

1 **Full title: Elevated aggression is associated with uncertainty in a**
2 **network of dog dominance interactions**

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12

13 **Abstract**

14 Dominance hierarchies are widespread in animal societies and reduce the costs of within-
15 group conflict over resources and reproduction. Variation in stability across a social hierarchy
16 may result in asymmetries in the benefits obtained from hierarchy formation. However,
17 variation in the stability and behavioural costs of dominance interactions with rank remain
18 poorly understood. Previous theoretical models have predicted that the intensity of
19 dominance interactions and aggression should increase with rank, but these models typically
20 assume high reproductive skew, and so their generality remains untested. Here we show in a
21 pack of free-living dogs with a sex-age graded hierarchy that the central region of the
22 hierarchy was dominated by more unstable social relationships and associated with elevated
23 aggression. Our results reveal unavoidable costs of ascending a dominance hierarchy, run
24 contrary to theoretical predictions for the relationship between aggression and social rank in
25 high skew societies, and widen our understanding of how heterogeneous benefits of
26 hierarchy formation arise in animal societies.

27

28 **Keywords:** dominance hierarchy, social network, agonistic interaction, social stability,
29 exponential random graph model

30

31 **Introduction**

32 Dominance hierarchies, in which high social rank confers priority of access to resources, are
33 a feature of animal societies from insects to primates (1–4). In many societies, dominant
34 individuals are easily recognised because they engage in conspicuous displays or frequent acts
35 of aggression towards other, subordinate group members (5,6). In other societies, dominance
36 is more difficult to infer because dominant individuals maintain their rank without resorting
37 to obvious aggression (7–9), or because dominant individuals are not necessarily the most
38 aggressive in the group (10).

39
40 Theoretical attempts to explain inter- and intraspecific variation in patterns of agonistic
41 behaviour proceed by making an explicit assumption of the function of aggression, dominance
42 or submission. The assumed function of agonistic interactions determines their predicted
43 patterns within groups. For example, where aggressive interactions serve directly to
44 outcompete or damage rivals, and submission signals a lack of motivation to challenge, one
45 might predict most aggression (and perhaps most submission) where competitors are most
46 unevenly matched. By contrast, if aggressive interactions primarily serve an information
47 function, such as to advertise resource holding potential (RHP), to reveal the quality of
48 opponents, or, in the case of submissive behaviour, to conceal information about the
49 motivation to challenge, one might predict most aggression and submission where the payoff
50 of winning is greatest and where competitors are most evenly matched (11,12).

51
52 Finally, while most models of dominance aggression assume a fixed hierarchy and examine
53 the costs and benefits of aggression to individuals of different rank, patterns of aggression
54 and submission may reflect instability or flux in social relationships within the group, or the
55 clarity of the hierarchy to its members. Unstable regions of the hierarchy can be detected by

56 there being fewer transitive relationships (A beats B, B beats C and A beats C) and more
57 cyclical relationships (A beats B and B beats C, but C beats A) than would be expected, based
58 on an overall network of hierarchical interactions (13). Rank instability may be a costly but
59 unavoidable feature of life in heterogeneous social groups in a dynamic social and ecological
60 environment. Particular regions of social hierarchies may be more or less susceptible to rank
61 instability, reducing or increasing the fitness payoffs associated with given ranks.

62
63 To investigate both the function of agonistic behaviour and patterns of stability requires data
64 on how patterns of aggression, dominance, and submission behaviours vary within social
65 hierarchies. Here we use data on social interactions in free-living dogs *Canis familiaris* to test
66 how dominance hierarchy stability varies with social rank and whether this carries
67 behavioural costs to individuals within particular regions of the hierarchy. Free-living dogs
68 frequently form multi-male multi-female social groups consisting of both related and
69 unrelated members (14,15). While they behave cooperatively (16,17), they typically exhibit a
70 promiscuous mating system (18), which would be expected to reduce reproductive skew.
71 Free-living dogs have previously been reported to exhibit a linear dominance hierarchy
72 (14,19,20,21), not dissimilar to that in wolves *Canis lupus* (22,23), in which older individuals
73 are dominant over younger ones and males are dominant over females of similar age.
74 However, unlike free-living dogs, wolves frequently live in closely-related family groups, in
75 which only the dominant pair reproduce (23). Aggressive interactions in group-living canids
76 are often influenced by motivation and context, for example by reproductive activity (24,25),
77 and as a result tend to deviate more from the expected linear hierarchy (19).

78

79 We employ social network analysis to investigate patterns of aggression, ritualised
80 dominance (here defined as ritualised behaviours intended to assert dominance without
81 resorting to aggression) and submission behaviours. Specifically, we (1) construct social
82 networks based on aggressive, ritualised dominance and submissive behaviours; (2) test how
83 ritualised dominance and aggressive behaviours vary with social rank; (3) determine regions
84 of instability in the network; and (4) examine whether rank instability is costly to individuals
85 through increasing the frequency of aggressive interactions. Our study of social behaviour in
86 dogs, where dominance is conspicuous and the costs of aggression can include prolonged,
87 energetically-costly interactions such as chasing and physical fighting (19) with that carry a
88 potential risk of injury (21), provides evidence for greater instability in dominance
89 relationships and increased aggression in the centre of dominance hierarchies. We suggest
90 that the patterns exhibited by dogs living in a complex social network may be a feature of
91 groups composed of animals of different ages and sexes, and have important implications for
92 the evolution of behavioural strategies within such groups, by generating rank-specific
93 variation in the benefits of hierarchy formation.

94

95 **Materials and Methods**

96 **Study System**

97 Behavioural observations were conducted on a free-living pack of domestic dogs in
98 Rome, Italy between April 2005 and May 2006 (197 days of observations in total). Individuals
99 in the pack were not owned by, or socialised with, humans and so could move and breed
100 freely, but were dependent on humans for food (provided daily by volunteer dog caretakers).
101 Over the course of the study, pack size ranged from 25 to 40 dogs. Our analysis focussed on
102 the 27 individuals that remained in the pack long enough to provide sufficient behavioural

103 data, comprising 6 adult males, 5 adult females, 4 sub-adult males, 1 sub-adult female, 6
104 juvenile males and 5 juvenile females. The age of individual dogs was ascertained from
105 knowledge of when they were born, if this was known. When not known, age was estimated
106 for trapped individuals by local veterinary public health officials using standard veterinary
107 methods (e.g. status of fur and tooth wear), or by trained field observers using physical
108 characteristics (e.g. individuals that were not fully-grown when first seen were aged as
109 juveniles, while individuals with worn teeth or grey muzzle hair were aged as adults) (19).

110

111 **Data collection**

112 Behavioural observations were carried out in three different social contexts: in the
113 presence of food, in the presence of receptive females and in the absence of any source of
114 competition (19). Data were collected using: i) a focal animal sampling method in the absence
115 of sources of competition, ii) a subgroup animal sampling method was used in the presence
116 of food and receptive females (totalling 282.5 hours of observation), and iii) an *ad libitum*
117 sampling method for behavioural interactions occurring outside focal sampling sessions,
118 which were considered important for the aim of the study (totalling 630.4 h of observation)
119 (see (19)). Focal observations of each individual were equally distributed over that full study
120 period, as well as across daytime between 0600 and 1800 h. Aggressive behaviour was
121 defined as threats (assuming a threatening posture: pointing, staring at, curling of the lips,
122 baring of the canines, raising the hackles, snarling, growling, and barking), chasing, physical
123 fighting and biting. Ritualised dominance behaviour included individuals displaying an upright
124 and stiff body posture with the head and tail held high and the ears pricked, individuals tail
125 wagging with the tail held high, and individuals placing their muzzle or paw on another
126 individual's back. Submissive behaviour (often associated with threats) comprised avoiding

127 eye contact, holding the head down, flattening the ears, holding the tail down or tightly
128 between the hind legs and against the belly, cringing, lying down and exposing the ventral
129 side of the chest or abdomen, avoiding and retreating. For all behavioural interactions, the
130 initiator and recipient of the behaviour were recorded.

131 Directed and undirected networks for these three behavioural categories were
132 calculated separately. Undirected networks used the total frequency of interactions between
133 two individuals (i.e. the total number of interactions, regardless of initiator/receptor) to
134 capture differences in the amount that different pairs of individuals interacted. Directed
135 networks connected the initiator of a behaviour to its receptor. Both binary (whether an
136 interaction occurred or not) and weighted (frequency of interactions) versions of the directed
137 networks were analysed.

138

139 **Calculation of rank**

140 The social rank of individuals was calculated according to the methods of (26), using data on
141 all submissive interactions. Submissive interactions provide the clearest distinction of
142 “winners” and “losers” and have been used in other studies in social canids, including this
143 study system (19). This method uses an algorithm that seeks to minimise the number of
144 inconsistencies in the rank order of individuals (i.e. where an individual of lower rank in a dyad
145 wins more interactions than the higher-ranking individual) and the strength of these
146 inconsistencies (the difference in rank between two individuals in an inconsistent dyad).

147

148 **Social Network Analysis**

149 Exponential random graph models were fitted to networks of interactions. These model the
150 probability of an interaction occurring (binary networks) or the frequency of interactions
151 (weighted networks) as a function of structural properties of the network, traits of the

152 individuals (nodes) and of the relationships between them (edges) (27,28). We fitted two
153 models for each of our three behavioural categories containing a mixture of structural and
154 individual-based terms: i) a model of the binary directed network using individual attributes
155 (sex and age) to explain the interactions an individual initiates, and ii) a model of the weighted
156 directed network using individual attributes (sex and age) to explain the interactions that an
157 individual initiates. We then fitted two additional models to networks of ritualised dominance
158 and aggressive interactions: iii) a model of the weighted directed network using rank (as
159 calculated using non-network methods as above) to explain the interactions that an individual
160 initiates and iv) a model of the weighted undirected network using rank to explain the
161 frequency of interactions between dyads. We did not fit these latter models to submissive
162 interaction networks, as these data were used to assign the social ranks used as explanatory
163 variables in them. ERGMs were fitted in R 3.2.0 (29) using the packages *ergm* (30,31) and
164 *ergm.count* (32), following the methods of (33). Statistical inference was based on the results
165 from the full models. Model convergence was tested using the function *mcmc.diagnostics*
166 (33). Full details of the models are provided in the supplementary information.

167 We then used model iii (rank-based) to explore how the ability to predict dominance-
168 related interactions changed across the hierarchy. The model was used to simulate 1000
169 directed networks for aggressive and ritualised dominance interactions using the function
170 *simulate* in *ergm.count* (32). This uses the parameters of the fitted model to simulate
171 networks with equivalent structural properties and enables the identification of regions of
172 the network that are least well explained by the model. The proportion of behaviours
173 performed by the more dominant individual in each dyad was then calculated for all null
174 networks. This statistic calculated from all simulated networks in which an interaction took
175 place was then compared to the equivalent proportion in the observed network, and the

176 median value of this comparison provided a measure of model of goodness of fit that was
177 used to determine how rank affected hierarchy stability. Goodness of fit provided a measure
178 of how well the model was able to predict the initiators of behavioural interactions for dyads
179 differing a) in their position in the dominance hierarchy and b) in their relative difference in
180 rank. This provided a measure of how well hierarchical relationships in particular regions of
181 the hierarchy matched the overall model, with the model over-fitting unstable regions and
182 under-fitting regions of increased stability.

183

184 **Results**

185 **The structure of free-living dog social networks**

186 We identified evidence for a sex-age graded linear dominance hierarchy from directed
187 networks of submissive interactions (Fig. 1). For all three interaction networks, transitive
188 interactions were significantly more likely and cyclical interactions significantly less likely than
189 expected by chance, and this influenced both the probability of interactions occurring and the
190 frequency of these interactions (Table 1). Networks of submissive interactions were most
191 linear, having the most negative estimates for cyclical interactions (meaning there were fewer
192 triads where $A > B$, $B > C$ and $C > A$) and a significant negative estimate for reciprocity (meaning
193 there were fewer dyads where both individuals initiated a behaviour). As expected, networks
194 of aggressive interactions were the least linear, showing more cyclical and reciprocal
195 interactions than either of the ritualised dominance or submissive networks (least negative
196 estimates for cyclical interactions and a positive rather than a negative estimate for mutual
197 interactions). Adults occupied the top ranks of a hierarchy based on submissive interactions
198 and tended to perform the most aggressive and ritualised dominance behaviours and the
199 fewest submissive behaviours, directing their submissive behaviours more towards other

200 adults. Juveniles occupied the bottom ranks of this hierarchy and initiated the fewest
201 aggressive and ritualised dominance interactions and the most submissive interactions,
202 directing ritualised dominance and aggressive interactions more towards other juveniles.
203 Males within each age class occupied higher ranks than females, and tended to perform more
204 ritualised dominance and fewer submissive behaviours than females, with their submissive
205 interactions more likely to be directed at other males.

206
207 Subadults targeted aggression, ritualised dominance and submission disproportionately
208 towards other subadults (significant Node match: Age – subadult terms). Although males
209 typically out-ranked females of the same age-class in hierarchies based on submissive
210 interactions, they tended to initiate aggressive interactions towards fewer different
211 individuals than females, and those that were initiated were targeted predominantly at other
212 males.

213

214 **Variation in hierarchy stability according to rank and behaviour**

215 Overall, simulated networks of behavioural interactions, using dominance ranks based on
216 submissive behaviour, accurately predicted the initiation of other dominance interactions,
217 especially for ritualised dominance behaviours. For all types of interaction, the goodness of
218 fit for predicted initiations from these simulations was, however, lowest for individuals that
219 were close in rank (Fig. 2). For aggressive interactions, reduced goodness of fit extended to
220 individuals further apart in rank than for dominance interactions. For ritualised dominance
221 interactions, when two individuals were adjacent in rank, the higher ranked individual was
222 often more likely to initiate a behaviour than the modelled expectations. In contrast, when
223 two individuals were close but not adjacent in rank and were towards the centre of the

224 hierarchy, the expected individual was less likely to initiate a ritualised dominance interaction
225 than expected (Fig. 2a, 2b).

226

227 Networks of aggressive interactions were harder to predict accurately, and there was less
228 systematic variation in when individuals did not behave as expected (Fig. 2c). However, there
229 was some tendency for the expected (higher ranking) individual to initiate fewer aggressive
230 interactions than expected towards the top of the hierarchy, and for dyads further apart, than
231 for ritualised dominance interactions, which may reflect the fact that males are less likely to
232 initiate aggressive interactions than females.

233

234 **Effects of rank on the levels of dominance behaviour and aggression**

235 Analysis of undirected interaction networks of ritualised dominance and aggressive
236 interactions (Fig. 3) revealed that for both behaviours, interactions tended to be more
237 frequent for dogs closer to the top of the hierarchy. For aggressive interactions, the frequency
238 of interactions was also higher for individuals closer to the middle of the hierarchy and closer
239 in rank (Fig. 4).

240

241 **Discussion**

242 Our network analysis found that the structure of dog hierarchy was less stable for
243 individuals close, but not adjacent, to one another in rank, especially in the central region of
244 the hierarchy. This central region of the hierarchy was characterised by elevated aggression
245 that is likely to reduce the benefits of hierarchical living, leading to heterogeneity in the
246 benefits obtained from hierarchy formation, and representing a cost of ascending rank in
247 groups without strong reproductive skew.

248

249 As predicted, networks of all agonistic interactions showed elevated transitivity and reduced
250 cyclicity of interactions as would be expected from a linear social hierarchy (13), and patterns
251 in the frequency or strength and assortativity of interactions were almost universally
252 supportive of the sex-age graded model of dominance relationships applying to this
253 population (19). Also in other social canids, social hierarchies are often influenced by sex and
254 age (23,34). Wolves differ in having hierarchies independently for males and females although
255 still graded by age, especially when packs are small and closely related (23). Dominance
256 hierarchies are important in determining access to resources in free-living dogs (35), perhaps
257 because of their promiscuous mating system (18) and tendency to live in unrelated as well as
258 related groups (14,15). In our study population, for example, dominant individuals were
259 occasionally observed stealing food from subordinates, with no behavioural reaction from the
260 subordinate individual (19).

261

262 Patterns of aggressive interactions (and to a lesser extent ritualised dominance interactions)
263 were less transitive and more cyclical than those of submissive interactions, suggesting that
264 they are be more dependent on context and motivation, and not always strictly tests of
265 dominance. In this population, aggressive interactions are rarely initiated in the absence of a
266 focus for competition, such as food (19). Contrary to the expected pattern in vertebrate
267 societies (36), female dogs tended to be aggressive to a greater number of different
268 individuals than males. We also found that males aimed the bulk of their aggressive and
269 ritualised dominance behaviour at other males, avoiding overtly aggressive encounters with
270 females. Anecdotal observations support this pattern: males in a different group of free-
271 ranging dogs were reported to “withdraw when the female made claims concerning food or

272 a resting site" (24). Further, reduced male aggression has also been demonstrated in other
273 social canids (37). The targeting of aggression towards other males might also be expected if
274 affiliative/non-aggressive social relationships increased breeding opportunities in a pack that
275 is promiscuous (18). In this situation, the costs of overt aggression are greater for males than
276 females, according with the "docile male hypothesis", that postulates that male aggression
277 toward females can harm reproductive success in some social systems (38–40).

278
279 We also showed how hierarchy stability varied with both rank, and difference in rank, for both
280 ritualised dominance and aggressive behaviours. In general, the initiation of aggressive
281 interactions was harder to predict than that of ritualised dominance interactions. This
282 highlights that not all aggressive behaviour is related to dominance interactions in this system
283 (19), and suggests that aggression is more likely for less well-established dominance
284 relationships. For individuals immediately adjacent in rank, the initiation of interactions
285 (ritualised dominance and aggressive) tended to be more one-sided than predicted by
286 models, with the expected individual being more likely to initiate an interaction than
287 anticipated, suggestive of winner-loser effects mediating dyadic behaviour among the most
288 closely matched individuals (41,42). In contrast, for individuals close in rank, but not adjacent
289 to one another, in the central region of the hierarchy, dyadic relationships were less stable
290 than would be expected. This difference in dyadic relationships between individuals adjacent
291 in rank and those close but not adjacent in rank, would most likely be explained by individuals
292 not adjacent in rank remaining relatively well matched, but having reduced information about
293 their "opponent's" relative strength or motivation to challenge (43). These unstable regions
294 may therefore arise as a consequence of temporal or contextual variation in factors
295 associated with the initiation or outcome of contests (41–43). In these free-living dogs,

296 instability in this region of the hierarchy may be explained by it containing predominantly
297 subadult individuals that are still establishing their dominance relationships, as is described
298 in other canids (44). This is supported by the tendency for subadults to target more
299 dominance interactions (of all types) at other subadult individuals.

300
301 Our results indicate that regions of instability in a dominance hierarchy may undermine the
302 benefit of reduced aggression for the individuals occupying those regions and may generate
303 differences among individuals in the benefits obtained from hierarchy formation. Previous
304 theoretical models have suggested that aggression should be greatest among dominant
305 individuals as the benefits of gaining rank are greater (5), and that aggression can be used as
306 a threat by dominant individuals to deter dominance challenges (12). The behavioural
307 (5,12,45) and consequent physiological (46,47) costs of maintaining dominance are well
308 established, and in this pack of free-ranging dogs, high social rank was associated with an
309 increased frequency of involvement in all types of behavioural interaction. However, in our
310 study, the central region of the hierarchy, in which hierarchical relationships were most
311 difficult to predict and less stable than expected, was also associated with elevated
312 frequencies of aggressive interactions. Therefore, for individuals of middling rank, rank
313 instability and its associated high levels of aggression may be an unavoidable cost incurred in
314 moving up the ranks and progressing towards higher social status.

315
316 The impact of rank stability is likely to vary depending on the nature of dominance hierarchies.
317 Many mammalian societies, especially those with more stable groups, are characterised by
318 matrilineal hierarchies in which changes in dominance are highly unusual (48). However, a
319 similar elevation of aggression amongst middle-ranking individuals has been found in birds,

320 in the sociable weaver *Philetairus socius* (49), and was suggested to be generated by either
321 the increased benefits of improved rank, or as a result of more numerous social relationships.
322 Similarly, in the cichlid fish *Neolamprologus pulcher*, increases in social rank were found to be
323 associated with temporary increases in aggression (45). It is therefore clear that across a
324 taxonomically diverse range of societies, high levels of aggression can be seen away from the
325 top of hierarchies, and that this variation in the expression of aggression is related not solely
326 to ascent in rank but to instability and uncertainty in the dynamics of hierarchical
327 relationships. Further work determining how this is related to the nature and fluidity of social
328 structure would be highly valuable, and this would benefit greatly from analytical approaches
329 that can incorporate modelling of the dynamics of dominance hierarchies (50,51).

330
331 We propose three mechanisms that may explain the pattern of instability in dyadic
332 dominance relationships in these free-living dogs. First, reduced stability might occur because
333 less information is available to assess dyadic relationships in a particular region of a hierarchy.
334 Hierarchical relationships tend to be more stable when individuals have more information
335 available to assess interaction outcomes (43,52). As highlighted, in our hierarchy of free-living
336 dogs, the unstable central region of the hierarchy was dominated by subadult individuals, and
337 it might be expected that these individuals are still in the process of forming their social
338 relationships. Second, if Resource Holding Potential (or a trait that correlates with RHPs, such
339 as body size) is normally distributed then we expect a preponderance of dyads with reduced
340 RHP asymmetries in the centre of a hierarchy. This may be analogous to the suggestion that
341 social relationships are more complex and numerous in the central part of a hierarchy (49).
342 Third, the central region might represent an area where dyadic dominance relationships are
343 highly dynamic and either social relationships within dyads change faster than it is possible to

344 measure, or these dynamic social relationships result in less accurate information about the
345 relative RHP of individuals. This is likely to be especially true if RHPs peak at a particular age
346 before declining (53). Since the unstable central region of the dominance hierarchy in our
347 study pack consists primarily of subadult individuals, this third mechanism is perhaps less
348 likely than those discussed previously.

349
350 We have revealed reduced linearity of dominance relationships and elevated
351 aggression for middle-ranking individuals. The pattern of elevated aggression in the central
352 region of a dominance hierarchy ran contrary to theoretical models of animal conflict
353 developed for animal societies with high reproductive skew, in which aggression is expected
354 to increase with hierarchical rank. Therefore, our results suggest that individuals in
355 hierarchical societies, especially those with low reproductive skew, pay an unavoidable cost
356 in order to assess social relationships, if or when they progress to higher ranks. A more general
357 understanding of the roles of dominance relationships in mediating the costs of group-living
358 requires theoretical frameworks and empirical approaches that recognise dominance
359 relationships as dynamic entities.

360
361

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366

367 **Author contributions:** All authors designed the study. SC and EN collected the data. MJS
368 analysed the data. MJS, MAC and RAM wrote the manuscript with all authors contributing
369 to revisions.

370

371 **Data accessibility statement:** Data and R code are provided in the supplementary material.

372

373 **Ethics:** This study complies with the Italian regulations regarding the ethical treatment of stray
374 domestic dogs. Research permission to conduct observations and handle animals was granted
375 by the Veterinary Public Service of Rome.

376

377 **Competing interests:** We have no competing interests

378

379

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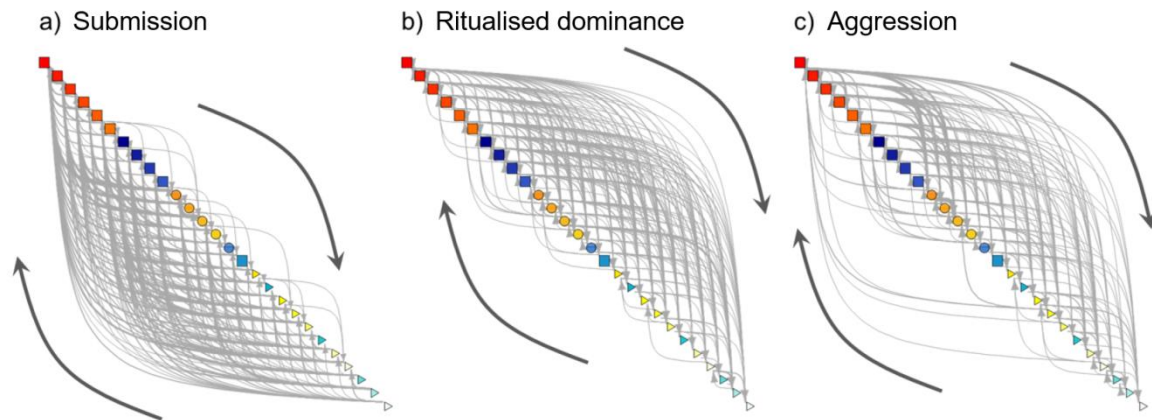
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504 **Figures and Tables**

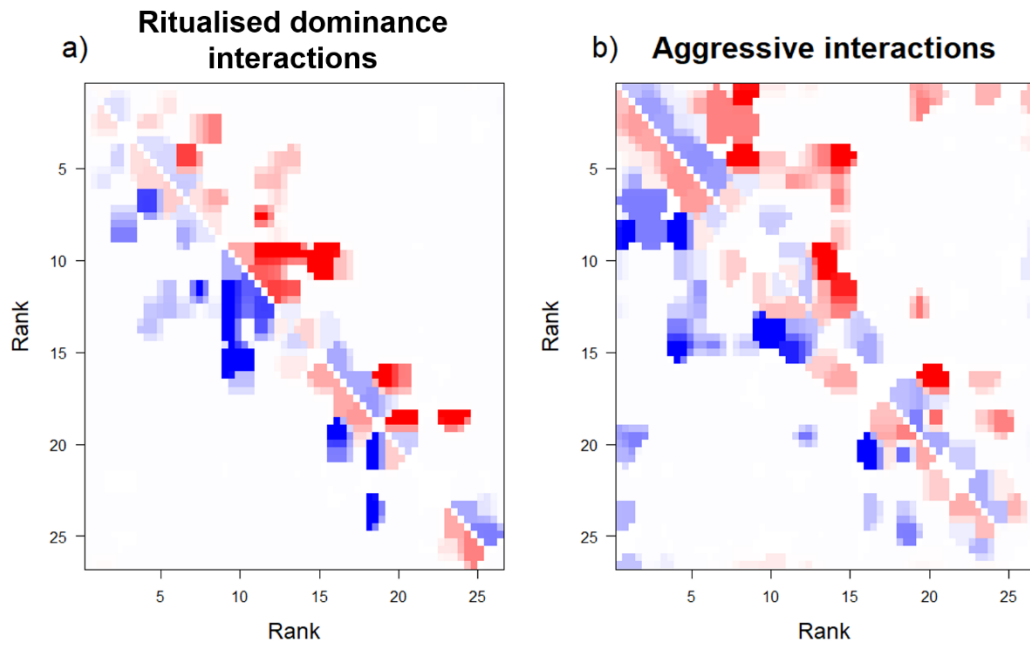
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507 **Figure 1.** Directed networks of agonistic behaviour in a pack of feral dogs, for submissive interactions (left),
508 ritualised dominance interactions (centre) and aggressive interactions (right). Edges are weighted in proportion
509 to the frequency of interactions. Nodes are coloured according to sex – males are red/yellow and females are
510 blue/green – and shaded to represent position in a hierarchy quantified using submissive interactions. Square
511 nodes represent adults, circles are sub-adults and triangles are juveniles.

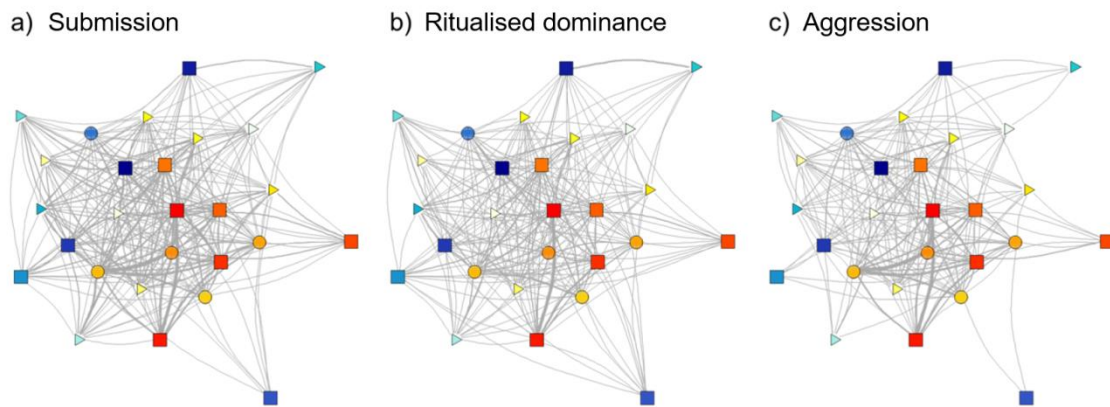
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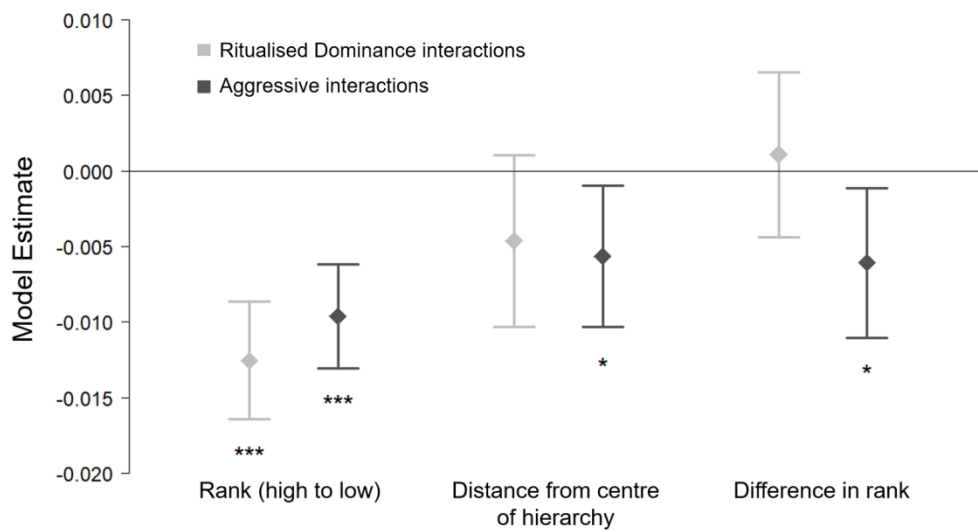
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514 **Figure 2.** Similarity in the proportion of a) ritualised dominance and b) aggressive interactions initiated by an
 515 individual in a pack of free-living dogs when compared to networks simulated from rank-based exponential
 516 random graph models. Goodness of fit of the observed data to the simulated network model is the median
 517 difference between proportion of behaviours initiated in the observed network and 1000 simulated networks.
 518 Red represents initiations of behaviour being more likely in the observed network than simulated networks and
 519 blue the initiations of interactions being less likely.

520



521
 522 **Figure 3.** Undirected networks showing the frequency of behavioural interactions in a pack of free-living dogs for
 523 a) submissive, b) ritualised dominance and c) aggressive interactions. Edges are weighted in proportion to the
 524 frequency of interactions. Nodes are coloured according to sex – males are red/yellow and females are
 525 blue/green – and shaded to represent position in the hierarchy quantified using submissive interactions. Square
 526 nodes represent adults, circles sub-adults and triangles juveniles.
 527



528

529 **Figure 4.** The effect of rank, rank distance from the centre of the hierarchy and difference in rank between two
 530 individuals on the frequency of involvement in ritualised dominance and aggressive interactions in a pack of free-
 531 living dogs. Models are from undirected networks of dominance-related interactions, and therefore individuals
 532 are recorded as interacting if they either initiated or were the recipient of a behaviour. Points represent the
 533 conditional estimates from the model and the error bars are the 95% confidence intervals of these estimates.
 534 Model estimates below zero mean that a change in the covariate reduces the number of interactions expected,
 535 and model estimates above zero mean that a change in the covariate increases the number of interactions
 536 expected.

537 **Table 1.** Summary of variation in the probability and frequency of **submissive, ritualised dominance and aggressive interactions** in directed networks of free-living dog social
538 interactions. Positive model estimates for the probability models mean that a given network configuration occurs more than expected, and positive estimates in the frequency
539 models mean given network configurations have greater edge weights than expected. Negative model estimates mean that given network configurations occur less
540 (probability model) or have lower edge weights (frequency model) than expected. Mutual terms were not fitted in the final weighted models as they caused the models to fail
541 to converge. Estimates that were significant are in bold (with asterisks showing the level of significance, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Term	Submissive interactions		Dominance interactions		Aggressive interactions	
	Probability	Frequency	Probability	Frequency	Probability	Frequency
Transitive interactions	0.07±0.01***	0.07±0.02***	0.07±0.01***	0.14±0.04***	0.07±0.01***	0.12±0.03***
Cyclical interactions	-0.61±0.09***	-0.36±0.03***	-0.47±0.09***	-0.35±0.04***	-0.18±0.08*	-0.11±0.03***
Mutual interactions	-1.52±0.41***	NA	-0.47±0.40	NA	0.43±0.34	NA
Node match: Age – Adult	-0.28±0.31	0.23±0.10*	-0.15±0.34	0.04±0.03	-1.20±0.28***	0.003±0.03
Node match: Age – Juvenile	-0.57±0.35	-0.13±0.04**	1.59±1.02	1.58±0.95	2.34±0.56***	0.69±0.18***
Node match: Age – Subadult	2.51±0.63***	0.04±0.02	1.46±0.63*	0.21±0.05***	1.57±0.61*	0.20±0.04***
Node match: Sex – Female	-1.04±0.31***	-0.03±0.04	-0.19±0.29	0.004±0.07	-0.51±0.26	0.03±0.08
Node match: Sex – Male	1.07±0.33**	0.13±0.02***	0.26±0.27	0.09±0.03**	1.28±0.24***	0.50±0.08***
Interactions: Male vs. Female	-0.28±0.14*	-0.02±0.02	0.46±0.20*	0.12±0.04**	-0.84±0.23***	-0.16±0.09
Interactions: Juvenile vs. Adult	0.64±0.19***	0.23±0.10*	-3.20±1.02**	-1.99±0.95*	-3.25±0.55***	-0.81±0.18***
Interactions: Subadult vs. Adult	0.38±0.16*	0.23±0.10*	-0.46±0.22*	-0.14±0.04***	-0.82±0.26**	-0.12±0.04**