Structured aggression and dominance dynamics in long-lived colonial African penguins (Spheniscus demersus)

Bálint Kovács

balintkovacs.elte@gmail.com

University of Pannonia

Borbála Kocsis

University of Pannonia

Péter Kollár

University of Pannonia

Ivett Pipoly

University of Pannonia

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Abstract

This study provides rare evidence from a long-lived seabird in captivity, extending insights beyond the short-lived model species that dominate social research. By mapping aggressive interactions as social networks, we demonstrate that dominance rank in African penguins is not determined solely by age or sex: rearing conditions exert long-lasting effects on an individual's position in the hierarchy. Contrary to the common assumption that artificial rearing impairs social competence, hand- and mix-reared birds consistently outperformed their parent-reared conspecifics. Our results also reveal the dynamic role of age, showing that younger penguins can dominate older individuals, reshaping how we understand the formation of social hierarchies. These findings have direct implications for conservation and zoo management, offering new strategies to improve welfare and social stability in captive penguin populations.

Introduction

A stable social structure is essential for fitness and reproductive success in social species (Armitage, 1986; Pusey & Packer, 1994; Alexander, 1974; Silk, 2007). In the wild, social hierarchies are shaped by multiple factors, including age, sex, predation pressure, sex ratio, and resource availability (Lott, 1991; Jordán et al., 2021). In captivity, however, social dynamics are often governed by different pressures (for example, habitat and population size), and understanding how these hierarchies form is particularly important for the welfare and conservation of threatened species (Carlstead, 1996; Mason et al., 2007; Zijlmans et al., 2019). For example, in African wild dogs *(Lycaon pictus)*, the loss of an alpha male led to the dissolution of a captive pack, whereas littermates relocated together formed a stable group (Zijlmans et al., 2019). Similarly, in captive western lowland gorillas (*Gorilla gorilla gorilla*), hierarchical position was strongly linked with social connectivity and behaviour: lower-ranked individuals were less socially connected and differed in social behaviour (Sweet & Cheyne, 2023). Such examples highlight the importance of socially informed management in ex situ conservation.

Among the traits influencing social behaviour, sex and age are frequently highlighted. Sex-based asymmetries in dominance and sociability are well documented across taxa, often linked to reproductive strategies and competitive behaviours (Biro & Stamps, 2008; Stockley & Jorgensen, 2011). Age can also influence social integration, with younger individuals sometimes being more competitive or exploratory, while older individuals may experience decline in dominance or become socially peripheral (Siracusa et al., 2023). However, in some systems, age is positively correlated with dominance or social position; for example, in female beef cattle (*Bos taurus*) dominance increases with age more strongly than with body mass (Šárová et al., 2013), and in bighorn ewe's (*Ovis canadensis*) older females typically occupy higher rank and more stable status (Favre et al., 2008).

Beyond intrinsic traits, early-life experiences can exert long-lasting effects on behaviour. In zoos, the rearing history, whether animals are raised by their parents, by hand, or through mixed strategies, may significantly influence their later social integration. Parent-rearing is generally considered the

conservation standard in ex situ programmes, as it is assumed to foster more natural social development and integration (Porton & Niebruegge, 2006; Hampson & Schwitzer, 2016). Evidence from mammals supports this view: hand-reared chimpanzees *(Pan troglodytes)* often show impaired social competence compared to parent-reared individuals (Bashaw et al., 2010), while in ravens *(Corvus corax)* hand-rearing negatively affects the development of social behaviours (Boucherie & Bugnyar, 2020). Similarly, in large felids, hand-rearing has been linked with reduced reproductive success (Hampson & Schwitzer, 2016). These findings suggest that parent-rearing promotes stronger social integration. Most research in this area has focused on mammals, reporting physiological or reproductive consequences of hand-rearing (Hampson & Schwitzer, 2016; Porton & Niebruegge, 2006), while studies on birds and other taxa remain scarce and often restricted to survival outcomes or methodological aspects (Utt et al., 2008). Despite the importance of rearing history in ex situ programmes, little is known about how it affects the social behaviour of long-lived, colonially breeding birds. This represents a critical gap, as social integration underpins both welfare and breeding success in captive populations.

African penguins *(Spheniscus demersus)* are an ideal model for addressing this question. As a colonial seabird with strong social bonds and frequent aggressive interactions during feeding (Eggleton & Siegfried, 1979), their behaviour is readily observable in captivity. Moreover, they are often hand-reared in zoos as part of conservation breeding programmes (Barham et al., 2008; Sherley et al., 2014), yet the behavioural consequences of these practices remain poorly understood. While previous studies on hand-rearing African penguins have primarily examined rearing techniques and survival (Barham et al., 2007; Sherley et al., 2014), none have addressed effects on social dominance.

In this study, we used behavioural observations to construct weighted, directed aggressive networks in a zoo-housed African penguin colony. We focused on three main predictors of social position: sex, age, and rearing history. By quantifying individual dominance using David's Score, we examined both the static dominance structure and temporal changes in rank over the study period. Specifically, we asked: (i) do sex, age, and rearing history predict dominance rank, and (ii) how do these factors influence temporal changes in dominance? Based on previous work, we expected males to attain higher dominance than females, and younger individuals to occupy higher ranks than older conspecifics. Given the frequent use of parent-rearing as a conservation standard, we hypothesised that parent-reared birds would integrate better socially and therefore achieve higher dominance than hand- or mix-reared conspecifics. Testing these predictions allows us to evaluate how both intrinsic traits and early-life history shape social organisation in a threatened seabird species.

Methods

Study area and objects

Behavioural observations were conducted in the African penguin enclosure at the Budapest Zoo & Botanical Garden (Budapest, Hungary). Feedings typically took place on land rather than in water, allowing most individuals to gather in a well-defined area simultaneously. This setting provided ideal

conditions for recording agonistic interactions (hereafter referred to as aggressive) before and during feeding and enabled the construction of weighted, directed social networks. The study group consisted of 29 individuals (16 males, and 13 females). Most penguins were individually identifiable by unique combinations of coloured wing bands, while in a few cases recognition was based on distinctive morphological traits (e.g. plumage pattern, bill shape). One individual had been blind since an early age. Ages ranged from 1 to 28 years, rounded to the nearest whole year. Birds were classified as juveniles (n = 4) if they had not yet moulted into adult plumage (Kemper & Roux, 2005). Rearing history was assigned to three categories: parent-reared (n = 12), hand-reared (n = 4), and mix-reared (n = 13). Parent-reared individuals were raised exclusively by their biological parents. Hand-reared birds were cared for solely by keepers from the first days after hatching. Introduction into the colony generally occurred later (around 1–2 weeks of age), but the precise timing was not systematically recorded. Mix-reared individuals experienced at least three weeks of exclusive hand-feeding in addition to parental care. For all subsequent analyses, these categories were labelled as “parent,” “hand,” and “mix,” respectively (see individual-level attributes in Online Resource 1).

Data collection

Observations were conducted between 8 April and 18 November 2022. Since the birds were most likely to congregate around feeding events, data collection was scheduled to occur before and during these periods. Morning feedings took place between 09:30 and 10:00, depending on the season, and afternoon feedings at 16:00. Each observation session began 30 minutes prior to feeding and ended once the last fish was consumed and the keeper had left the enclosure, resulting in approximately 45 minutes of observation per session.

In total, data were collected on 97 sampling days, each comprising two feeding events. During these sessions, we recorded only aggressive interactions (Eggleton & Siegfried, 1979), including the identities of both initiator and receiver. Interaction intensity was coded on an ordinal scale reflecting the assumed physical cost and risk of each behaviour (Zahavi & Zahavi, 1998). Each interaction was assigned an edge weight as follows: 1 = displays without physical contact, 2 = chasing without contact but involving higher aggression, and 3 = fights or pecks involving direct physical contact (Table 1). All sampling events were recorded on a voice recorder in Hungarian and subsequently transcribed into a digital database with each interaction linked to the corresponding initiator, receiver, and interaction weight.

Table 1
Aggressive behaviours recorded in African penguins, adapted from Eggleton & Siegfried (1979). Each behaviour was assigned an ordinal edge weight (1–3) reflecting escalating intensity, from non-contact displays to physical fights.

Interaction	Description	Edge weight
point threat	Aggressive posture, when the initiator points its beak directly towards the object of its aggression.	1
extended point	The individual stretches toward the other individual while showing a point threat.	1
retracted point	Threatening posturing during nesting, the beak is directed upwards, and the bird may draw back with its flippers held away from its sides for balance.	1
sideway stare	Threatens with the individual's head turned to the side, while the beak is pointed towards the other penguin, usually just below the horizontal.	1
alternate stare	Head-turning threats at the rate of one or two per second, usually during nesting.	1
chase	One penguin aggressively chases another without physical contact.	2
peck	One penguin pecks another; physical contact is present.	3

Aggressive network models

We constructed daily aggressive social networks based on dyadic aggressive interactions between two individuals. These were represented as directed edges from aggressor to recipient in a graph, with nodes denoting individuals and edges denoting social ties (Wey et al., 2008). In total, 97 weighted and directed networks were generated, with edge weights corresponding to the ordinal aggression scale defined in Table 1. To quantify social positions within these networks, we calculated David's Score (DS) for each individual on each observation day (David, 1987). DS is a widely used dominance index in animal behaviour research, derived from the rates of dyadic aggressive interactions. It accounts for both the frequency and intensity of wins and losses, providing a continuous measure of hierarchical position within the social structure (Gammell et al., 2003; Bang et al., 2010; Paoli et al., 2006). This local-level index enables meaningful comparisons of individuals' dominance ranks across time and is particularly well-suited for directed, weighted aggressive networks (Sánchez-Tójar et al., 2018). Moreover, DS is robust to incomplete sampling and unbalanced interaction matrices, which are common challenges in observational studies of animal behaviour (Sánchez-Tójar et al., 2018). Thus, aggressive interactions represent the behavioural basis, while DS provides an individual-level dominance index summarising these interactions.

Statistical analyses

All statistical analyses were conducted in R version 4.3.2 (R Core Team, 2023). To quantify individual dominance ranks, we calculated DS from the aggressive interaction matrices using the “ANTs” package (Sosa et al., 2020). To test the effects of sex, age, and rearing type (parent, hand, or mix) on individual social position, we fitted generalized linear models (GLMs) with DS as the dependent variable. To account for non-independence in social data, we employed a permutated generalized linear mixed model (PGLM) with 1000 randomisations, also implemented in the “ANTs” package. To assess the temporal stability of individual dominance ranks, we calculated the linear trend in DS for each individual by fitting simple linear regressions with DS as the response variable and observation day (1–97) as the predictor. The resulting slopes represented the direction and magnitude of individual changes in dominance rank over the study period. These slope values were then used as individual-level response variables in a second permutation-based GLM, where sex, age, and rearing type were included as predictors (trend ~ sex + age + rearing; see details in DS trajectories in Online Resource 2–4). Finally, we conducted post-hoc pairwise comparisons between rearing categories using permutation tests (using the “ANTs” package as well) to evaluate differences in both mean DS values and temporal DS trends.

Ethics declaration

This observational study complied with the ethical standards of the Budapest Zoo & Botanical Garden; no invasive procedures were performed. No specific ethical approval was required, as the study was purely observational and conducted under the standard husbandry permissions of the institution.

Strange summary

The subjects’ origin, age/sex composition, rearing categories, and housing are detailed above (and in Online Resource 1); individuals were identified by colour bands, therefore blinding was not feasible.

Results

Across 97 observation days, we recorded a total of 21,183 aggressive interactions and constructed daily directed and weighted social networks (summarised in Fig. 1). Dominance ranks among individuals were calculated using DS (Fig. 2). We modelled DS as a function of sex, age, and rearing category using a PGLM. Sex had a strong, significant effect on DS, with males exhibiting higher dominance scores than females ($\beta = 7.076 \pm 0.465$ SE, $t = 15.214$, $p < 0.001$; Table 2). Age negatively influenced DS ($\beta = -0.625 \pm 0.037$, $t = -16.690$, $p < 0.001$; Table 2), indicating that younger individuals occupied higher dominance ranks and engaged in more aggressive interactions than older ones. Regarding rearing type, both hand-reared ($\beta = 2.606 \pm 0.776$, $t = 3.360$, $p = 0.004$) and mix-reared ($\beta = 3.170 \pm 0.518$, $t = 6.124$, $p < 0.001$) individuals showed significantly higher DS values compared to the parent-reared group. Pairwise comparisons (Table 3) showed that mix-reared penguins had the highest DS, although the difference between hand-reared and mix-reared individuals was not statistically significant ($\beta = 0.564 \pm 0.842$, $t =$

0.670, p = 0.50). Thus, both hand- and mix-reared birds were more dominant than parent-reared individuals, but mix- and hand-reared birds did not differ significantly.

We further analysed individual temporal trends in DS (Fig. 3) using a PGLMM with the same predictors. Sex showed a significant effect, with males exhibiting positive trends in dominance over time compared to females (β = 0.083 ± 0.035 SE, t = 2.391, p = 0.043; Table 4). This result indicates that males increased their involvement in aggressive interactions and consolidated their dominance status during the study period. Rearing type also influenced dominance trajectories (Table 4): mix-reared individuals showed significantly increasing DS trends over time compared to parent-reared birds (β = 0.112 ± 0.039, t = 2.885, p = 0.041), while no significant differences were detected between hand- and parent-reared (β = − 0.075 ± 0.058, t = − 1.290, p = 0.153) or between mix- and hand-reared individuals (β = 0.037 ± 0.063, t = 0.597, p = 0.322). Age did not significantly predict DS trends (β = − 0.003 ± 0.002, t = − 1.195, p = 0.841).

Table 2
Parameter estimates from the permutated generalised linear mixed model (PGLMM) predicting DS based on sex, age, and rearing category in the captive African penguin population. The table shows estimates (β), standard errors (SE), t-values, and p-values for each predictor.

Predictor of DS	ß	SE	t value	p value
reference (female-parent)	-0.467	0.556	-0.840	0.301
male	7.075	0.465	15.214	< 0.001
age	-0.625	0.037	-16.689	< 0.001
hand	2.606	0.775	3.360	< 0.001
mix	3.169	0.517	6.124	< 0.001

Table 3
Pairwise comparisons of rearing categories (parent-, hand-, and mix-reared) for dominance scores (DS) and temporal dominance trends (DS trend). Estimates represent mean differences between groups, with associated standard errors (SE), t-values, and permutation-based p-values from PGLM models.

pairwise- comparison	model	estimate	SE	t-value	p-value
hand - mix	DS	0.563	0.842	0.669	0.5
	DS trend	0.037	0.062	0.597	0.322
hand - parent	DS	-2.606	0.775	-3.360	0.004
	DS trend	-0.075	0.058	-1.290	0.153
parent mix	DS	3.169	0.517	6.124	< 0.001
	DS trend	0.112	0.038	2.885	0.041

Table 4
Parameter estimates from the permutated generalised linear mixed model (PGLMM) predicting individual temporal trends in DS index based on sex, age, and rearing category. Estimates (β), standard errors (SE), t-values, and p-values are shown.

predictor of DS trends	ß	SE	t-value	p-value
reference (female-parent)	-0.086	0.041	-2.148	0.113
male	0.083	0.035	2.391	0.043
age	-0.003	0.002	-1.195	0.841
hand	0.075	0.058	1.290	0.113
mix	0.112	0.038	2.885	0.046

Discussion

Dominance as a measure of social integration

In social animals, dominance position often reflects the degree of social integration within the group, because high-ranking individuals typically engage in more interactions, attract more partners, and are central in the social network (Silk 2007; Ilany et al. 2021). Although dominance and integration are conceptually distinct, they can covary when hierarchical relationship's structure opportunities for affiliation and coalition formation (Sapolsky 2005). In such systems, rank change represents not only competitive success but also a proxy for the individual's capacity to become socially embedded and maintain group membership. We therefore interpret temporal changes in dominance rank as indicators of changing social integration within the colony, acknowledging that this link is probabilistic rather than deterministic and may vary across taxa and contexts. Demonstrating this connection in a colonial bird provides valuable insight into how social position, competitive behaviour, and developmental history interact to shape social organisation.

In this study, we showed that sex, age, and rearing history significantly shape dominance status in zoo-housed African penguins. Using social network analysis of 97 days of observations, we found that males consistently attained higher dominance ranks than females, younger birds outranked older conspecifics, and both hand- and mix-reared individuals were more dominant than parent-reared ones. Although hand- and mix-reared penguins did not differ significantly in their overall dominance ranks, rearing history still predicted temporal trajectories: mix-reared individuals increased in rank over time relative to parent-reared birds. These findings highlight the role of both intrinsic traits and early-life history in shaping aggressive networks in a threatened seabird species. Additionally, the results may point out the importance of early-life social history and treatments for social species in ex situ conservation efforts and/or in conservation biological studies.

Sex effects on dominance and temporal dynamics

Male penguins were consistently more dominant than females, and only males showed increasing dominance trajectories during the study period. This sex asymmetry is consistent with patterns in many taxa where males engage more intensively in aggressive interactions to secure access to resources or mates. For instance, in red junglefowl *(Gallus gallus)*, male competition drives rank differences (McDonald et al., 2019), whereas in spotted hyenas (*Crocuta crocuta*), rank strongly predicts access to resources and social integration (Ilany et al., 2021). In penguins, however, males may gain dominance advantages by defending food during feeding events or through higher competitive motivation, potentially underpinned by hormonal profiles (e.g., Mauget et al. 1994). The fact that male dominance increased over time suggests that they do not simply start higher in the hierarchy but actively reinforce their positions, with implications for management, as escalating male competition may destabilise group dynamics if not monitored.

Age-related decline in dominance

We also observed a strong negative relationship between age and dominance, with younger individuals more frequently occupying high ranks. This contrasts with many mammalian systems, where older individuals often retain dominance (e.g. rhesus macaques (*Macaca mulatta*): Siracusa et al. 2023). In our population, the highest DS values were recorded among juveniles, an unexpected pattern that may reflect early-life strategies in captive environments where food is predictable and older birds have less incentive to compete. Rather than active exclusion, older penguins may experience passive marginalisation due to declining condition or reduced motivation. Highlighting this age effect is important, as it reveals that social integration in captivity does not simply mirror wild hierarchies but may shift towards youthful dominance in stable, resource-rich conditions.

Rearing effects on dominance structure

Rearing history also shaped social positioning. Both hand- and mix-reared penguins achieved higher dominance scores than parent-reared conspecifics, and mix-reared birds displayed the strongest increasing dominance trends over time. This contrasts with most zoo literature, where hand-rearing has often been associated with impaired social competence, as seen in chimpanzees (; Bashaw et al. 2010) or ravens (; Boucherie & Bugnyar 2020). Additionally, in California condors *(Gymnogyps californianus)*, parental rearing promoted stronger dominance interactions (Utt et al. 2008). Our results suggest that in African penguins, artificial rearing may instead foster more competitive behavioural styles in food acquisition situations, potentially through differences in early provisioning or human exposure. The finding that mix-reared birds showed the most pronounced dominance trajectories hints that hybrid strategies may combine the affiliative benefits of parental care with the assertiveness promoted by the exclusively hand-rearing. These findings challenge assumptions of universally adverse effects of artificial rearing and highlight the importance of species-specific developmental pathways.

Implications for zoo management and conservation

Dominance asymmetries have direct implications for welfare, access to food, and breeding opportunities in captive colonies. Our results indicate that groups dominated by hand- or mix-reared individuals may

exhibit stronger competitive interactions, which could increase stress or injury risk, but may also facilitate integration and prevent marginalisation. Recognising these trade-offs is crucial for conservation breeding programmes, where socially competent and behaviourally resilient individuals are needed for potential reintroduction. Continuous monitoring of social hierarchies, especially among males and younger individuals, can help understand group dynamics, prevent instability and improve management. Social network analysis provides a robust framework for such monitoring by capturing both static hierarchies and temporal dynamics.

Limitations and future directions

Recent work has raised concerns about the indiscriminate use of permutation procedures in animal social network analysis (Weiss et al. 2021; Hart et al. 2022; Redhead et al. 2025). These studies emphasise that datastream permutations can inflate Type I error rates when applied to regression models or when non-independence is not fully accounted for. In the present study, permutations were not used to generate formal null-hypothesis tests in a regression framework but rather to assess robustness and approximate uncertainty under non-independence among dyads. We follow the recommendation of Sánchez-Tójar et al. (2018) and treat our results as inferentially cautious but biologically informative. Future work could complement this approach with model-based simulations or Bayesian hierarchical methods that explicitly model social dependencies.

Our study was restricted to a single zoo colony observed over eight months, which limits the generality of our conclusions. Longer-term and multi-population studies are needed to assess the consistency of these patterns. Moreover, we focused solely on aggressive behaviour and dominance; these interactions were recorded exclusively during feeding events, a special context that may not fully represent the overall social dynamics of the group. Affiliative interactions such as allopreening, which likely buffer aggression and stabilise groups, can also be important to integrate into future analyses. Finally, while dominance is often linked to reproductive output in social animals (Beck et al. 2021), we did not assess direct fitness correlates. Future research would benefit from examining how rearing history and dominance interact with pair bonds and breeding success, providing a more detailed picture of the welfare and conservation implications of social structure in African penguins.

Strange statement

Sampling around feeding events may elevate aggression rates and introduce self-selection, so generalisability beyond feeding contexts should be interpreted with caution.

Conclusions

By linking aggressive interactions to dominance indices, our study shows that sex, age, and rearing history shape social organisation in zoo-housed African penguins. Males consolidated their dominance over time, while juveniles and young adults occupied higher ranks than older conspecifics. Additionally, rearing history exerted lasting effects, with hand- and mix-reared individuals being more dominant than

parent-reared birds. These findings underscore the complexity of managing captive populations and the importance of incorporating early-life history into welfare and conservation strategies.

Declarations

Competing interests

The authors have no competing interests to declare.

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Ethics Approval

This purely observational study was conducted under the standard husbandry permissions of the Budapest Zoo & Botanical Garden (Hungary). No invasive procedures were performed, and therefore, formal ethical approval was not required.

Data availability

Data and R scripts are available at Zenodo (DOI: 10.5281/zenodo.17339385).

Contributions

Conceptualisation -B Kovács, B Kocsis, Methodology-B Kovács, B Kocsis, Investigation - B Kovács, P Kollár, Formal analysis – B Kovács, Supervision – I Pipoly, B Kocsis; Writing – original draft – B Kovács, B Kocsis; Writing – review & editing – I Pipoly, P Kollár.

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Figures

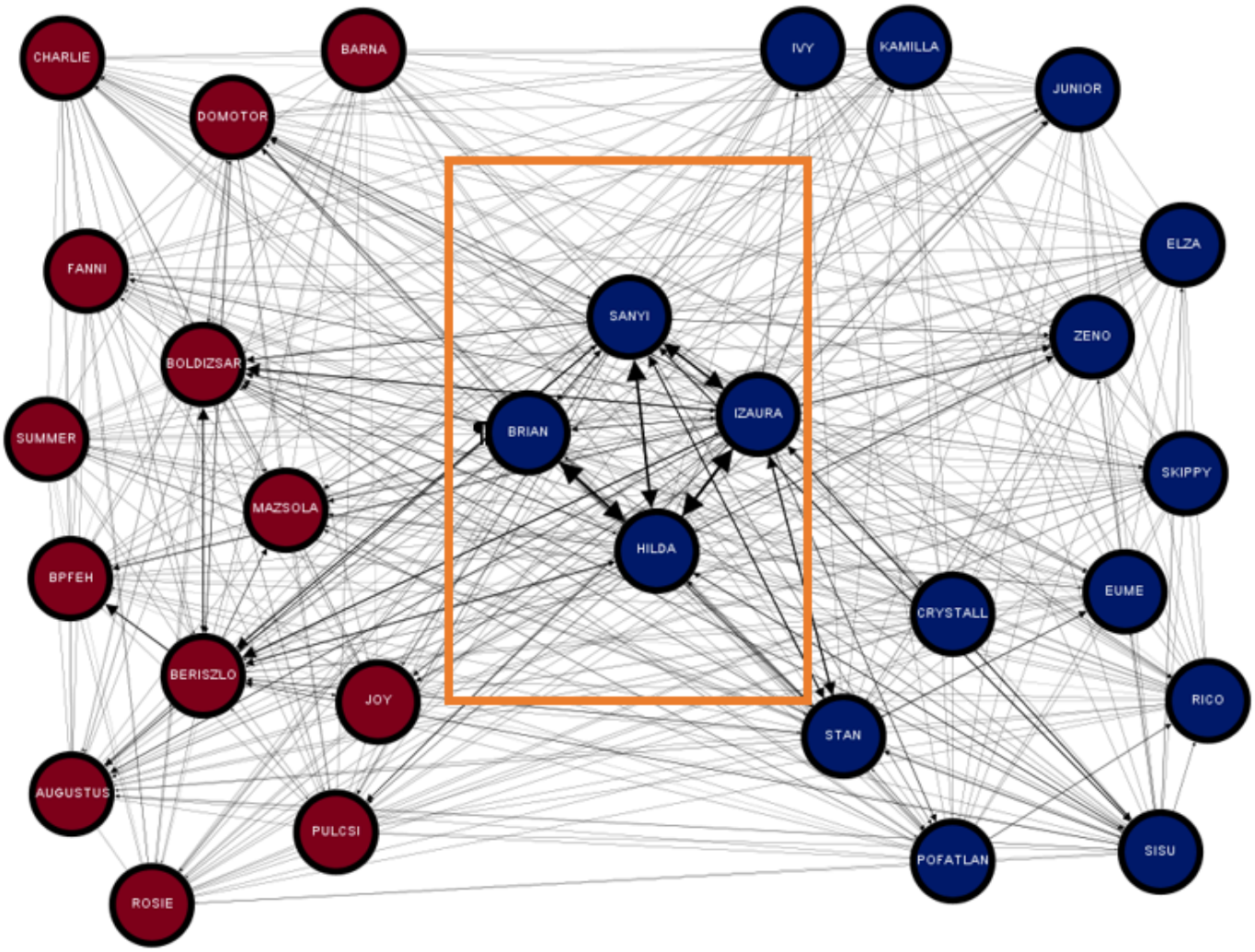

Figure 1

The summarised aggressive social network in the zoo–housed African penguins over the 97-day study period. Node colour codes: red – females, blue – males. Orange square – juvenile individuals. The thickness of the edges represents the edge weights, and the arrows show the directions from initiators to recipients.

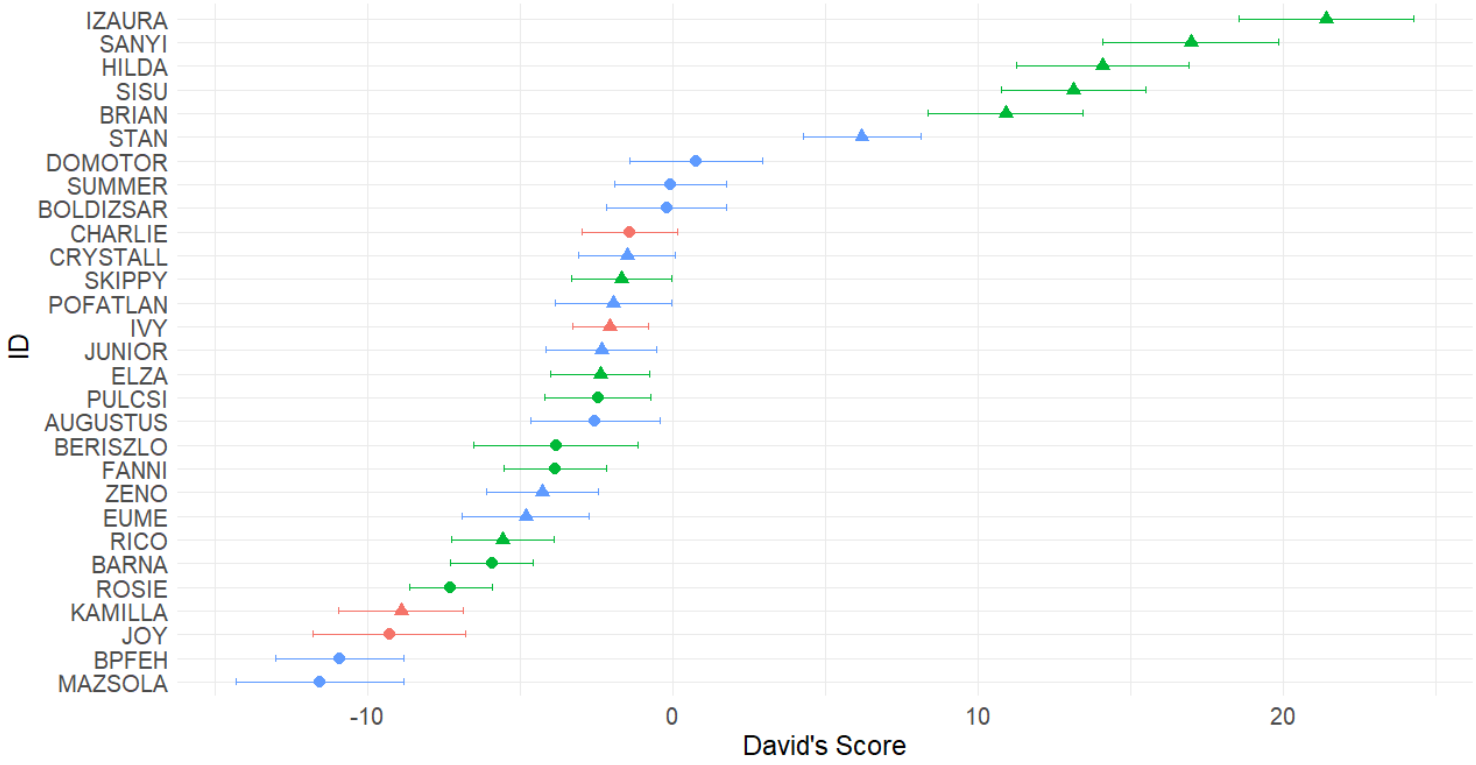

Figure 2

Dominance ranks (DS) of African penguins. Each point represents an individual, with 95% confidence intervals shown. Shape indicates sex (triangle = male, circle = female), and colour indicates rearing type (green = mix, red = hand, blue = parent). Individuals are ranked from lowest to highest DS, with lowest meaning the least dominant/aggressive, and highest meaning the most dominant/aggressive behaviours/relationships.

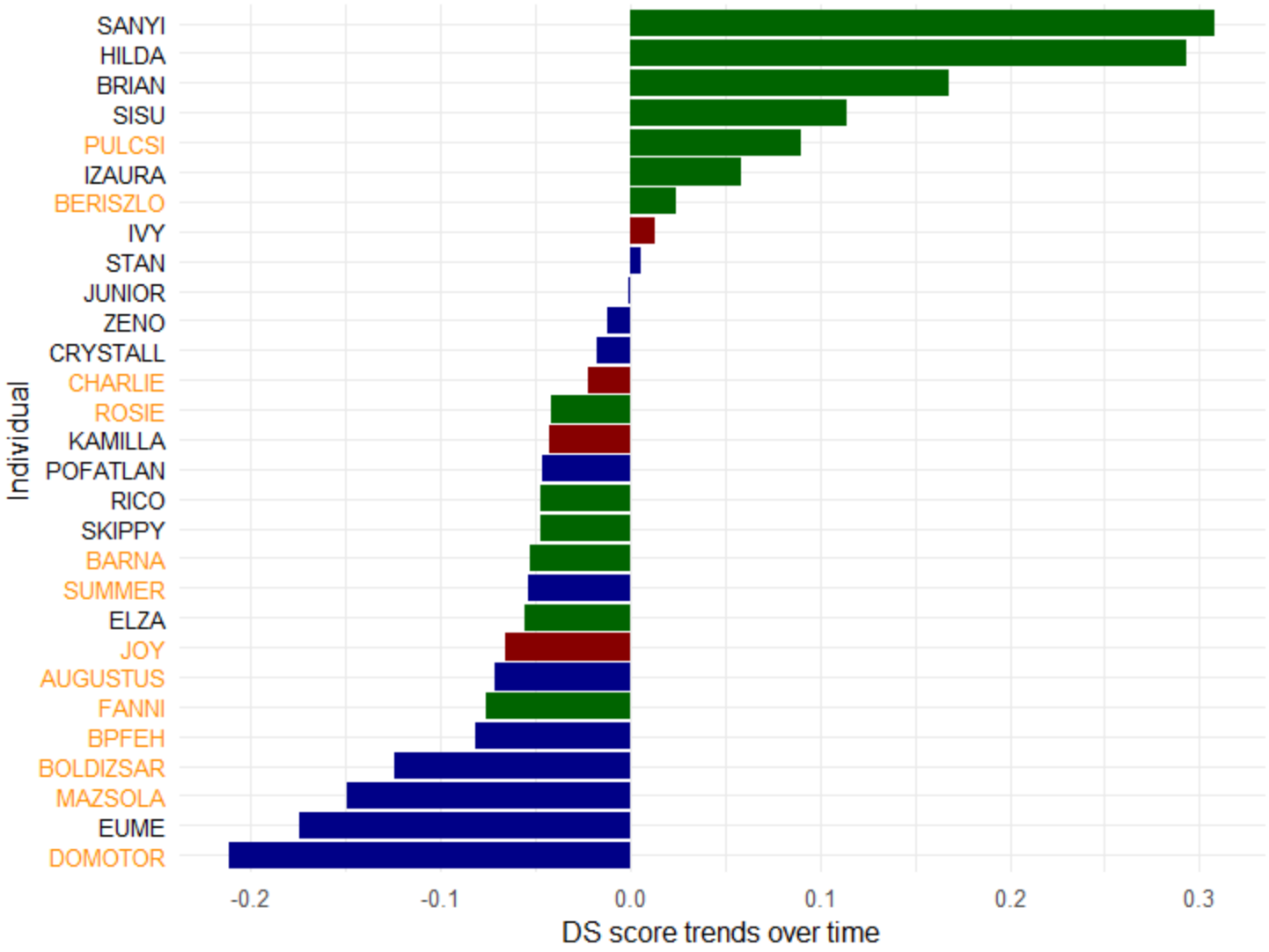

Figure 3

Trends in dominance rank (DS) over time in African penguins. Each bar represents an individual's rate of change in DS starting from zero. Name colour indicates sex (black = male, orange = female). Bar colour indicates rearing history (blue = parent-reared, red = hand-reared, green = mix-reared). Individuals with negative values became less dominant over time, whereas individuals with positive values increased their dominance.

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