Long-term stability of dominance hierarchies in a wild parrot with fission-fusion dynamics

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Abstract

Dominance hierarchies allow animals living in stable groups to limit the costs of fighting over access to resources. However, little is known about whether hierarchies are maintained in more open, fission-fusion societies, where individuals interact with large numbers of individuals. We recorded social associations and aggressive interactions in a highly social, communally roosting parrot, the sulphur-crested cockatoo (*Cacatua galerita*). By following 515 individuals across three neighbouring roosts and recording social interactions during foraging, we show that sulphur-crested cockatoos form clear linear hierarchies. Hierarchies are primarily roost based, but also incorporate birds from outside the roost. We find that an individual's dominance rank is affected by sex and age, with males ranking higher than females and adults ranking higher than juveniles. Finally, we find despite highly dynamic social associations (fission-fusion dynamics) among individuals, hierarchies are stable, with

dominance ranks being highly repeatable across years. This study demonstrates that stable and/or closed group membership are not pre-requisites for dominance hierarchies to emerge.

Introduction

Contests over limited resources are a fact of life for most social species (Ward and Webster, 2016), and can potentially be costly for the animals involved. As a result, many animals have evolved mechanisms to assess competitors, allowing them to target a subset of potential competitors to engage with and decrease overall level of aggression (Drews, 1993; Arnott and Elwood, 2009; Dehnen et al., 2022). Dominance hierarchies are one such mechanism, and dominance rank is thought to give the most precise information on competitive ability (Parker, 1974). However, the formation of dominance hierarchies requires memory of repeated interactions between individuals (Hobson, 2020). This complexity means that dominance hierarchies are generally thought to only emerge in animals that form stable groups with relatively closed membership. This is because in more open societies, where social associations are drawn from a potentially large pool of individuals, the cognitive challenge of keeping track of many individuals over extended periods of time is thought to limit the ability (de Silva et al., 2017) — or alleviate the need (Boehm, 1999) — for individuals to form hierarchies.

Assumptions about limits to social cognition are challenged by growing evidence that animals can form and maintain differentiated social relationship and complex multi-level social structures (Papageorgiou et al., 2019; Papageorgiou & Farine, 2021; Camerlenghi et al., 2022). In multi-level societies (where groups interact with other groups) and in societies where individuals form large fission-fusion groups (Smith et al., 2008; Loretto et al., 2017; Aplin et al., 2021; Penndorf et al., 2022), individuals have been shown to maintain long-term preferred social associations with both in- and out-group members, likely based on individual recognition (Izawa & Watanabe, 2008; Kerth et al., 2011; Carter et al., 2013; Loretto et al., 2017; Aplin et al., 2021). However whether animals living in societies containing hundreds of potential social associates can also form and maintain stable dominance hierarchies remains under-explored.

Parrots represent an excellent taxa in which to investigate this question. Many parrot species exhibit strong pair bonds, while also interacting within communal roosts and with individuals from the broader population, with the resulting variable flock sizes ranging from several individuals to aggregations of thousands (Hardy, 1965; Noske et al., 1982; Rowley, 1990; O'Hara et al., 2019). Given this variable sociability, coupled with longevity (Wirthlin et al., 2018; Smeele et al., 2022) and complex cognition (Olkowicz et al., 2016), parrots are often referenced in discussions on social complexity (e.g., Krasheninnikova et al., 2013; Hobson et al., 2014; Aplin et al., 2021). Yet studies of dominance patterns among wild parrots remain rare (but see Diamond and Bond, 1999; Penndorf

et al., 2022), and it has often been assumed that species which form large communal roosts cannot have stable dominance hierarchies (Noske et al., 1982). Studies in captivity are more common, but results are mixed: some species form linear or quasi-linear hierarchies (e.g., budgerigars: Soma and Hasegawa, 2004; cockatiels: Seibert and Crowell-Davis, 2001; Senegal parrot: Lantermann, 1998) and others not (e.g., keas: Tebbich et al., 1996, blue-fronted amazons: de Souza Matos et al., 2017). The most detailed examination of this question comes from a series of captive studies on captive monk parakeets, revealing that groups of 11-21 individuals can form linear social hierarchies based on memory of past interactions (Hobson et al., 2014; Hobson and DeDeo, 2015; Hobson et al., 2021; van der Marel et al., 2023). However, groups in captivity are necessarily much smaller and more stable than those in the wild, and captivity has been shown to induce the formation of linear hierarchies even in egalitarian species (Horová et al., 2015; but see Boucherie et al., 2022). Wild studies are therefore vital to our understanding of dominance interactions in parrots.

Here, we investigate the potential for dominance hierarchies in wild sulphur-crested cockatoos (SC-cockatoos; *Cacatua galerita*. SC-cockatoos are large, long-lived parrots that live in year-round communal roosts of 50-1000 birds (Aplin et al., 2021). Within roosts, SC-cockatoos display fission-fusion dynamics with variable flock sizes (Noske et al., 1982; Styche, 2000). Birds also regularly forage with individuals of different roosts, and can engage in between-roost movements (Aplin et al., 2021; Penndorf et al., 2022). Yet, despite these fission-fusion dynamics, SC-cockatoos maintain long-term social relationships beyond the pair bond that are strongly suggestive of social recognition, including with kin and non-relatives, and with birds from other roosts (Aplin et al., 2021; Penndorf et al., 2022), suggesting that they should also have the capacity to form dominance hierarchies. In this study, we address four aims. First, we record aggressive interactions from 515 individuals across three neighbouring roosts and ask whether roosting-communities of wild SC-cockatoos form linear dominance hierarchies. Second, we test for individual predictors of dominance rank, including age and sex. Third, we test the repeatability of dominance ranks for moving individuals across the visited locations. Forth, we re-measure interactions across (i) two periods over two months (July and September 2019), and (ii) two periods over 3 years (2019-2022) to assess the short- and long-term stability of any emergent hierarchies.

Methods

Study population

The study was conducted at three neighbouring roost-sites in north Sydney, Australia (Table S1). At each roost site, birds were habituated to the observer and then individually paint-marked with non-toxic dye (Marabu Fashion Spray, MARABU GmbH) using methods detailed in Penndorf et al. (2022). In addition to paint-marked birds, 144 birds had previously been wing-tagged at the Royal

Botanic Gardens as part of an ongoing citizen science study *Big City Birds* (Davis et al., 2017; Aplin et al., 2021). The number of marked birds at each site varied from 42 - 165. Age (juveniles: <7 years, adults: >7 years) and sex of birds were assessed by eye-colour (Berry, 1981). Additionally, feathers were collected, from which DNA was extracted for molecular sexing and to match individuals across the two study periods.

Social data collection

Data on social associations and aggressive interactions were collected from all three sites in 2019 over two 10 day periods (July 8-20 and September 19 to October 2), and at on site (Clifton Gardens) in 2022 over 12 days (July 7-20). During these periods, birds were attracted to forage on the ground by scattering small amounts of seed over an approximate 385-500m^2 area of grass in parks close to the roost (300-680m distance). Foraging flocks were then observed daily for 2.5 to 3 hours. During each daily sample, the identity of all birds present — e.g. identifiable within the study area — was recorded every 10 minutes (Altmann, 1974). Between presence scans, aggressive interactions were recorded using all occurrence sampling (Altmann, 1974). For each interaction, we recorded the time and the identities of winners and losers.

Presence scans were collated and used to construct social networks using a gambit-of-the-group approach and a simple ratio to weight edges between 0 (never observed in the same group) and 1 (always observed in the same group) (Cairns & Schwager, 1987; Farine & Whitehead, 2015). We then identified social network communities using the (*igraph* package, Csardi, Nepusz, et al., 2006). These social network communities clearly correlated to roosting groups, and so we assigned the roost membership (residency) of each bird according to which social network community they were assigned to (Figure 1a).

Dominance hierarchies

We calculated a separate dominance hierarchy for each of the three roost-sites and observation periods. In order to obtain reliable dominance hierarchies, we only included individuals with ten or more agonistic interactions at a given roost-site (BA: N_{ind}=126; CG: N_{ind_2019}=93, N_{ind_2022}=59; ; NB: N_{ind}=74; Sánchez-Tójar et al., 2018). Hierarchies were calculated using randomized Elo-ratings (R-package *aniDom*, Sánchez-Tójar et al., 2018; sigma: 1/300, K: 200, randomisations: 10,000). We measured the robustness of the hierarchy by using the functions *'repeatability by splitting'* and *'repeatability by randomisation'*. Furthermore, we assessed the transitivity of the hierarchy following McDonald and Shizuka 2013 and Shizuka and McDonald 2015 (see Section S1).

To test whether rank was correlated with residence status, sex or age, we ran a generalised linear mixed model using the R-package *lme4* (Bates et al., 2015). We tested whether standardised rank was predicted by age, sex or residency. Since individuals could appear in the hierarchies of several

sites and across years, we included site (BA, CG 2019, CG 2022, NB) and individual ID as random variables.

To assess the stability of dominance hierarchies over time, we calculated the hierarchy at each roost location separately for each observation period (July and September 2019 for short-term stability; 2019 and 2022 at Clifton Gardens for long-term stability), incorporating information about prior dominance scores into hierarchy inferences, following suggestions from Strauss and Holekamp (2019a). Using the *DynaRankR*-package (Strauss and Holekamp, 2019a), we tested dyadic similarity between hierarchies between each time period at each site and each randomisation of the Elo-Rating (randomisation = 10,000). To calculate the random expectation, we created 10,000 hierarchies for each site and time period by random sampling, before calculating the dyadic similarity obtained through random sampling. Finally, using the *rptR*-package (Stoffel et al., 2017), we tested the individual repeatability in dominance rank between each roost they visited.

All analysis were conducted in R v 4.3.0 (R Core Team, 2023).

Results

The number of birds included in the hierarchy at each site (i.e. $\geq$10 observed interactions) varied between 59 and 126 (Table S1). We recorded 6,402 (2019, 3 sites) and 2,087 (2022, 1 site) aggressive interactions across all birds, of which 5,447 and 1,935 respectively were between individuals that were included in the same dominance hierarchy ($N_{ind2019}$ = 265, $N_{ind2022}$ = 59). Most agnostic interactions were between males ($N_{males2019}$ = 114, $N_{interactionsmales2019}$ = 1,590, $N_{interactionsknownsex2019}$ = 3,607, $N_{males2022}$ = 25,$N_{interactionsmales2022}$ = 848, $N_{interactionsknownsex2022}$ = 1,960).

Cockatoos form clear dominance hierarchies

We found that, within roosting communities, SC-cockatoos formed robust and highly transitive hierarchies (robustness: Figures 2a,b, S2 a,c,d,f & Table S2; transitivity $\geq$ 0.8 — Table S3). Further evidence for the robustness of the hierarchies comes from focusing on individuals present in the dominance hierarchies of several roosting communities. We found that these individuals were repeatable in their dominance rank across the different roosts (R=0.56 [0.20-0.78], P=0.003 — Figure **??**), with simulations showing that this result was not due to sampling (see Supplementary material S2, Figure S1).

Predictors of dominance rank

Sex and age were significant predictors of rank. Males ranked higher than females (β= -0.43; P<0.001 Figure S2 a,c,d,f), and adults ranked higher than juveniles (β= -0.14; P=0.006). When repeating

the same analysis for each sex separately, we found again that age (β_{males}= 0.38, P_{males}<0.001, $\beta_{females}$= 0.21, $P_{females}$0.07) correlated with dominance rank.

Steepness of the hierarchy

Given the sex-based segregation of the dominance hierarchies, and that most interactions occurred within individuals of the same sex, we calculated the steepness of the hierarchies separately for each sex. In male hierarchies, individuals typically had a chance of >60% to win an aggressive interaction against a male one rank lower than themselves (p >0.6; Figure 1b-e). However, this probability increased relatively rapidly with increasing rank difference, reaching 0.9 with a rank difference between 4 and 16 (Figure 1b-e). In females (hierarchy only possible at Clifton Gardens in 2019 and 2022), the probability of winning against an individual of one rank below or above was more variable (2019: 0.5, 2022: 0.8), and reached 0.9 for a rank difference of 3 (2022) or 6 (2019) (Figure S3a,b).

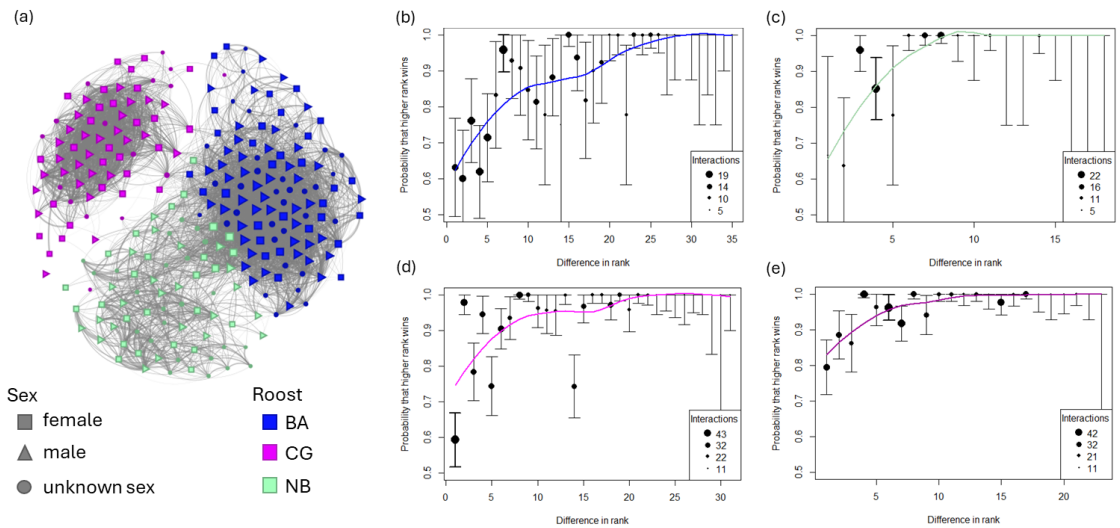

Figure 1: Social association network and steepness of social hierarchies. (a) Social network of Sulphur-crested cockatoos in 2019, constructed using a gambit-of-the-group approach and a simple ratio to weight edges between 0 (never observed in the same group) and 1 (always observed in the same group) (Cairns & Schwager, 1987; Farine & Whitehead, 2015). The colour of the nodes represented the three network communities identified using the *igraph* package (Csardi, Nepusz, et al., 2006) (Blue: BA, pink: CG, green: NB). The shapes of the nodes represents the sex of the individuals (square: female, triangle: males, circles: individuals of unknown sex). The graphic was constructed in Gephi (Bastian et al., 2009). For visual clarity, only edges above 0.1 are represented. (b-e) The steepness of the male social hierarchy is represented at 3 roosting locations (b: BA, c: NB, d-e: CG) across two years (b-d: 2019, e: 2022)

Stability of dominance hierarchies over time

Within each roosting community, dominance ranks were highly repeatable over a period of two months (July-September 2019; similarity >0.81, Table S4), which was significantly higher than expected by chance (R ≈ 0.5, Table S4). Similar repeatability was found when repeating the analysis within each age (juvenile/adult) and sex (males/females) class (Table S4), suggesting that this effect was not driven by predictable age and sex differences in dominance rank. In the roosting community visited again after a period of 3 years 2022, dominance ranks were remarkably similar in their repeatability (2019-2022, similarity: 0.84 [0.83-0.86], random expectation: 0.50 [0.43-0.57], Figure 2c, Table S4).

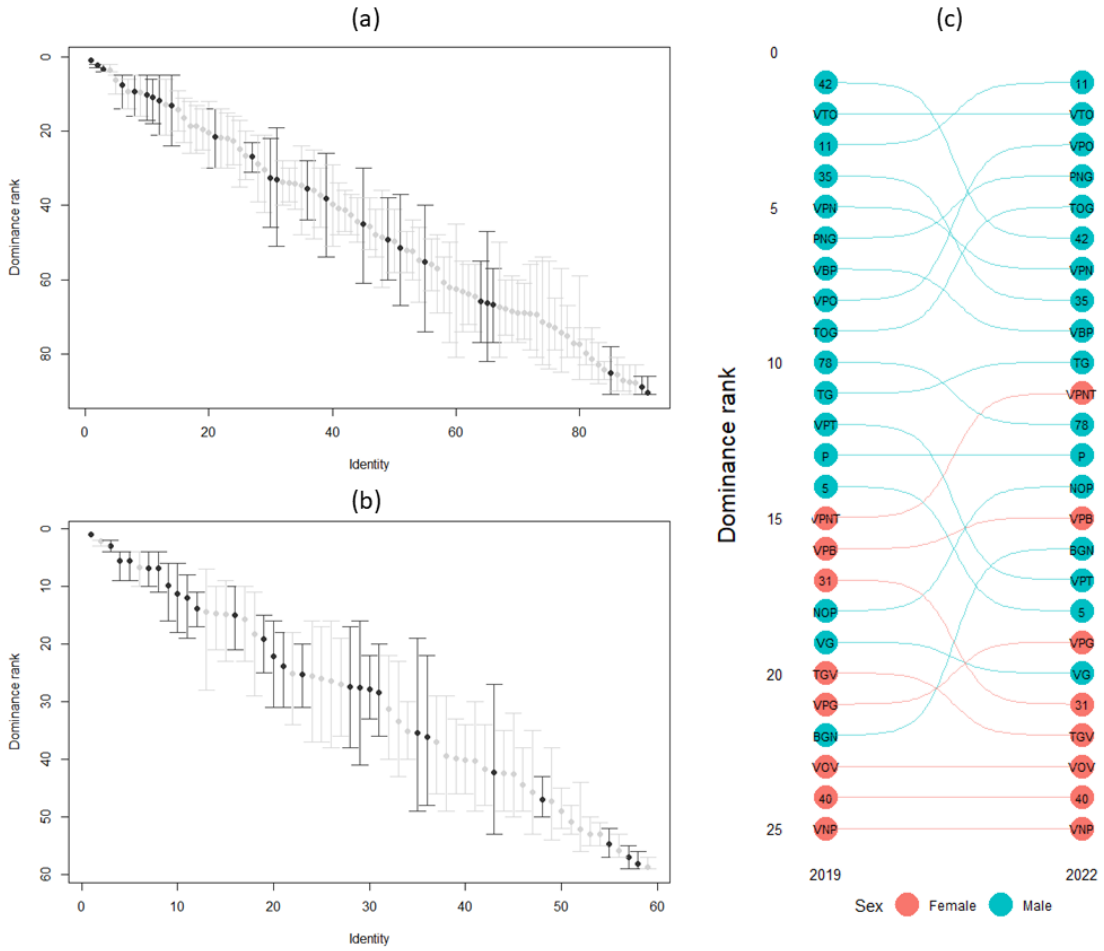

Figure 2: Dominance hierarchy at Clifton Gardens in 2019 (a) and 2022 (b). Individuals present in both study periods are shown in dark grey, and changes in their relative dominance rank across years is shown in (c). Males are represented in blue, and females in red.

Discussion

We found that, despite their largely open social structure, SC-cockatoos formed clear dominance hierarchies. These hierarchies were structured by sex and age, with males and adults higher in the hierarchy than females and juveniles. We also found that hierarchies were stable across periods of months to years. Our findings imply that wild SC-cockatoos can keep track of an impressively large number of conspecifics. The inferred hierarchies in our population in 2019 included 59, 74 and 126 individuals, suggesting that SC-cockatoos of our study population can deal with at least 100 conspecifics. If so, this would constitute a memory for conspecifics comparable to that of ravens (Boucherie et al., 2022), elephants (McComb et al., 2000) and humans (Hill and Dunbar, 2003, but see Lindenfors et al., 2021).

Whether hierarchies rely purely on social recognition and memory of past interactions requires further exploration. For example, in a sex- and age-segregated hierarchy such as found in our study, a categorisation of dominance relationships (e.g. only remembering the exact dominance ranks of conspecifics of the same age and sex) would significantly reduce cognitive requirements that comes with making social decisions in an open society with significant fission-fusion dynamics (Aureli & Schino, 2019). In our case, this rule would reduce the requirement for individual recognition substantially, for example to 19 (1 site, NB) to 77 (all sites) individuals for adult males. However it should also be noted that our roost sizes, while typical for our study population, are relatively small for SC-cockatoos, where roost sizes have been reported as reaching well over one thousand individuals. Further study is needed to determine what strategies animals can use to reduce the cognitive demands of living in dynamic societies, and whether stability and/or linearity of hierarchies break down at larger social scales.

Further evidence for the social cognitive ability of SC-cockatoos comes from individuals that exhibited social mobility between roosting communities (Penndorf et al., 2022). Some individuals in our study were present in two or three dominance hierarchies, and their ranks were significantly repeatable across roosting communities. These results suggest that individuals are likely to be familiar with individuals across a much broader social landscape than just their own roosting community. Further, if hierarchy is memory based, it also suggests that such individuals can deal with up to 300 conspecifics across at least three social contexts.

Recent studies have demonstrated the importance of social relationships in the acquisition and maintenance of dominance ranks. For example, dominance ranks in captive monk parakeets rely on social history, rather than individual factors (van der Marel et al., 2023). In this case, it is suggested that this is because individuals rely on social support to achieve rank (Strauss & Holekamp, 2019b) and buffer against stressful events (Cohen & Wills, 1985; Testard et al., 2021; van der Marel et al., 2023). Our study extends these finding by suggesting that individuals may be able to use social memory (e.g. past exposures to specific roosting communities) to maintain dominance ranks in

large, open societies, and that their memories can be expressed in two or more hierarchies (or social communities).

Wild SC-cockatoos can form stable long-term relationships (Aplin et al., 2021), and maintain some social relationships even after dispersal into different roosting communities (Penndorf et al., 2022). Our results build upon these previous findings by indicating that SC-cockatoos also form and maintain clear and stable dominance relationships with a large number of conspecifics, and retain their dominance rank over periods of at least three years. Taken together, these studies provide ample evidence that large-brained bird species that exhibit fission-fusion dynamics, such as common ravens (Boeckle and Bugnyar, 2012) and SC-cockatoos (this study) possess substantial cognitive ability that allows them to navigate a complex social landscape with both within- and between-community social interactions. Future studies should attempt to elucidate the cognitive load of maintaining dominance hierarchies in such systems, with the potential to substantially contribute to ongoing debates about the evolution and ecology of socio-cognitive complexity.

Data accessibility

All the raw data and scripts used in this study will be made available upon publication.

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Supplementary material

S1 Transitivity of the hierarchy

In order to assess the transitivity of the hierarchy, we used a directed 1/0 matrix, based on the majority of wins (McDonald and Shizuka, 2013), with the modification that when two individuals won the same number of contests against each other, they both received scores of 1 (Shizuka and McDonald, 2015). This produced a directed network where a dominant-subordinate relation was represented by an edge directed from the dominant to the subordinate individual. We used the package *compete* (Curley, 2016) to infer transitivity of dominance relationships both at group level, and within each sex. Emphasis was on the proportion of transitive triangles relative to all triangles (Pt, defined by McDonald and Shizuka, 2013) is given by:

$$P_t = \frac{N_{transitive}}{N_{transitive}+N_{cycle}}$$

where $N_{transitive}$ is the number of transitive dyads, and N_{cycle} is the number of cyclic triangles. In a random network, P_t is expected to be 0.75 (McDonald and Shizuka, 2013). Therefore, transitivity was scaled so that it runs from 0 for the random expectation to 1 (all triangles are transitive), by the following triangle transitivity metric (t_{tri}):

$$t_{tri} = 4 \times (P_t - 0.75)$$

S2 Simulations

To assess the repeatability of dominance rank between resident and visited roost, we based the structure of the simulated data on the observational data, keeping constant: (i) the overall number of individuals in the population (N=277) and in the hierarchy of each roost site, and (ii) the number of moving individuals (defined as appearing in the dominance hierarchy of either 2 (N=25) or 3 (N=2) roosting communities.

Each iteration comprised six steps. 1) A dominance rank was randomly attributed to each agent, resulting in hierarchy spanning across the entire sub-population (N= 277) 2) Each agent was randomly assigned to a roost, keeping the distribution of the original dataset (N_{BA}=126 individuals; N_{CG} = 91; N_{NB}=77). 3) Each agent was randomly assigned a sex class, keeping the same number of males, females and individuals of unknown sex as in the original data set (N_{males} = 92; $N_{females}$ = 73; $N_{unknown}$ = 112) 4) Moving individuals, e.g. individuals appearing in two (N=25) or three (N=2) dominance hierarchies were randomly selected. For those individuals, we assigned one resident roost and one (or two) visited roosts. 5) Based on their population-level dominance rank, individuals were

re-ranked within their assigned roost and sex-class. We then calculated the standardized dominance rank (]0-1], with 0 being the highest ranking agent, 1 the lowest ranking) 6) Lastly, for the moving individuals, we calculated the repeatability of the dominance rank between their resident and visited roost(s) using the *rptR*-package (Stoffel et al., 2017)).

We conducted 1000 iterations. The results are presented in Figure S1.

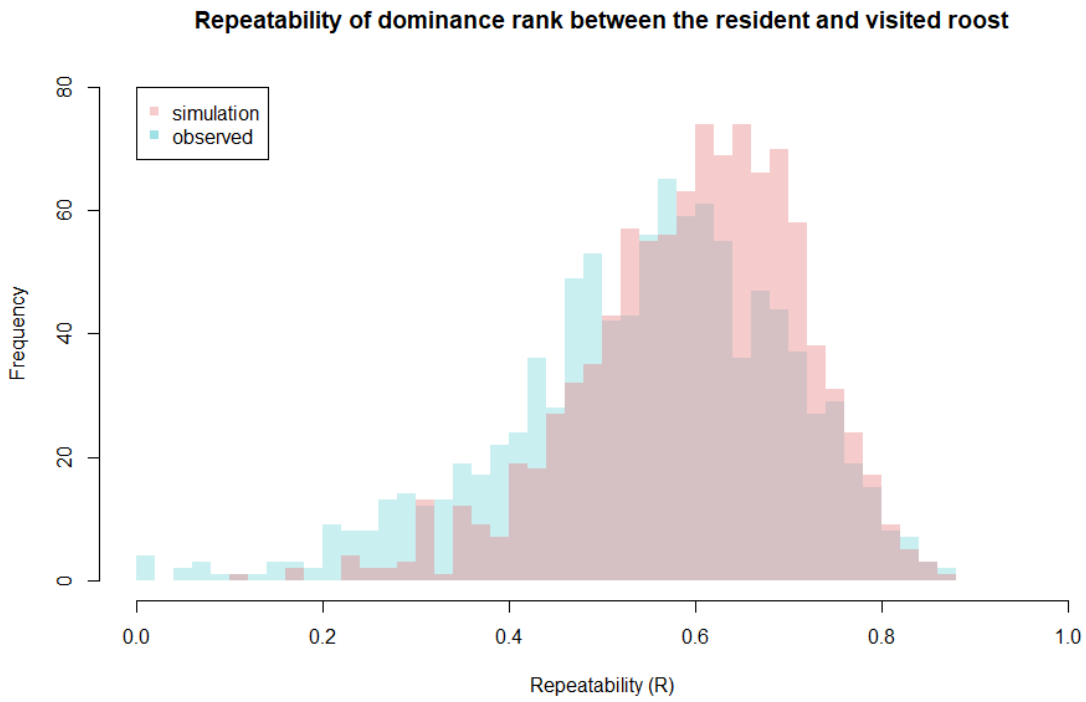

Figure S1: Repeatability of between the dominance rank of moving individuals at their resident vs visited roost. The observed data is plotted in blue, the simulated data in red.

Table S1: Location of the three study roosts and the estimated number of SC-Cockatoos at each site. The two letter code between parentheses represents the abbreviation for each roost site. At each site, we conducted roost counts by attracting birds to the ground at dawn, and recording the number and identities of all birds present. These roost counts were then used to estimated the number of birds at each site, as well as the percentage of marked birds (2019). As individuals regularly visit other different sites, the number of birds marked at one specific site can be larger than the number of individuals roosting at this location. P: paintmarked; W: wingtagged; R: recognizable feature. For Northbridge, the number between brackets represent the number and percentage of marked individuals of the satellite roost.

Year	Roosting site (abbreviation)	GPS location	Number of marked birds	Roost size	Percentage marked
2019	Balmoral Beach (BA)	-33.828494, 151.253983	209P, 12W, 6R	88-165	94-96%
2019	Clifton Garden (CG)	-33.841444, 151.252889	86P, 12W, 1R	42-111	92-95%
2022	Clifton Garden (CG)	-33.841444, 151.252889	92P, 13W, 0R	NA	NA
2019	Northbridge (NB)	-33.817167, 151.221694	78P, 2W, 4R	56-72 (+21-27)	93-98 % (100%)

Table S2: Uncertainty of SC-cockatoo social hierarchies measured at each of the three roost sites. Correlations above 0.8 (repeatability by randomisation) and 0.5 (repeatability by splitting) suggest robust hierarchies (Sánchez-Tójar et al., 2018)

Year	Roosting site	Repeatability by randomisation	Repeatability by splitting (CI)	$N_{individuals}$	$N_{interactions}$
2019	BA	0.96	0.80 (0.75-0.85)	126	1,737
2019	CG	0.98	0.88 (0.84-0.91)	93	2,735
2022	CG	0.97	0.86 (0.80-0.91)	59	1,935
2019	NB	0.97	0.77 (0.70-0.84)	74	1,005

Table S3: Transitivity of aggression networks at SC-cockatoo group level, calculated for all individuals present at one site (overall), or within each sex.

Year	Roosting site	Overall	Males	Females
2019	BA	0.80	0.8	/
2019	CG	0.85	0.88	0.73
2022	CG	0.88	0.99	0.74
2019	NB	0.88	0.96	/

Table S4: Dyadic similarity in social hierarchy within months (July and September 2019) or years (2019-2022), calculated using the *DynaRankR*-package (Strauss & Holekamp, 2019a)

Level	Time period	Roosting site	Similarity	Random expectation
All ages and sexes	July & September 2019	BA	0.81 [0.79-0.84]	0.5 [0.42-0.58]
	July & September 2019	CG	0.84 [0.83-0.85]	0.5 [0.44-0.55]
	July & September 2019	NB	1	0.51[0.19-0.83]
	2019 & 2022	CG	0.84 [0.83-0.86]	0.50 [0.43-0.57]
Juveniles	July & September 2019	BA	0.88 [0.77-0.99]	0.5 [0.26-0.74]
	July & September 2019	CG	0.83 [0.78-0.88]	0.5 [0.36-0.64]
	July & September 2019	NB	/	/
	2019 & 2022	CG	/	/
Adults	July & September 2019	BA	0.86 [0.83-0.89]	0.5 [0.37-0.63]
	July & September 2019	CG	0.88 [0.86-0.90]	0.5 [0.42-0.58]
	July & September 2019	NB	/	/
	2019 & 2022	CG	0.86 [0.84-0.88]	0.5 [0.43-0.57]
Females	July & September 2019	BA	0.91 [0.84-0.98]	0.5 [0.37-0.63]
	July & September 2019	CG	0.67 [0.60-0.74]	0.5 [0.38-0.62]
	July & September 2019	NB	/	/
	2019 & 2022	CG	0.83 [0.77-0.89]	0.5 [0.36-0.64]
Males	July & September 2019	BA	0.86 [0.81-0.91]	0.5 [0.37-0.63]
	July & September 2019	CG	0.86 [0.84-0.88]	0.5 [0.42-0.58]
	July & September 2019	NB	/	/
	2019 & 2022	CG	0.80 [0.77-0.83]	0.5 [0.41-0.59]

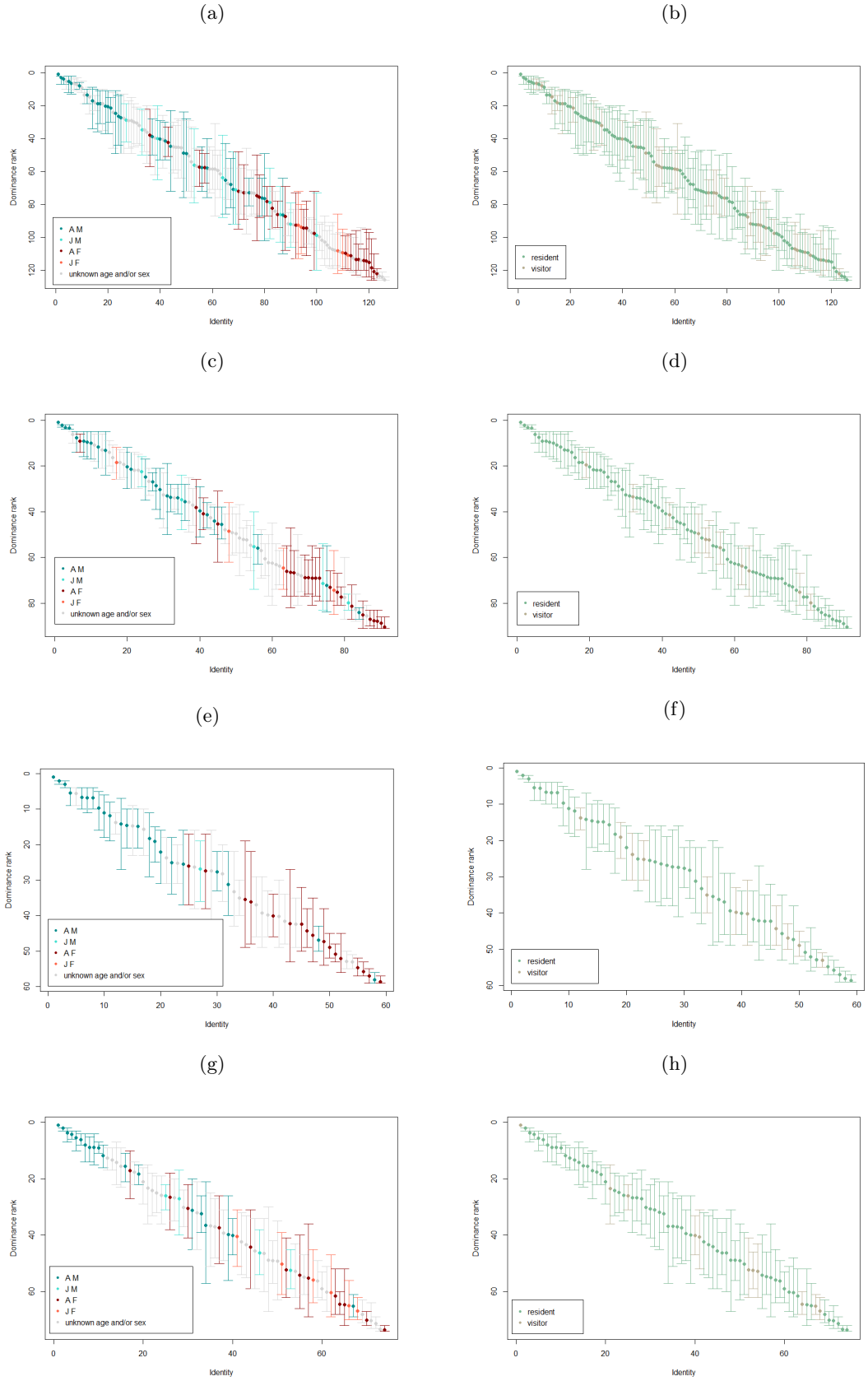

Figure S2: Hierarchies coloured by age and sex (left column) or residence status (right column) in three roosting communities of SC-cockatoos: a-b: Balmoral Beach (BA), c-d: Clifton Gardens (CG) 2019, e-f: Clifton Gardens 2022, g-h: Northbridge (NB).
AM: adult male, JM: juvenile male, AF: adult female, JF: juvenile female. All individuals for whom information about age and sex were incomplete or absent are represented in grey (left column).

(a) (b)

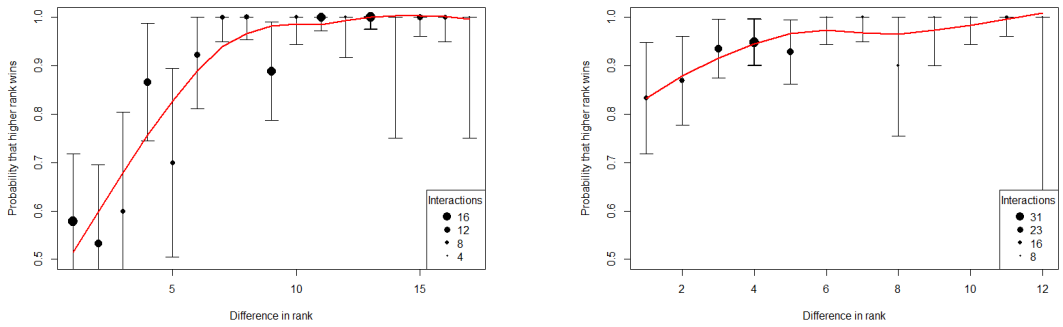

Figure S3: Shapes of female hierarchies measured at the CG-roost across two years: a: 2019, b: 2022

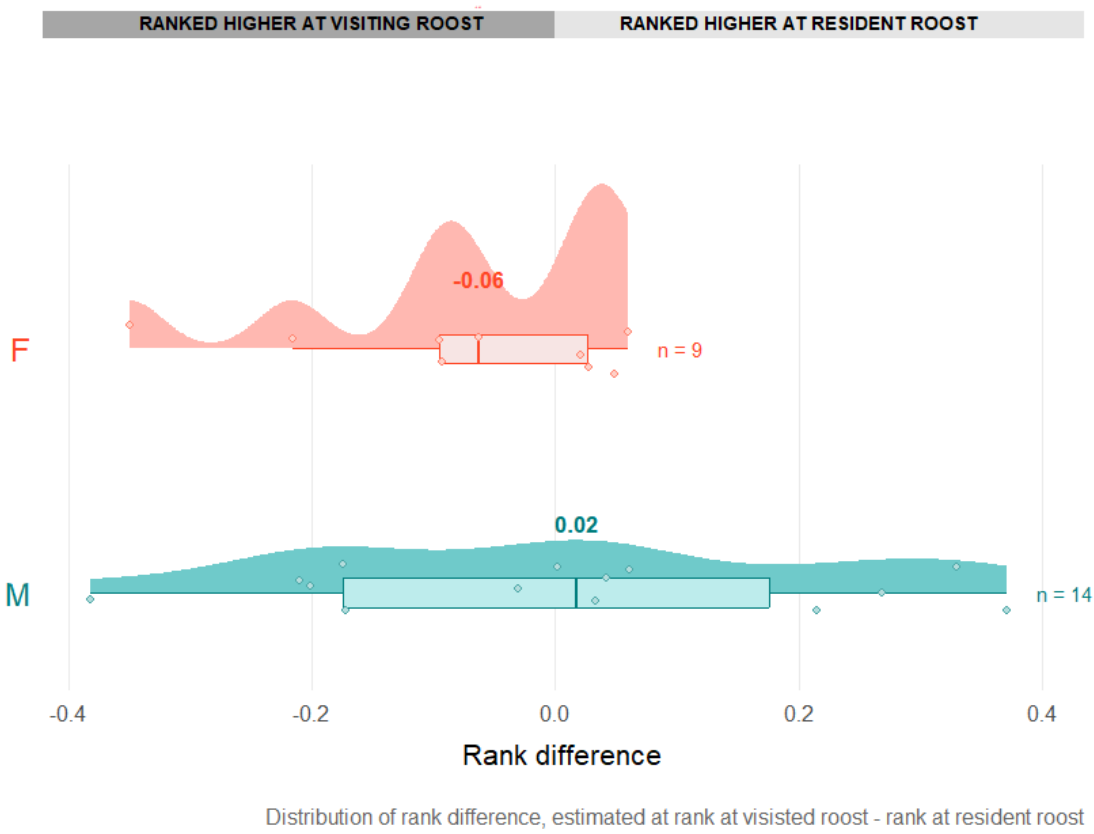

Figure S4: Rank differences between the visited roost and the resident roost, represented as function of sex (F: females, M: males).