birds showed a much greater absolute change in aggression balance (mean ± SE = 0.58 ± 0.10, range [0.005-0.99], n = 15 birds) than the remaining group members (0.17 ± 0.01, [0.0002–0.82], n = 117 birds); LR test: $\lambda = 59.4$, $P < 0.001$). Birds (both focal birds and group members) in top-ranked trials (0.26 ± 0.02, [0.001-0.99], n = 126) showed a greater change in aggression balance than birds in middle/low-ranked trials (0.09 ± 0.02, [0.0002-0.48], n = 66; LR test: $\lambda = 81.8$, $P < 0.001$). Lastly, we found a significant interaction effect between focal rank (top- or middle/low-ranked) and subject (focal or remaining group member, LR test: $\lambda = 25.3$, $P < 0.001$; Fig. 2b). Top-ranked focal birds showed a greater change in aggression balance than group members from middle/low-ranked trials while middle/low-ranked focal birds showed a similar change in aggression balance to group members from top-ranked trials.

To ascertain if the group responded differently to individual birds compared to its rank, we compared the total number of agonistic interactions received between the focal birds upon reintroduction and similar ranked birds prior to the focal's reintroduction. We found that the rank of the focal bird resulted in different aggression responses. Focal birds received more aggression (mean ± SE = 533.2 ± 83.9, range [143-1110], n=15) than similarly ranked birds (218.4 ± 38.7, [90-640], n=15; LR test: $\lambda = 15.65$, $P < 0.001$; Fig. 2c). We also observed more agonistic interactions overall during top-ranked trials (461.6 ± 81.0, [96-1110], n=18) compared to middle/low-ranked trials (247.1 ± 38.9, [90-478], n=12; LR test: $\lambda = 7.65$, $P = 0.02$; Fig. 2c). We found no interaction effect for received aggression between the rank of the focal birds and the subject (LR test: $\lambda = 1.99$, $P = 0.16$; Fig. 2c). Focal birds and similar ranking birds received aggression from a similar number of distinct birds (proportion controlled for by group size, mean ± SE = 0.82 ± 0.02, [0.6-0.95], n = 30; SI4). Most of the group members aggressed against focal birds and similar ranking birds.

Across the groups, we detected all three social dominance patterns during the 77 assessment periods. The most common pattern was the downward heuristic (45%, attack any individual lower-ranked than self), followed by the bullying pattern (33%, preferentially attack much lower-ranked individuals), and the close competitors pattern (22%, attack slightly lower-ranked individuals; see Table 1). When we did not experimentally perturb the social groups, we found that groups 2020 and 2021 non-experimental phase did not shift their dominance patterns during the observation period. The two groups differed in the dominance patterns they followed (Table 1): one consistently followed a bullying pattern (Fig. 3a) and the other a downward heuristic pattern (Fig. 3b until period 10). When we performed our perturbation experiments, we detected a total of six dominance pattern shifts in our 2021 experimental phase. The group followed a bullying pattern in 50% of the assessment periods and the downward heuristic pattern in the other half of the assessment periods (Table 1). Four of the six shifts occurred directly following a perturbation (Fig. 3b). We found that dominance patterns in our two 2022 groups also changed over time. Both groups switched between all three possible dominance patterns but exhibited different propensities to follow each dominance pattern (Table 1, Fig. 3c,d). We detected a total of ten dominance pattern shifts in group 2022-1 and five of those occurred directly following a perturbation. In group 2022-2, we detected 14 shifts of which seven occurred directly following a perturbation.

Social role and perturbation type drive pattern shifts

The focal bird’s rank affected the social dominance patterns in the 2022 groups. 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 5 out of 6 shifts after top-ranked perturbations and 2 out of 6 shifts after middle/low-ranked perturbations. Across both groups combined, we found that top-ranked perturbations resulted in dominance pattern shifts in 67% of a total of 12 perturbations compared to shifts in 33% middle/low-ranked perturbations (Fig. 4). When we analysed how directed aggression at the group-level changed by rank, we found that the groups switched to or kept a bullying pattern in 8 out of 12 (67%) top-ranked perturbations (Fig. 4a). 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 67% of trials; Fig. 4b). We included the results by rank and perturbation type in Supplemental Information 5 (Fig. SI5) and summarized the dominance pattern transitions across all trials and social groups (Fig. SI6). As top-ranked perturbations resulted in more social upheaval (i.e., most pattern shifts, Fig. 4, SI5 and SI6), we focused on these trials to study how top-ranked perturbations affected the dominance patterns dynamics.

To test whether top-ranked removals and reintroductions differentially affected pattern dynamics, we quantified the observed number of shifts across the three experimental social groups. We then compared these observed pattern transitions to a reference model where we randomized the patterns over 1000 iterations per group (see methods and SI7). Across all top-ranked trials, we observed a similar number of shifts prior to and after removals and reintroductions (Fig. SI6). In both cases, we observed shifts in a total of 6 out of 9 trials (67%). However, the use of dominance patterns after removals and reintroductions differed (Fig. 5a, b). After removal, we found that in 5 out of 9 trials, the dominance pattern shifted to or remained a downward heuristic pattern (Fig. 5a). After reintroduction, the dominance pattern shifted to or remained a bullying pattern in 8 out of 9 trials (Fig. 5b). When we compared the shifts to expectations if dominance pattern changes were randomly ordered (Fig. 5c, 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. 5e). 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. 5f). 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.

Discussion

We assessed social plasticity in captive parakeet groups by determining if 1) individual aggression decisions and dominance patterns changed over time within social groups, 2) we could induce these changes using social perturbation experiments, and 3) rank of the removed/replaced focal bird resulted in different changes in social dominance. We found that individual aggression decisions could change over time and groups could shift their dominance patterns, and these changes were associated with our experimental perturbations. For example, the amount of aggression received by top-ranked focal birds upon reintroduction was much higher compared to the amount of aggression received by middle/low-ranked birds upon reintroduction and compared to similarly ranked birds prior to reintroduction of the focal bird. These findings are in line with previous results showing that rank determinants in monk parakeets are more based on the history of social interactions than on individual characteristics (10, 18). Additionally, we found that the rank of the perturbed bird affected both the propensity of the group to shift patterns and the pattern the group shifted to. In contrast to one of our predictions, we found that the number of pattern shifts were the same after removals and reintroductions, but that reintroductions resulted in different social dominance pattern use compared to removals. Our results highlight that groups subjected to experimental manipulations of social conditions led to predictable changes in aggression dynamics.

Our results across multiple replicate groups provide evidence that monk parakeet groups shifted between dominance patterns over time. We documented 29 shifts in dominance patterns, with evidence for shifts within the same group from multiple groups. These results confirm that dominance patterns are plastic features of a social group. 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 (19). However, if a group can adaptively respond to changes in socioecological 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 (20–22).

We found that many of the dominance pattern shifts were observed directly following a change in group composition. While most shifts followed perturbations, they did not exclusively occur after a perturbation, and not all perturbations resulted in shifts. Although monk parakeets can be subjected to frequent changes in group compositions via fission-fusion dynamics (14), and thus expected to be robust to group membership changes, our results suggest that perturbing just one individual in the group could drive the group to shift to a different pattern. Overall, a group's response to the perturbation of a group member may be species- and context-dependent (23–31), where the social system and environment (e.g., resource availability (32)) may influence whether a species is resilient to a perturbation.

Our experiments provide insight into how the ranks of the perturbed individuals and perturbation type affected group responses. Even though not all perturbation events triggered a dominance pattern shift, the perturbations of top-ranked birds (key individuals) made up most perturbations that triggered a shift. Other animal groups are also susceptible to perturbations of top-ranked individuals (23, 24, 27, 29, 32). For example, in pig-tailed macaques (*Macaca nemestrina*), key individuals manage conflict within groups and their removal results in overall destabilization of the social structure (23, 27). Similarly, targeted removals of key individuals compared to random individuals in killer whale (*Orcinus orca*) networks resulted in fragmented groups, which disrupts social structure and potentially threatens population viability (24). In our monk parakeet groups, the perturbation of key individuals affected individual aggression decisions, the propensity of a group to shift as well as which dominance pattern the group shifted towards.

In contrast to our prediction that removals would result in pattern shifts but not reintroductions, we found a similar number of shifts after removals and reintroductions. This finding suggests that both perturbation types break the group's information and either force, or allow the opportunity for, the remaining group members to update their rank. Shifts in dominance patterns after key individual removal may suggest there is a vacuum and remaining groups members change their aggression to seize the opportunity to update their rank (33). Perhaps during the reintroduction, social history of past interactions is still important and the group members want to keep their updated rank and do not want to lose it again to the reintroduced bird (10). While removal of individuals from the group has been extensively studied (23–26, 28–31, 34), the introduction of new individuals through birth and immigration or the return of absent group members has received less attention as these processes in wild populations are harder to follow (but see (26, 35). Our study now highlights that particularly the reintroduction of individuals has group-level consequences on hierarchical organization and dominance patterns and has the potential to destabilize social structure.

While we found consistent evidence that the rank of the perturbed bird affected the group's responses, the current suite of experiments cannot determine why these differences in responses might exist. Neither can they explain how different responses might be beneficial for the functioning of the group. One potential explanation for groups to shift patterns 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 using this pattern may help individuals preserve their own ranks. For example, it might be beneficial for individuals to switch to a close competitors pattern if the perturbation leads to conditions that are conducive to rank overthrow because this pattern could reduce the chances of rank challenges from close-ranked opponents. Alternatively, 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.

The shifts towards bullying a previously top-ranked reintroduced individual, which occurred the most in this study, may be beneficial for group members as it may allow group members to 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 (36). Our results contradict simple copying of aggressive targets because we observed 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 (37) or to deter potential opponents from aggressing (38). Previous work with monk 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 (18) and that rank in these groups appears to be an outcome of social history in the groups (10). 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 found 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 (37). 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 (38). Thus, bullying may be a method for individuals to signal their rank to uninformed individuals or potential opponents.

Using social perturbation experiments, we provide evidence that monk parakeets show social plasticity in structured aggression in response to changing social environments. Our results showed that individuals adjusted their aggression decisions, 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. Many animal species face changes in the social and physical environment through both internal and external factors, such as naturally occurring demographic processes or through threats associated with urbanization and climate change (5, 39, 40). Social plasticity may be one way for species to show resiliency to changing environments (20, 21).

Tables and Figures

Table 1. Summary of the social dominance patterns across four social groups of captive monk parakeets. We show the dominance pattern distribution in % and the number of transitions after removals, reintroductions, and between perturbations during the stabilization period.

Group	Total 3-day periods	Downward heuristic	Close competitor	Bullying	No. shifts after removals	No. shifts after reintroductions	No. shifts after perturbation	No. shifts without perturbation
2020 (non-experimental group)	3	-	-	100%	-	-	-	0
2021 non-experimental phase	10	100%	-	-	-	-	-	0
2021 experimental phase	12	50%	-	50%	1	3	4	0
2022-1 (experimental group 1)	26	34.6%	42.3%	23.1%	3	2	5	5
2022-2 (experimental group 2)	26	38.5%	23.0%	38.5%	3	4	7	7
Total	**77**	**45.5%**	**22.1%**	**32.5%**	**7**	**9**	**16**	**13**

Figure 1. Aggression rate remained relatively stable for each social group. Each panel represents a different social group and shows the rate of directed aggression controlled for hours observed and group size (see Table inset) with the overall mean aggression rate (for panels (a) and (b) in grey, and for panel (c) horizontal dashed lines). Vertical lines indicate the timing of nonexperimental perturbations (dotted lines), and the experimental perturbations for removals (dashed lines) and reintroductions (solid lines). Note the different y-axis scale for panels a and b compared to panel c.

Group	2020	2021 non-experimental phase	2021 experimental phase	2022-1	2022-2
Agonistic interactions	3,148	18,858	23,076	42,280	42,403
Hours observed	61.4	220.9	255.5	458.5	464.4
Group size	20	22/20	20	11	11
Mean ± SE aggression rate	2.42 ± 0.09	4.02 ± 0.29	4.59 ± 0.24	8.83 ± 0.58	9.01 ± 0.67

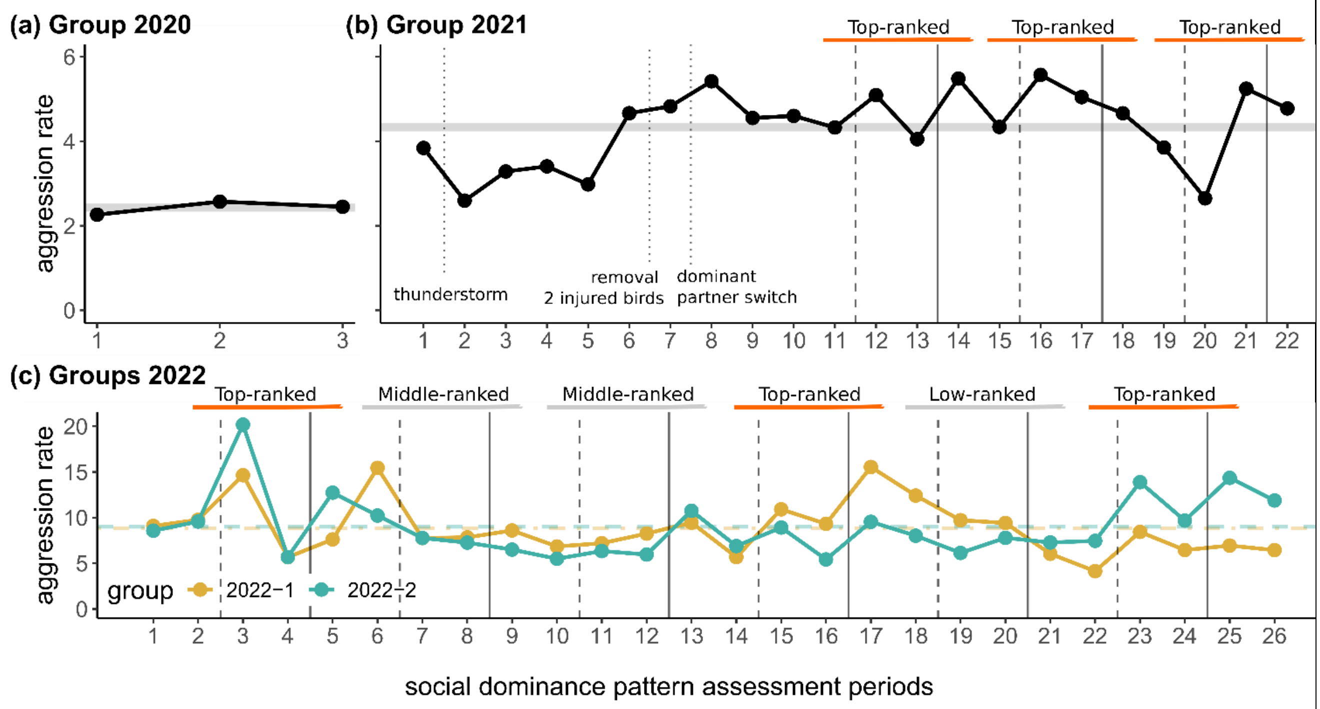


Figure 2. Aggression summary after perturbation experiments in captive monk parakeets. In panel (a) we show the aggression network for the first experimental trial in Group 2021. The nodes are ordered by their respective power score with higher ranking birds closer to 1. The focal bird is highlighted in blue. The edge width represents the total number of agonistic events between two individuals. The blue edges represent the rule-followers (higher-ranking birds aggress against lower-ranking birds), and the red edges represent the rule-breakers (lower-ranking birds aggress against higher-ranking birds). Panel (b) shows the change in absolute aggression balance for the experimental groups, where we perturbed top-ranked or middle/low-ranked birds. We calculated the change in the aggression balance upon reintroduction minus the aggression balance before removal. We included the three social groups where we performed experimental perturbations. Panel (c) reports the total number of aggressive events toward the focal birds during the assessment period upon reintroduction and toward the similar ranked bird in the assessment period prior to reintroduction of the focal bird.

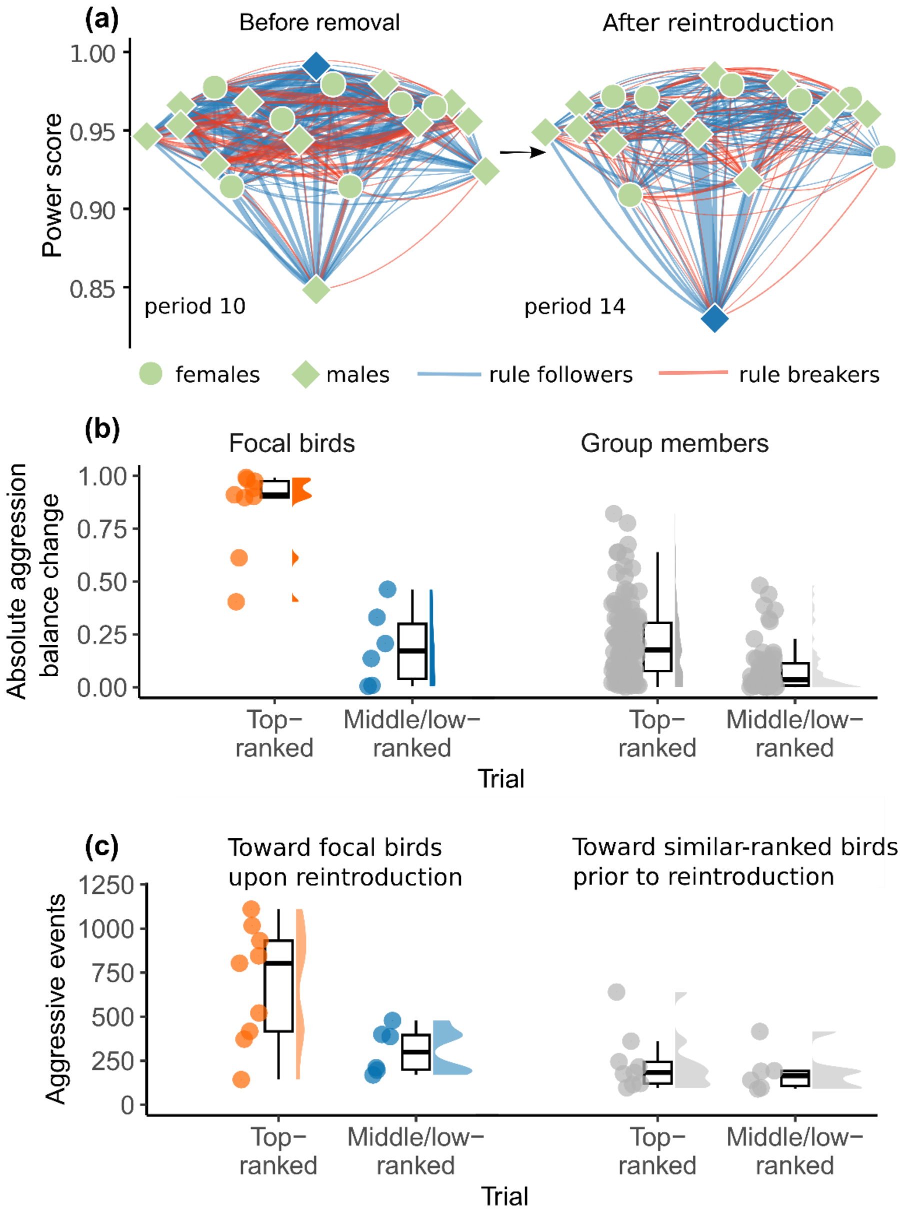


Figure 3. Dominance patterns primarily changed over time when group composition was experimentally perturbed. Each panel represents a different social group with the dominance patterns for each assessment period. The dotted lines in panel (b) represent nonexperimental perturbations (a thunderstorm, removal of 2 injured birds, and finally a dominant partner switch). 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. The total number of observed pattern shifts across total assessment periods is included.

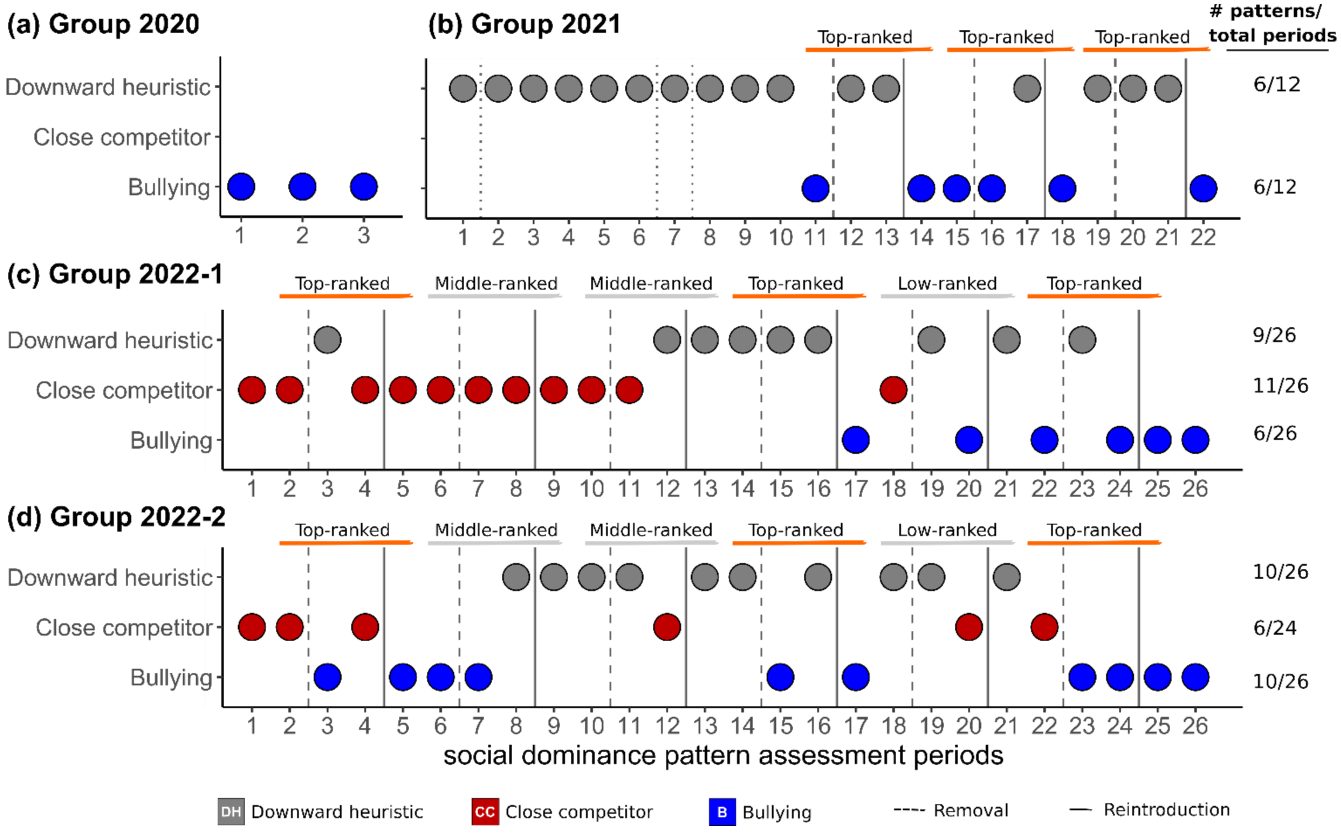


Figure 4. Perturbations of top-ranked monk parakeets resulted in more shifts than perturbations of middle/low-ranked birds. Using transition diagrams, we summarized dominance pattern transitions for both 2022 groups after perturbations (removals and reintroductions combined) of (a) top-ranked and (b) middle/low-ranked focal birds. The proportions represent the number of shifts out of the total perturbations.

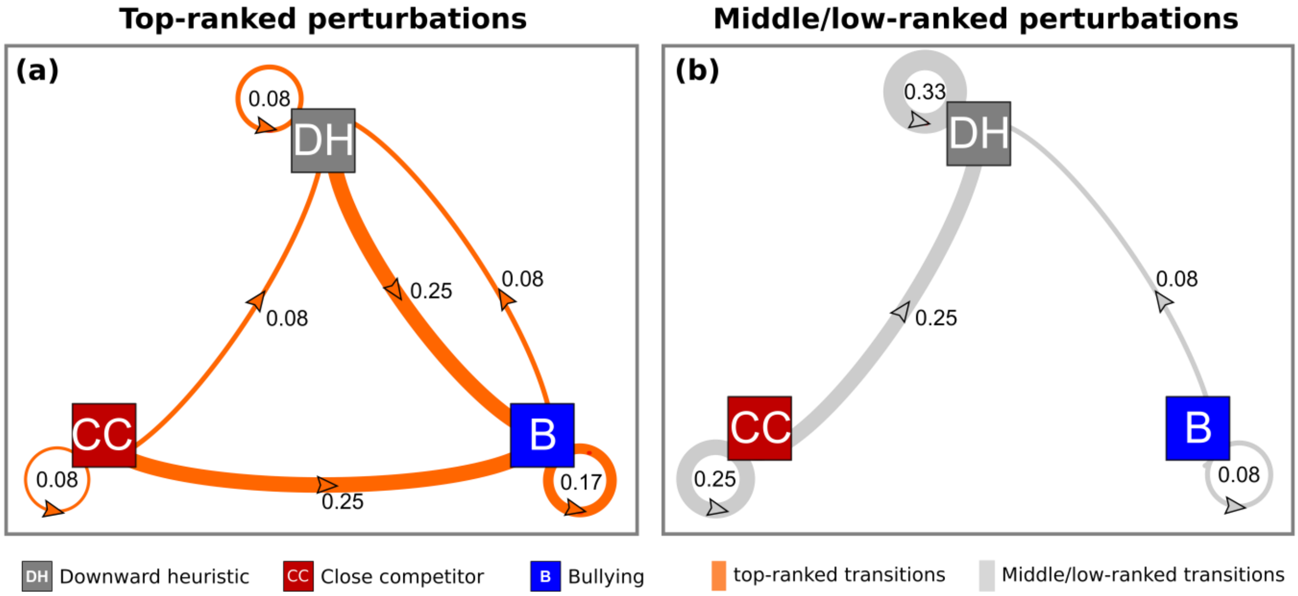
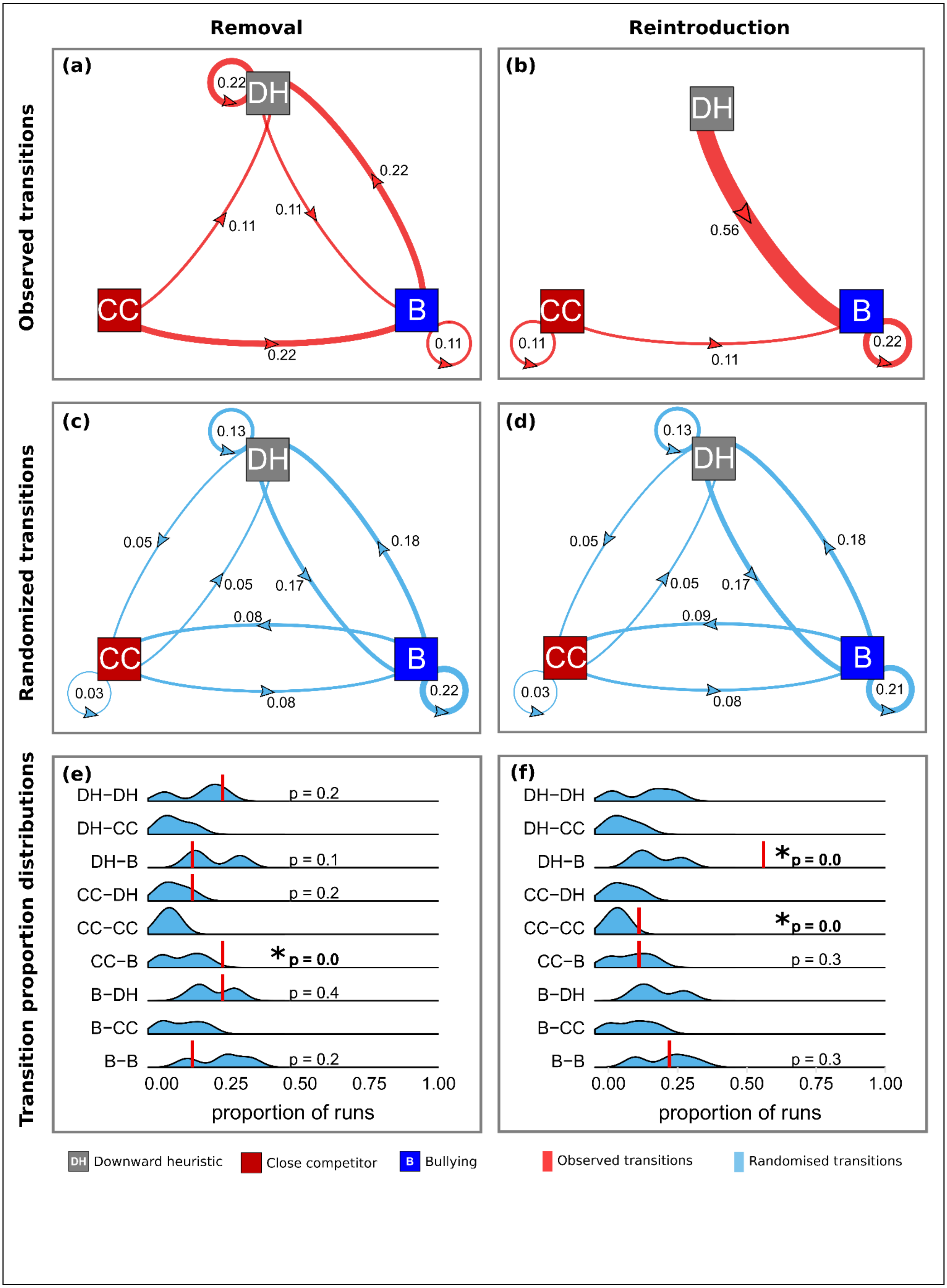


Figure 5. Effect of perturbation type on dominance pattern dynamics across all nine top-ranked perturbations. The transition proportions of the observed dominance patterns (a) after removal and (b) upon reintroduction. The average transition proportions of the randomized dominance patterns across all nine trials (c) after removal and (d) upon reintroduction. The bottom panels show the distributions of the proportion pattern changes (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. 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.


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

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. We performed all analyses in R version 4.1.2 (41) and created the figures using ggplot2 (42), diagram (43), and ggridges (44).

Social groups

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. 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.

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 for a total of 191.3 person hours across 12 days, with an average of 20.5 ± 3.6 (SD) hours of observation per three-day assessment periods (n = 3 periods). 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 for a total of 832.8 person hours across 31 days, with an average of 22.1 ± 2.4 (SD) hours of observation per three-day assessment period (n = 10 periods). 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. Second, we removed two injured birds (both lower-ranked) to receive professional care after our first capture event. The third unplanned 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.

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 in 2021 (see paragraph above, Table SI1.2). We performed the perturbation experiment from May until July 2021 and we started the perturbation experiment after the birds had interacted for 31 days in the flight pen. In total, we observed over 940.3 person hours in 37 days, with an average of 21.3 ± 2.3 (SD) hours of observation per three-day assessment period (n = 12 periods, from period 11 onward).

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 (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 over 793.9 person hours in 77 days, with an average of 17.6 ± 3.2 (SD) hours of observation per three-day assessment period (n = 26 periods). In group 2, we observed for 771 person hours in 78 days, with an average of 17.9 ± 3.7 (SD) hours of observation per three-day period (n = 26 periods).

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 (45) using the Animal Observer application (Diane Fossey Gorilla Fund v1.0, (46)). Observers identified the birds using a unique body color combination made with nontoxic permanent markers (Sharpie, Inc.®) (47). We recorded agonistic interactions with a clear winner (decided aggression events (48)). 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 (16). We combined crowds and displacements for further analyses, removed duplicate observations, and retained the interactions where both the actor and the receiver were identified (see for details (10)).

Rank-based removals

To start our perturbation experiments, 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 (7, 10, 49). 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. In our 2021 experiment, we performed removal/reintroduction trials of three top-ranked birds (focal bird). In 2022, we performed trials of three top-ranked, two middle-ranked and one low-ranked bird per group. We randomized the order of the trials prior to the start of the field season.

To remove the focal bird, we caught all birds in the morning using mist nets and removed 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 remaining group members to interact undisturbed for eight days which is sufficient time for the social structure to restabilize (47). We did not use the observations of the day of the trapping for our analyses as this event may have been stressful for the birds. We reintroduced the removed bird at the same time (8:30) and location each time after the 8-day removal period. We recorded observations immediately after the reintroduction of the focal to investigate the group's response to the reintroduced bird. We then allowed the birds 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 focal for the next trial (Table SI1.2 and SI1.3).

Social dominance pattern assessment

We used the agonistic interaction events binned across three days of observations to assess the dominance patterns. We used the function *domstruc* from the 'Domstruc' package (49) to calculate the global dominance patterns (7). This function uses two parameters. First, it calculates *focus*, which measures the distribution of the relative rank difference between the aggressor and the receiver. A value closer to 1 means that the receivers of aggression are all two ranks down the hierarchy from the aggressors, while the focus will decrease when the aggression is more equally distributed across all ranks in the hierarchy. Second, the function calculates *position*, which reflects where aggression is most focused relative to the aggressor's rank. Recent work has categorized rank-based group-level aggression into three categories (7): 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 (7). If the group follows a bullying pattern, the value of position would be closer to 1, whereas if the group follows a close competitor pattern, the value would be closer to 0. To assess whether and which dominance pattern a group follows, the function compares the observed focus and position values to the values simulated by reference models. This reference model results in a downward heuristic pattern and generates 95% CI for that model for the two parameters. To account for systems where aggression could move up the hierarchy instead of down the hierarchy as is defined for the downward heuristic pattern, a tuning parameter is implemented in the model. This tuning parameter is the fraction of aggressive interactions that are randomly allocated, because individuals could make mistakes or are opportunistic in their aggression decisions (see for example the rule breakers in Fig. 2a). When the tuning parameter is 0, individuals aggress completely at random, whereas a value of 1 means that individuals aggress only individuals ranked lower than themselves. If the observed focus and position parameters fall inside the convex hull of the 95% CIs as the tuning parameter is varied from 0 to 1, we classified the group as having a downward heuristic pattern. If the quantities fall above the convex hull (higher relative rank difference) the pattern classified as a bullying pattern and if is the quantities are lower, as a close competitors pattern.

Summarizing individual aggression patterns

For each group and pattern assessment period, we calculated aggression rate (controlled for by hours observed and group size) and aggression balance (i.e., aggression give/aggression given + received). For the aggression rate, we tested whether the rate differed between the bigger (n = 20 birds) and smaller groups (n = 11 birds) using a generalized linear mixed model (GLMM) for gamma distribution. We used group size as a fixed factor and group ID and the 3-day periods as random factors. For the aggression balance, a value of 1 means that the bird only aggressed, while a value of 0 means the bird only received aggression.

For the experimental groups only, we analyzed how aggression given and received changed for individual birds. First, we constructed aggression networks using the 'igraph' package (58) as directed and weighted association matrices where the strength of the association was the total amount of agonistic events per dyad. As edges, we included the rule followers (amount of aggression that follows the dominance hierarchy where higher-ranking birds aggress against lower-ranking birds) and rule breakers (lower-ranked birds aggress against higher-ranked birds). Next, we analyzed the change in absolute aggression balance between the pattern assessment period just before removal and upon reintroduction using a GLMM for beta distribution. As dependent variables, we included an interaction term between focal rank (top-ranked or middle/low-ranked trial) and subject (focal or remaining group member). We included a crossed random term of social group and bird ID to account for differences in group size and for birds (n = 14) that were used in both the 2021 and 2022 field seasons. We used the package 'glmmTMB' (50) to implement the model, checked model diagnostics with the 'Dharma' package (51), and tested for significance using the likelihood ratio test (LR) (52). We then compared the total amount of aggression received for the focal birds upon reintroduction and birds that were similar ranked to the focal birds but in the period just prior to the focal's reintroduction. We used GLMM for negative binomial distribution to compare number of agonistic events received for focal birds or similar ranked birds including an interaction with the rank of the focal bird. We included group ID as random factor. We used the 'lme4' package (53) to implement the model, checked model diagnostics with the 'Dharma' package (51), and tested for significance using the likelihood ratio test (52). Similar to above, we also analyzed the number of distinct aggressors for focal birds and similar ranked birds using GLMM for beta distribution. We controlled for group size by dividing the number of aggressors by group size as the group size for the focal bird included one extra bird. We included an interaction effect between subject (focal bird or similar ranked bird) and focal rank (top-ranked trial vs middle/low-ranked trial), and group ID as random effect. We used the package 'glmmTMB' (50) to implement the model, checked model diagnostics with the 'Dharma' package (51), and tested for significance using the likelihood ratio test (52).

Testing the rank and perturbation type effects on social dominance pattern dynamics

We summarized the dominance pattern changes between assessment periods using transition diagrams (43). We included the results by removal and reintroduction and rank for the 2022 groups in SI4. 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 SI6).

To study the general patterns of how the groups respond to perturbation type (removals and reintroductions), we combined the top-ranked trials across the three experimental groups (2021-group and the two 2022-groups), resulting in 9 removals and 9 reintroductions. We analysed whether the observed pattern transitions prior and after the perturbations were different from random (see SI7 for the conceptual figure). First, we randomized the order of the observed dominance patterns 1000 times (Fig. SI7 *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 removal and reintroduction separately (Fig. SI7 *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. SI7 *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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