Perturbations highlight importance of social history in parakeet rank dynamics

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Lay summary

Dominance rank can influence many aspects of an individual's biology, but what factors determine rank can vary widely across species. We manipulated group membership to determine whether rank is the product of a group's social history (memory of past interactions) in captive monk parakeets. After reintroducing removed individuals, no removed bird could immediately re-take their rank, and bodyweight did not correlate with rank. Our results provide support that social history shapes rank in monk parakeets.

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Abstract

Dominance hierarchies can provide many benefits to individuals, such as access to resources or mates, depending on their ranks. In some species, rank can emerge as a product of the history of social interactions within a group. However, it can be difficult to determine whether social history is critical to rank in observation-based studies. Here, we investigated rank dynamics in three captive groups of monk parakeets (*Myiopsitta monachus*). We used experimental social perturbations to test whether social history shapes rank emergence in these groups. Using targeted removals and reintroductions, we tested whether differently ranked individuals could re-take their ranks in hierarchies after reintroduction following their removal period from the group. We performed perturbations that consisted of an eight-day removal and an eight-day reintroduction period of 15 differently ranked focal birds. We found that no focal birds could regain their previous rank immediately following reintroduction and that the top-ranked birds showed greater relative rank loss than middle/low-ranked birds. We also found that morphology, specifically bodyweight, was unassociated with rank. Combined with previous results, this experiment supports the hypothesis that rank in monk parakeet dominance hierarchies is more likely to be an emergent outcome of past interactions and memory rather than based on individual characteristics. Gaining a better understanding of how individuals achieve and maintain rank can give insight into the role of cognition on rank acquisition, as rank position can have significant biological effects on individuals in hierarchically structured groups.

Keywords

Animal aggression, dominance hierarchy, dominance rank, monk parakeet, *Myiopsitta monachus*, parrot, sociality, social manipulation

Introduction

Dominance hierarchies structure aggression in many social groups across the animal kingdom (Shizuka and McDonald 2012; Holekamp and Strauss 2016; Hobson et al. 2021). The ranks that individuals hold in these hierarchies, and the aggression one receives based on rank, can affect their access to resources (Pizzari and McDonald 2019), health (Cavigelli and Caruso 2015; Simons et al. 2022), and reproductive success (Hodge et al. 2008; Sukmak et al. 2014). These effects demonstrate that rank can have significant biological consequences on individuals in social groups.

Understanding how and why individuals achieve high rank has been an area of active research (Strauss et al. 2022). In some species, rank may be a product of *social history*, where memory of past interactions is critical in structuring rank. Rank then becomes an emergent property of group interactions (Chase et al. 2002; Hotta et al. 2014; Massen et al. 2014; Hobson and DeDeo 2015; Tibbetts et al. 2019). We refer to this process as the social history hypothesis. Memory of social history can be encoded via shifts in neural and physiological mechanisms (Dwortz et al. 2022) or general behavior following wins and losses in fights, and does not necessarily require high cognitive skills (Korzan et al. 2007; Hotta et al. 2014). However, in systems with individual recognition (Kogan et al. 2000; Tibbetts 2002), rank may be based off a combination of experiences and observations of interactions among individuals, where the outcomes and types of interactions serve to structure future behaviors (Hobson and DeDeo 2015; Tibbetts et al. 2019; Hobson et al. 2021). In this case, individuals may need to rely on their cognitive abilities to achieve and maintain rank. Greater cognitive processing is required in these systems as decisions on who to fight at the individual level are made using emergent rank information by observing the interactions among other individuals (Chase and Seitz 2011; Massen et al. 2014; Hobson and DeDeo 2015; Reichert and Quinn 2017; Hobson et al. 2021). Individuals in these systems may use perception, recognition of group members, memory of past interactions, and transitive inference to infer the rank of others. The use of social history is hypothesized to be primarily present in species that have small, stable social groups as individuals would not require as much cognitive processing to recognize their group members due to interacting repeatedly with one another (Sheehan and Bergman 2016). However, social history can also be an important factor in groups that have high fission-fusion dynamics or multilevel societies where group membership and group size are fluid (Shultz and Gersick 2016; Chaine et al. 2018; Boucherie et al. 2022). To better understand the factors that underlie rank in a particular species, we need to investigate the relative importance of how social history may affect an individual's rank.

Different methods exist to understand the relative importance of social history in structuring rank emergence and maintenance. In most social species, it is more feasible and straightforward to measure an individual-level characteristic and quantify its association with rank compared to trying to determine the effect of social history on rank. Rank can be strongly correlated with an *individual characteristic*, such as body size, weapon or ornament size, age, motivation, or maternal inheritance (Engh et al. 2000; Chase and Seitz 2011; Reddon et al. 2011; Santos et al. 2011; O'Connor et al. 2015). We refer to this process as the individual characteristics hypothesis. An absence of a strong correlation could then signify that social history may shape rank supporting the social history hypothesis, but it could also mean that the salient characteristic that affects rank was not identified, measured, and tested (Chase and Seitz 2011). Additional methods are needed to reach a conclusion in support of social history. For example, observational studies and natural perturbations to social groups could identify the effect of social history on rank (Strauss and Holekamp 2019; Boucherie et al. 2022). However, this observational approach generally requires long-term study and still cannot definitively separate individual characteristics that may change over an individual's lifetime from the effects of social history.

Other approaches to identifying the potential for social history's importance in rank emergence have used computational methods. For example, using observations of agonistic interactions in monk parakeet groups, Hobson and DeDeo (2015) used computational methods by organizing aggression relationships into “chains” of aggression to detect that the parakeets could benefit from incorporating information about the relationships of others into their aggression decision-making. They also found that this information structures aggression. However, this study could not address whether disruption to the information in the group causes changes in the social ordering that is then reflected by changes in aggression behavior because these analyses were conducted while the hierarchy was stable.

Experimental tests of the social history hypothesis can be used to parse apart social history and individual characteristics as potential drivers structuring rank. Experimental perturbations allow for an examination of, for example, the type of information individuals use, how rank is inferred, and how social groups respond to changes in their group composition (Flack et al. 2005; Barrett et al. 2012; Hellmann et al. 2015; Kubitza et al. 2015). Here, we test the social history hypothesis using a series of social manipulations to experimentally perturb the social history of individuals in groups and investigate the changes in individuals’ ranks.

We used experimental perturbations of social groups that show the potential for social and cognitive complexity and that exhibit dominance hierarchies to better clarify whether social history shapes rank. We tested this idea in monk parakeets (*Myiopsitta monachus*), a small neotropical, parrot native to South America with a global distribution that readily forms dominance hierarchies in captivity (Hobson et al. 2013; Hobson et al. 2014; Hobson et al. 2015; Hobson and DeDeo 2015). Monk parakeets live in fission-fusion societies with pairs as their primary social unit and show the potential for social and cognitive complexity (Hobson et al. 2013; Hobson et al. 2014; Hobson and DeDeo 2015). As summarized above, previous work has indicated that social history is likely important in the emergence of rank in this species (Hobson and DeDeo 2015; Hobson et al. 2021), but experimental manipulation would provide additional support to this hypothesis.

We tested the social history hypothesis in three groups of monk parakeets. In each trial, we identified an individual according to their rank, removed it from the group, and reintroduced it after an 8-day absence. We hypothesized that if shorter-term social history (remembering the more current interactions during the removal period when the focal was absent) was important in achieving and maintaining rank, the removed individuals would not immediately be able to re-take their previous ranks upon reintroduction because the remaining group members would have shifted in rank during the removed bird's absence and would defend their new ranks against the reintroduced bird. In contrast, if longer-term social history (remembering the interactions with the focal bird prior its removal) was important in rank dynamics, we predicted that these removed birds would be able to re-take their ranks immediately on re-joining the group as all the birds would remember these individuals and their agonistic relationships. To differentiate the effect of longer-term social history and the effect of individual characteristics that might determine rank, we also measured the bodyweight of the birds at each capture event. If the bodyweight of the birds determined their ranks, we predicted we would find a significant association between bodyweight and rank. We also predicted that the effect of social history would be most pronounced for top-ranked individuals and less pronounced for middle/low-ranked birds because all group members would benefit from the removal of a top-ranked bird. This finding would provide more support for social history as the remaining group members could adjust their behavior according to the previous social standing of the removed birds. This experimental approach combined with a lack of association between individual characteristics and rank, can provide stronger indications that social history is important to rank in this species.

Methods

The social experiments and observations took place at the United States Department of Agriculture, Wildlife Services, National Wildlife Research Center (USDA WS NWRC), Florida Field Station, in Gainesville, FL, USA. We performed the experiments on monk parakeets that were captured by the

USDA WS NWRC from four feral populations in southern Florida (n = 33 birds) in February 2021. All animal-related research activities were approved by the University of Cincinnati (IACUC protocol #AM02-19-11-19-01) and the USDA NWRC (Quality Assurance #3203).

Social groups

We performed the social experiments in 2021 and 2022. In both years, we used the same experimental timeline but the number of social groups, group sizes, the size of the flight pens, the time of year, the number of trials, and the ranks of removed individuals differed.

In 2021, we experimentally perturbed a single large group of 20 parakeets. Observations took place from April through July 2021 with a group of seven females and 13 males (sexes were unknown prior to the field season and the observers were blind to sexes throughout the field season). This large group was housed in a 45 x 45m semi-natural outdoor flight pen (hereafter “large flight pen”). We allowed the large group to interact and the social structure to stabilize in the large flight pen for 44 days prior to starting our perturbation experiments. We conducted three social perturbations of three top-ranked birds in the large group between 16 May and 5 July 2021. A team of four observers collected parakeet behaviors between 08:00 and 19:00 from blinds arrayed around the flight pen (see below for data collection methods).

In 2022, we perturbed two medium groups of eleven parakeets each. Each group contained five females and six males. Of these 22 birds, 14 birds were ones that had participated in our 2021 experiment in the large group; 8 birds were new to the experiments and were not involved in the 2021 experiment (Supplemental Material (SM) 1). These social groups were housed in two medium-sized 10 x 4.5 x 3m flight pens (hereafter “medium flight pen”). We allowed these groups eight days to interact and form their social structure before starting the social perturbations. We performed six perturbation trials (three top-ranked, two middle-ranked, and one bottom-ranked bird) in each of the medium social groups between 26 January and 5 May 2022. We randomized the order of the rank removals prior to the start of the social perturbation experiment and performed the same type of rank removal on both social groups. A team of two observers collected parakeet behaviors between 09:00 and 18:00 from blinds located outside each medium flight pen, with 4 observers rotating between the two medium social groups.

Social interaction data collection

To facilitate individual identification, we marked each parakeet on the head, cheeks, and neck with a unique color combination using nontoxic, permanent markers (Sharpie, Inc.®) (Hobson et al. 2013). This unique color combination represented a unique letter ID for each bird combining the three different colors chosen from blue, green, orange, and purple. Color combinations were randomly assigned to each individual within years and individuals that participated in both 2021 and 2022 were given new randomly assigned color combinations in the second year. All marks were re-applied at each capture event, when necessary (see section below for more detail on capture events).

Observers recorded all dyadic agonistic interactions using all-occurrence sampling (Altmann 1974). We entered the data directly into electronic format using an iPad and the Animal Observer application (Diane Fossey Gorilla Fund v1.0), which we customized to record all-occurrence observations (van der Marel, O'Connell, et al. 2022). We recorded two types of directed agonistic interactions: *crowding events*, where the actor approached a target, but the target moved away before the actor was within striking range, and *displacement events*, where the actor aggressively approached another bird within striking distance and supplanted it from its location with a strike. From these observations, we excluded any interaction where either of the two interactants was unknown (keeping only interactions where the actor and the target were positively identified).

We then filtered the data to exclude duplicate observations. Because we had more than one observer simultaneously monitoring each group to better capture the entire interaction history, different observers could record the same aggressive event. To remove duplicate observations, we determined the maximum number of aggressive interactions (including both crowds and displacements) between each pair of individuals (dyads) recorded by each observer during each minute of observation. Combining both crowds and displacements was a more conservative method to remove duplicates as it resulted in fewer interactions but excluded the instances where two observers observed the same interaction but one coded it as a "crowd" and the other as "displacement". For any minute of observation where aggression between a particular dyad was recorded by more than one observer, we retained the observations of aggression from the observer that observed and recorded the most aggressive events for that dyad in that minute (see van der Marel et al. 2021). The prevalence of duplicated (and subsequently removed) agonistic events are summarized in Table SM2.1.

Rank-based removals

For all groups, we used a consistent experimental timeline. Each perturbation cycle lasted 17 days, including a day where we captured the group and removed the focal bird, followed by an 8-day removal and an 8-day reintroduction period (SM2). We pooled aggression data into a series of 3-day bins (i.e., rank assessment periods, SM1). Each perturbation cycle consisted of four 3-day rank assessment periods.

To find the dominance rank of each bird, we used both crowd and displacement aggression events collected for each rank assessment period. We included both crowd and displacement interactions in our rank calculation because our analyses indicated that we could treat these two behaviors as interchangeable (see SM3, using methods in van der Marel et al. 2021). We quantified rank for each individual using power, which is an interval measure bounded between 0 and 1 (Hobson and DeDeo

2015; Hobson et al. 2021). We calculated each individual's power score using a modified version of PageRank centrality implemented in the 'Domstruc' package (Hobson et al. 2021; Mønster et al. 2021). We created directed aggression networks for each assessment period. From these aggression networks, we used the function 'dom_ec' to calculate a centrality score ranging from 0 to 1 that included both direct and indirect aggressive interactions for each bird to all other birds in the network. A high centrality score (closer to 1) translates to a low power score (closer to 0), which could be interpreted that a bird with a low power score (low-ranking bird) receives aggression from other birds, whereas a bird with a high power score (high-ranking bird) is the instigator of agonistic interactions with other birds. We used the continuous power score measure instead of ordinal rank measures because in an ordinal ranking method, each individual is ranked in a linear order, which would not allow us to discern between cases where individuals have similar power scores. For example, individuals with rank positions 1 and 2 could have very similar or dissimilar power scores. For the analyses, we primarily used the continuous measure, power score, but we also incorporated ordinal ranking to highlight rank positions.

We used rank and power score information from the 3-day rank assessment period just prior to a removal day to determine which individual to remove. On each removal day, we trapped all the parakeets in the large and medium flight pens using mist nets, removed the focal parakeet for the current perturbation trial, and released the remaining birds back into the flight pen. As we caught and handled all birds on capture days, which is potentially stressful for the birds, we allowed the birds to recover in the afternoon after trapping and excluded the interactions recorded on capture days from our analyses. The removed focal bird was housed in its standard housing cage during the removal period (2 x 2m wire cage within an aviary), which is where the parakeets normally reside when they are not in the flight pen. The removed bird was housed near other parakeets (not involved in the social experiment) but away from the social group remaining in the flight pen. After eight days, we reintroduced the removed bird by releasing it back into the social group.

Testing whether social history underlies rank

We quantified all birds' rank and power score dynamics in the group throughout our social experiments. To test whether individuals could re-take their previous rank position in the dominance hierarchy following an absence, we quantified all parakeets' ranks and power scores in the group prior to each removal and following each reintroduction (e.g., rank assessment periods 2 and 5, Fig 1 and 2). The timing of the power score, relative rank, and weight recovery measurements of the focal bird of trial three in 2021 (rank assessment period 14) was slightly delayed by a tropical storm (see Figure 1 for timeline visualization and SM1 for additional timeline details). Before the storm, we moved all birds to their holding cages after rank assessment period 13 and released them back into the flight pen after two days. We calculated the focal bird's recovery using a two-day observation period (rank assessment period 14). We excluded rank assessment period 14 from the rest of our analyses, but we included the power score assessment for this period in Figure 1.

For all trials, we compared the focal birds' absolute power score changes to the remaining group members using a generalized linear mixed model (glmm) for a beta distribution. We used the absolute power score change as our dependent variable and an interaction between focal rank (either top-ranked or middle/low-ranked) and subject (either focal or remaining group member) as fixed factors. For our random term, we performed model selection to select the best random term as we had three different social groups, where some group members were used in different years. We included both a crossed term to account for birds that were used in both years (n = 14 birds) and a nested random term to account for the variation of birds within each group, only the crossed, and only the nested term. We found that the model with the crossed random term showed the lowest Akaike's Information Criterion (AIC*c*; Table SM4). We then selected whether the model with an interaction or without an interaction between focal rank and subject was best using AIC*c* (Table SM4). Model selection was performed using the package "AICcmodavg" (Mazerolle 2020). We used the package 'glmmTMB' (Brooks et al. 2017) and we checked the model fit using the ‘Dharma’ package (Hartig 2017). We then tested for significance for each fixed factor using the likelihood ratio test (Zeileis 2002).

Ruling out the effects of individual characteristics on rank

We compared our results for the importance of social history on rank to additionally test for the effect of individual characteristics on rank. We used bodyweight as an individual characteristic for two analyses (see SM5 for justification of bodyweight). First, we tested whether bodyweight was correlated with rank in these groups of monk parakeets. Second, we compared bodyweight changes across the trials to those of the remaining group members.

On removal days when all individuals were captured, we measured the bodyweight of each bird in grams using a digital scale. We excluded seven data points in 2021 and three data points in 2022 with incorrectly recorded bodyweights (SM5). We calculated the mean of each bird’s bodyweight across the capture events each year (mean ± SD = 110.1 ± 6.8 g in 2021, and 113.5 ± 7.9 g in 2022). We used a *t*-test to test for a sex difference in mean bodyweight as bodyweight was normally distributed. We tested for sex differences in bodyweight by genetically sexing all individuals with feather samples (IQGenetics, Inc., Miami, FL, USA) because monk parakeets are sexually monomorphic. Bodyweight did not differ between females (110.6 ± 1.2 (SE), n = 12) and males (112.8 ± 1.1, n = 16; T test: $T = -0.99$, p = 0.32), therefore we excluded sex from further analyses.

If individual characteristics underlie rank in the parakeets, then rank should be associated with individual characteristics and the birds that were used in both years should obtain similar power scores and relative rank positions in both years. To test this, we correlated power score and bodyweight just prior to removals per trial and per group using Kendall’s correlation because this correlation measure is robust for small sample sizes (Bonett and Wright 2000). We also used a Kendall’s correlation to test for a correlation in power scores and rank position that were standardized to account for the different group sizes (n = 20 and n = 11 birds) at the start of the social experiment in 2021 and 2022 of the 14 repeat birds. If bodyweight determines rank, we should see a change in bodyweight if rank is not correlated, therefore, to control for the effect of bodyweight on rank, we correlated bodyweight for the birds that were used in both 2021 and 2022. We performed a Pearson's correlation at two timepoints: 1) on the days that the birds were released into the flight pens, and 2) at the start of the social experiments.

We investigated the dynamics of rank with changes in bodyweight because removal/reintroductions could be stressful to the birds and could result in bodyweight changes. If bodyweight contributed to rank and power, a change in bodyweight could then result in a change to that bird's power score. To investigate the relationship between changes in bodyweight of the focal birds, we measured the bodyweight of all removed focal birds at several time points per trial: 1) at each group capture event (removal days), 2) just prior to reintroduction to the group, and 3) at the following group capture event (normally 8 days after reintroductions, except for trial 3 in 2021, see above). This method allowed us to detect changes in bodyweight that occurred during the removal phase, during the reintroduction phase, and across the entire 17-day trial. Due to a mistake during data collection, we had to exclude the bodyweights of the two focal birds of trial 3 in 2022 (SM5).

We tested for a difference in the percent bodyweight change during removal and reintroduction of the focal birds and between top-ranked and middle/low-ranked focal birds. We had one bird that was a focal bird both in 2021 and 2022 but testing the bodyweight change difference using group and ID as random factors resulted in a singular fit of the model. Therefore, we used an ANOVA with an interaction term between perturbation type (removal or reintroduction) and focal rank (top-ranked or middle/low-ranked). As a comparison to the weight change of the focal birds, we quantified the percent weight change (difference between weight at capture event 1 and 2, etc.) across all the birds in the group, with bodyweights measured at each group capture event for both focal birds and remaining group members. We used percent weight change as our dependent variable and an interaction term between subject (focal bird or remaining group member) and focal rank as our independent variables. We used trial as a fixed factor to account for bodyweight changes over time, with group and ID as a crossed random factor design as we had multiple weight measures per bird and we had multiple birds that were used in both years. We used 'fitDist' function in the 'gamlss' package (Rigby and Stasinopoulos 2005) to fit the best distribution of percent bodyweight change. We fitted our model in *gamlss* with a normal exponential t distribution. We visually inspected model fit and tested for significance using a likelihood ratio test.

Data availability

We performed all analyses in R version 4.1.2 (R Core Team 2021) and created the figures using ggplot2 (Wickham 2016). The data and code are available on the GitHub repository (*link will be provided after the double-blind review process*).

Results

We performed removal/reintroduction trials for a total of nine unique top-ranked birds, four unique middle-ranked birds, and two unique bottom-ranked birds. After data cleaning, we used over 100,000 aggressive events to quantify rank. In 2021 in our group of 20 birds, we perturbed three top-ranked birds and quantified rank and power scores using 24,317 agonistic interactions across 13 3-day bins, with 21.3 ± 2.3 (SD) hours of observation effort per rank assessment period. In 2022 in our two groups of 11 birds, we perturbed three top-ranked birds and three middle/low ranked birds in each social group and quantified rank and power scores using 42,280, and 42,402, interactions for group 1 and 2, respectively (SM2), over 18.5 ± 4.4 (SD, n = 26 bins) observation hours per rank assessment period.

Across all 15 trials and in all three of our social groups, none of the removed birds were able to re-take their previous rank immediately after reintroduction (Fig. 1 and 2, Table 1). During the 8 days after reintroduction, 13 focal birds (87%) increased their power scores but of these birds only five (38%) also gained rank positions (Table 1, Fig. 1 and 2). The model that best explained absolute power score changes after removal (the lowest AIC value) was explained by an interaction between focal rank and subject (Table SM5). The results for removed/reintroduced focal birds differed from the rank dynamics of other birds that remained within the social groups. The focal birds ($n = 15$) dropped much more in power score and showed greater absolute power score changes (mean ± SD = 0.15 ± 0.09, range [0.03-0.32]) than the birds that remained in the flight pen for the duration of the 17-day trial (0.04 ± 0.04, range [0.00005 - 0.37]; LR test: $\lambda = 51.51$, $p < 0.001$; Fig. 3). The interaction between focal rank and subject was not significant (LR test: $\lambda = 0.51$, $p = 0.5$).

We also found an effect of the removed parakeet's (focal bird's) rank on its power score immediately after reintroduction. Removal and reintroduction of top-ranked parakeets resulted in a greater absolute power score change (0.05 ± 0.06, range [0.0002-0.32]) compared to the middle/low-ranked removal trials (0.04 ± 0.05, range [0.00003-0.28]); LR test: $\lambda = 18.07$, $p < 0.001$; Fig. 3).

Table 1. Change in measured variables between different timepoints for each focal bird for (a) changes between removal and reintroduction (e.g., difference between rank assessment periods 5 and 2, Fig. 1) and (b) changes between reintroduction and the next focal removal (e.g., difference between rank assessment periods 6 and 5). Columns show changes in power score, ordinal rank, and weight (negative values indicate losses, positive values indicate gains and are highlighted in bold, 0 indicates no change).

				(a)			**(b)**		
Group	Trial	Focal rank	ID	Power score	Rank	Weight	Power score	Rank	Weight
2021	1	Top	BBB	-0.16	-20	**+0.40**	**+0.01**	0	-6.60
2021	2	Top	GPG[1]	-0.05	-16	-2.30	**+0.03**	**+7**	**+0.20**
2021	3	Top	OPP	-0.16	-20	**+0.57**	**+0.02**[2]	0[1]	-7.37[2]
2022-1	1	Top	PBO[1]	-0.08	-7	-8.19	-0.03	-1	-3.70
2022-1	2	Middle	OOO	-0.06	-4	**+2.90**	**+0.03**	0	-1.74
2022-1	3	Middle	PGG	-0.11	-4	**+1.46**	**+0.03**	**+1**	NA[3]
2022-1	4	Top	GPO	-0.22	-10	**+4.80**	**+0.16**	**+4**	-6.47
2022-1	5	Bottom	OPP	-0.03	0	**+3.93**	**+0.05**	**+1**	-1.03
2022-1	6	Top	BBB	-0.28	-10	-4.71	**+0.13**	0	**+1.82**
2022-2	1	Top	BBO	-0.19	-8	-6.68	-0.02	-1	-6.02
2022-2	2	Middle	OBB	-0.09	-3	-1.19	**+0.01**	0	-1.76
2022-2	3	Middle	PBP	-0.20	-5	**+6.58**	**+0.14**	**+1**	NA[3]
2022-2	4	Top	GOO	-0.19	-10	**+0.80**	**+0.05**	0	-1.77
2022-2	5	Bottom	OGO	-0.08	-1	-5.50	**+0.05**	0	**+2.61**
2022-2	6	Top	GOP	-0.32	-10	-3.66	**+0.10**	0	-1.78

[1] This bird was the same bird that was a top-ranked focal in 2021 and in 2022. None of the other 14 repeat birds were a focal in both years.

[2] The recovery values were calculated using a two-day observation period (rank assessment period 14, Fig. 1) collected after the birds were placed back into their holding cages for two days due to a tropical storm.

[3] We excluded an erroneous weight measure which did not allow us to measure the weight change after reintroduction.

Figure 1. Dominance rank changes over time for the group of 20 birds in 2021. Each rank assessment period includes power score assessments calculated over three days of observations. Three perturbation trials are shown where a top-ranked focal was removed and reintroduced. Each of the focal birds are highlighted with bolder power score lines and the insets represent the change in ordinal rank positions. Circles show the power scores (i.e., modified PageRank score) of focal birds prior to removals; diamonds show the power scores following reintroductions; colored dashed lines show the change in power score for each focal prior to removal compared to following their reintroduction to the group; grey dashed lines show removal points; grey solid lines show reintroduction points.

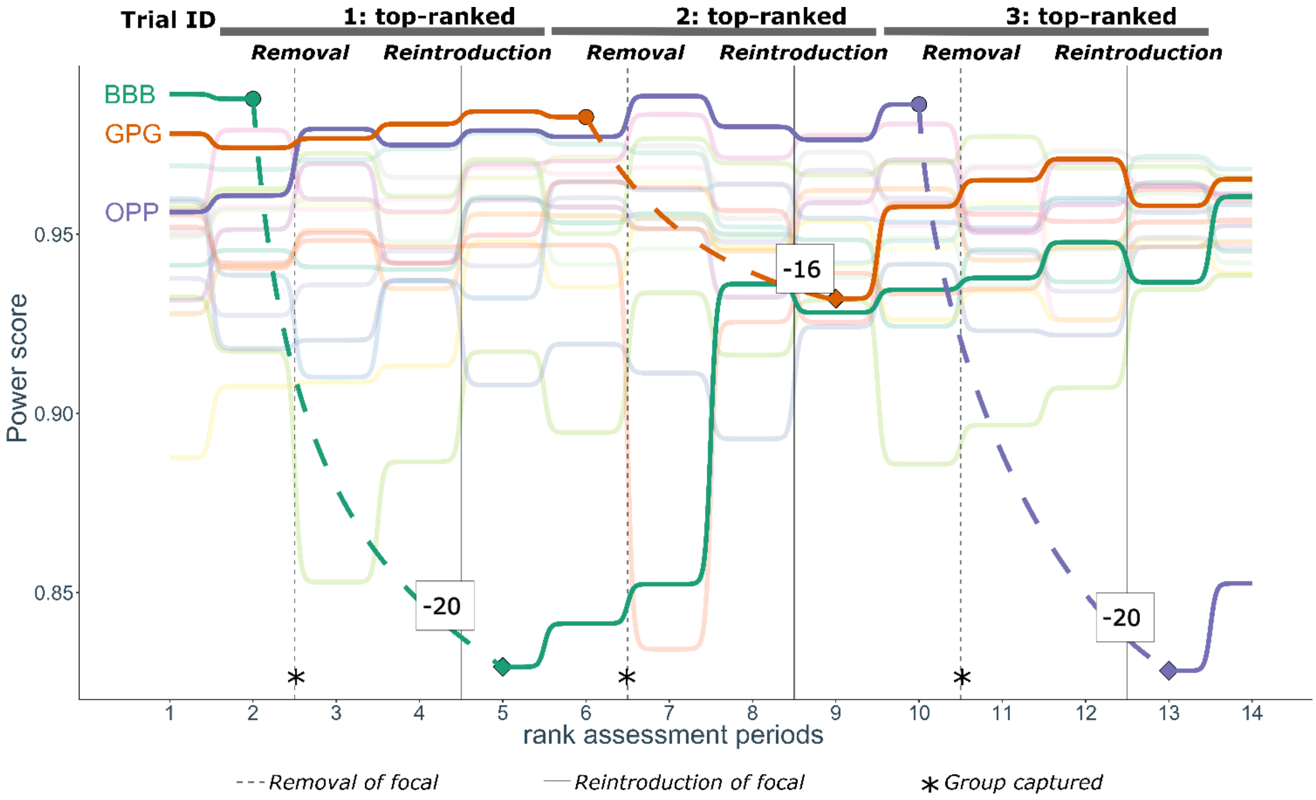
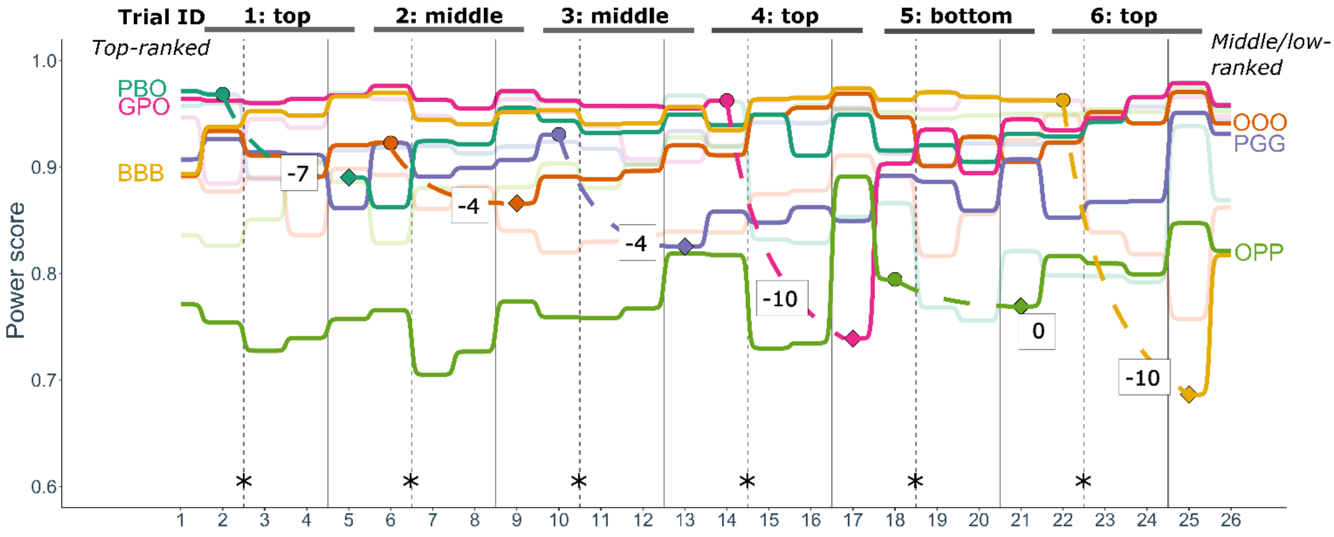


Figure 2. Dominance rank changes over time for the two medium groups of 11 birds in 2022. Each rank assessment period includes power score assessments calculated over three days of observations. Six perturbation trials are shown for each group where three top-ranked focal birds (‘top’) and three differently ranked focal birds (2 ‘middle’ and 1 ‘bottom’-ranked) were removed and reintroduced. Each of the focal birds are highlighted with bolder power score lines and the insets represent the change in ordinal rank positions. Circles show the power scores (i.e., modified PageRank score) of focal birds prior to removals; diamonds show the power scores following reintroductions; colored dashed lines show the change in power score for each focal prior to removal compared to following their reintroduction to the group; grey dashed lines show

removal points; grey solid lines show reintroduction points.

(a) Group 2022-1



(b) Group 2022-2

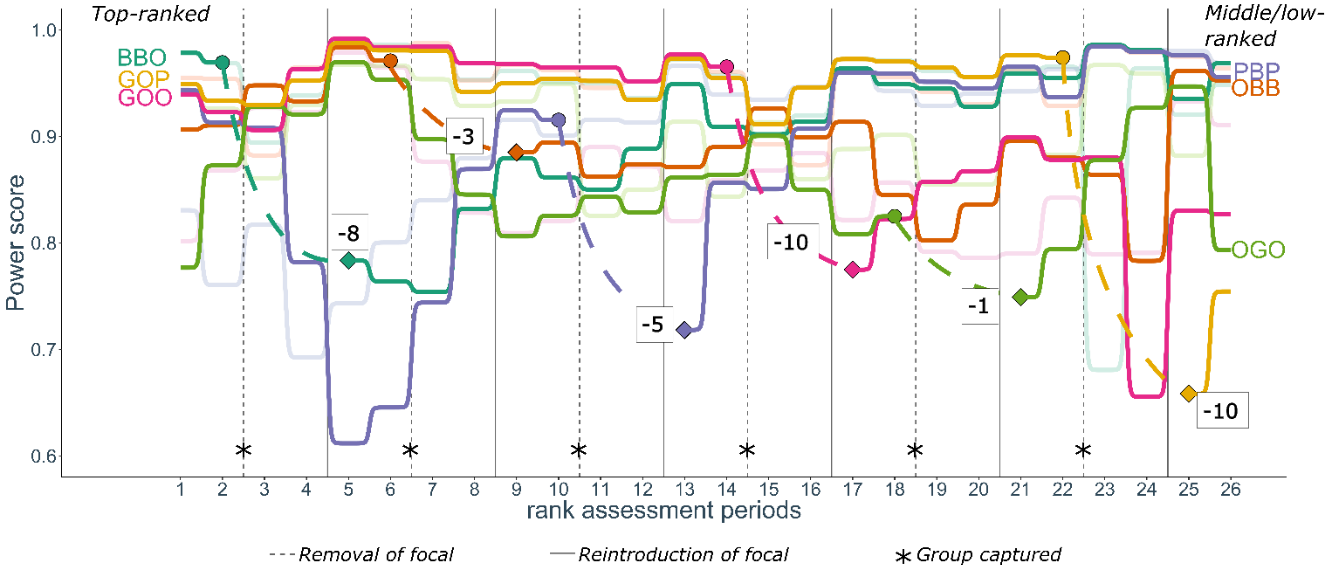
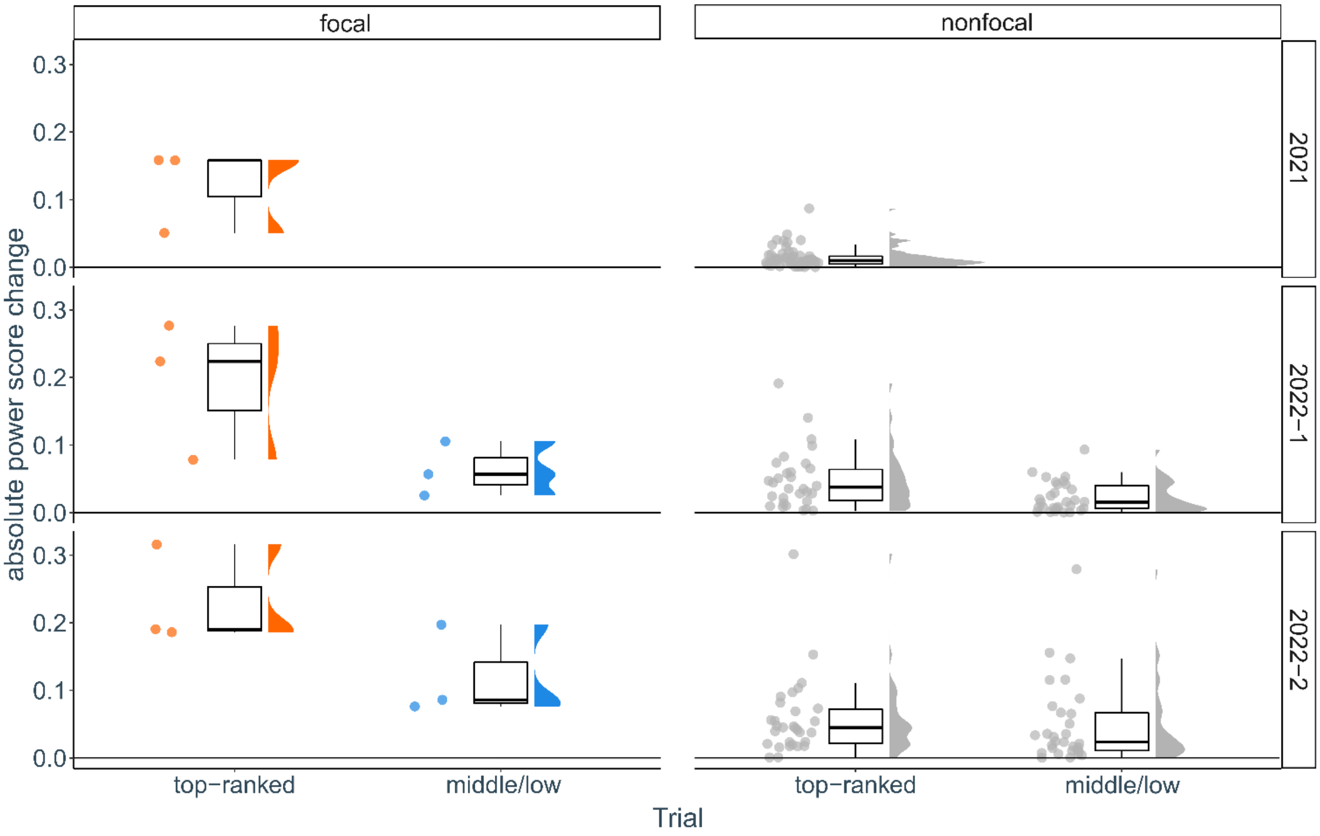


Figure 3. A raincloud plot of the change in absolute power score for focal birds and the remaining group members (nonfocal) by focal rank (top-ranked and middle/low-ranked). Absolute power score changes represent the power score change between the rank assessment periods upon reintroduction and the period just prior removals (e.g., rank assessment periods 5 and 2).

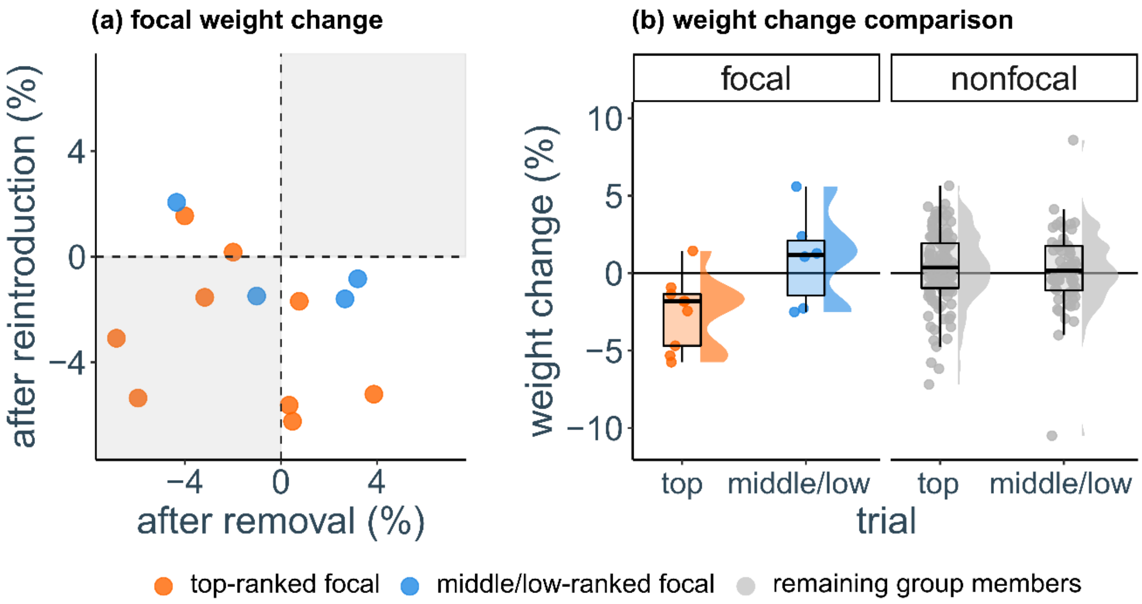


We found no consistent evidence that the individual characteristic, bodyweight, influenced rank. First, we rarely found a correlation between power score and bodyweight; birds in only one trial (trial 1 in 2021) out of 15 trials showed a significant correlation between bodyweight and power score (SM6). Second, for the birds that were used in both experimental years (n = 14 birds), we found that the power score or rank at the start of the experiment (3-day period prior to first removal; bin 2) did not correlate between the experimental years (power score: τ = -0.23, p = 0.28; rank: R = -0.26, p = 0.37), nor did it correlate during the period with the same number of days after initial introduction into the flight pens (power score: $\tau = 0.19$, $p = 0.39$; rank: $R = 0.21$, $p = 0.48$), but that bodyweights on the day that the birds were introduced into the flight pens and on the start date of the social experiment were significantly correlated between the experimental years ($R = 0.79$, $p = 0.002$ and $R = 0.62$, $p = 0.02$, respectively). Thus, power score changes occurred without changes in bodyweight. Both results indicate that rank is not correlated with bodyweight in these captive groups of monk parakeets.

When we tested whether bodyweight changed over time in the focal birds, we found no difference in percent weight change during the 8-day removal (mean ± SE = -0.61 ± 0.96 %) nor during the 8-day reintroduction period (-2.22 ± 0.76 %; $F_{1,24} = 1.9$, $p = 0.2$; Fig. 4a). We did find an effect of the rank position of the focal birds on bodyweight change ($F_{1,24} = 5.4$, $p = 0.03$; Fig. 4a), where the perturbation of a previously top-ranked focal bird resulted in a greater bodyweight loss (-2.42 ± 0.74 %) than of the control focal birds (0.55 ± 0.92 %); However, we found no interaction between removal or reintroduction period and focal rank ($F_{1,24} = 0.1$, $p = 0.8$; Fig. 4a).

When we compared the percent weight change across all the remaining group members (nonfocal birds in the group) across the 17-day trials to the weight change of the focal birds, we found a significant interaction in percent bodyweight change between focal rank and subjects (LR test: $\lambda = 8.22$, $p = 0.006$). The focal birds lost 1.36 ± 0.93 (SE) percent of their bodyweight during their respective trials, while the remaining group members (excluding focal birds for their respective trial) gained on average 0.31 ± 0.21 (SE) percent bodyweight per trial. Top-ranked focal birds had a significant decrease in percent bodyweight (mean ± SE = -2.96 ± 0.91 %) compared to increases for control focal birds (1.04 ± 1.48 %) and remaining group members in a top-ranked trial (0.36 ± 0.25 %) or control trial (0.23 ± 0.39 %; Table 1; Fig. 4b). Trial number did not have a significant effect on percent bodyweight changes (LR test: $\lambda = -0.48$, $p = 1$), and, therefore, bodyweight for all birds did not significantly change during the social experiment. The random factors group and bird ID explained a significant amount of variation in the bodyweight data (LR test: $\lambda = 5.75$, $p = 0.047$ and $\lambda = 0.0$, $p < 0.001$, respectively), which suggest that group and individual variation existed. Overall, the perturbation trials influenced the bodyweight of the top-ranked focal birds, but not the middle/low-ranked focal birds nor the remaining group members for both focal rank perturbations.

Figure 4. Bodyweight changes across time of the focal birds and across all individuals in the group. Panel (a) shows the percent bodyweight change for each focal following the removal period, comparing bodyweight at reintroduction to bodyweight on removal, and following the reintroduction period, comparing bodyweight at the next capture event to bodyweight on reintroduction. The shaded quadrants reflect where individuals either lost or gained weight after both removals and reintroductions. Panel (b) shows the percent weight change across capture events for the focal birds and all remaining group members ('nonfocal', excluding the focal birds). A positive weight change indicates weight gain, and a negative weight change indicates weight loss. Top-ranked trials are indicated in orange, the control trials in blue, and the nonfocals in grey for both trials.



Discussion

Using a social perturbation experiment, we show strong support that social history (the memory of past interactions) shapes rank in captive monk parakeets. We conducted two kinds of removal experiments. In 2021, we removed and consequently reintroduced only top-ranked focal birds and quantified the resulting rank dynamics. To differentiate between rank dynamics caused by the social perturbations from those caused by removing birds of high rank, we repeated the experiment in 2022, this time randomly selecting whether to remove a top-ranked or middle/low ranked bird during each removal. None of the removed birds could re-take their previous rank and all focal birds dropped significantly in power score immediately upon reintroduction. We also found that bodyweight was generally not associated with rank. These results are consistent with previous observational and computational studies in this species (Hobson and DeDeo 2015; Hobson et al. 2021). Our 2022 experiment, in which we removed individuals of different ranks in multiple groups, showed that all focal birds suffered rank loss and a drop in power score, which indicates that it was not the perturbation of only top-ranked birds that caused these changes. However, we found that these changes were more extreme for previously top-ranked birds. Top-ranked birds also lost significantly more percent bodyweight than control birds and the remaining group members. Focal birds eventually regained power score and rank over time despite not re-taking their previous rank position immediately upon reintroduction. The regaining of rank and power score by focal birds could indicate that social ascent and aggressive interactions may be costly (Fialkowski et al. 2021; Humphries et al. 2021; Milewski et al. 2022), take time to accomplish, and involve an understanding of current social dynamics and connections. Together, these findings provide strong support for the importance of social history in monk parakeets.

Another line of evidence, besides the perturbation trials, shows support for the social history hypothesis in the three monk parakeet groups. As we used 14 birds in both experimental years, we were able to follow their rank dynamics over a longer time frame and within different social group compositions. We did not find that power score and rank correlated between the two years, while bodyweight was correlated. As an illustration of year-to-year rank effects, the bottom-ranked bird in 2021 became the top-ranked bird in trial 1 in the next year (in group 2022-2). It is possible that another unmeasured individual characteristic, such as age, could have influenced these rank dynamics. However, we were unable to include chronological age in our analytical approach because the monk parakeets were captured from feral populations as adults (i.e., exact age unknown). Moreover, if other unmeasured individual characteristics influenced rank, our perturbation experiments should have shown that removed individuals could more easily and quickly re-take their ranks and we should have found a correlation between year 1 and year 2 ranks.

Additional factors could explain the rank dynamics we observed during the perturbation trial. The first potential mechanism is stress experienced during the removal and/or the reintroduction period. Focal birds might not re-take their rank position immediately if the removal period was stressful because of the potential separation from the social group. A response to a stressor (in this case, the removal from or reintroduction into the social group) could be decreased food intake or increased heat production and activity (Harris 2015), leading to changes in bodyweight. However, we found bodyweight of the removed birds did not decrease when we compared the focal bird's bodyweights on removal and at reintroduction. Experimental manipulation of bodyweight, for example, by artificial mass loading or by adding satellite tags, can affect dominance rank in some (Portugal et al. 2020) but not other species (Sergio et al. 2015). In our study, the loss in rank upon reintroduction is more likely due to the focal bird's history with its group members than bodyweight alone because half of the focal birds gained weight during removal and, thus, were heavier upon reintroduction. Birds may have gained weight during removal because the focal birds were not involved in intense movement (e.g., flight) and had more direct access to food than while in a flight pen with conspecifics. This lack of consistent bodyweight loss during the removals may indicate that removed birds were not overly stressed or negatively affected by the removal period itself. It is possible that some other unmeasured stress mechanism such as hormone levels could have changed over the 8-day removal period, but in that case, rank and power score loss for both top-ranked and middle/low-ranked removed birds should have been equally affected. In contrast, we found a stronger effect of removals on power score and rank in reintroduced top-ranked birds, which supports the effect of social history rather than a generalized effect across all perturbed focal birds.

Stress could also have influenced the rank and power score dynamics of focal birds in the period after reintroduction. However, only two (both top-ranked focal birds) out of 15 focal birds also lost power score during their reintroduction period, indicating that the majority of the focal birds could regain some amount of power after reintroduction. Top-ranked focal birds did lose significantly more weight during their reintroduction period than middle/low-ranked birds, but this may have occurred primarily because of the high physical activity due to displacement from the feeders in the first couple of days upon reintroduction as we found that the group focused their aggression on the reintroduced top-ranked focal bird in the first three days after reintroduction (van der Marel, Francis, et al. 2022). Increased aggression following reintroduction did not result in physical injury to any of the reintroduced birds (van der Marel, personal observation). Future studies could test whether this loss in bodyweight is more due to the remaining group members preventing focal birds from feeding when they are first reintroduced. Similar to the results during removal, we found a differential response to the reintroduction for top-ranked and middle/low-ranked birds, suggesting that our results support the effect of social history rather than a generalized effect across all perturbed focal birds. Overall, in combination with previous results showing that the outcomes of experienced and observed fights contained information about rank (Hobson and DeDeo 2015; Hobson et al. 2021), these results suggest that our measured individual characteristic was not the main driving factor of rank in captive monk parakeets.

A second potential mechanism that could explain the rank dynamics we observed during the perturbation trial is the role of social support. Having social support in the form of affiliative partnerships could buffer negative and stressful events (Cohen and Wills 1985; Seeman and Mcewen 1996), such as perturbations (Testard et al. 2021), and could improve rank and fitness (e.g., spotted hyenas, *Crocuta crocuta,* Strauss and Holekamp 2019). In the parakeet groups, relationships between the focal and the remaining group members may have affected the removed individual's ability to retake rank. Individuals that had strong and stable partnerships before removal and that can re-join on reintroduction may be able to reintegrate at a similar rank position in the hierarchy when they return from an absence. Further research is needed on the role that social support may play in the rank dynamics upon reintroduction.

By performing controlled experiments in captivity, we found that social history shapes rank, but we do not know to what extent captivity influenced our results (Webster and Rutz 2020). We do not think that captivity influenced bird behavior in our study as our results within our three captive groups were consistent with each other and with the results from two groups of long-term captives in 2015 (Hobson and DeDeo 2015). Additionally, dominance structure and social dominance patterns across species show no evidence that they are consistently affected by captivity (Shizuka and McDonald 2015; Hobson et al. 2021). Thus, the observed patterns consistently emerge despite changes in group size, cage size, habitat complexity, and the origins of the birds (long-term captives in 2015 and newly caught birds in this study). The captive experiments indicate that the parakeets have the capability of using social history and information about each other to make their aggression decisions and structure their groups, but whether they use these same behaviors to structure wild groups is still an open question. Social history might be important in shaping rank in wild groups of monk parakeets as it would allow faster formation of dominance hierarchies during integration of immigrants in species with fission-fusion dynamics (Hobson and DeDeo 2015; Shultz and Gersick 2016; Hobson et al. 2021), but this requires further investigation.

Using experimental social perturbations, we found that shorter-term social history matters in this potentially cognitively complex species. We found that interactions that occurred during the removal period had a greater effect on rank dynamics than interactions that occurred prior to removals. Yet, we do not know to what extent cognitive processing is required to respond to these perturbations or the duration that the birds were able to infer the rank of their group members. For example, even in systems where rank is based on individual characteristics (e.g., cichlid fish, *Astatotilapia burtoni;* Fernald 1977), cognitive ability and performance can vary with rank position (Wallace et al. 2022), suggesting that throughout the rank continuum, i.e., the various determinants that can influence rank from individual characteristics to social history (Holekamp and Strauss 2016), cognitive abilities may play an important role in rank acquisition and retention. A better understanding of the mechanisms that influence rank may provide insight into the role of cognitive processes and social systems on rank acquisition and maintenance.

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Data availability

The data and code are available on the GitHub repository (annemarievdmarel/Monk_rank_socialVSchar; van der Marel 2022).

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Supplemental Material

Perturbations highlight importance of social history in parakeet rank dynamics

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Supplemental Material 1. Group composition

Supplemental Material 2. Experimental schedule

Supplemental Material 3. Results decision framework pooling agonistic interactions

Supplemental Material 4. Model selection power score change

Supplemental Material 5. Justification of using body mass as individual characteristic

Supplemental Material 6. Correlation results of power score and body mass per trial

Supplemental Material 1: Group composition

Table SM1.1. The group composition of the three social groups. The social group in 2021 was comprised of 20 birds that were captured from feral population in southern Florida and the two groups of 11 birds each were comprised of birds previously used in 2021 and that were held in their holding cages in 2021. In total, 68.2% (n=14) of the birds were used in the social experiments in both years.

Band ID	**Sex**	**Site captured**	**Mark '21**	**Band ID '22**	**Mark '22**	**Group '22**
BB1248	male	Goulds	GPG	BB1248	PBO	1_west
BB1211	female	Florida City		BB1211[2]	PPO	1_west
BB1245	male	Perrine	OOO	BB1245	BBB	1_west
BB1251	male	Galloway	OPP	BB1257	GGP	1_west
BB1218	female	Florida City	PBO	BB1218	GPO	1_west
BB1252	female	Galloway	PPB	BB1252	POP	1_west
BB1242	male	Perrine	PPO	BB1242	OPO	1_west
BB1155	male	Florida City	PPP	BB1155	BOB	1_west
BB1157	male	Florida City		BB1157	OOO	1_west
BB1210	female	Florida City		BB1210	OPP	1_west
BB1212	female	Florida City		A200	PGG	1_west
BB1250	female	Goulds	GGG	BB1250	PBP	2_east
BB1246	female	Goulds	GGO	BB1246	OOP	2_east
BB1159	male	Florida City	GOO	BB1159[3]	PPP	2_east
BB1156	male	Florida City	GOP	BB1156	GOP	2_east
BB1158	male	Florida City	OBB	BB1158	BBO	2_east

BB1255	male	Galloway	POO	BB1255	GPG	2_east
BB1241	female	Perrine	POP	BB1241	GOO	2_east
BB1152	female	Florida City		BB1152	GGG	2_east
BB1215	female	Florida City		BB1215	OBB	2_east
BB1214	male	Florida City		BB1214	OGO	2_east
BB1216	male	Florida City		BB1247	POO	2_east
BB1253	male	Galloway	BBB	BB1253[4]		
BB1240	male	Perrine	BOB	NA[1]		
BB1154	male	Florida City	OGO	NA[1]		
BB1254	female	Goulds	OOP	BB1254		
BB1249	female	Goulds	PBB	NA[1]		
BB1244	male	Perrine	PGG	NA[1]		

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[1] The “NA” represents birds not present in our 2022 field season.

[2] This bird was included in group 1 instead of BB1217 (excluded due to health concerns) on day 1

[3] This bird was included in group 2 instead of BB1253 on day 2.5

[4] This bird was excluded on day 2.5 due to health concerns, swapped with BB1159

Supplemental Material 2: Experimental schedule

Table SM2.1 The experimental setup of our social perturbation experiment in monk parakeets. Each perturbation cycle lasted 16 days with an 8-day removal and an 8-day reintroduction period. We observed in total for 6 days during the removal and 6 days during the reintroduction period. We pooled three days to assess rank (rank assessment periods). In 2021, we found 6393 (22.1%) duplicated agonistic events. In 2022, in group 1 we found 6170 (19%) and in group 2 8196 (19%) duplicated agonistic interactions.

Start date	End date	Trial	Period	Days	Hours observed	Birds	Agonistic events
2021-04-05	2021-05-18	na	Initial group formation + social structure stabilization	41			
2021-05-16	2021-05-18	1	rank assessment 1	3	22.85	20	1977
2021-05-19		1	capture 1	1			
2021-05-20	2021-05-22	1	rank assessment 2	3	21.82	19	2111
2021-05-23	2021-05-24	1	days off	2			
2021-05-25	2021-05-27	1	rank assessment 3	3	22.58	19	1738
2021-05-28	2021-05-30	1	rank assessment 4	3	26.7	20	2928
2021-05-31	2021-06-01	1	days off	2			
2021-06-02	2021-06-04	2	rank assessment 5	3	21.38	20	1856
2021-06-05		2	capture 2	1			
2021-06-06	2021-06-08	2	rank assessment 6	3	20.95	19	2218
2021-06-09	2021-06-10	2	days off	2			
2021-06-11	2021-06-13	2	rank assessment 7	3	19.68	19	1887
2021-06-14	2021-06-16	2	rank assessment 8	3	18.37	20	1713
2021-06-17	2021-06-18	2	days off	2			
2021-06-19	2021-06-22	3	rank assessment 9	3.5	20.97	20	1615
2021-06-23		3	capture 3	1			
2021-06-24	2021-06-26	3	rank assessment 10	3	17.82	19	897
2021-06-27	2021-06-28	3	days off	2			
2021-06-29	2021-07-01	3	rank assessment 11	3	21.38	19	2131
2021-07-02	2021-07-04	3	rank assessment 12	3	20.98	20	2005
2021-07-05	2021-07-08	3	captures 4 and 5; birds moved to holding cages due to tropical storm	2			
2021-07-09	2021-07-10	3	Rank assessment 13	2	14.43	20	1241

Start date	**Trial**	**Rank assessment period**	**Hours observed**	**Birds**	**Agonistic events**	
					Group 1	Group 1
2022-01-19		1	35.05	11	2175	2050
2022-01-26	1	2	16.07	11	1725	1692
2022-01-30	1	3	11.70	10	1245	1715
2022-02-04	1	4	18.83	10	1068	1071
2022-02-07	1	5	17.90	11	1500	2507
2022-02-12	2	6	18.48	11	3142	2080
2022-02-16	2	7	18.78	10	1458	1459
2022-02-21	2	8	19.20	10	1505	1395
2022-02-24	2	9	19.22	11	1817	1374
2022-03-01	3	10	19.55	11	1472	1182
2022-03-05	3	11	19.40	10	1171	1031
2022-03-10	3	12	9.77	10	806	582
2022-03-14	3	13	14.45	11	1503	1709
2022-03-19	4	14	17.07	11	1067	1294
2022-03-23	4	15	19.23	10	2098	1714
2022-03-28	4	16	20.37	10	1899	1105
2022-03-31	4	17	19.68	11	3366	2066
2022-04-05	5	18	19.00	11	2595	1676
2022-04-09	5	19	16.70	10	1623	1025
2022-04-14	5	20	17.72	10	1668	1380
2022-04-17	5	21	19.98	11	1328	1600
2022-04-22	6	22	20.30	11	924	1665
2022-04-26	6	23	19.45	10	1370	2254
2022-05-01	6	24	21.28	10	1373	2060
2022-05-04	6	25	18.90	11	1443	2985
2022-05-09		26	13.25	11	939	1731

Supplemental Material 3. Results decision framework pooling crowds and displacements

We used the observations of crowd and displacements for the 3-day bins during the stable phase with 20 birds (bins 1, 5, and 9) in 2021 to determine whether we could pool the two behaviors into one agonistic behavioral context following the methods as described in van der Marel et al. (2020).

Step 1: Here, we determined whether basic characteristics of crowds and displacements were similar. We found that crowds were the rarer behavior type but both behaviors were highly correlated (Table. SM3.1). These results provide initial support for pooling behaviors, allowing us to move to Steps 2 and 3 of our decision framework.

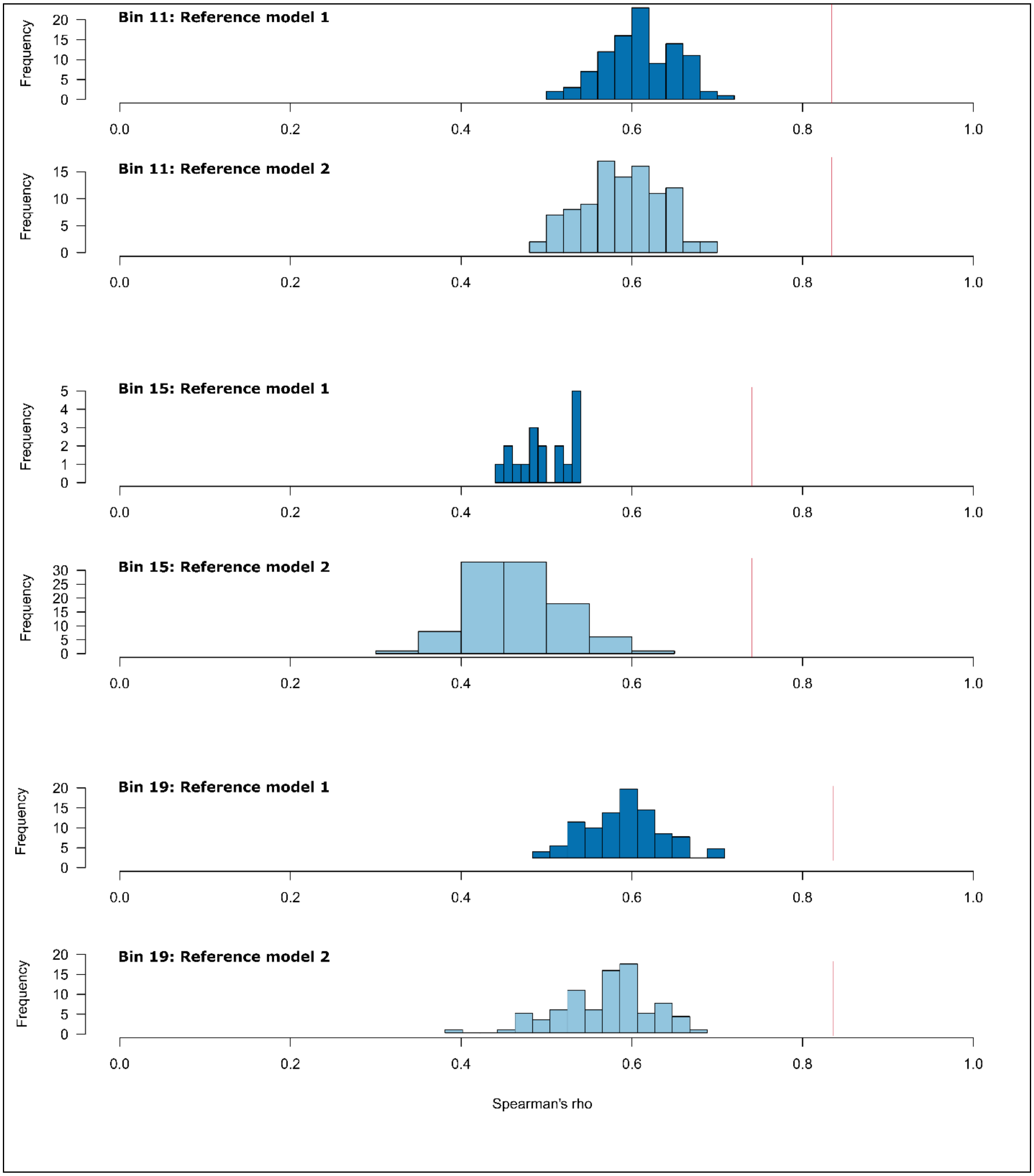
Table SM3.1. Descriptive summary of crowds and displacements for the 3-day bins during the stable phase with 20 monk parakeets.

Bin	Crowds	Displacements	Total aggression	Mantel correlation
1	1210	1797	3007	0.83
5	819	1150	1969	0.74
9	700	981	1681	0.82

Steps 2 and 3: Here, we created 2 reference models. Reference model 1 allowed us to see whether the behaviors are interchangeable and reference model 2 told us whether the results of reference model 1 is due to uneven number of events for crowds and displacements.

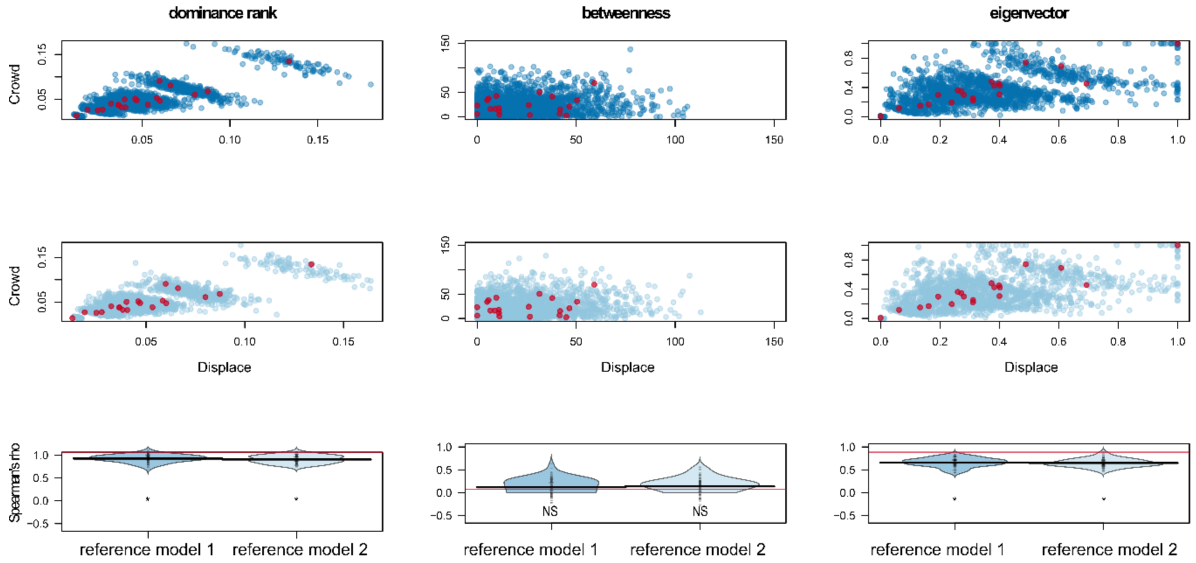
First, we investigated whether the aggression matrices of crowds and displacements were correlated. We found that the observed value fell higher than the distribution of both reference models for all 3 bins (Fig. SM3.1). These results are another indication that the two behaviors are functionally similar.

Figure SM3.1. Mantel correlations of the aggression matrices of each run for reference model 1 (dark blue) and reference model 2 (light blue) with the observed correlation depicted with the red vertical bar. For all three bins and both reference models, the observed correlation was much higher than the randomized correlation, suggesting that we could pool the 2 behaviors.



Second, we studied whether the behaviors were interchangeable using different individual-level social measures, such as modified eigenvector centrality as the measure for dominance rank, betweenness centrality, and eigenvector centrality. Here, we provide the results of bin 11. The results are similar for all 3 bins, where dominance rank and eigenvector centrality are highly correlated for both reference models and the observed values were significantly higher than the reference model distributions (Fig. SM3.2). Betweenness centrality was not correlated, and the observed value fell within the reference model distribution. These results tell us we could pool the 2 behaviors.

Figure SM3.1. This figure shows from the left to right columns the following individual social metrics: modified PageRank as dominance measure, betweenness centrality, and eigenvector centrality. The top and middle rows are scatterplots between crowds and displacement for reference model 1 (dark blue) and reference model 2 (light blue), respectively. The bottom row represents the matrix correlation strength for each reference model. Observed values are indicated in red. An asterisk shows where the observed correlation fell outside the correlation values of the reference models and NS shows that the observed value fell within the reference model distribution.



Third, we investigated whether the behaviors were interchangeable using different group-level hierarchy measures, such as linearity, steepness, and triangle transitivity. We received some contrasting results (Fig. SM3.3). The pooled values were significantly different from the behaviors separately, except for triangle transitivity. Furthermore, only displacements were the same for the observed data as the reference model distribution. This tells us that triangle transitivity is the same, but that linearity and steepness values are lower for the behaviors separately compared to when they are pooled.

Finally, we investigated the social dominance patterns for crowds, displacements, and crowds and displacements combined. Again, we ran 100 reference models and compared the observed pattern to the percentage of runs with the reference model dominance patterns. The observed patterns corresponded with the majority of reference model runs (Fig. SM3.4). Plus, for 2/3 of the trials, the dominance patterns were the same for crowds, displacements, and both behaviors pooled.

Figure SM3.2. This figure shows the group-level hierarchy metrics, linearity, steepness, and triangle transitivity from the left to right column, respectively. The top row shows the results for bin 11, the center row for bin 15, and the bottom row for bin 19. Observed values are indicated in red and the distributions show values from reference model runs. The observed value falls within the distribution of the reference model runs when P<0.05 (noted as asterisks) and falls outside the range when P>0.05 (noted as NS).

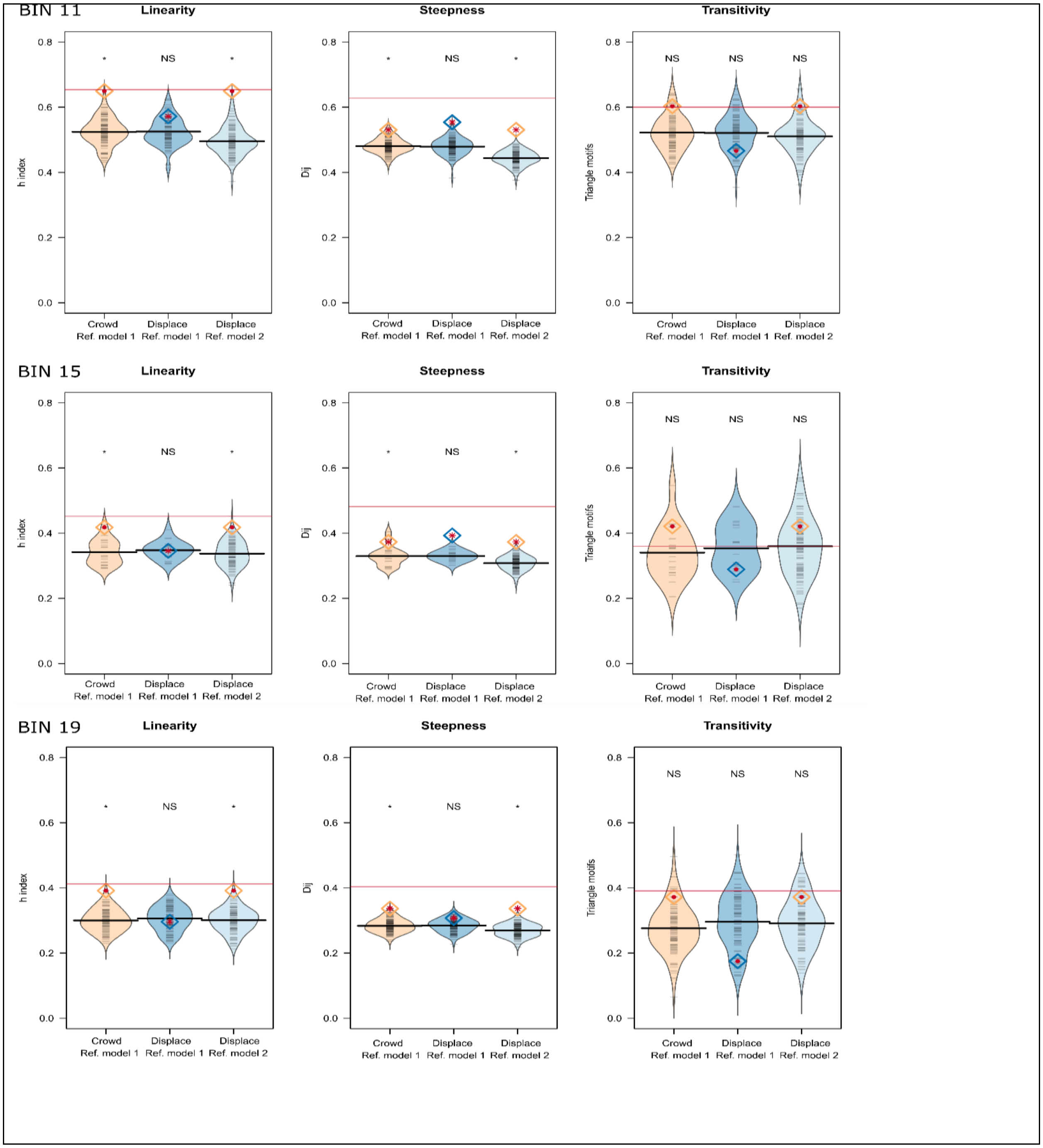
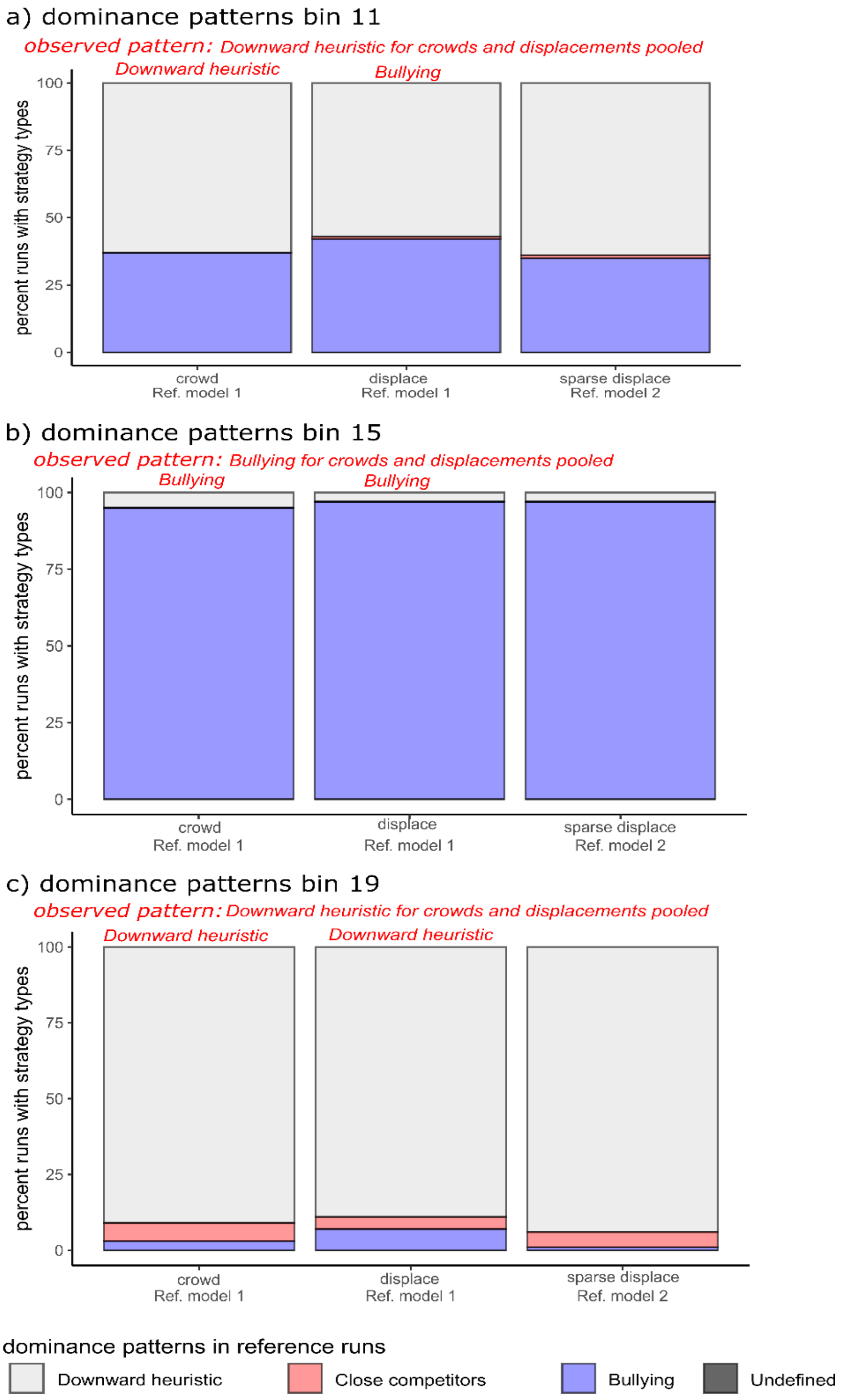

BIN 11
Linearity
Steepness
Transitivity
BIN 15
Linearity
Steepness
Transitivity
BIN 19
Linearity
Steepness
Transitivity
h index
Dij
Triangle motifs
0.0
0.2
0.4
0.6
0.8
*
NS
Crowd
Ref. model 1
Displace
Ref. model 1
Displace
Ref. model 2

Figure SM3.3. The percent runs with dominance patterns of the reference models. The observed patterns are the same in 2 out of 3 stable periods (bin 15 and 19) for crowds and displacements separately and when pooled (indicated in red in italics). Plus, the observed patterns are the same as the majority reference runs. These results suggest we could pool the behaviors.



Supplemental Material 4. Model selection power score change

Table SM4. AIC model selection using the package "AICcmodavg" for the random term in the model looking at power score change between focal birds and remaining group members and top-ranked and control trials.

Model	K	AIC*c*	delta	weight	Cumulative weight	logLik
Abs power ~ rank * subject + (1|group) + (1|ID) + (1|group/ID)	7	-888.68	0	0.28	0.28	451.64
Abs power ~ rank * subject + (1|group) +	**7**	**-888.68**	**0**	**0.28**	**0.55**	**451.64**

Supplemental Material 5. Justification of using body mass as individual characteristic

Justification of using body mass as individual characteristic

We decided to use body mass as an individual characteristic over other morphometric measurements for multiple reasons: 1) mass change can happen on a short timescale while morphometrics take time to change. Within the timespan of the trials (e.g., 48 days in 2021 and 82 days in 2022), body mass could have changed while we would not expect other morphometric measures (e.g., tarsus) to change; 2) other morphometric measurements were not as reliable measures in monk parakeets. For example, tarsus is not a reliable measure in parakeets (EAH, personal observation) and wing cord and tail length are variable because feathers can tear due to captivity. We took two culmen measurements that refer to the beak size (Hobson and DeDeo 2015): culmen length, which is affected by captive conditions because the animal care personnel trimmed their beaks when necessary, and culmen width, which would be a measure that we could have used besides body mass as a proxy of body size and to create a relative body size measure. Below we provided the analyses to determine whether body size or condition underly rank and the causality of the direction of this relationship using our 2021 data. As we did not find significant results using this dataset, we did not perform the analyses using our 2022 data.

Culmen width repeatability and relative body size assessment

We used the repeatable package to assess repeatability of culmen width. Culmen width (mean ± SD = 12.93 ± 0.61 mm, n = 4 -5 measures per ID) was significantly repeatable (R = 0.34, se = 0.12, CI = [0.092 – 0.549], $p < 0.001$). Body mass and culmen width were positively correlated (Pearson's correlation: r^2 = 0.22, p = 0.03). As we did not expect culmen width to change throughout the duration of the social experiment, we performed a correlation between average culmen width and power at the end of the initial group formation period prior to first removal. We then got the residuals of the linear regression of body mass and culmen width as a proxy for relative body size and performed the same analyses for body mass in the manuscript using relative body size instead.

Exclusion of body mass data points

Upon checking our morphometrics data frame, we identified multiple instances, where we potentially reported a wrong body mass. These instances may have been due to incorrect reporting of the mass of the bird bags or the mass of bird bag and bird together and on some days we had strong winds which could have caused an incorrect weight. Other times, we may not have tared the scale correctly. As a precaution, we excluded the following points in our dataset:

- BBB on 2021-04-05 with a bird bag weight of 112.08 g, resulting in a bird weight of 105.8 g, and on 2021-07-05 with a bird weight of 86.8 g, which are lower compared to the bird's other weights (always above 110g).
- POP on 2021-06-23 with a bird bag weight of 129.94 g, resulting in a bird weight of 121.4 g, which is higher compared to other weights of this bird (always below 107 g).
- BOB on 2021-07-08 with a bird bag weight of 169.77, resulting in a bird weight of 109.1 g, which is lower compared to other weights of this bird (always above 100 g).
- OOO on 2021-06-23 with a bird weight of 72.82 g, which is low compared to other weights of this bird (always above 115 g)
- PPB on 2021-04-05 with a bird weight of 86.2 g, which is low compared to other weights (always above 100g)
- GPG on 2021-04-05 with a bird weight of 89.2 g, which is low compared to other weights (always above 110g)
- PBP on 2022-03-14 with a bird weight of 139.55, which is high compared to other weights (always below 130g)

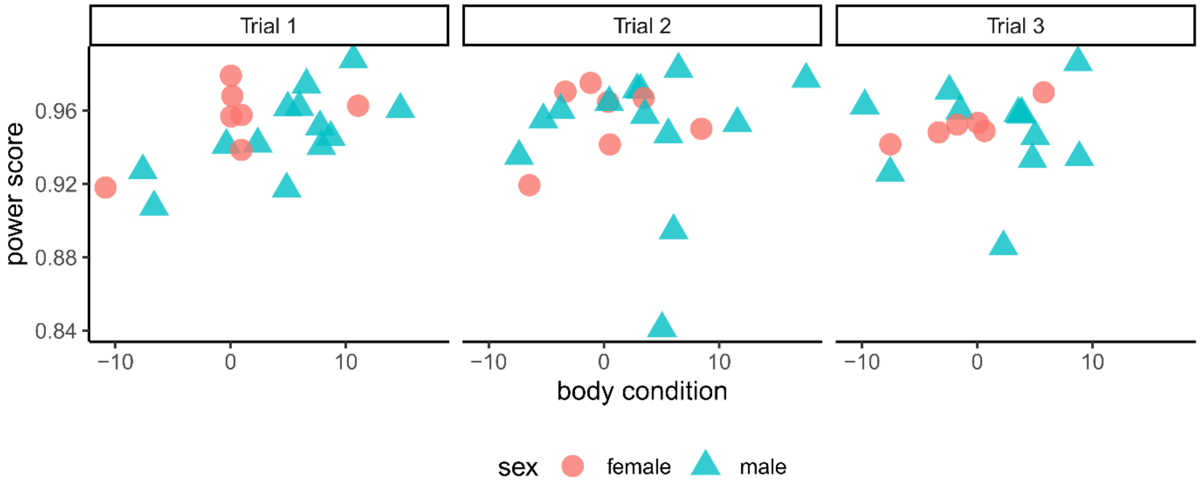
- PGG on 2022-03-14 with a bird weight of 145.18, which is very high compared to others (always below 120g)
- OOO on 2022-05-12 with a bird weight of 97.50, which is very low compared to others (always above 106g). This bird did have a long infection, we still excluded this weight as the next weight is 106g again.
- PPO on 2022-02-15 with a bird weight of 92.88, which is very low compared to others (always above 106g).

Does culmen width or relative body size underly rank?

We did not find a correlation between average culmen width and power at the end of the initial group formation period, when social structure was stable (Kendall's tau = -0.001, p = 0.97). Therefore, we did not include culmen width in further analyses.

We found partial support for a relationship between relative body size and power. Relative body size and power were correlated at trial 1 (Kendall's tau = 0.33, p = 0.05), but not at trial 2 (tau = 0.08, p = 0.63) or trial 3 (tau = 0.09, p = 0.65; Fig. SM6), which was similar to the body mass results in 2021 (Table SM6).

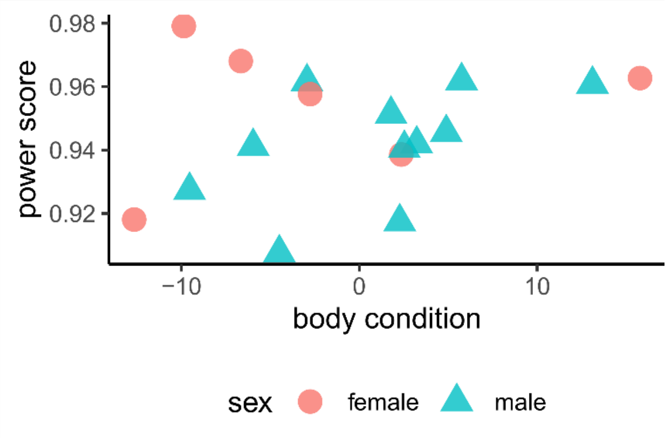
Figure SM5.1. Assessing the relationship between relative body size and power score in monk parakeets. The figure shows the correlation between relative body size and power score just prior to removals 1, 2, and 3, respectively. Females are denoted with pink circles and males with blue triangles.



Can we determine the direction of causality?

We investigated the direction of causation of the association. First, we tested whether initial relative body size predicted power at the end of the initial group formation period. We measured their body weight and culmen width at five different capture events. Relative body size was on average 0.41 ± 6.9 g. We found that relative body size did not predict power prior to first removal (LRT: $\lambda = 0.38$, $p = 0.54$, estimate ± SE = 0.01 ± 0.01, Fig. SM5.2).

Figure SM5.2. Assessing the direction of causality between rank and relative body size. Beta regression of initial relative body size in gram on power score calculated during the 3-days at the end of the initial group formation period just prior the first removal. Females are denoted with pink circles and males with blue triangles.



Second, we tested whether relative body size could be an outcome of rank position. Power and relative body size change were not correlated both when the focal was included (trial 1: Kendall's tau = 0.17, p = 0.32; trial 2: Kendall's tau = -0.02, p = 0.94) and excluded (trial 1: Kendall's tau = 0.08, p = 0.68; trial 2: Kendall's tau = -0.03, p = 0.90). We found that 40 % and 45% of the birds for trials 1 and 2, respectively, followed the prediction that if rank influences relative body size, then birds should either show an increase in relative body size and an increase in power or alternatively, show a loss of power and a decrease in relative body size (Fig. SM5.3). Compared to the relative body size change of the remaining birds in the flight pen across the entire perturbation trial, all three focal birds showed relative body size loss (trial 1 change in relative body size = -5.61; trial 2 = -2.69; trial 3 = -5.79) but this loss was similar to the loss of some of the remaining group members (trial 1: mean ± SD = -0.67 ± 2.81 [-4.89, 4.40]; trial 2: -1.92 ± 3.31 [-8.59, 3.39]; trial 3: -5.04 ± 3.37 [-11.23, 0.49], n = 17; Fig. SM5.4).

Fig. SM5.3. The correlation between power score changes and relative body size changes for trials 1 and 2, respectively. The colored points represent the ordinal rank of the individuals at the start of the trial with top-ranked birds in red and bottom-ranked birds in blue. The grey rectangles represent the quadrants where we would expect the datapoints to fall in if relative body size is an outcome of rank. The grey rectangle in the left bottom corner represents when individuals lose rank and relative body size and the grey rectangle in the right upper corner represents when individuals gain relative body size and rank. We found that 40 % and 45 % of birds for trial 1 and 2, respectively followed our prediction that if individuals lose or gain power they will then show an decrease or increase in relative body size.

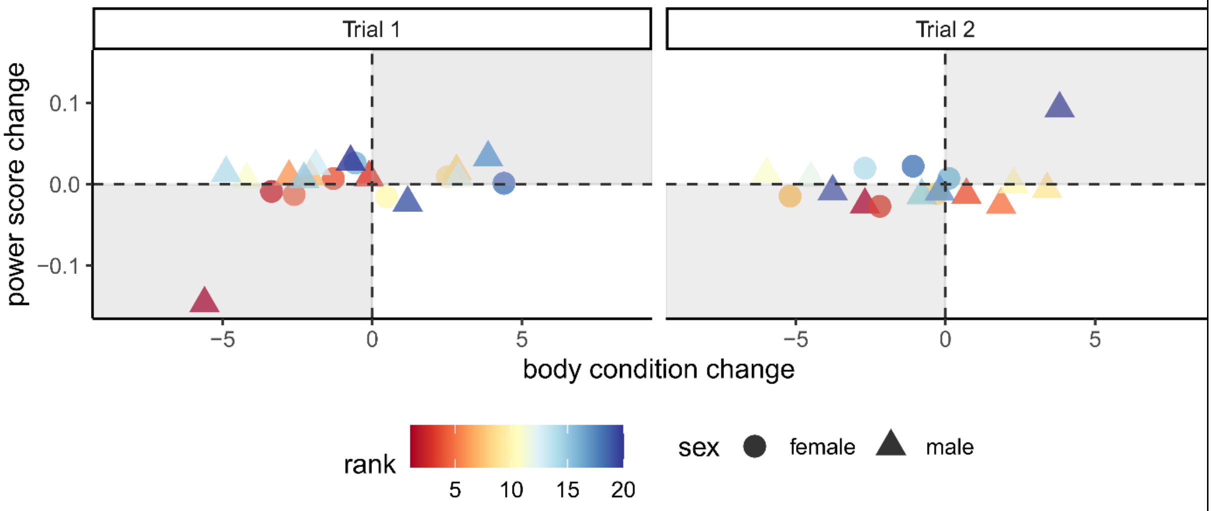
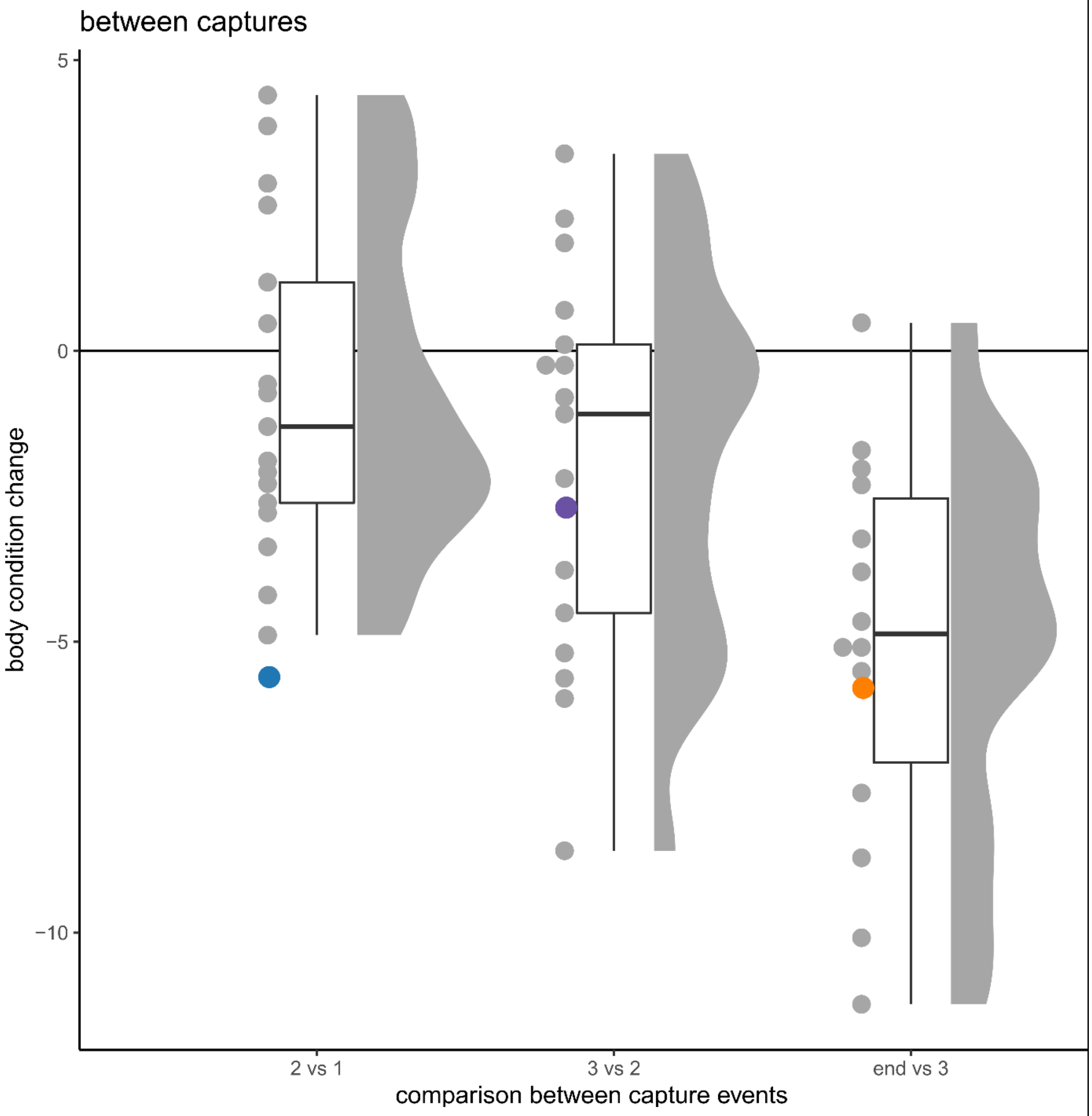


Fig. SM5.4. Relative body size changes across time in the focal birds and across all individuals in the group. The relative body size change across capture events for all group members with the focal birds highlighted in color. A positive value indicates an increase in relative body size and a negative value indicates a decrease in relative body size.



Supplemental Material 6. Correlation results of power score and body mass per trial

Table SM6. Correlation between power score and body mass per group and per trial. Significant correlations are in bold.

group	trial	Kendall's tau	p-value
2021	1	**0.33**	**0.04**
2021	2	0.19	0.26
2021	3	0.08	0.65
2022-1	1	0.13	0.65
2022-1	2	0.13	0.65
2022-1	3	-0.13	0.65
2022-1	4	-0.27	0.28
2022-1	5	-0.24	0.36
2022-1	6	0.13	0.65
2022-2	1	-0.16	0.54
2022-2	2	-0.09	0.76
2022-2	3	0.02	1.00
2022-2	4	-0.16	0.54
2022-2	5	-0.09	0.76
2022-2	6	-0.20	0.45

Figure SM6. Correlation between power score and body mass for each group and trial separately.