Perturbations of key individuals trigger shifts in group-level dominance patterns

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Summary

Dominance hierarchies direct and structure aggression in a myriad of species (Shizuka and McDonald 2015; Hobson et al. 2021). Recent computational approaches have been able to detect additional aggression patterns within animal dominance hierarchies based on relative rank differences between individuals (Hobson et al. 2021). Within species, distinct groups can follow different social dominance patterns, indicating that these patterns should not be thought of as a species-specific characteristic, but rather as a characteristic of that group (Hobson et al. 2021). Yet, we know little about how and why a particular social dominance pattern emerges within a group, why groups show variation in their patterns, and whether these patterns are flexible. A better understanding of the conditions under which a group might shift from one pattern to another would provide insight into the flexibility of these group-level patterns. We tested whether the removal and reintroduction of a single key group member (individuals that have a disproportionately large effect on group dynamics, Modlmeier et al. 2014) could be sufficient to trigger a shift in the social dominance pattern in a captive group of monk parakeets (*Myiopsitta monachus*). Social perturbations have been used to determine how a group's social structure responds to the removal of key individuals (e.g., Flack et al. 2005; Goldenberg et al. 2016). We found that the group was more resilient to the removal of a top-ranked individual but responded more consistently to the reintroduction of those key individuals. We show that perturbation experiments can assess the impact of key individuals on group-level aggression and identify conditions associated with shifts in the group's social dominance pattern.

Results and Discussion

Our social perturbation experiment where we removed and subsequently reintroduced a single 'key' group member shows that the perturbations did not result in a total collapse of the monk parakeet social structure. The group's level of aggression remained relatively stable despite both perturbations, i.e., removals and reintroductions (Fig. 1a, Table SI1.1). Additionally, the general structure of the aggression networks remained stable (Fig. 2): the aggression matrices before and after the removal and reintroduction of each focal bird were significantly correlated (Table 1). Also, the percentage of rule followers (where higher-ranked individuals aggress against lower-ranked individuals, mean ± SD = 59.6 % ± 4.5 %) was overall consistently higher than the percentage rule breakers (where lower-ranked individuals aggress against higher-ranked individuals, mean ± SD = 40.5 ± 4.5 %) throughout the experimental period, except for the reintroduction period of trial 2 the percentage of rule breakers were higher than the percentage rule followers (Fig. 2; Table S3.1). Mainly the identity of the target of aggression changed during our social experiment (Fig. 2).

Table 1. Mantel correlations using the Spearman method of the aggression matrices of the 3-day period immediately before and following perturbations (removals and reintroductions) of the focal monk parakeet.

Trial	**Before vs. after removal**		**Before vs. after reintroduction**	
	Mantel correlation	*P*	*Mantel correlation*	*P*
1	0.69	<0.001	0.66	<0.001
2	0.65	<0.001	0.51	<0.001
3	0.66	<0.001	0.71	<0.001

Effects of the removal of a key individual

The group was relatively resilient to the removal of a key individual: in 2 out of 3 trials, the social dominance pattern remained the same prior to and following the removal of the top-ranked individual (Fig. 1b). The observed pattern changes before versus after removal were not unusual compared to a random distribution of pattern changes (Star methods *Pattern changes*; Fig. 3a and b, Fig. SI4.1a and b). For example, only for trial 3 (periods 9 to 10; Fig. 1b) the observed pattern remained a downward heuristic pattern after removal (33% of all trials), while for the randomised distribution of pattern changes 26% of randomisations (out of a 1000) across all three trials showed this pattern transition (Fig. 3a). Furthermore, we found that 876 of the 1000 randomisations showed the same transition from bullying to bullying that was observed in only 1 of the 3 trials (33 %; Fig. 3b). Overall, we found that the randomised social dominance pattern dynamics showed the exact same dynamics for all three trials in only 2.9% of the randomisations as observed after removal. The removal of individuals could reflect natural demographic processes, such as the death or dispersal of a group member (Shizuka and Johnson 2020). Resilience to the removal of key individuals is also seen in ants (Naug 2009), great tits (Firth et al. 2017), chacma baboons (Barrett et al. 2012), Savannah elephants (Wiśniewska et al. 2020), and white-lipped peccaries (Grossel et al. 2022). However, it can also result in instability of the group structure, as seen in pigtailed macaques (Flack et al. 2005; Flack et al. 2006), killer whales (Williams and Lusseau 2006), Columbian ground squirrels (Manno 2008), and house sparrows (Kubitza et al. 2015). In leaf-roosting bats, the group's resilience to targeted attacks depends on the roosting resources, where the species with the least resources show unstable group structure after targeted removals (Chaverri 2010). Therefore, the group's response to the removal of a group member may be species- and context-dependent, where the social system and resource availability may influence whether a species is resilient to the removal.

Effects of the reintroduction of a key individual

In contrast to the relative stability following removals, reintroductions changed the group-level social dominance patterns in monk parakeets. We found that the reintroductions of a single key individual were sufficient to consistently shift the social dominance pattern of the group. The group was more consistent in their response to the reintroduction of those key individuals: in all three perturbations, groups followed a downward heuristic (aggress indiscriminately against others ranked below themselves) just before reintroduction but altered to a bullying pattern (aggress preferentially to those far below in rank) just after reintroduction (Fig. 1b). The amount of aggression directed toward the reintroduced bird is consistent with the result of a bullying pattern after reintroduction (Fig. 2). The observed pattern changes for all three trials were significantly different from a random distribution of pattern changes (Star methods *Pattern changes*; Fig. 3c and d, Fig.SI4.1c and d). For example, in all three trials the observed pattern transitioned in a similar fashion but only in 27% of the 1000 pattern transition randomisations did we find the same pattern change (Fig. 3c). Of the 1000 randomised pattern distributions, we only found that 26 randomisation runs (2.6%) showed the pattern transition from downward heuristic to bullying for all three trials, which is the same as the observed pattern transition (Fig. 3d). The change in social dominance pattern from downward heuristic to bullying following the reintroduction of the removed bird may indicate that this captive group of monk parakeets could use the history of social interactions to adjust their decision-making with whom and when to aggress upon a reintroduction. This possibility is in line with previous results that show that rank determinants in monk parakeets are more based on the history of social interactions than on individual characteristics (Hobson and DeDeo 2015; van der Marel, Francis, et al. 2022). Together these results show that the group is more sensitive to the reintroduction than to the removal of a top-ranked bird. This difference in response to the removal compared to the reintroduction may be expected if the birds that improved in rank due to the absence of the top-ranked bird value their newly obtained rank positions, which may provide greater benefits such as resource access, but this requires further investigation.

While removal of individuals from the group has been extensively studied, 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 Firth et al. 2017; Boucherie et al. 2022). For example, in ravens, returning birds after an absence receive more aggression but primarily when they are juveniles, suggesting that in the fission-fusion society of ravens, both social history (tenure) but also individual characteristics (age) influences reintegration into a group (Boucherie et al. 2022). In great tits, reintroduced birds reassociate with their same flock mates as before their removal (Firth et al. 2017). In monk parakeets, returning previously top-ranked birds after an absence suffer an extreme drop in rank (van der Marel, Francis, et al. 2022) and receive more aggression. Future experiments are now testing whether the group responds similarly to the reintroduction of differently ranked individuals, or the introduction of a stranger and these results will help untangle the effects of specific individuals in the group and their effect on the group's social dynamics. Especially, as key individuals may influence group dynamics and resilience of species that show the potential for cognitive and/or social complexity, such as eusocial insects, elephants, primates, and whales (Flack et al. 2005; Williams and Lusseau 2006; Goldenberg et al. 2016; Annagiri et al. 2017), and now also in a parrot species. Thus, species- and context-dependent factors, such as social dynamics and demography, may also be factors integral to the behavioral responses from social groups towards the reintroduction of previously absent group members.

Conditions associated with changes in social structure

Distinct monk parakeet groups can show different social dominance patterns, e.g., a close competitor pattern (Hobson and DeDeo 2015) or a bullying pattern (van der Marel et al. 2021), suggesting that these patterns are group-specific and potentially plastic (Hobson et al. 2021). We identified one condition associated with shifts in the group's social dominance pattern within the same group: social upheaval, especially by the reintroduction of a key individual altered social dominance patterns within the same social group. Reintroduction of a key individual may not affect other social groups within the same species or different species the same because species vary in their social systems (Kappeler and Schaik 2002; Wolff and Sherman 2007), their resource and space use (Lacey and Sherman 2007; de Silva et al. 2016; Webber and Vander Wal 2017), and their ability to respond to perturbations. Some species or groups may not respond the same as monk parakeets to natural or experimental demographic processes, while others may respond more strongly to a change in environmental conditions (e.g., Testard et al. 2021). Further research could detect what type of perturbation, and what social role of the perturbed individual or group of individuals, induce a change in social dominance patterns and whether the group responds similarly to the introduction of a new individual that could reflect immigration.

Social structures are dynamic and change over time due to changes in group membership or due to changes in the strengthening and weakening of relationships (Ebensperger et al. 2009; de Silva et al. 2011; Pinter-Wollman et al. 2013; Aguilar-melo et al. 2018; Shizuka and Johnson 2020), but the direction and magnitude of social changes are often difficult to predict. Determining what factors cause changes in animal societies may help us understand how animals cope with or adjust to changing environments, particularly because animals are faced with an increasing number of threats, such as those associated with urbanization and climate change. For example, species that are introduced to new habitats (Kolar and Lodge 2001; Vahsen et al. 2018) or species that experience habitat and/or climate changes (Previtali et al. 2010; Bourne et al. 2020; Rat et al. 2020; Van de Ven et al. 2020) must adjust to a new environment. Forecasting the direction and magnitude of social change is particularly important for societies organized hierarchically because disruption to the hierarchical order can destabilize a population's social structure. Predicting the effect of perturbation events and consequently the identification of network resilience may allow us to prevent future instability from emerging, but also to reduce potential costs if the system does collapse.

Figures

Figure 1. Despite removal of the top-ranked monk parakeet, dominance patterns remained the same in 2 out of 3 trials while upon the reintroduction of the removed monk parakeet, dominance patterns changed from a downward heuristic to a bullying pattern. Panel a shows the time points where the top-ranked individual (3 different birds) was removed and reintroduced, the rate of directed aggression controlled for both hours observed (totaled over all four observers) and group size (removal: n = 19 birds; reintroduction: n = 20 birds), and the overall mean aggression rate (in grey). Panel b shows the social dominance patterns for each assessment period. Individuals can randomly aggress against others below self (*downward heuristic* pattern), can direct aggression toward individuals nearby in rank (*close competitor*), or toward individuals much farther below them in rank (*bullying*).

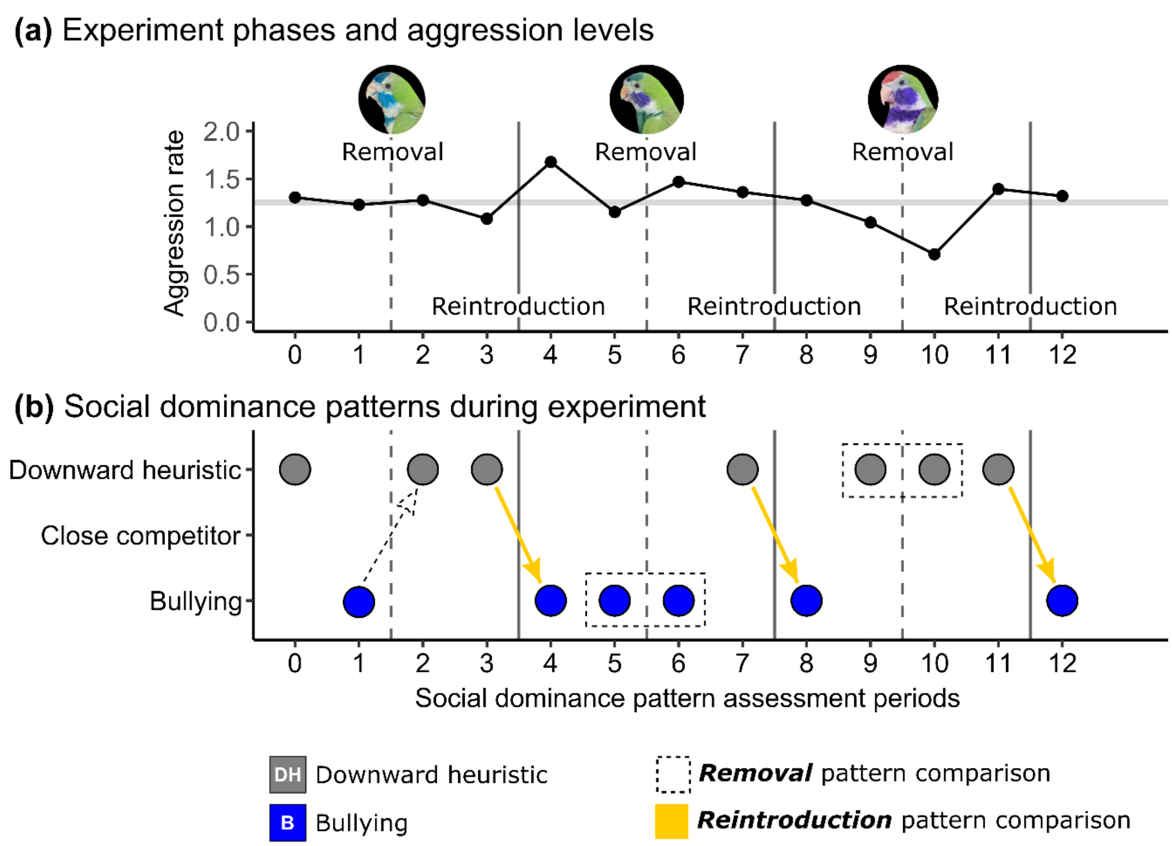


Figure 2. The monk parakeet aggression networks are consistent throughout the social experiment.

Panel (a) shows the aggression networks for the 3-day periods before and after removal and panel (b) the networks for the periods before and after reintroduction. The nodes are ordered by their respective power score with higher ranking birds closer to 1. For the periods before removal and after reintroduction (N = 20 birds), the focal birds are highlighted in blue (trial 1), purple (trial 2), and orange (trial 3). 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). The period numbers are the social dominance pattern assessment periods (see Fig. 1).

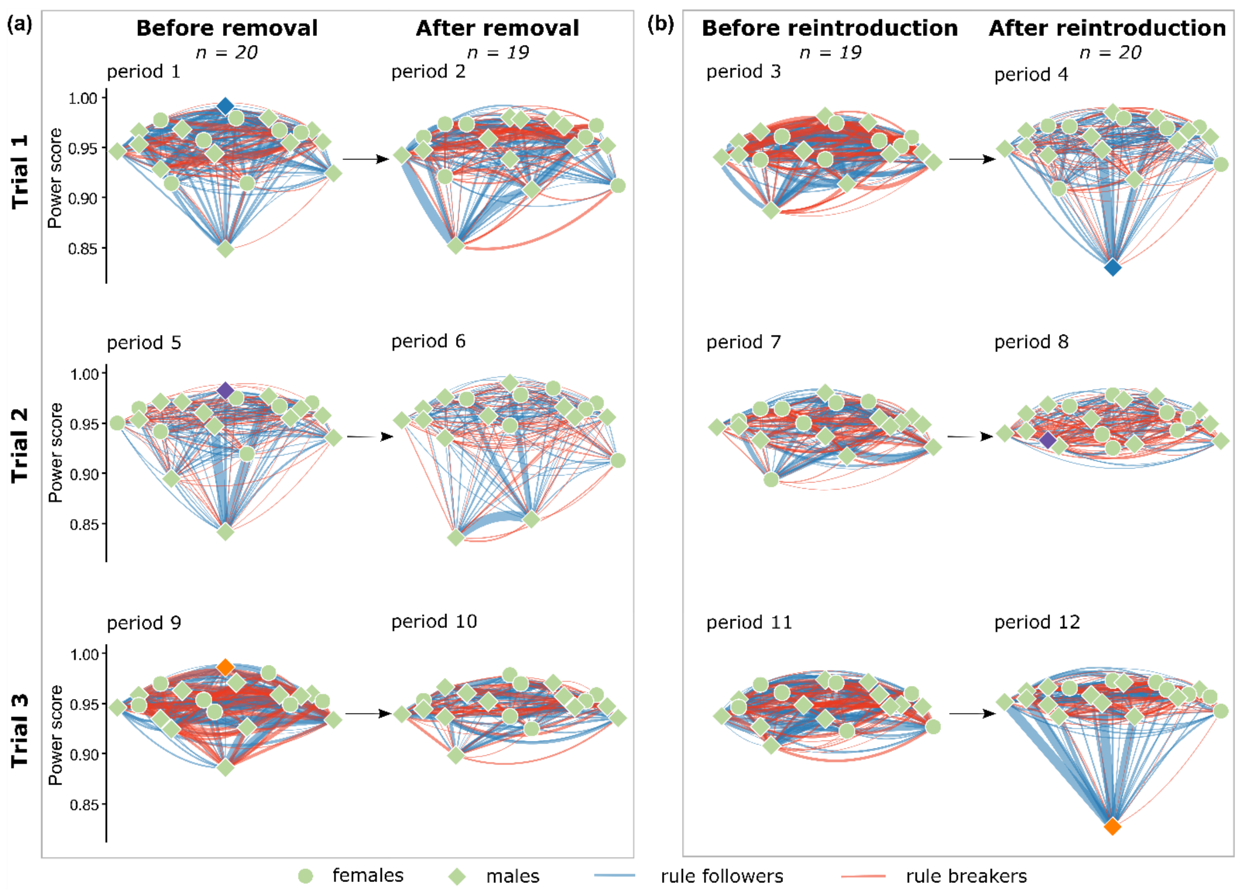
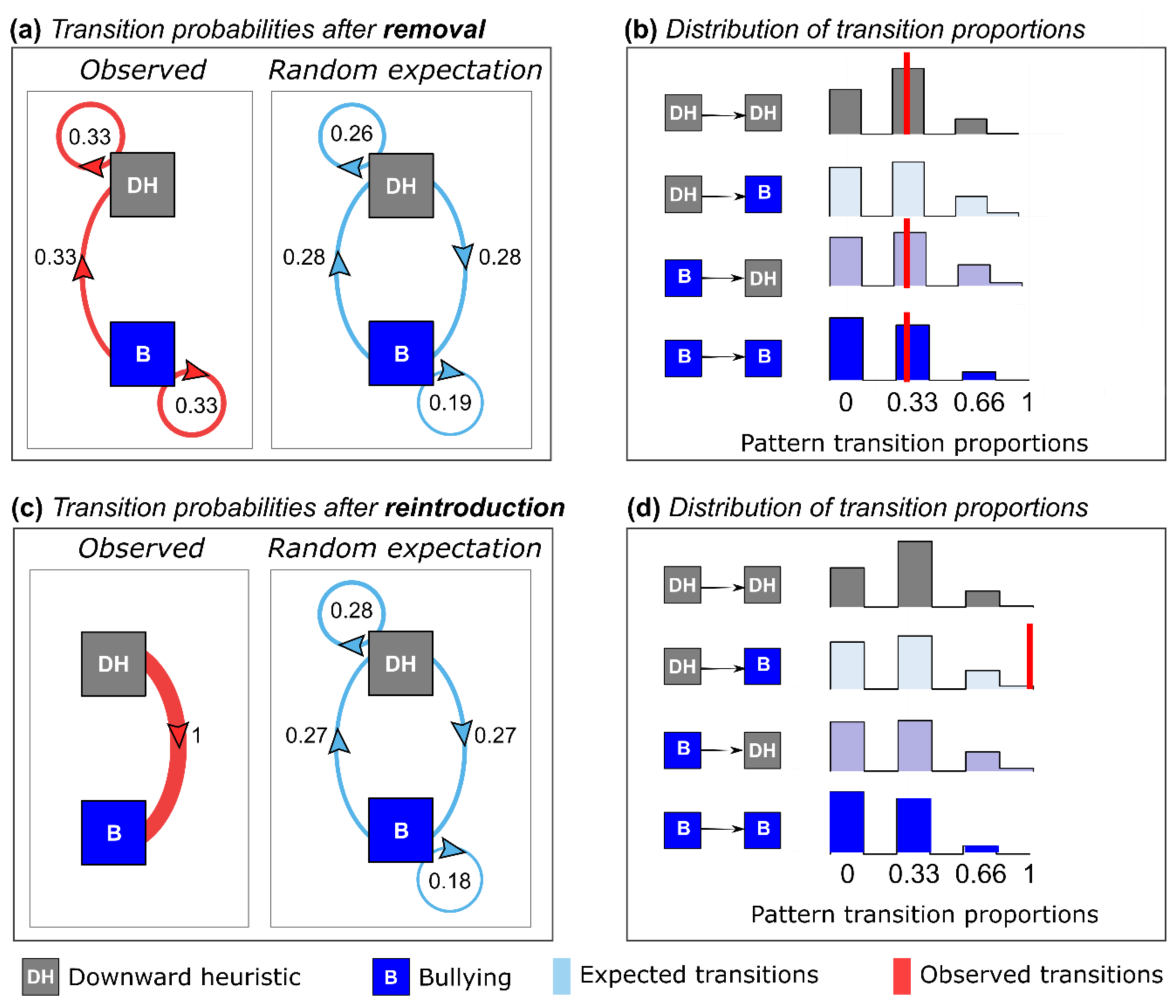


Figure 3. The observed social dominance pattern changes after removal are not different from a randomised distribution, while the observed pattern change after reintroduction is unusual compared to the randomised pattern changes. The transition proportions of the observed and randomised dominance patterns (a) after removal and (c) upon reintroduction. The values in the random expectation represent the average proportion combining all three trials across the 1000 runs. The right panels (b and d) show the distributions of the proportion pattern changes, which is the number of trials with that specific pattern transition divided by the total number of trials (n = 3), per run (b) after removal and (d) 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 three trials.



Methods

Study species

We experimentally manipulated a captive group of 20 monk parakeets (*Myiopsitta monachus*), a highly social neotropical parrot that readily forms dominance hierarchies in captivity (Hobson et al. 2014; Hobson et al. 2015; van der Marel, Francis, et al. 2022). We performed the social perturbation experiments at the United States Department of Agriculture National Wildlife Research Center in Gainesville, FL, USA from May 10th through July 5th, 2021. For individual identification, each bird received a steel leg band and a unique color combination on the feathers using nontoxic permanent markers (Sharpie, Inc.®) (Hobson et al. 2013).

Data collection

Four observers performed daily observations approximately between 08:00 and 19:00 from three different blinds in a 45 x 45 m seminatural outdoor flight pen. The observers recorded dyadic interactions using all-occurrence sampling (Altmann 1974) using the Animal Observer application (Diane Fossey Gorilla Fund v1.0, van der Marel et al. 2022). 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 the framework described in van der Marel et al. (2020) to ascertain that crowds and displacements were functionally similar and thus part of the same behavioral context. We combined crowds and displacements for further analyses (van der Marel, Francis, et al. 2022) and retained the interactions were both the actor and the receiver were identified.

Having multiple observers improved sampling effort but could also result in observers recording the same interaction. To remove duplicate observations, we first summarised the number of agonistic interactions (crowds and displacements combined) that were observed in the same minute for each observer. We then kept the observations of the observer with the highest number of observations, removing duplicated observations of the other observers.

Quantifying rank

We allowed the birds to interact for 44 days in the flight pen prior to first removal allowing for enough time for the dominance hierarchy to stabilize (Hobson et al. 2013). To start our experimental perturbations, we identified the top-ranked bird by calculating the dominance rank of each bird using a modified version of PageRank using the 'Domstruc' package (Hobson et al. 2021; Mønster et al. 2021; van der Marel, Francis, et al. 2022). To identify the individual ranks, we used agonistic interaction events binned across three days of observations prior to removals (see Fig. SI1). Only one of the observers (AM) performed the dominance rank analyses and was aware of the complete dominance hierarchy, the other observers were blind to the standing of the remaining group members in the dominance hierarchy.

Experimental design

To remove the top-ranked bird, we caught all birds using mist nets in the morning and removed only the top-ranked bird (the focal). We placed the focal back in its standard housing cage (2 x 2m wire cage) near other parakeets (that were not part of this experiment) but away from the birds in the flight pen. We then released all birds back into the flight pen except for the focal. We allowed the birds (n = 19) to interact undisturbed for eight days which is sufficient time for the social structure to restabilize (Hobson et al. 2013). We reintroduced the removed bird at the same time (8:30) and location each time after the 8-day removal period (e.g., day 9, Fig. SI1). 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).

Statistical analyses

We performed all analyses in R version 4.1.2 (R Core Team 2021) and created the figures using ggplot2 (Wickham 2016), diagram (Soetaert 2020), ggridges (Wilke 2021), and ggraph (Pedersen 2021). All data have been deposited at https://github.com/annemarievdmarel/Monk_dompattern (van der Marel and Hobson 2022).

Dominance patterns

Social dominance patterns emerge from the sum of individual aggression decisions and are a property of the social group. Across animal species, individuals may simply follow the general *downward heuristic* pattern of dominance hierarchies (aggress indiscriminately against others ranked below themselves). However, individuals can also use relative rank differences between themselves and potential targets to be more specific about who they aggress against: using a *close competitor* (aggress preferentially to others ranked slightly below themselves) or *bullying* (aggress preferentially to those far below in rank) pattern (Hobson et al. 2021).

We assessed the social dominance pattern at four different timepoints in each perturbation trial (n = 3 trials). We used agonistic interaction events binned across three days of observations prior to removals, after removals, prior reintroduction, and after reintroduction (see Fig. SI1). This binning allowed for enough agonistic interactions to assess the social dominance patterns (mean ± SD = 2007 ± 527 agonistic events assessment period). In total, we used 25059 agonistic interactions over 277 hours and 1023 person hours across 40 days, averaging 21.3 ± 2.2 (SD) hours of observation per 3-day period to determine the group's social dominance pattern (see Table S1.1 for the summary per period). We used the function *domstruc* from the 'Domstruc' package (Hobson et al. 2021; Mønster et al. 2021) to calculate the global dominance patterns (Hobson et al. 2021). This function calculates two measures of aggression: focus measures the distribution of the relative rank difference between the aggressor and the receiver, and position reflects where aggression is most focused relative to the aggressor's rank. Using focus and position, the function derives the dominance pattern that is used by the group 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 reference model. The group directs aggression differently if the observed dominance pattern deviates from what is expected under the reference model, where the group could either follow a bullying, where aggressors could target individuals much lower than themselves in rank, or close competitor pattern, where aggressors target individuals close to themselves in rank.

Aggression networks

We constructed aggression networks using the ‘igraph’ package (Csárdi and Nepusz 2006) 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). We compared the before and after removal, and the before reintroduction and upon reintroduction aggression matrices with a mantel correlation test with the Spearman method using the ‘vegan’ package (Oksanen et al. 2019). For the aggression matrices where the top-ranked bird is removed, we included a row and column for the removed focal bird and filled these with zeros to create similar-sized matrices of 20 birds.

Pattern dynamics

To answer whether the removal and reintroduction of a top-ranked bird could change the social dominance patterns, we analysed whether the observed pattern transitions prior and after the perturbations were different from random. We did these analyses separately for removal and reintroduction. For the conceptual figure of these analyses see SI3. First, we randomised the order of the observed dominance patterns 1000 times (Fig. SI3.1 *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 before and after reintroduction for each trial separately (Table SI1.1; Fig. SI3.1 *step 2a*). We calculated the proportion of randomised pattern transitions and averaged these across the three trials, which we then visualised. Next, per reference model run, we summarised the number of trials (out of 3 trials) that showed a particular social dominance pattern change, either a change from downward heuristic to downward heuristic, from downward heuristic to bullying, from bullying to downward heuristic, or from bullying to bullying. We included all four possible pattern changes per run and calculated the proportion of pattern changes per run across all three trials. We visualised this reference distribution and included the observed pattern changes (Fig. SI3.1 *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 (removal or reintroduction). Finally, we summarised the percentage of runs where we observed the exact same pattern changes as observed for all three trials.

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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.

Author Contributions

- Conceptualization: EAH, AM
- Data collection: AM, XF, CO, COE
- Analyses: AM
- Writing: AM, EAH
- Comments: AM, XF, CO, COE, CC, EAH

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Supplemental Information

Supplemental Information 1: Experimental schedule

Table SI1.1. The experimental social perturbation schedule in monk parakeets. In total, we performed three perturbation trials, which lasted 16 days with an 8-day removal and an 8-day reintroduction period. We pooled three days to assess social dominance patterns rendering 12 social dominance pattern assessment periods.

Start date	End date	Trial	Period	Days	Hours observed	Birds	Agonistic events
2021-04-28	2021-05-18	na	Initial group formation	21		20	
2021-05-16	2021-05-18	1	assessment 1	3	22.85	20	1977
2021-05-19		1	capture 1	1			
2021-05-20	2021-05-22	1	assessment 2	3	21.82	19	2111
2021-05-23	2021-05-24	1	days off	2			
2021-05-25	2021-05-27	1	assessment 3	3	22.58	19	1738
2021-05-28	2021-05-30	1	assessment 4	3	26.7	20	2928
2021-05-31	2021-06-01	1	days off	2			
2021-06-02	2021-06-04	2	assessment 5	3	21.38	20	1856
2021-06-05		2	capture 2	1			
2021-06-06	2021-06-08	2	assessment 6	3	20.95	19	2218
2021-06-09	2021-06-10	2	days off	2			
2021-06-11	2021-06-13	2	assessment 7	3	19.68	19	1887
2021-06-14	2021-06-16	2	assessment 8	3	18.37	20	1713
2021-06-17	2021-06-18	2	days off	2			
2021-06-19	2021-06-22	3	assessment 9	3.5	20.97	20	1615
2021-06-23		3	capture 3	1			
2021-06-24	2021-06-26	3	assessment 10	3	17.82	19	897
2021-06-27	2021-06-28	3	days off	2			
2021-06-29	2021-07-01	3	assessment 11	3	21.38	19	2131
2021-07-02	2021-07-04	3	assessment 12	3	20.98	20	2005

Supplemental Information 2: Summary of network measures

Table SI2.1. For each social dominance pattern assessment period the density, and the percentage rule breakers, where lower-ranking individuals aggress against higher-ranking individuals, and rule followers, where higher-ranking individuals aggress against lower-ranking individuals.

period	density	rule breakers (%)	rule followers (%)
1	0.64	32.23	67.77
2	0.66	38.33	61.67
3	0.66	38.94	61.06
4	0.69	36.88	63.12
5	0.62	40.00	60.00
6	0.62	41.78	58.22
7	0.64	44.09	55.91
8	0.57	51.38	48.62
12	0.60	40.17	59.83
10	0.52	39.89	60.11
11	0.65	41.52	58.48
12	0.60	40.17	59.83

Supplemental Information 3: Creating random distribution of observed social dominance patterns

Figure SI3.1. A conceptual figure of the analysis to test how unusual the observed pattern changes are.

We created a reference model that randomised the observed social dominance patterns for 1000 iterations (Step 1). We compared the social dominance patterns for the 3-day period immediately before the perturbation (removal or reintroduction) to the 3-day period immediately after the perturbation. Using these 1000 random pattern change distributions; we calculated the transition probabilities across all 1000 runs (Step 2A) and the proportion of pattern changes out of 1000 runs (Step 2B).

1. Create a randomized distribution out of the observed patterns

Trial	Period	Perturbation	Observed patterns
1	1	Before removal	Downward heuristic (D)
1	2	After removal	Downward heuristic
1	3	Before removal	Downward heuristic
1	4	After removal	Bullying (B)
2	1	Before removal	Downward heuristic
... 3	...4	...after reintro	....

Randomize observed patterns 1000 times →

Randomization 1	Randomization 2	Randomization 3	....	Randomization 1000
Bullying	Downward heuristic	Downward heuristic		Bullying
Downward heuristic	Downward heuristic	Downward heuristic		Downward heuristic
Downward heuristic	Bullying	Downward heuristic		Downward heuristic
Downward heuristic	Downward heuristic	Bullying		Downward heuristic
....etc	...etc	...etc		..etc

2. A) Average transitions probabilities (separate for removal & reintroduction)

Trial	Observed pattern change After removal	Proportion pattern change
1	D - D	1/3 trials = 0.33
2	B – D	1/3 trials = 0.33
3	B – B	1/3 trials = 0.33

Trial	Random pattern change After removal	Proportion pattern changes
1	D - D	179/1000 = 0.18
1	D - B	301/1000 = 0.30
1	B – D	266/1000 = 0.27
1	B – B	254/1000 = 0.25
2	...etc	...etc

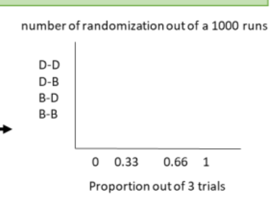
Summarize average proportion across the 3 trials

Random pattern change After removal	Average proportion pattern changes
D - D	0.26
D - B	0.28
B – D	0.28
B – B	0.19

2. B) Distribution of transition proportions (separate for removal & reintroduction)

Trial	Observed pattern change After removal	Proportion pattern change
1	D - D	1/3 trials = 0.33
2	B – D	1/3 trials = 0.33
3	B – B	1/3 trials = 0.33

Randomization #	Random pattern change After removal	No. trials (has to sum up to 3 trials for each run)	Proportion out of 3 trials
1	D - D	0	0.00
1	D - B	1	0.33
1	B – D	2	0.66
1	B – B	0	0.00
2	...etc	...etc	



Supplemental Information 4: Distribution of transition proportions

Figure SI4.1. The observed pattern changes after removal are not different from a randomized distribution, while the observed pattern change after reintroduction is unusual compared to the randomised pattern changes. The transition proportions of the observed and randomized dominance patterns (a) after removal and (c) upon reintroduction. The values in the random expectation represent the average proportion combining all three trials across the 1000 runs. The right panels show the distributions of the proportion pattern changes out of four different pattern transitions per run (b) after removal and (d) after reintroduction. The x-axis in b and d represent the proportion of pattern changes per run, which is the number of trials divided by the total number of possible pattern changes (4 possible pattern changes). The y-axis represents the number of runs out of a 1000 that shows the specific pattern transition in at least one of the three trials. To illustrate the plot in more detail, we provide an example: only for one trial the observed pattern remained a downward heuristic pattern after removal (33% of all trials), while for the randomised distribution of pattern changes 26% of the 1000 randomisations across all three trials showed this pattern transition (Fig. a). We found that 438 of the 1000 randomisations showed the transition from bullying to bullying in 1 out of the 4 different observed pattern changes (25 %; Fig. b).