Social decision-making in a wild parrot relies on both individual recognition and intrinsic markers

Penndorf, J.[a,b], Farine, D. R.[b,c,d], Martin, J. M.[e], Aplin, L. M.[a,b,c]

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[a] Cognitive and Cultural Ecology Research Group, Max Planck Institute of Animal Behavior, Radolfzell, Germany.
[b] Division of Ecology and Evolution, Research School of Biology, Australian National University, Canberra, ACT, Australia.
[c] Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland.
[d] Department of Collective Behavior, Max Planck Institute of Animal Behavior, Konstanz, Germany.
[e] Hawkesbury Institute for the Environment, Western Sydney University, NSW, Australia.

Contact details: julia.penndorf@anu.edu.au
Division of Ecology and Evolution,
The Australian National University,
46 Sullivans Creek Rd,
Acton ACT 2601,
Australia

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Abstract

Dominance hierarchies allow group-living animals to limit the potential costs of fighting over access to resources, but can these be maintained in more open, fission-fusion societies, where individuals have incomplete social information? We recorded social associations and aggressive interactions in a highly social, large-brained parrot, the sulphur-crested cockatoo *(Cacatua galerita)*. By following 411 individuals across three neighbouring roosts, we show that sulphur-crested cockatoos form shallow, but stable, hierarchies that incorporate birds from within and outside the roost. We find that hierarchies are maintained via a two-fold strategy when initiating or reacting to an aggression: initiate and escalate interactions based on rank difference when familiar, and direct and escalate interactions based on weight similarity when unfamiliar. Our results demonstrate the association between complex cognition, social memory, and the maintenance of dominance hierarchies in fission-fusion systems.

Key-words: *Cacatua galerita*, dominance hierarchy, fission-fusion dynamics, social behaviour, social cognition, psittaciformes, social heuristics

Introduction

Contests over limited resources are a fact of life for almost all social species (Ward and Webster, 2016), and can potentially be extremely costly for the animals involved. Various mechanisms should therefore have evolved that allow animals to better assess competitors and more accurately target a subset of individuals to engage with, decreasing the overall level of aggression (Arnott and Elwood, 2009; Dehnen et al., 2022). There have been two main mechanisms proposed to decrease the cost of aggressive interactions. The first is the so-called *badge-of-status* (reviewed by Santos et al., 2011). Here, individuals exhibit signals that correlate with fighting ability, allowing opponents to assess their probability of winning without any need for social recognition or memory. These typically consist of differences in plumage, skin colouration or enlarged ornaments. For example, house sparrows (*Passer domesticus*) display a variably sized bib patch (Liker and Barta, 2001; though see Sanchez-Tojar et al., 2018), great tits (*Parus major*) have a prominent black breast-stripe that varies in width (Järvi and Bakken, 1984; but see Wilson, 1992), and some wasp species display their quality in their facial patterning (Tibbetts and Lindsay, 2008). The second mechanism is the formation of stable dominance hierarchies, which are shaped by memory of repeated interactions and potentially by observations of the interactions amongst others (Cheney & Seyfarth, 2008). Hierarchies can either be based entirely on social recognition and memory (Barnard and Burk, 1979; Tibbetts and Dale, 2007), or a combination of social recognition and some intrinsic and predictable markers (e.g. age or sex; Chiarati et al., 2010). However, the relative importance of memory and badge-of-status in determining aggressive interactions within free-living animal populations remains unclear.

The type of social system individuals live in should be an important determinant of which mechanism to assess competitors is more advantageous. Within stable groups, dominance hierarchies will allow for the best up-to-date assessment of the status of group co-members (Drews, 1993). In open societies or in very large groups, by contrast, a badge-of-status can provide a short-cut that, while perhaps not as accurate, does not require previous interactions or individual recognition (Sheehan and Bergman, 2016). Recent work has suggested that animals may also have context-dependent mixed mechanisms, especially in species that may encounter a mixture of familiar and unfamiliar individuals. Experimental manipulation of colourful crown patches in blue tits (*Cyanistes caeruleus*) and golden-crowned sparrows (*Zonotrichia atricapilla*) found that the crown patch size mediates contest outcomes amongst strangers, but is less important in determining contest outcomes between birds caught in the same area (Vedder et al., 2010; Chaine et al., 2011; Chaine et al., 2018). These results suggest that animals may use individual recognition to mediate interactions with familiar group members, and use status symbols to mediate aggressive interactions with relative strangers (Chaine et al., 2018). However, such mixed-strategies have not been observed or reported in natural interactions in the wild.

In birds, there is now increasing evidence that species can maintain complex multi-level social structures (Papageorgiou et al., 2019; Papageorgiou & Farine, 2021; Camerlenghi et al., 2022), in which groups interact with individuals from other groups, or form very large fission-fusion groups. For example, many corvids and parrots exhibit classic *communal roosts*, where individuals breed and/or sleep at highly stable communal roost sites with potentially hundreds of individuals, forage in smaller fission-fusion subgroups, and occasionally also interact with members of other neighbouring roosts (Loretto et al., 2017; Aplin et al., 2021). Similarly, colonial nesting seabirds and marine mammals may interact with large numbers of colony members at sea and on land, while also potentially interacting with individuals from other colonies while at sea (McKinnon et al., 2006). There have been various arguments and mixed evidence for what strategies individuals may use to mediate aggressive interactions under these circumstances. First, the ability to segregate spatially into subgroups with flexible membership may decrease the cost of competition to the extent that the need for stable hierarchies or a badge-of-status is weakened (de Silva et al., 2017) or entirely absent (Boehm, 1999). Alternatively, complex social cognition may allow individuals to remember large numbers of interactions and individuals, for example as has been argued for ravens (Boeckle and Bugnyar, 2012). A third and understudied possibility is that individuals use mixed strategies, with memory-based dominance hierarchies determining dominance outcomes among familiar individuals (e.g. at the roost-, or group-level) and with individuals either (i) deploying no assessment strategies towards relative strangers, (ii) assessing strangers by using a badge-of-status, or (iii) assessing strangers using a set of cues to their state. The potential existence of mixed strategies could help explain how animals navigate the social complexity associated with living in open societies, as well as helping to explain the mixed-evidence for the importance of badges of status (Sanchez-Tojar et al., 2018).

Parrots are an intriguing taxa to investigate the link between social dynamics and mechanisms to mediate aggressive interactions. Many parrot species are highly social, exhibiting strong pair bonds, but also interact 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 well-established 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). While parrots do not show any apparent inter-individual variation in plumage or ornamentation that could be clearly interpreted as a badge of status, they do show ultraviolet fluorescence (Pearn et al., 2001; Berg and Bennett, 2010), but the latter is largely thought to be used as a sexual signal (Berg and Bennett, 2010; Delhey et al., 2017).

Studies of interaction patterns among wild parrots are very rare (but see Diamond and Bond, 1999), and it has often been assumed that the species that form large communal roosts do not have stable dominance hierarchies (Noske et al., 1982). Studies in captivity are more common, but results are mixed, with some species appearing to be able to 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, with results suggesting that this species forms linear social hierarchies (Hobson et al., 2014), and that individuals use rank inference to preferentially direct aggression towards individuals close-by in rank (Hobson and DeDeo, 2015; Hobson et al., 2021). However, social groups in captivity are necessarily much smaller and more stable than 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 instrumental to our understanding of social cognition in general, and parrots are an under-explored taxa despite their potential to yield profound insights into how animals navigate complex social environments.

Here, we investigate patterns of aggressive interactions within and between three neighbouring roost groups of wild sulphur-crested cockatoos (*Cacatua galerita*). Sulphur-crested cockatoos (SC-cockatoos) are large, white, sexually monomorphic parrots that exhibit no clear plumage variations between individuals that might represent a social signal of status (Figure 1). Like many other parrots, SC-cockatoos form year-round communal roosts of up to 500 birds (possibly more), with breeding pairs (a minority of the population) nesting close to the roost site (Aplin et al., 2021). Within these roosts, SC-cockatoos display highly fluid fission-fusion dynamics, with flock size varying between 2 and 500 individuals (Noske et al., 1982; Styche, 2000). In addition, as roosts can be very close to each other (1.5-5km, see Penndorf et al., 2022), birds also regularly engage in between-roost movements, as well as foraging with individuals of different roosts (Aplin et al., 2021; Penndorf et al., 2022). Despite these larger dynamics, individuals maintain stable, long-term relationships beyond the pair bond that are strongly suggestive of social recognition, including with birds from other roosts (Aplin et al., 2021). However, the patterning of aggressive interactions in this species has to date not been assessed.

In this study, we addressed two aims. First, we asked whether roosting-groups of wild SC-cockatoos form linear dominance hierarchies, and tested for individual predictors of dominance, including weight, age, and sex. We then measured dominance interactions across two periods over two months to assess the stability of any emergent hierarchies. Second, we used aggressive interactions and incidences of escalations in aggressive interactions to ask what assessment mechanisms SC-cockatoos use when engaging in aggressive interactions across different levels of social knowledge.

Methods

Study population

The study was conducted in an urban population of SC-cockatoos in Sydney, Australia, an area within the native range of the species. SC-cockatoos in this area use communal sleeping roosts of up to 200 individuals. These roosts are maintained year round and likely over many decades, and consist of non-breeding and breeding birds, with breeding individuals nesting in tree-hollows in close proximity to the main roost (Aplin et al., 2021). In this area, roosts tend to located 1.5-5km apart, with birds generally foraging in an approximate 3km radius around the roost (Aplin et al., 2021), and returning to the roost regularly throughout the day. Our study was focused on three similar sized neighbouring roost-sites in north Sydney, located at Balmoral Beach (BA), Clifton Gardens (CG), and Northbridge (NB): Figure 1a, Table S1.

At each of the three roost sites, birds were habituated to the researchers and subsequently marked using non-toxic dye (Marabu Fashion Spray, MARABU GmbH) using methods detailed in Penndorf et al. (2022). Each individual was marked with an unique combination of one to four coloured dots, applied with sponges on the middle of the back (Figure 1b). As part of a parallel project run at the same time, birds were also habituated and marked at two roost-sites outside of the focal study area

(Table S1), in Manly (MA) and the Royal Botanic Gardens (BG; Table S1). In addition to paint-marked birds, 144 birds had been wing-tagged at the Royal Botanic Gardens between 2011-2018, as part of the ongoing citizen science study *Big City Birds* (Davis et al., 2017; Aplin et al., 2021, Figure 1c).

Overall, 411 individually identifiable birds were included in the study across the three roost locations, which we estimate to be between between 92 and 98% of the local population (Table S1). Of these 411 birds, 373 were paint-marked, 28 were wing-tagged, and 11 had distinctive physical features that meant marking was not required (e.g., healed injuries): Table S1. Age (juveniles: <7 years, adults: >7 years) and sex of birds were assessed by eye-colour (Berry, 1981). Additionally, feathers were collected for a parallel study, and genetic sexings was used to sex juveniles (BA: n=68, CG: n=55, NB: n=41, Penndorf et al., 2022). Finally, we recorded the weight of individuals by training them to step on a flat scale that read at 1g accuracy in exchange for a food reward (e.g. sunflower seeds). This resulted in 214 birds being weighed 1 to 17 times each (mean: 4.3) over the 4 months across the three primary roost-sites (BA, CG, NB). Weight was highly repeatable within individual (0.78, 95% CI=0.72-0.82, R-package *rptR*, Stoffel et al., 2017, no. bootstraps=1000) and ranged from 717g to 1054g. Males tended to weigh more than females, and adults more than juveniles (Figure 1c).

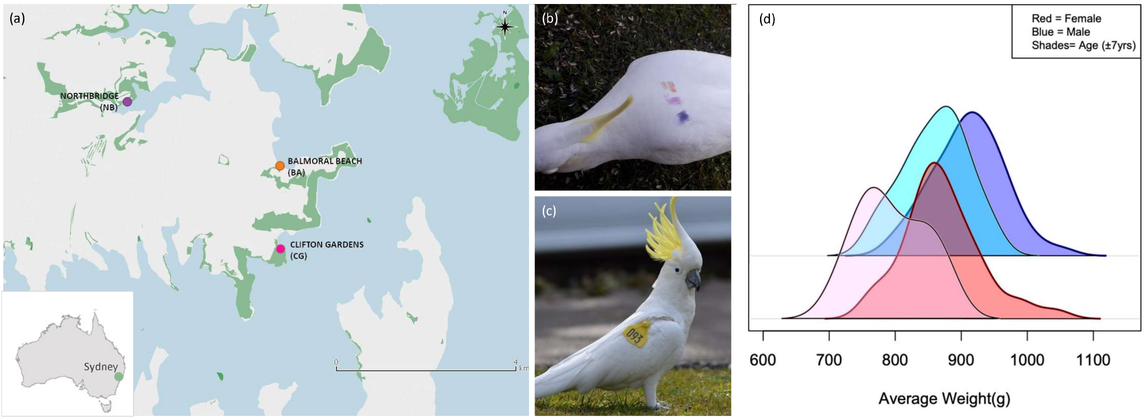

Figure 1: Study locations and marked birds and their respective weights. (a) Map of the three roosting communities included in the study, (b) Example of marking with temporary dye, Violet Pink Orange - horizontal, that remains visible for 3-4 months. (c) Example of wing-tagged bird — 093 Albie. (d) Distribution of average weights of individuals in grams, across age and sex classes. Dark blue are adult males (>7yrs, n=137), light blue are juvenile males (<7yrs, n=49), dark red are adult females (>7 yrs, n=116), and pink are juvenile females(<7yrs, n=30).

Social data collection

Social association and interaction data were collected over two 10 day periods from July 8th - 20th and September 19th - October 2nd 2019. 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 over a 3 hour (July) or 2.5 hour (September) daily sampling period.

During each sampling period, the identity of all birds present was recorded every 10 minutes (Altmann, 1974). We defined present as being identifiable within the park. Between presence scans, aggressive interactions were recorded using all occurrence sampling (Altmann, 1974). For each interaction, we recorded the time, the identities of the individuals involved, as well as the sequence of the interaction. All aggressive behaviours recorded in the study, as well as their definitions, can be found in Table S2. If several dyads interacted very close in time, we prioritized recording the identities of winners and losers.

All procedures were approved by the ACEC (ACEC Project No. 19/2107).

Dominance hierarchies

We calculated a separate dominance hierarchy for each of the three roost-sites, combining interaction data from both observation periods. In order to obtain reliable dominance hierarchies, we only included individuals with ten or more agonistic interactions at a given roost-site location (BA: N_{ind}=126; CG: N_{ind}=93; 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'* of the same package. Furthermore, we assessed the transitivity of the hierarchy following McDonald and Shizuka 2013 and Shizuka and McDonald 2015 (see Section 1).

To explore whether rank was correlated with sex, age, or weight, we ran a generalized linear mixed model using the R-package *lme4* (Bates et al., 2015). We tested whether standardized rank was predicted by the sex, age, or average weight of an individual, as well as the interaction between age and average weight. Since individuals could appear in the hierarchies of several sites (26 individuals present in two hierarchies, two individuals present in three hierarchies), we included site and individual ID as random variables.

Stability of hierarchies over time

To assess the stability of dominance hierarchies over time, we calculated the hierarchy at each roost location separately for each observation period. The dominance rankings of both periods were then compared between each period using a correlation test. Only individuals with ten or more interactions at a specific location within each of the two time periods were included.

Social decision-making

Decisions about interactions were made at two levels. First, an individual (hereafter *initiator*) decides whether to engage in an aggressive interaction. Second, the individual that is being aggressed (hereafter *receiver*) chooses whether to retreat or reciprocate. Decision-making in both cases is based either on an assessment of the opponent's resource holding potential (RHP, Green and Patek, 2018) or on memory, including prior experience or knowledge of relative rank (Chaine et al., 2018).

We hypothesised that in the absence of local knowledge, individuals would use assessment of RHP to decide on whether or not to engage in an aggressive interaction. We further hypothesised that when individuals had knowledge about the social environment, they would instead base their decision-making on the dominance hierarchy. In order to test these hypotheses, we considered two instances of decision making: the decision of the initiator about whom to aggress, and the decision of the receiver about how to react to the aggression.

As aggressive interactions involving females were relatively rare, we restricted interactions to male-male dyads only. As a proxy for RHP, we used an individual's average weight, which is likely to be correlated to overall body size. As a proxy for familiarity, we considered an individuals familiar with the social environment at the site if they were present in at least 5% of the scans conducted at the site. Else, individuals present in fewer than 5% of scans at the site were considered unfamiliar with the social environment.

Deciding whom to aggress

To test which cues SC-cockatoos are most likely to base their decisions to initiate an aggressive interaction upon, we used a two step approach. First, we tested the influence of weight on decision-making. For this, the data was divided into two groups: 1) interactions where the initiator had no social knowledge, and 2) interactions where the initiator had social knowledge. In a second step, we focused only on interactions where the initiator had social knowledge to test whether familiar individuals use an alternative, rank-based, interaction strategy.

In order to test the strategic use of aggressions for each of the above described scenarios, we adapted the method developed by Hobson et al. (2021) and modified by Dehnen et al. (2022), consisting of several steps. First, we calculated the difference between individuals in weight or rank as:

- (weight initiator) - (weight receiver) for the analysis on weight
- (rank initiator) - (rank receiver) for the analysis on rank.

The interaction data were used to count the number of observed directed interactions across each pairwise combination of individuals. To generate expected interaction patterns, we implemented a permutation procedure, where each iteration (n=1,000) randomly selected one interaction, and then randomly selected a new receiver of the interaction among all individuals present (i.e. individuals present in the scan just before and just after the interaction, including the original receiver but not the initiator). Permutations were limited to interactions where at least three were present at the site at the time of the interaction (including the original initiator and receiver).

We ran 10,000 permutations before calculating the difference between observed and permuted datasets. If the observed tendency to interact follows a random pattern, the confidence intervals should overlap zero. A positive or negative value that does not overlap zero indicates that interactions between individuals of that rank difference occurred more or less often than expected by chance. As interaction strategies towards individuals positioned higher or lower than oneself in the hierarchy may differ (Dehnen et al., 2022), we fitted separate smoothing splines for positive and negative rank differences (*smooth.spline* R-function, d.f.=3, lambda=0.04).

Analysis of escalations

To examine the decision of the receiver, we identified escalation events. These were defined as interaction sequences in which the receiver responded aggressively towards the initiator of the interaction, independent of who eventually won the interaction. Across all roost sites, this resulted in 3,845 interactions between 396 individuals (Table S1).

We first tested the influence of weight and familiarity on the likelihood of an interaction to escalate. Therefore, we tested whether escalation events were predicted by the absolute weight difference (in grams), the knowledge status of both receiver and initiator, whether the initiator was of higher/lower weight than the receiver, as well as the interactions between all terms.

In a second step, we focused only on a subset of interactions, where both individuals were knowledgeable of the social environment to test the influence of rank difference on the likelihood of escalation. Therefore, we tested whether escalation events were predicted by the the absolute rank difference the knowledge status of both receiver and initiator, whether the initiator was of higher/lower rank than the receiver, as well as the interactions between all terms.

For both analyses, we constructed binomial GLMMs (package *lme4*, Bates et al., 2015) that included the base predictor for each hypothesis (absolute weight or rank differences) and all possible combinations of additional predictors (familiarity and whether the initiator was heavier for the weight hypothesis, and whether the initiator was heavier or higher in rank for the rank hypothesis) that could contribute to an escalation. We then compared models using AIC to identify which set of additional predictors were important in modulating the role of the hypothesised heuristic (e.g. does familiarity affect the role of weight difference?).

Results

The number of birds included in the hierarchy at each site (i.e. >10 observed interactions) varied between 74 and 126 (Table S1). We recorded 6,402 aggressive interactions across all birds at each of the three roost sites, of which 5,447 were between individuals in the same dominance hierarchy (n = 265 birds). Of these, 3,859 observations had a full sequence starting with information about the initiator and receiver (see Table S1 for a subset of birds per site). From the 265 individuals in the local hierarchies, the weight of 176 was known.

Aggressive networks were sparse when both sexes were considered together (density: 0.19-0.64, Table S4), likely because there was a low incidence of aggressive interactions involving females. When only males were considered, the density of aggressive networks was much higher (density:0.39-0.80, Table S4).

Dominance hierarchies

We found that SC-cockatoos form robust hierarchies, both at group level and within males (Figure 2 & Figures S1a,c; Table S3). At roost-level, hierarchies were stable for at least two months (≥ 0.70; Table S5), and highly transitive (≥ 0.8) (Table S7), suggesting that wild SC-cockatoos form stable, quasi-linear hierarchies.

Overall, hierarchies were significantly segregated by sex and age, with males ranking higher than females (β= -0.40; P<0.001 Figures 2, S1a,c), and adults ranking higher than juveniles (β= 0.12; P=0.020). Resident individuals also ranked higher than visiting individuals (β=-0.12, P=0.040). Standardized weight, however, was not significantly correlated with rank (β= -0.0002; P=0.570). When repeating the same analysis within males only, we found neither age (β= 0.19, P=0.11), residency (β=0.014, P=0.91) or weight (β=-0.0005, P=0.63) predicted dominance rank in males. Given the sex-segregated hierarchy, and that most interactions occurred within individuals of the same sex, the subsequent analyses were conducted only on males.

The shallowness of the male hierarchy is evidenced from individuals having only a chance of >60% to win an aggressive interaction against an individual one rank lower than themselves (BA=0.6, CG=0.75, NB=0.75; Figure S1b,d,f). However, this probability increased relatively rapidly with increasing rank difference, reaching 0.9 with a rank difference between 6 and 16 (Figure S2b,d,f). Similarly, in females (hierarchy calculable at CG only), the probability of winning against an individual of one rank below or above was 0.5, and reached 0.9 for a rank difference of 6 (Figure S3b).

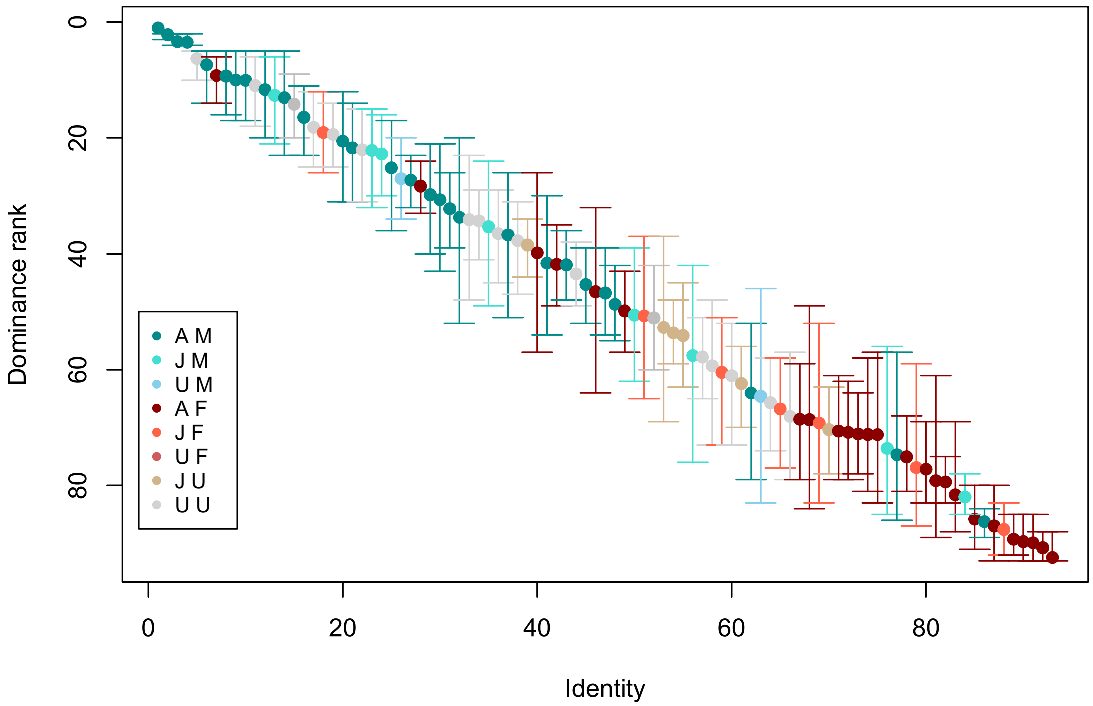

Figure 2: Dominance hierarchy for the CG roosting community of sulphur-crested cockatoos. The dots represent the rank for each individual, with the associated confidence intervals. Each node is coloured by age and sex class. A: adult, J: juvenile, F: female, M: male, U: unknown (can be either unknown age or unknown sex). The hierarchies of the two BA and NB roosting communities are presented in Figure S1.

Social decision making

Initiation of interactions

If the initiator was not knowledgeable of the social environment, they preferentially targeted other individuals close in weight (-170g - 200g; Figure S4a). By contrast, interactions initiated by knowledgeable individuals (present in >5% of the scans at that specific location), showed no significant influence of weight on the decision to initiate an aggressive interaction, though there was a tendency of individuals to initiate interactions with others that were slightly lighter (<80g, Figure S4b). Rather, when individuals were knowledgeable of the social environment, relative rank difference was a better predictor of social interactions. In this case, individuals directed aggressive interactions towards lower ranking individuals, while avoiding aggressing those higher in rank (Figure S4c).

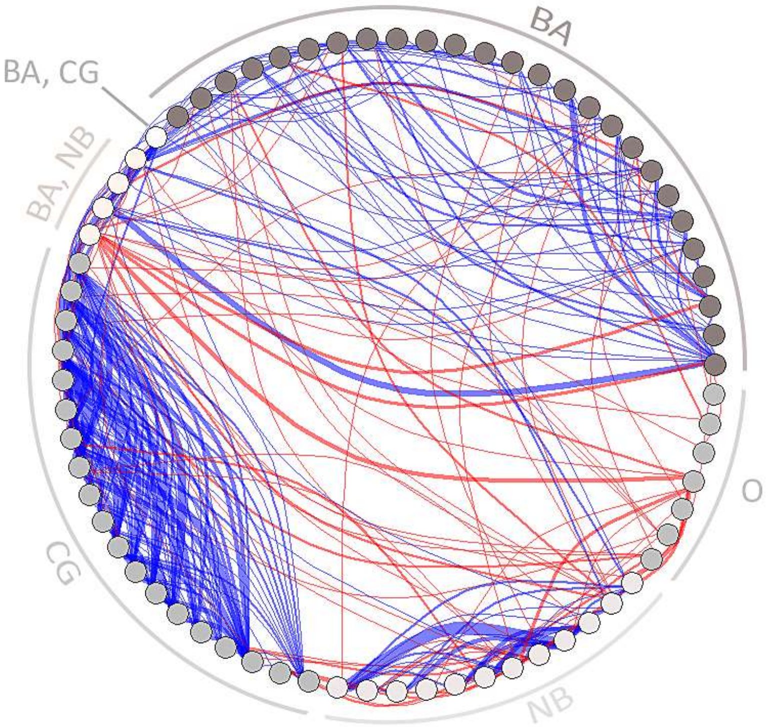

Figure 3: Aggressive interactions between males. Nodes are coloured by the familiarity of the individual with specific social environment(s), indicated as label for each node (BA, CG, NB). Individuals that where transient at all three sites are marked as "O" (other roost-membership). Edges are coloured depending on the familiarity with the social environment. Blue edges represent interactions between familiar individuals. Red edges represent interactions between unfamiliar individuals.

Escalation of interactions

The model of escalation most supported by the data included an interaction between absolute weight difference and familiarity, plus a term capturing whether the initiator was higher or lower in weight. This suggests that familiar and unfamiliar individuals had different tendencies to escalate interactions for a given difference in weight. Specifically, we found that escalation events in our dataset were best predicted by an interaction between weight difference and familiarity, and whether the initiator was heavier than the receiver of the interaction (Figure 4a). That is, if one individual in the dyad had no social knowledge, then interactions were much more likely to escalate if individuals were close in weight. This probability of escalation was also higher if the receiver was heavier than the initiator (Figure 4a). If both individuals were familiar with the social environment, escalations were also more likely to escalate if the receiver was heavier, independent of the weight difference. There was a possible trend towards a higher probability of escalation when the weight difference was large (Figure 4a), however this was entirely driven by two interactions between the same dyad.

Second, we focused on a subset of the data containing only interactions between individuals familiar with the social environment to test whether rank differences can predict escalations of aggressive interactions. For the effect of rank difference, the model most supported by the data included an interaction between absolute rank difference and whether the initiator was higher ranked than the receiver. Specifically, we found that if the initiator was higher ranked, interactions were very unlikely to escalate, and escalations only occurred if individuals were close in rank (Figure 4b). If, on the other hand, the initiator was ranked below the receiver in the hierarchy, the probability of escalation was high and increased with increasing rank difference (Figure 4b).

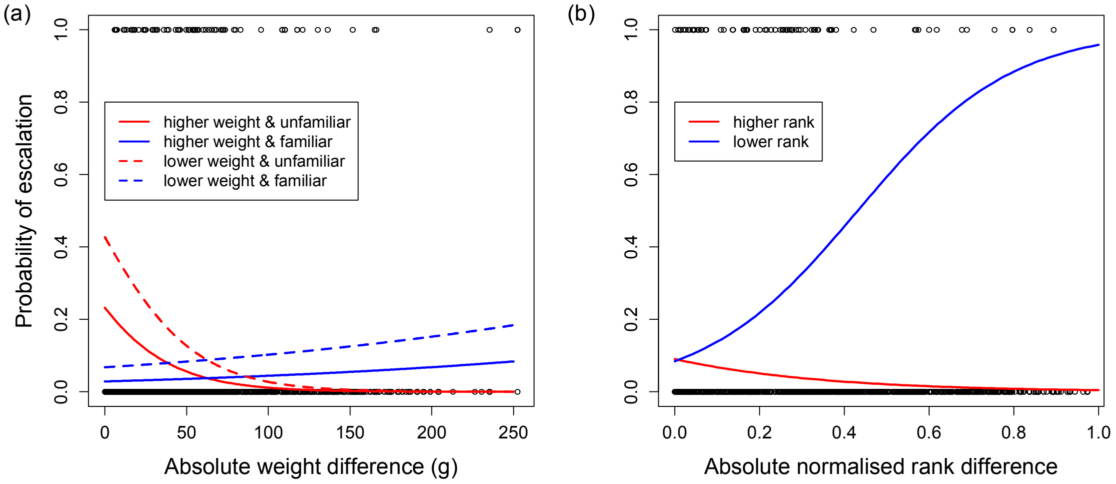

Figure 4: Probability for interactions to escalate depending on differences in weight and rank, and whether birds were familiar or not. (a) We found that escalations were generally more likely if the initiator had a lower weight than the receiver (dashed lines versus solid lines). In the absence of social knowledge (red lines; unfamiliar), we further found that escalations were more likely if the two individuals were closer in weight. (b) Escalation in interactions between knowledgeable individuals were only likely to occur if the initiator was lower in rank (blue line), with this probability increasing as this difference in rank increased. Line colours are labelled from the perspective of the initiator.

Discussion

We found that SC-cockatoos used mixed decision-making strategies in their aggressive interactions. First, for dyadic interactions where at least one individual was not knowledgeable of the social environment (i.e. a visitor to the roost site), individuals disproportionately directed aggression towards those close above and below themselves in weight, peaking at 90g heavier. Within these interactions, the probability of escalation depended on whether the individuals were close in weight, with this probability being higher if the receiver was higher in weight. This contrasted the interactions among familiar individuals. Here, weight had little correspondence with whom individuals directed aggression towards. Weight only affected the probability of escalations when the initiator was considerably lower in weight than their aggressor. Second, within regularly interacting individuals, we found that SC-cockatoos formed quasi-linear dominance hierarchies that were shallow but stable over at least 2 months. These hierarchies were structured by sex and age, with males engaging in most interactions, and within sex, individuals' social rank was not predicted by weight. Individuals were less likely to direct aggression towards those above them in the hierarchy than expected by chance, and were more likely to direct aggression towards those below them, with this peaking at 15-45% rank difference. Escalation to received aggression was only likely to occur when the receiver was much higher ranked than their aggressor. Together with our results on interactions between less familiar individuals, these results provide evidence that SC-cockatoos were engaging in a mixed strategy that depends on the familiarity between interacting individuals. When facing less familiar individuals, decisions to interact — or escalate — were based on the relative weight difference. Simultaneously, social decisions between familiar individuals were based on social recognition and memory, and individuals were generally aware of relative rank differences between themselves and others.

Interactions with strangers: using proxies for resource holding potential

When interacting with non-residents, SC-cockatoos used body size (weight) in their aggressive decision-making. This suggests that: (i) there are limits to social cognition in SC-cockatoos, with individuals unable to retain (or not using) memory of relative rank for individuals outside of their group, despite being members of nearby roosts and therefore potentially having interacted previously to our observation period, and (ii) SC-cockatoos are assessing these individuals using a set of cues to their state, including sex and weight. This finding contributes to the growing evidence of mixed strategies in systems with fission-fusion dynamics (Vedder et al., 2010; Chaine et al., 2011; Chaine et al., 2018), but extends this body of work by giving evidence for the existence of such strategies even in the absence of clear status signals. This is particularly intriguing, as it has been suggested that the use of social recognition could constraint the evolution of open social systems, while the use of quality signals may facilitate the evolution of open social systems (Sheehan & Bergman, 2016).

While we show an effect of assessment of body size (as estimated by weight) on decision-making, we cannot exclude the possibility that weight is correlated to a yet undescribed status signal in this species. One possibility could be crest length or colour, given its importance for signalling across Cacatuidae (Liévin-Bazin et al., 2018; Bertin et al., 2020). Another potential status signal might be UV-reflective plumage (Pearn et al., 2001; Berg and Bennett, 2010). Such fluorescent patches are found in a majority of parrot species (140 out of 143 species examined by Mullen and Pohland, 2008). SC-cockatoos have yellow feathers on their cheek, under-wing, and crests that exhibit ultraviolet fluorescence (Figure 1b) (Mullen and Pohland, 2008). The function of this fluorescence in SC-cockatoos has not been studied. However, UV-reflective plumage is used to inform mate choice in Budgerigars (Pearn et al., 2001), and it is largely thought to be a sexual signal (Berg and Bennett, 2010; Delhey et al., 2017). Whether it could also signal dominance in parrots warrants further investigation. However, based on our recorded interaction sequences, it seems unlikely to be the primary cue or signal. We observed no obvious movement or display of cheek patches during aggressive interactions. Crest movements are often induced by surprising or alarming stimuli (Liévin-Bazin et al., 2018), and are utilised in breeding displays at nest hollows (*personal observation*). These observations are further strengthened by our data, as only 16% of all aggressive interactions included crest-erection (15% of interactions involving familiar individuals, and 19% of interactions involving unfamiliar individuals).

Interactions with familiar individuals: relying on social cognition instead of proxies for rank

Our results from interactions between relative strangers suggest that SC-cockatoos are able to assess body size (for which we used weight as a proxy), and perhaps use this as a signal of RHP. Yet within roosts, weight did not determine dominance rank. This may seem surprising, given (i) that flocks of wild SC-cockatoos have been suggested to be too large to form dominance hierarchies (Noske et al., 1982), (ii) the high degree of fission-fusion dynamics in this species means individuals may encounter hundreds of others over days and weeks(Aplin et al., 2021; Penndorf et al., 2022), and iii) that weight does partly influence decisions to initiate and/or escalate aggressive interactions. One potential explanation is that weight-based hierarchies tend to be restricted in terms of maximum group size when weight differences become too small to assess (Ang and Manica, 2010). Groups of SC-cockatoos may therefore be too large for primarily weight-based hierarchies to be useful. By contrast, SC-cockatoos could have the cognitive ability to learn and remember their position in the dominance hierarchy. Previous work has suggested that SC-cockatoos exhibit preferred social associates (Penndorf et al., 2022), and form stable long-term relationships (Aplin et al., 2021); work in other parrot species also suggests extensive individual recognition (Wanker et al., 1998; Buhrman-Deever et al., 2008).

This suggests that SC-cockatoos may possess sufficient memory of past interactions to allow them to track dominance relationships in large social groups (Hobson, 2020).

Hierarchies were robust and stable, yet hierarchy steepness was low in all groups measured. This may be, at least partially, due to the experimental and ecological conditions. It has been suggested that strong linear hierarchies are more likely to form when individuals compete for monopolizable food sources (Wrangham, 1980; Boucherie et al., 2022. Here, we measured aggressive interactions in a context that attempted to mimic natural ground foraging behaviour, where groups dig for roots – or feed on the seeds – of grasses. These resources (similar to most of their foraging resources), are non-monopoliseable. Indeed, aggressive interactions in the study were mostly of low intensity, and only 6% involved body contact. In comparison, competition for tree hollows can be fierce, with nesting sites constituting a highly limited resource (Davis et al., 2013). These interactions often involve physical fights, with injuries being observed in adults just before and at the start of the breeding season (*personal observation*). It may therefore be possible that SC-cockatoos form multiple context-dependent hierarchies; this remains to be described.

Conclusions

Our previous work has shown that wild SC-cockatoos form stable long-term relationships (Aplin et al., 2021), and maintain some social relationships even after dispersal into different roost groups (Penndorf et al., 2022). This suggest that SC-cockatoos possess extensive memory of past interactions — an ability displayed by other large-brained bird species that exhibit fission-fusion dynamics, such as common ravens (*Corvus corax* Boeckle and Bugnyar, 2012). However, even with good memory, given the open society of SC-cockatoos, a mixed strategy that depends on the frequency of encounter might be more adaptive than a sole reliance on social recognition and memory, as it may reduce errors from inaccurate recollection or outdated information.

In Sheehan and Bergman (2016), the authors suggested that, after dispersal, juveniles should rely on quality signals when interacting with unfamiliar individuals, but once juveniles are settled, interactions reoccur, which should favor social recognition over quality signals. Empirical evidence for an existence of such a mixed strategy was provided by a recent study in golden-crowned sparrows (*Zonotrichia atricapilla*), where badges-of-status affected dominance among strangers, but not familiar flock mates (Chaine et al., 2018). However, that study inferred familiarity from spatial proximity, and did not explore whether individuals formed dominance hierarchies within familiar flocks. Here we substantially extend this study by showing the expression of mixed strategies in the wild, and the conditions under which one or the other is expressed, in a species with no obvious badge-of-status, and where stable, quasi-linear dominance hierarchies are maintained within roosting groups. Taken together, our results suggest that social knowledge remains an important determinant of aggressive interactions, even under such high fission-fusion dynamics, but that individuals can flexibly incorporate other potential cues of competitive ability when recent knowledge is lacking.

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