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Faculty of Science

**The Effect of Season and Dominance Hierarchy on
Strategic Interaction Among Birds in Mixed-species
Aggregation**

Master's thesis

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Annotation

The effect of the dominance hierarchy and the season was studied on different aspects of mixed-species bird aggregation at feeders, such as the group size, feeding propensity, and strategic interaction among birds. To achieve these goals two types of feeders namely: gauze ball feeders and bottle feeders were used. The study was conducted in winter accounting for the non-breeding season and spring for the breeding season in three sites around České Budějovice, Czech Republic.

Declaration

I declare that I am the author of this qualification thesis and that in writing it I have used the sources and literature displayed in the list of used sources only.

Date:13-04-2023

České Budějovice,

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1 **1. Introduction**

2 Mixed species aggregation (MSA) in birds occurs when more than one species gather around
3 a resource or specific location (Powell, 1985). MSA, in nature, is seen around food resources
4 clumped in space, such as mass-fruiting trees, water bodies, termite swarms or mineral licks,
5 and artificially available sources like bird feeders (Willis & Oniki, 1978; Robb et al., 2008;
6 Goodale, Beauchamp, & Ruxton, 2017). As the resources are limited to a specific location,
7 there is a need for competition between participating members for food acquisition. This results
8 in dominance interactions such as aggressive and agonistic interactions which are displayed
9 through physical combat or visual signals respectively (Miller et al., 2017; Kenyon & Martin,
10 2022). Aggressive interactions include display of dominance behaviours such as pecking,
11 striking, and chasing (Duncan & Wood-Gush, 1971; Kaufmann, 1983; Diniz, 2020), and
12 agonistic interactions include behaviour involving visual postures or signals such as
13 confronting or advancing towards the opponents, and spreading wings with vocalisations to
14 display threat (Scott & Deag, 1998; Kenyon & Martin, 2022). The propensity to win such
15 interactions establishes a dominance hierarchy, where the dominant species (the winner species
16 representing higher rank in the hierarchy) has better access to limited resources compared to
17 its subordinates (Richner, 1989; Francis et al., 2018). Thus, the species' rank in the hierarchy
18 determines its access to resources such as food (Francis et al., 2018) and breeding territory
19 (Rabinowicz et al., 2020), indirectly influencing the life history and fitness of the participating
20 species (Schneider, 1984; Ekman, 1987; Zhang et al., 2021). However, the dominance
21 interactions are costly and energy-consuming (Riechert, 1988; Kenyon & Martin, 2022). This
22 is especially true for aggressive interactions as they involve in physical combat, hence
23 energetically demanding (DeCarvalho, Watson, & Field, 2004; Georgiev et al., 2013).
24 Moreover, species involved in aggressive interactions increase the risk of injury or death and
25 they are also vulnerable to predation (Robertson, Gibbs, & Stutchbury, 1986; Hof & Hazlett,
26 2012; Diniz, 2020), besides the depletion of energy reserves. Hence, the type of interaction
27 must be displayed strategically based on the opponent's position in the dominance hierarchy,
28 such that they attain maximum benefits with minimum energy costs.

29 Past empirical studies have shown that the dominance rank is strongly predicted by the body
30 mass across species (French & Smith, 2005; Miller et al., 2017; Francis et al., 2018; Moreno-
31 Opo, Trujillano, & Margalida, 2020) and that feeding propensity and access to quality
32 resources increase with an increase in their ranking status in the hierarchy (French & Smith,
33 2005; Francis et al., 2018). With respect to strategizing dominance interactions, studies on

34 intraspecific interactions in group-living species demonstrate a ‘close competitor strategy’
35 where the individuals express highly costly interaction such as chasing and pecking towards
36 individuals of similar rank and lower aggressive interaction such as displacing and gaping as
37 the difference between the ranks increases (Hobson & DeDeo, 2015; Wright et al., 2019;
38 Dehnen et al., 2022). However, these studies are limited to group-living species and
39 intraspecific interactions, suggesting a gap in testing the ‘close competitor’ strategy in MSAs.
40 Despite this, we expect to see that, during the dyadic dominance interactions, high-cost
41 interactions i.e., aggressive interactions are exhibited towards species that are immediately
42 positioned to them in the hierarchy, and that the tendency to express such interactions is
43 reduced and taken over by gradual switch to agonistic interactions with an increase in the rank
44 difference. This is expected to be so, as the dominance between distant ranks is well-established
45 and less susceptible to change, unlike closely positioned ranks.

46 Although the aforementioned studies show that dominance rank plays a significant role in both
47 feeding propensity (in the case of MSAs) and strategic expression of different types of
48 interaction (in the case of group living animals) these studies are restricted to nonbreeding
49 season i.e., winter. This could be an oversimplification as the species interactions in the
50 communities might not be permanent, especially in the temperate region (Saavedra et al.,
51 2016), where the availability of food, temperature, and duration of the day varies with the
52 season (Lack, 1954; Jansson, Ekman, & von Brömssen, 1981; Haftorn, 1992). In response to
53 seasonal variation, species exhibit strong responses such as: migration shaping the species
54 composition, reproduction changing the species’ behaviour, and changes in dietary preference
55 influencing resource exploitation (Slater, 1995; Holland et al., 2006; Canoine et al., 2007).
56 Therefore, it is important to understand the feeding propensity and use of strategic dominance
57 interactions along the hierarchy in the context of seasonality.

58 Hence, in this study, we aim to assess the response of species’ feeding propensity and close
59 competitor strategy in MSA in relation to seasonality. In order to achieve this, we are interested
60 in investigating 1) variation in group size as a function of seasonality, 2) the effect of
61 seasonality and dominance rank on the feeding propensity of participating species, 3) the
62 importance of rank difference and seasonality on the strategic use of interaction types.

63 To achieve this, two types of feeders differing in accessibility and food quality to particular
64 bird species are used, and observations are made on the dyadic interactions at each feeder (see
65 Appendix 3 for feeder images). It is expected that there is an increase in the group size in winter

66 and in ball feeders, in general. This is assumed to be associated with the decreased food
67 availability and harsh weather conditions in winter (Lack, 1954; Haftorn, 1992) and availability
68 of higher nutrient and fat content in gauze ball feeder (Alatalo & Moreno, 1987; Francis et al.,
69 2018). It is also hypothesized that dominance rank and season have an impact on feeding
70 propensity. In general, the feeding propensity is expected to increase with dominance rank
71 following the body size as suggested in previous studies (Miller et al., 2017; Francis et al.,
72 2018; Moreno-Opo et al., 2020). Furthermore, the feeding propensity is assumed to correlate
73 with the season, i.e., reduced in spring as a response to increased alternative food availability
74 in the surroundings (Hinde, 1956; Seward et al., 2014; Barras, Candolfi, & Arlettaz, 2022).

75 In winter, we expect to see the species follow the ‘close competitor’ strategy, where aggressive
76 interactions (high cost) are more likely towards species closely positioned in the hierarchy, and
77 agonistic interaction (low cost) towards species further below themselves. This is based on the
78 assumption that ranks of the species positioned closely in the hierarchy is unstable and
79 vulnerable to change due to similar body size, therefore, in order to establish constant
80 dominance, species closely positioned in the hierarchy tend to defend aggressively (Hughes,
81 1996; Hemelrijk, 2000; Wright et al., 2019). On the other hand, we expect to see either of the
82 two possible patterns in spring: The tendency to be aggressive decreases even between species
83 from closely positioned ranks, and it is to be taken over by agonistic interactions. This
84 assumption is based on the availability of food in the spring, as the food abundance increases,
85 the dependency on the feeder is expected to reduce, hence, there is a poor need to exert high-
86 cost aggressive interactions towards closely located species in the hierarchy. Alternatively, the
87 pattern may be similar to winter, following ‘close competitor’ strategy, showing aggressive
88 interaction between closely positioned species in the hierarchy. This assumes that although
89 increased availability of food in spring can decrease the dependency on the feeder hence could
90 possibly reduce the tendency to be aggressive, increased levels of hormones such as androgen,
91 estrogen, and testosterone in the breeding season makes species’ territorially aggressive in
92 order to protect resources, mating partner, nest and the chicks (Harding, 1981; Balthazart, 1983;
93 Canoine & Gwinner, 2002). Hence, the tendency to interact aggressively is expected to remain
94 between closely ranked species in spring. We also assume that lower-ranking species express
95 cooperative interactions (such as joining the individuals at the feeder or attending the feeder
96 right after the departure of the individuals at the feeder leaves) opportunistically, towards
97 higher-ranking species from the farthest rank in the hierarchy, in order to gain access to the
98 feeder. But this is expected to be limited to winter, as this kind of interaction is risky due to

99 their interaction with larger species, increasing the chances of injury (Robertson et al., 1986;
100 Hof & Hazlett, 2012), and we assume that the lower-ranking species are forced to exhibit this
101 interaction as an outcome of attributes of harsh conditions related to winter.

102 **2. Methodology**

103 **2.1 Study area**

104 The study was conducted in three localities in České Budějovice, Czech Republic, namely: 1)
105 Branišovský les (48.979N, 14.418E), representing a mixed forest predominated by oak
106 (*Quercus sp.*), spruce (*Picea abies*) and pine (*Pinus sylvaticus*), 2) Mladohaklovský rybník
107 (48.993N, 14.437E), representing mixed stands of aspen (*Populus tremula*) and birch (*Betula*
108 *sp.*) with willow shrubs (*Salix sp.*), and 3) U Švába (48.967N, 14.444E), which is a draw stand
109 of shrubs and trees between crop fields with the predominating elder (*Sambucus niger*),
110 blackthorn (*Prunus spinosa*), aspen and oak. During my observations, the crop fields
111 surrounding this line of vegetation were freshly sown with barley (*Hordeum vulgare*) and
112 rapeseed (*Brassica napus*) or left ploughed (see Appendix 1 and 2 for map and images of study
113 site)

114 **2.2 Data collection**

115 Two types of bird feeders were deployed for the experiment (see Appendix 3 for feeder
116 images): bottle feeder, composed of a mixture of sunflower seeds, wheat millet, and flax; and
117 gauze ball feeder, composed of hardened vegetable fat and a mixture of ground seeds same as
118 the bottle feeder. In each of the aforementioned locations, seven of each feeder type were
119 installed at random, separated by at least 100 meters for feeders of the same type and 50 meters
120 for feeders of different types. The feeders were installed two weeks prior to the observations
121 to allow birds to get accustomed to the food availability and visit feeders regularly. Moreover,
122 they were available throughout the duration of the study as they were regularly monitored and
123 refilled/replaced. The study was conducted between December to mid-March accounting for
124 the winter season (non-breeding period for all focal bird species) and mid-March to May
125 corresponding to the spring season (breeding period).

126 At each feeder, data on 1) the winner and loser species of dyadic dominance interaction at the
127 feeder, 2) the type of behaviour expressed by the winner species during the dominance
128 interaction (Table 1), and 3) mixed species group size and composition within 10 m distance
129 to the feeder was collected. This data was recorded in the morning during the first four hours
130 after sunrise. A video recorder and binoculars were used by the observer to ensure maintaining

131 a distance of 15 m from the feeder to prevent any disturbance. Since the occurrence of the
132 Mixed species aggregations of birds (MSAs) at the feeders is opportunistic, we adopted ad
133 libidum observation-based recordings. We collected five such opportunistic recordings per
134 feeder and each season, with each recording lasting four minutes on average (mean = 4.40,
135 SD= 0.76). In total, 431 recordings were gathered with each feeder representing at least five
136 recordings (mean= 5.13, SD= 0.37) (see Appendix 4 for a table summarizing all observations
137 on particular feeder, feeder type and season). However, 10 recordings from two feeders (one
138 ball feeder and one bottle feeder) did not show any interaction in the spring season as there was
139 no aggregation.

140 Here, an individual is considered to be a winner if it successfully displaced the individual at
141 the feeder. The individual that is displaced is termed a loser. The dominance behaviour
142 exhibited by the winner to displace the loser is distinguished into seven behaviours as listed
143 below (Table 1). Further, these Seven dyadic dominance behaviours were categorized into
144 three types of interaction (Table 1): aggressive, agonistic, and cooperative interactions, based
145 on the energy consumed, and physical contact. Aggressive interactions are considered to be
146 behaviours such as pecks, strikes and chasing behaviour, as they are costly in terms of energy
147 consumed or potential physical injury (Duncan & Wood-Gush, 1971; Kaufmann, 1983;
148 DeCarvalho et al., 2004; Hof & Hazlett, 2012). While agonistic interactions include behaviours
149 such as confronting and advancing towards the opponent and wing spread with vocalization.
150 Agonistic interaction is comparatively less costly in terms of energy consumed and require no
151 physical contact (Scott & Deag, 1998; Kenyon & Martin, 2022). On the other hand, cooperative
152 interaction is scored when an individual joins the other individual at the feeder without any
153 displacement effect. The risk of injury with this type of interaction is based on the opponent's
154 tolerance towards the joining individual, if successful both the participants are benefited at the
155 feeder unlike the outcome of the aggressive and agonistic interactions. Apart from this,
156 vegetation mapping was performed at each feeder to collect data on the composition and
157 number of trees and understorey shrubs within the 10-meter radius of the feeder. The tree and
158 understorey density were estimated (see Appendix 4). We also extracted the mean daily
159 temperature for every recording duration of the study period from World Weather Online
160 (World Weather, 2016) (available at: <https://www.worldweatheronline.com/>).

161

Interaction type	Behaviour	Definition
aggressive	peck	A pecks head or other body parts of B
	strike	A strikes the head or other body parts of B with its feet
	chase	A chases B
agonistic	wings spread	A displays widely spread wings with vocalization to B, and B retrieves
	advance	On arrival of A to less than 0.5 m to the feeder, B retrieves
	confront	A displaces B from the feeder on its arrival at the feeder
cooperative	cooperative	A joins B, which is already feeding at the feeder

163 Table 1: The list of dyadic behaviours observed at the feeders are categorized into 3 interaction
 164 types. A represents the winner individual and B the loser individual which is the recipient of
 165 the behaviour

166 **2.3 General data structure**

167 2559 observations were made on different kinds of dyadic interactions from 431 recordings
 168 from 42 feeders in both seasons. 431 group sizes and group composition of mixed species
 169 aggregations were assessed. Of 2559, 1099 interactions were categorized as “opportunistic”
 170 where the species “A” present in less than 5 meters distance approached the feeder and
 171 subsequently species “B” present at the feeder left within 3 seconds. However, “opportunistic”
 172 behaviour had to be removed from the dataset since the behaviour could not be accurately
 173 measured due to various constraints such as observers’ error due to the visibility of species
 174 “A”, and lack of objective precision in accountability of such behaviour. Hence leaving us with
 175 1460 dyadic interactions within and between species. These interactions included: agonistic
 176 interactions, aggressive interactions, and cooperative interactions (see Table 1 for a
 177 description). Of 1460 interactions, 657 are interspecific interactions and 803 are intraspecific
 178 interactions.

179 **2.4 Data analysis**

180 **2.4.1 Dominance hierarchy**

181 To construct the dominance hierarchy, data on 657 interspecific dyadic interactions was used
 182 from both the seasons and feeder types. As previous studies have indicated hierarchy to be

183 strongly shaped by body size (Miller et al., 2017; Francis et al., 2018; Moreno-Opo et al., 2020),
184 we assumed that there is no difference in hierarchy towards season or feeder. Since cooperative
185 interactions (122) does not indicate a winner or loser species, the cooperative interaction was
186 filtered out from this data which left us with 535 interspecific interactions.

187 Given that the dyadic interaction dataset was also used to assess the effect of rank difference
188 on the type of interaction expressed, and as robust dominance hierarchies can be generated
189 using comparatively fewer observations (Sánchez-Tójar, Schroeder, & Farine, 2018; Dehnen
190 et al., 2022), we split the interspecific dyadic interaction data (without cooperative interaction)
191 randomly into two subsets of 25% and 75%. The first subset (i.e., 25% data) was used to
192 construct the dominance hierarchy while the rest was used in calculating the tendency to
193 express different types of dominance interactions.

194 As complete randomization in splitting the data would lead to first subset being biased towards
195 the most common species that interact very frequently and represent the least number of
196 interactions by species participating less frequently, randomization with respect to species was
197 performed. (Sánchez-Tójar et al., 2018) was followed to create a stable hierarchy with an
198 optimal dataset, where 15 interactions were randomly chosen for the most common species, 10
199 interactions for comparatively uncommon species, and all available interactions for rare
200 visiting species such as *Certhia familiaris* (Eurasian Treecreeper) and *Lophophanes cristatus*
201 (Crested Tit) (two and five respectively). In total 139 (25% data) winner-loser, dyadic
202 interactions were used to construct a dominant hierarchy.

203 To produce the rank-based dominance hierarchy, I employed the method suggested by
204 (Sánchez-Tójar et al., 2018), i.e., the ‘randomized Elo-rating’ which used 139 winner-loser
205 dyadic interaction data for 15 species and iterated Elo-ranks 500 times. From this, mean
206 dominance rankings were calculated. This was performed in R software using Elo-score
207 function from the aniDom package.

208 Since the dominance hierarchy is used as a predictor in the analysis, the robustness and
209 certainty of the dominance hierarchy were tested using ‘estimate_uncertainty_by_splitting’
210 (with probability to repeat 500 randomizations) from aniDom package. Further, we also
211 assessed the steepness of the dominance hierarchy using the and ‘plot_hierarchy_shape’
212 function in aniDom package. These functions incorporated the first subset of data on winner
213 and loser interaction (i.e., 25% data). Additionally, many studies namely, (Miller et al., 2017;
214 Francis et al., 2018; Moreno-Opo et al., 2020) have shown that body size can be used as a proxy

215 for ranking where the relation between dominance hierarchy and body size of respective bird
216 species is linear, hence, we performed Spearman's correlation test using 'cor.test' function in
217 R to confirm the certainty of the hierarchy indirectly.

218 2.4.2 Group size

219 The group size was determined for each recording as the total number of participants found at
220 the feeder within a radius of less than 10 m. From 431 recordings at 42 bottle and ball feeders,
221 431 group sizes were made in total. The effect of various predictors such as season, feeder type,
222 tree density, shrub density, and temperature were tested on the group size using the analysis of
223 variance. The step-wise selection was performed using the 'add1' function to choose the model
224 with the parsimonious predictors. Moreover, the group size data were log transformed to
225 achieve normal distribution, and to account for the variation caused by the site, the chosen
226 model was subjected to the analysis of variance with the 3 sites as a random effect.

227 2.4.3 Feeding tendency

228 Feeding tendency is the propensity of the species to feed at the feeder given its presence in the
229 mixed species aggregation (MSA) around the feeder. It is calculated by dividing the number of
230 times a species was seen feeding at the feeder by the number of times it was seen in the
231 aggregation around the feeder. It was determined for each participating species per feeder per
232 season based on all the observations from 5 recordings at a given feeder. Following (Stanley
233 Cramp, Perrins, & Brooks, 1982; S. Cramp, 1988; Isenmann, 1994), the diet of the birds was
234 classified as omnivores, insectivores, primary granivores, and strict granivores. Dominance
235 rank constructed from 25% of the interspecific dyadic dominance interaction data was used for
236 the analysis.

237 The effect of environmental factors such as season, feeder type, tree density, and understory
238 density and species traits such as dominance rank, and diet at the feeder was tested on the
239 feeding tendency. To achieve this, step-wise selection of parsimonious predictors using linear
240 regression models was performed. Finally, the chosen predictors were tested with random
241 factor such as site, to account for the random effect.

242 2.4.4 Dyadic strategic interactions

243 The second subset of the interspecific dyadic dominance interaction data (75% data = 396) was
244 combined with the rest of the data that comprised cooperative interspecific interactions (122)
245 and all intraspecific dominance interactions (803). In total, we used 1321 dominance

246 interactions between and within species. To calculate the rank difference, the species were
247 replaced by their ranks and the winner species rank was subtracted from the loser species' rank.
248 As a result, the rank difference ranged from -9.5 to +6.7 where - indicates the interaction is
249 displayed by the species from a higher rank, while + is by species from a lower rank. Regardless
250 of the sign (+/-), the number in the rank difference suggests the difference between two species
251 in the hierarchy. Higher the number, the larger the rank difference between any given species
252 dyad.

253 The tendency to exhibit particular dyadic interaction is the proportion of particular interaction
254 displayed out of all types of interactions displayed. It was calculated for each type of
255 interaction, for every rank difference by dividing the number of a given type of dyadic
256 interaction (i.e., agonistic, aggressive, or cooperative interaction) displayed by species from a
257 given rank difference by the total number of interactions displayed for the same (i.e., the
258 summation of aggressive, agonistic, and cooperative interaction). It is to note that in spring,
259 there is no observation of interactions displayed by lower ranking species towards high-ranking
260 species, hence the tendency to show any kind of interaction is not assigned to the rank
261 differences ranging from 0.55 to 7.

262 To test for the effect of rank difference, season, and feeder type on the tendency to display
263 three types of interactions, we employed 'step' function and performed generalized linear
264 models using quadratic regression for aggressive interaction and logistic regression for
265 agonistic interaction and cooperative interaction. These interactions were then plotted using
266 loess models (span= 0.58), to visualize the effect of rank difference, season, and feeder type.

267 **3. Results**

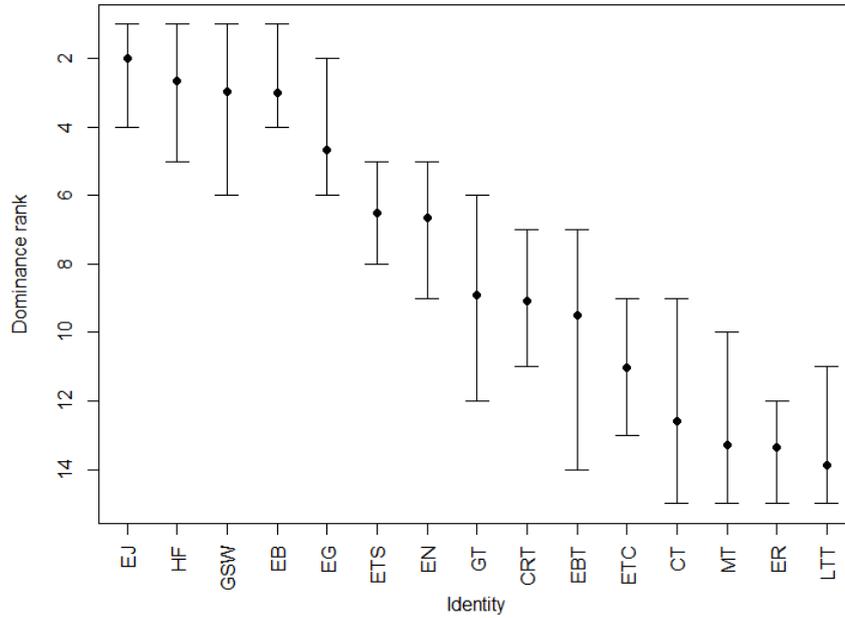
268 **3.1 Dominance hierarchy**

269 The dominance hierarchy of the 15 participating species is shown in the Table 2 with the
270 highest-ranking species being Eurasian Jay (*Garrulus glandarius*) and the lowest-ranking
271 species being Long-tailed Tit (*Aegithalos caudatus*) (Figure 1). Based on the correlation score
272 ($\rho = 0.79$) calculated using the 'estimate_uncertainty_by_splitting' function, it is clear that
273 the dominance hierarchy is robust and certain. Hence, it can be used as a predictor in the main
274 analysis. In accordance with the 'plot_hierarchy_shape' function, the probability of winning is
275 more than 90% only when the rank difference is 3 or more (Appendix 5). The Spearman's
276 correlation test confirms that there is a strong correlation between dominance hierarchy and the
277 body size of species ($\rho = -0.88$, $p < 0.001$) (French & Smith, 2005; Miller et al., 2017; Francis

278 et al., 2018; Moreno-Opo et al., 2020). Therefore, with an increase in the body size, there is an
 279 increase in the rank of the species (1 being the highest) (Figure 2).

Species	Scientific names	Species code	Body size	Diet	Mean rank
Eurasian Jay	<i>Garrulus glandarius</i>	EJ	159.5	Omnivore	2.02
Hawfinch	<i>Coccothraustes</i> <i>coccothraustes</i>	HF	56.6	Strict granivore	2.58
Great Spotted Woodpecker	<i>Dendrocopos major</i>	GSW	74.9	Omnivore	2.99
Eurasian Bullfinch	<i>Pyrrhula pyrrhula</i>	EB	24.3	Strict granivore	3.03
European Greenfinch	<i>Chloris chloris</i>	EG	26	Strict granivore	4.63
Eurasian Tree Sparrow	<i>Passer montanus</i>	ETS	21.4	Primary granivore	6.56
Eurasian Nuthatch	<i>Sitta europaea</i>	EN	20.4	Omnivore	6.59
Great Tit	<i>Parus major</i>	GT	16.3	Omnivore	8.96
Crested Tit	<i>Lophophanes cristatus</i>	CRT	11	Omnivore	9.1
Eurasian Blue Tit	<i>Cyanistes caeruleus</i>	EBT	11.1	Omnivore	9.51
Eurasian Treecreeper	<i>Certhia familiaris</i>	ETC	9	Insectivore	11.07
Coal Tit	<i>Periparus ater</i>	CT	9.2	Omnivore	12.53
Marsh Tit	<i>Poecile palustris</i>	MT	11.1	Omnivore	13.27
European Robin	<i>Erithacus rubecula</i>	ER	17.7	Insectivore	13.31
Long-tailed Tit	<i>Aegithalos caudatus</i>	LTT	8.6	Insectivore	13.84

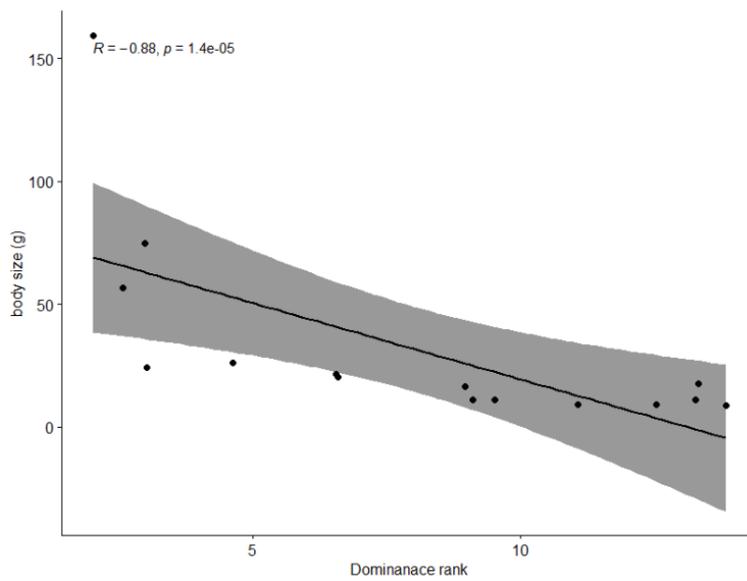
280 Table 2: A list of dominance hierarchy of the 15 participating species along with their body
 281 size in grams. The rank of each species is the mean rank calculated from 500 iteration of the
 282 dominance rank. The body size of the participating species is extracted from (Dunning Jr, 2007)
 283 and the diet from (Stanley Cramp et al., 1982; S. Cramp, 1988; Isenmann, 1994)



284

285 Figure 1: Dominance hierarchy with mean ranks. The identity refers to the species code which
 286 is listed in table 2. The points are mean ranks with 95% confidence interval as whiskers

287



288

289 Figure 2: Correlation between body size and dominance rank of participating species in mixed-
 290 species aggregations.

291

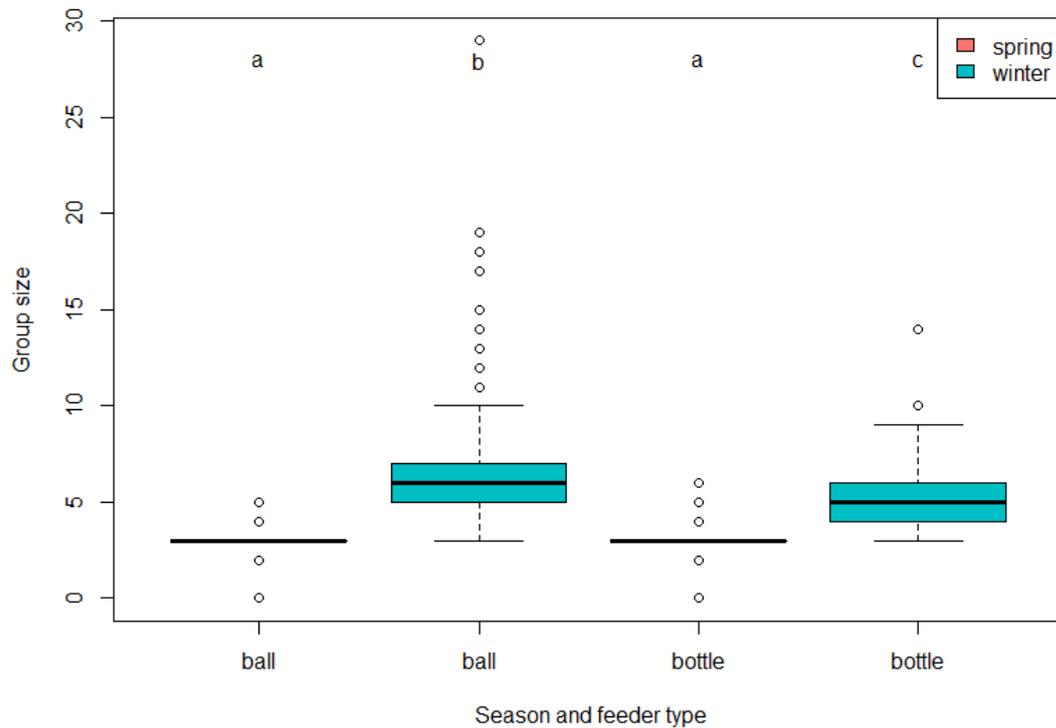
292 **3.2 Group size**

Model	Predictor	AIC	F value	Adj. R ² (%)
Null	-	518		
Model 1	Season	278.1	322.9 _(1, 429)	42.8
Model 2	Season + feeder type	273.5	166.9 _(2, 428)	43.6
Model 3	Season + feeder type + tree density	252.3	125 _(3, 427)	46.4
Model 4	Season * feeder type + tree density	246.7	97.11 _(4,426)	47.2

293 Table 3: ANOVA models explaining the variability in group size generated using stepwise
294 selection

295 As seen in Table 3, four models were generated using step-wise selection, from which the
296 Model four was chosen as a parsimonious model to explain most variation (AIC= 246.7, adj.
297 R²= 47.2%). This model showed season (p<0.001, F_(1, 426) = 349.77), feeder type (p=0.005, F_(1, 426) = 7.09), and tree density (p<0.001, F_(1, 426) = 24.01) as the main predictors to explain the
298 variation in group size. When the site was included as a random effect in ANOVA model, the
299 effect of tree density was no more significant (P=0.68, F_(1, 424) = 0.167), while season (P <
300 0.001, F_(1, 424) = 364.0), feeder type (P= 0.005, F_(1, 424) = 7.70) and their interaction (P=0.006,
301 F_(1, 424)=7.4) were found to be highly significant.
302

303 Based on this, the season is the strongest predictor of the group size and it increases by 0.65
304 times in winter on average. The group size of birds visiting the ball feeder is by 0.9 larger than
305 the bottle feeder on average. Overall, in the winter, the group size increased in both feeder
306 types (Figure 3). Additionally, Tukey test was performed to assess the difference in group size
307 as a function of pairwise interaction between season and feeder type. As a result, it was found
308 that, each feeder type showed significant difference in the group size based on the season
309 (p>0.001). Moreover, it was found that in the winter season, there is a significant difference in
310 group size between bottle and ball feeders (p<0.001), however, there is such no difference in
311 the spring (p=0.9). To conclude, there was no difference between the feeder types in spring
312 (although the group size was small for both compared to winter) unlike in the winter season.



313

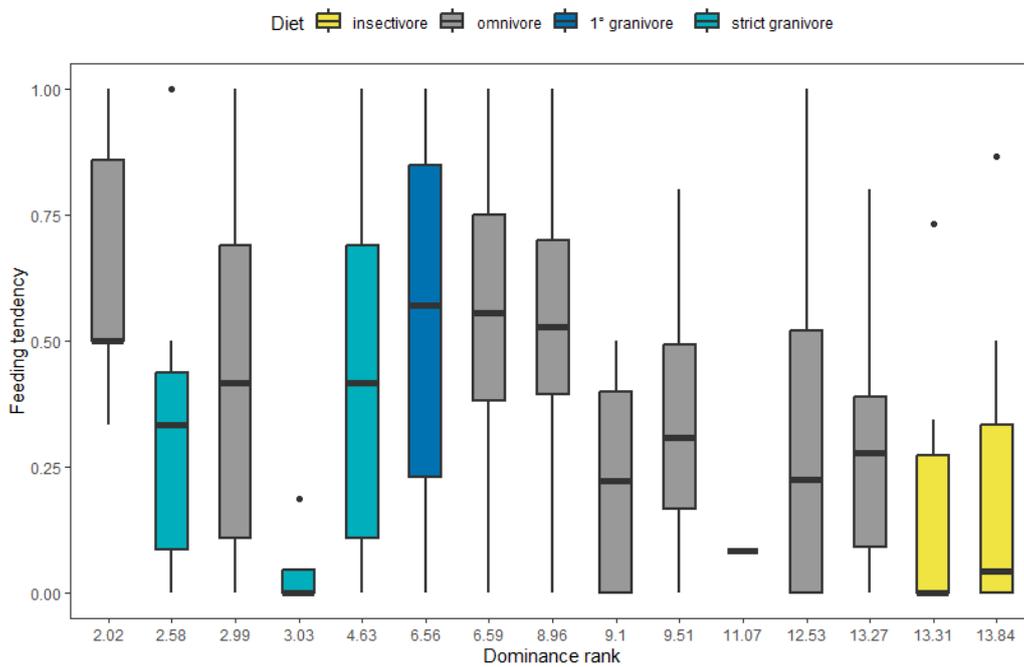
314 Figure 3: Effect of season and feeder type on the group size of MSA of birds. “a”, “b” and “c”
 315 represents the pair-wise interactions of the Tukey test

316 3.3 Feeding tendency

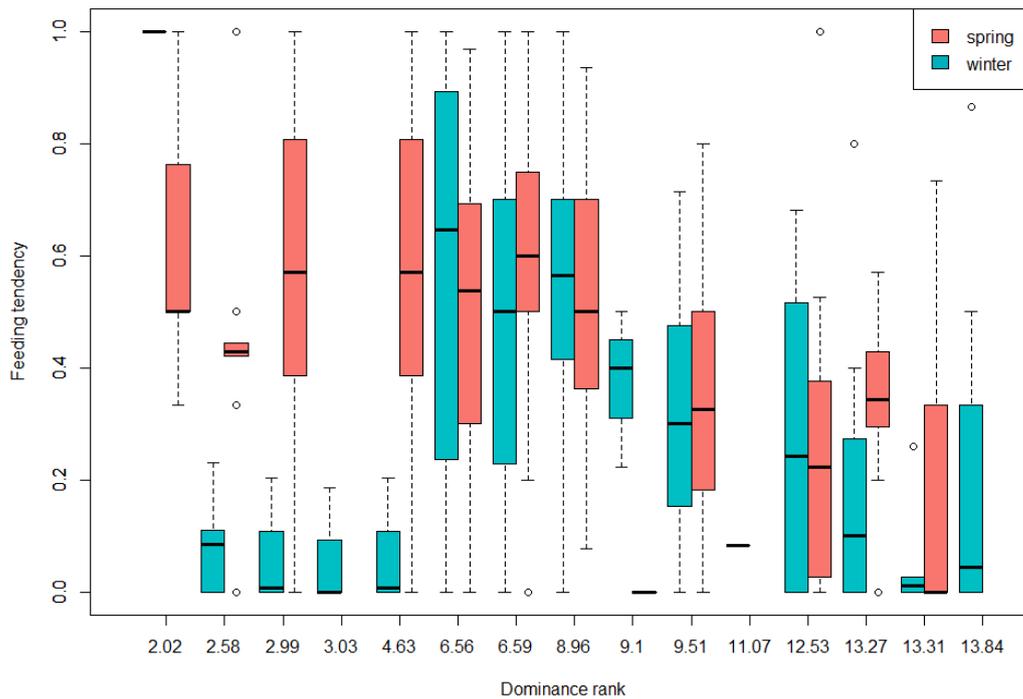
317 The step-wise selection and interaction models produced four models (Table 4), which showed
 318 dominance rank, season, and diet as significant predictors of feeding tendency. However, due
 319 to the singularity of diet showing an absolute correlation with ranks, the inclusion of diet did
 320 not improve the model value (model three) or the amount of variation explained. Therefore,
 321 based on the AIC and the adj. R^2 value model four was chosen as the parsimonious model with
 322 main predictors: rank ($P < 0.001$, $F_{(14, 343)} = 8.67$), season ($P = 0.02$, $F_{(1, 343)} = 5.09$), and the
 323 interaction between them ($P < 0.001$, $F_{(11, 343)} = 3.90$). After accounting for the random effect of
 324 the site, it can be seen that dominance rank is the strongest predictor of feeding tendency
 325 ($P < 0.001$, $R^2 = 24.24$, $F_{(14, 341)} = 8.89$), with a general trend of decrease in the feeding rank with
 326 a decrease in the dominance rank position (13.8 being the lowest) (Figure 4). However, season
 327 which has a poor overall negative effect on the feeding tendency ($P = 0.03$, $R^2 = 0.9$, $F_{(1, 341)} =$
 328 4.68), interacts with rank and has a significant mixed effect on the trend caused by rank
 329 ($P < 0.001$, $R^2 = 8.34\%$, $F_{(11, 341)} = 3.89$) as seen in the graph (Figure 5).

Model	Predictors	AIC	F value	Adj. R ²	Data used as singularity
Null	-	136	-	-	-
Model 1	Rank	63.89	7.87 (14, 355)	20.7	-
Model 2	Rank + season	61.04	7.74 (15, 354)	21.5	-
Model 3	Rank + season + diet	61.04	7.74 (15, 354)	21.5	diet
Model 4	Rank * season	39.41	6.52 (26, 343)	28	-

330 Table 4: List of linear regression models explaining the variability in feeding tendency
331 generated using the step-wise selection



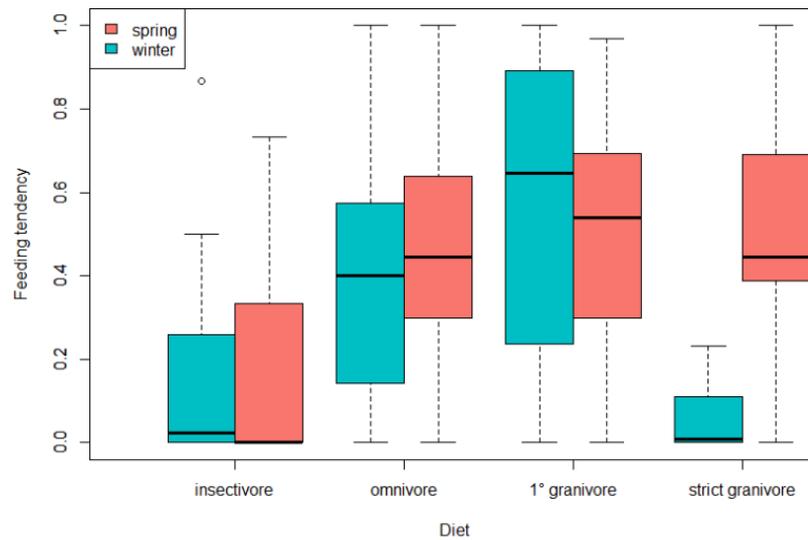
332
333 Figure 4: The effect of mean dominance rank on the feeding tendency. The colours represent
334 species' diet



335

336 Figure 5: The effect of mean dominance rank and season on the feeding tendency

337 To address and understand the minor deviations in the general trend of rank-based feeding
 338 propensity and mixed effects as a result of interaction with season (Figure 5), the diet of the
 339 species was used as the underlying factor to explain the variation. As diet is embedded within
 340 ranks, we first decoupled the effect of rank on diet by using random effect ANOVA with the
 341 main predictors: diet, season and their interaction and rank as random effect. From the results,
 342 we found that there is a significant effect of interaction between diet and season on the feeding
 343 tendency ($p < 0.001$, $F_{(3, 351)} = 5.97$). Based on the pairwise comparisons using post hoc test, it
 344 is found to be especially true for strict granivores (rank: 2.58, 3.03, 4.6) where the feeding
 345 tendency follows the ranking order and it increases by 0.31 in spring ($P < 0.001$) (Figure 6).
 346 While the omnivores and primary granivores follow the feeding tendency with the ranking
 347 order but are not affected by the season ($P < 0.05$). On the other hand, the insectivores (rank:
 348 11.07, 13.31, 13.84) fall on the lowest rank and show the least feeding tendencies in both
 349 seasons ($p = 0.030$) as a result of ranking order and diet preference. Therefore, when these results
 350 are interpolated onto the interaction of rank and season, the mixed effect of the interaction
 351 between rank and season on feeding tendency can be explained.



352

353 Figure 6: The effect of the bird species' diet and season on the feeding tendency

354 **3.4 Strategic interaction**

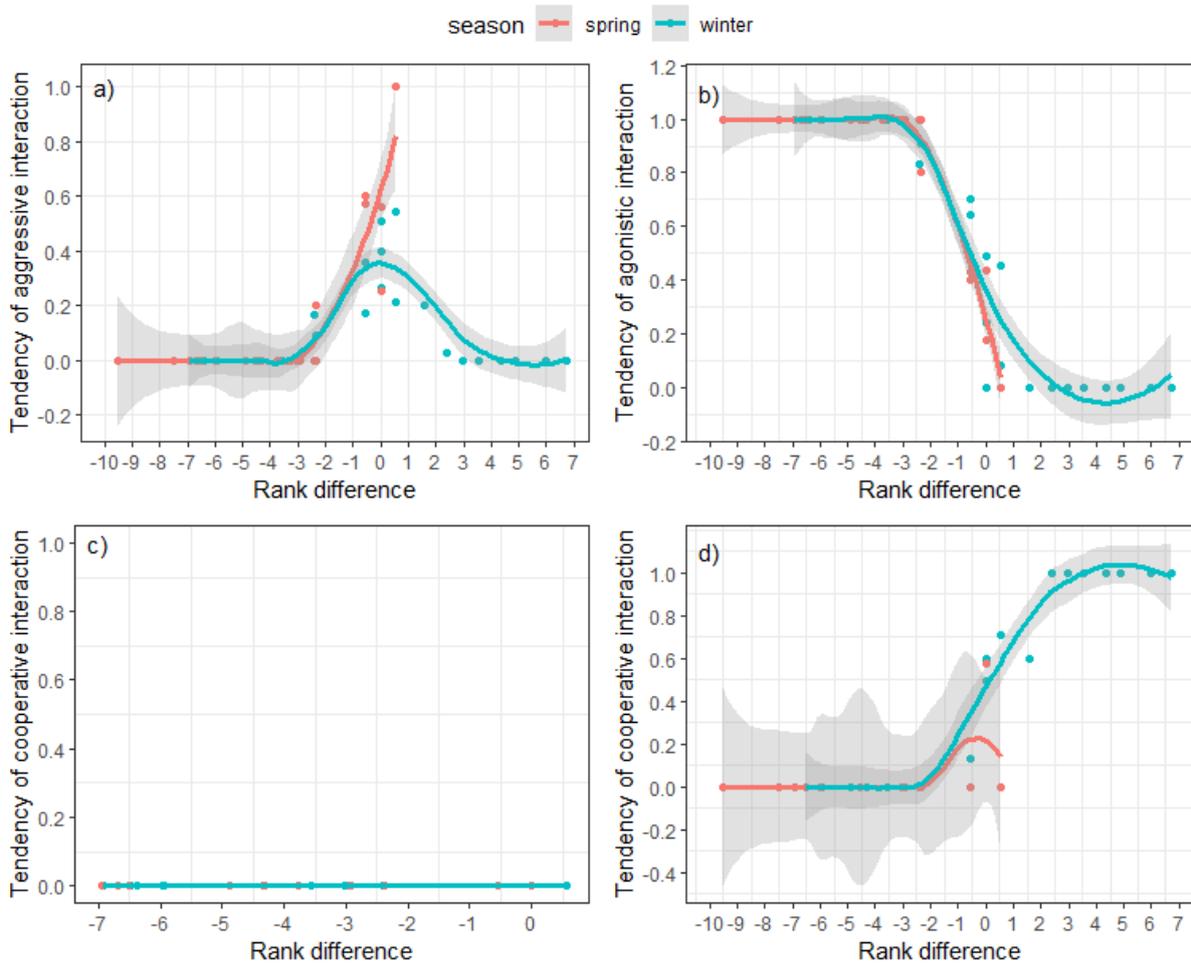
Interaction type	Models	Predictors	AIC
Aggressive	Null	-	42.04
	Model 1	Rank difference*	22.61
Agonistic	Null	-	78.86
	Model 1	Rank difference	15.07
Cooperative	Null	-	61.2
	Model 1	Rank difference	17.19
	Model 2	Rank difference + feeder type	15.53

355 Table 5: List of all the models explaining the variability in the occurrence of different types of
 356 strategic interactions generated using 'step' function. * indicates that the predictor is raised to
 357 two as a part of the quadratic equation.

358 3.4.1 Aggressive interaction

359 Using the generalized linear-quadratic models in step function showed that the effect of the
 360 rank difference is quadratic with unimodal distribution and that it is the only significant factor
 361 in explaining the tendency to display aggressive interaction (AIC= 22.61) (Table 5). This effect
 362 is also prominent in the loess curve from the graph below (Figure 7-a), where, the tendency to
 363 be aggressive is highest when the rank difference is -0.55, and it gradually decreases to 0 with
 364 an increase in the rank difference to -/+ 2.4 (in both directions). Although the tendency to be

365 aggressive is higher in spring (tendency: 1 at 0.55) from the loess curve, it is solely driven by
 366 a single rank difference (0.55). Moreover, according to the step function, the effect of the
 367 season is not significant or parsimonious ($p>0.5$). Therefore, we assume that seasonality has
 368 no effect on the tendency to be aggressive.



369

370 Figure 7: Loess models showing the effect of rank difference and season on the tendency to
 371 display different types of interactions, strategically, namely a) aggressive interaction b)
 372 agonistic interaction, c) cooperative interaction at bottle feeders, and d) cooperative interaction
 373 at gauze ball feeders. The pink and blue loess curve represent spring and winter season,
 374 respectively. The grey bands represent 95% confidence interval

375 3.4.2 Agonistic interaction

376 Step function generated a parsimonious model where, only the rank difference predictor had a
 377 significant logistic effect on the feeding tendency (AIC= 16, $P<0.001$) (Table 5). On visualizing
 378 this relation through the loess model (Figure 7-b), a general trend was observed where the
 379 tendency to be agonistic is at its maximum (the tendency of agonistic interaction = 1) when the

380 rank difference between the species is high i.e., less than -2.4 and the winning species is from
381 the higher rank. With the decrease in the rank difference between interacting species located
382 closely in the ranking order i.e., more than or equal to -2.4 and less than 0.55, the tendency to
383 be agonistic is gradually reduced from 1 to 0.08 but still prominent. However, species from the
384 lower rank with a rank difference of more than 0.55, do not express any kind of agonistic
385 interaction.

386 3.4.3 Cooperative interaction

387 Based on the generalized linear model with binomial distribution, model 2 with the rank
388 difference ($P = 0.04$) and feeder type ($P_{\text{(ball feeder)}} = 0.30$, $P_{\text{(bottle feeder)}} = 0.99$) predictor showed
389 the least AIC value (15.53) compared to the other models (Table 5). Although the feeder type
390 does not show a significant p-value, on comparing the loess model-based graphs (Figure 7-c &
391 7-d) we can see that bottle and ball feeders produce two different curves. i.e., bottle feeder has
392 no impact on cooperative tendency as there is no cooperative interaction displayed at bottle
393 feeders by any ranks, in any season. On the other hand, at ball feeders, the rank difference
394 shows a logistic regression on the cooperative tendency. As the bottle feeder shows absolutely
395 no effect, the GLM was rerun with the rank difference and season for the ball feeder alone, and
396 the rank difference was found to be the only significant explanatory factor ($P=0.046$) in ball
397 feeders.

398 From the loess model plotted for the ball feeder as seen in Figure 7-d, it is clear that in both
399 seasons the tendency to display cooperative interaction is 0 by species from higher ranking
400 order, with a ranking difference of less than -0.55. And in general, when the species are found
401 in the same rank (intraspecific interaction) or adjacent to each other in the ranking hierarchy (-
402 0.55 to 1.55) the tendency to be cooperative is low but gradually increasing (tendency: 0.12 to
403 0.6). And it is exclusively expressed (tendency= 1) by species with a rank difference of more
404 than 1.55.

405 Although the GLM suggests no significant effect of season in gauze ball feeders, from Figure
406 7-d, we can see that in winter the effect is purely logistical, and the scope of cooperative
407 interaction is comparatively highest (tendency: 1) and spread along broad rank difference (0 to
408 7). The cooperative interaction is expressed in 3 instances following a power curve: a) when
409 the species is from higher ranking order, yet rank difference is very low i.e., more than -0.5, b)
410 when the species rank difference is 0, c) when the rank difference is more than 0 with species
411 exhibiting this behaviour are from lower ranking order. The tendency to express this is at its

412 highest peak (1) when the rank difference is of more than 1.55, suggesting that lower-ranking
413 species while interacting with species with more than 1.55 rank difference tend to be
414 cooperative. However, in spring, this interaction is restricted to only one case where the species
415 are from the same rank (tendency: 0.6).

416 **4. Discussion**

417 **4.1 Dominance rank**

418 The dominance hierarchy follows past studies showing a strong correlation between body size
419 and ranking order (French & Smith, 2005; Miller et al., 2017; Francis et al., 2018; Moreno-
420 Opo et al., 2020). Therefore, it can be used as a proxy for ranking species. The steepness of the
421 dominance hierarchy is weakly linear and shallow as the probability of winning is more than
422 0.9 only when the rank difference is more than 3. This is due to the similarity in body size
423 between species positioned close to each other in the hierarchy (Hughes, 1996; Hemelrijk,
424 2000). As a result, closely ranked species are also required to spend high energy by displaying
425 aggressive interactions in order to gain access to food as observed in the study.

426 **4.2 Group size**

427 The season is the strongest contributor explaining the variation in group size at the feeder. The
428 group size in winter which represents the non-breeding period for all focal birds (starting from
429 December to mid-March) is 0.65 times higher than the spring season which corresponds to the
430 breeding period covering mid-March to May. From past studies, it is widely understood that
431 seasonality in temperate regions is a critical driving factor influencing the winter survival and
432 fitness of birds through two effects, i.e., directly by thermoregulation (Bakken, Murphy, &
433 Erskine, 1991; Robinson, Baillie, & Crick, 2007) and indirectly by variation in food availability
434 (Lack, 1954; Carrascal, Seoane, & Villén-Pérez, 2012). In winter season, there is a shortage of
435 food in the surroundings (Lack, 1954) and shorter daylight period for foraging, (Jansson et al.,
436 1981). This regulates the foraging efficiency of birds (Lack, 1954; Pakanen et al., 2018).
437 Additionally, low temperature also challenges the bird to acquire fat reserves to fuel
438 metabolism for maintaining stable body temperature and increasing chances of survival
439 (Haftorn, 1992; Brodin, Nilsson, & Nord, 2017). (Newton, 1998; Robb et al., 2008) also
440 showed the importance of bird feeders and supplementary feeding as food source for birds
441 during harsh periods like winter. As the species are limited by resource, provisioning of food
442 at bird feeders plays a critical role in determining important life history traits like survival,
443 fecundity and reproductive performance (Newton, 1998; Robb et al., 2008). These factors

444 potentially contribute to birds feeding at the feeder, hence, increasing the aggregation size at
445 the feeder in winter. On the other hand, as the spring season approaches, the aggregation size
446 at the feeder decreases. As the species become territorial, and defend their territory and
447 resources in the breeding season i.e., spring (Hinde, 1956) as a result of territoriality, the
448 aggregation size at the feeder is observed to reduce. Moreover, Enoksson and Nilsson (1983)
449 shows that with the increase the food abundance the territory size reduces. With the increase
450 in the food abundance in the surrounding (Seward et al., 2014; Barras et al., 2022), the species,
451 in general, are also not forced to attend feeders unlike in winter. All these factors support the
452 results of decreased aggregation size in spring.

453 With regards to the feeder type, in winter, the change in the group size at the gauze ball feeder
454 is slightly more pronounced than at the bottle feeder. The gauze ball feeder is nutritionally rich
455 containing hardened vegetable fat and a mixture of ground and unground seeds (carbohydrates)
456 (Alatalo & Moreno, 1987; Francis et al., 2018). Hence, feeding at the ball feeder provides
457 higher fat deposits required to fuel metabolism for thermoregulation in winter. Additionally,
458 the handling time of food at the ball feeder is comparatively shorter, which makes it easier for
459 participating birds to prefer ball feeders over bottle feeders (Woodrey, 1990; Francis et al.,
460 2018). Moreover, more than one individual can access and feed at the ball feeder, potentially
461 improving the aggregation size, unlike in the bottle feeder where the access to the feeder is
462 limited to only one individual at a given time. All these factors facilitate increased group size
463 at gauze ball feeders. However, this is only restricted to winter due to narrowed seasonal food
464 preferences in most participating species as mentioned above.

465 **4.3 Feeding tendency**

466 The dominance hierarchy or dominance rank, which is estimated by winning of dyadic
467 interactions shows increased feeding tendency with increased rank order (1 being highest). This
468 suggests the position in the dominance hierarchy can influence the feeding tendency of the
469 participating species. As expected, the results indicate that the dominant species are more likely
470 to gain access to the feeder compared to the subordinate species. Since the dominance hierarchy
471 is strongly correlated with the body weight of the species, it could be used as a proxy to
472 understand the feeding tendency. Although the feeding tendency is affected by dominance
473 rank, there is a heterogenous shift in the feeding tendency as a result of interaction with the
474 season. This is contradictory to our hypothesis that there will be an increased feeding tendency
475 in winter. This is due to the heterogeneity in the diet and diet preference of the participating

476 species leading to variation in the general trend of rank based-feeding and hence, the variation
477 is explained using diet. The strict granivores falling in the higher rank (*Coccothraustes*
478 *coccothraustes* - Hawfinch, *Pyrrhula pyrrhula* - Eurasian Bullfinch, *Chloris chloris* - European
479 Greenfinch), follow the rank-based feeding tendency only in spring but not in winter; on
480 average, they show 0.31 higher feeding tendency in spring compared to winter ($P=0.03$). While
481 the omnivores and primary granivores follow the feeding tendency with the ranking order but
482 are not affected by the season ($P= 0.503$, $P= 0.209$). On the other hand, the insectivores
483 (Eurasian Treecreeper, *Erithacus rubecula* - European Robin, Long-tailed Tit) fall on the
484 lowest rank and show lower feeding tendencies in both seasons ($p=0.030$) as a result of ranking
485 order and diet preference.

486 Seeds and buds are a prominent part of the diet in strict granivores such as Hawfinch, Eurasian
487 Bullfinch, and European Greenfinch (Newton, 1967). In the breeding season, nestlings are also
488 fed predominately with crushed seeds and invertebrates with the proportion of seeds increasing
489 with the chicks' age (Mountfort, 1957; Kirby et al., 2018). The breeding of these granivores is
490 hence dependent on the availability and abundance of seeds (Newton, 1967). In the non-
491 breeding season, the granivores travel large distances in search of patches with high seed
492 availability (Blendinger & Ojeda, 2001). The availability of the seeds in the farmlands after the
493 harvest period act as the source of food during the winter. However, the abundance of seeds
494 continuously declines over winter and is not replenished until the following summer, hence
495 creating a 'hunger gap' in early spring (Hulme, 1998; Powolny et al., 2018). Given that
496 majority of their diet and the chicks' diet being composed of seeds, in spring, the feeder acts
497 as a crucial resource point for food. Hence, the feeder attendance or feeding tendency of
498 granivores at the feeder is observed to be significantly higher in spring. Bullfinch presents an
499 exception to this conclusion as it does not feed at feeders in the spring season although its major
500 diet comprises seeds and buds (Newton, 1967). It is assumed that this is due to the species'
501 inability to perch at the bottle feeder as the species shows foraging behaviour of perching and
502 feeding from tree branches and cover (Newton, 1972; Newton, 1993; Marquiss, 2007). Hence,
503 it is not suitable for the type of feeder chosen in this study. On the other hand, insectivores have
504 a feeding preference toward invertebrates and only a minority of their diet is composed of seeds
505 (Ehrenroth, 1976; S. Cramp, 1988). Since the feeder is not composed of food that is suitable
506 for such a diet, it explains the lower feeding tendency at the feeder in the winter season and
507 lower (European Robin) or no feeding tendency in spring (in the case of Eurasian Treecreeper
508 and Long-tailed Tit). Overall, omnivores and primary granivores show higher feeding

509 tendencies compared to insectivores (and the feeding tendency follows the dominance rank
510 order) but exhibit no variation with seasons. This could be due to broad variation in the feeding
511 preference among these species (S. Cramp, 1988; Erard, 2008; del Hoyo, Elliott, & Christie,
512 2011). Some of the omnivores also display species-specific variation, i.e. Eurasian Jay and
513 Crested Tit, which showed decreased feeding tendency in spring and *Dendrocopos major*
514 (Great Spotted Woodpecker) and *Poecile palustris* (Marsh Tit) showing increased feeding
515 tendency in spring. In the case of Eurasian jay and Crested Tit, the decrease in the feeding
516 tendency at the feeder is expected to be due to their nestlings' narrowed diet consisting of
517 invertebrates. Hence, the feeder acts as a minor representation of the diet (Atiénzar et al., 2009;
518 Schodde, 2010). However, in the case of Woodpecker and Marsh Tit, the factors influencing
519 this pattern are not clear and we speculate that the increased feeding tendency could be
520 attributed to the territorial behaviour increasing the access to the feeder. Therefore, there is a
521 need to incorporate the effect of territoriality at the feeder points in order to assess its
522 importance, in further studies. Overall, besides feeding tendency being positively affected by
523 rank, diet of the species interacts with the season to explain the variation in the feeding
524 propensity.

525 **4.4 Strategic interaction**

526 Based on the results, one can confirm that rank difference can be used as a strong predictor of
527 the tendency to be aggressive and agonistic. Individuals with a rank difference of -0.55 show a
528 higher tendency to be aggressive and it reduces to 0 gradually with an increase in the rank
529 difference to $-/+2.4$. This follows the 'close competitor' strategy as suggested in past studies
530 on intraspecific interactions in group-living animals, where the individuals closely positioned
531 in the hierarchy compete aggressively (Wright et al., 2019; Dehnen et al., 2022). Closely
532 positioned ranks are more likely to be unstable and change since they have similar body sizes
533 and compete for the same resource (Hemelrijk, 2000; Hobson, 2020). Hence, in order to
534 constantly establish and maintain the rank position, there is an escalation in aggression in the
535 ranks positioned immediately adjacent in the hierarchy. When the rank difference is less than
536 -2.4 (i.e., -2.4 to -10), individuals exhibited a higher tendency to be agonistic suggesting
537 indicating that, with the increase in the rank difference, the tendency to be agonistic is
538 predominant. Since a larger rank difference means competing with species that possess greater
539 body size differences (Francis et al., 2018) and an increased probability of losing (as addressed
540 in the steepness of the hierarchy), it suggests that the opponent's position is well established
541 and highly stable (Dehnen et al., 2022). Hence, low-cost behaviour expressing agonistic

542 interaction is more profitable for both the winner and loser species as it helps exert minimal
543 energy for the winner species and prevents the risk of injury for the loser species (Parker, 1974;
544 Hobson, 2020). The observations on cooperative interaction were restricted only to ball feeders
545 and not bottle feeders as bottle feeders offer no place for sharing food at the feeder due to the
546 limitation of perching space. In ball feeders, the tendency to display cooperative interaction is
547 observed in 1) species which are very closely positioned in the dominance hierarchy (-0.55),
548 2) individuals with the same rank in the hierarchy (0), and 3) subordinate species with a
549 minimum rank difference of 0.55. And it is at its highest when the rank difference is more than
550 1.55. This suggests that cooperative interaction is a strong submissive behaviour expressed by
551 species that are positioned in the lower hierarchy, poorly towards species that are positioned
552 closely but at a higher rank in the hierarchy, and strongly towards species that are positioned
553 on the higher and distant hierarchy. Although the model does not depict the impact of season,
554 it is clear from the loess curve that the trend is prominent only in the winter season, and
555 insignificant in the spring (Figure 7-d). Despite the higher risk of injury to species that initiate
556 cooperative interaction, under the circumstance of poor food availability in the surroundings,
557 poor thermoregulation and shorter daylight in winter (Lack, 1954; Jansson et al., 1981; Haftorn,
558 1992), the species might be pushed to express cooperative behaviour towards higher-ranking
559 species. In spring, cooperative interaction is only seen between individuals when the rank
560 difference is 0. This suggests intraspecific cooperation as a result of territoriality and the
561 formation of mating pairs in spring (Hinde, 1956). Besides this, the increase in the food
562 abundance in spring promote the species to aggregate less (Seward et al., 2014; Barras et al.,
563 2022) and hence avoid interactions with species from higher ranking order, as to prevent the
564 risk of injuries, unlike in winter. However, since there is no data available on the interactions
565 expressed by subordinates with a rank difference of more than 0.55, more data needs to be
566 collected to confirm the conclusions.

567 Extending the findings of previous studies on group-living animals (Wagner & Gauthreaux Jr,
568 1990; Hobson & DeDeo, 2015; Dehnen et al., 2022), this study confirms the prevalence of
569 strategic interaction based on the rank differences in mixed-species aggregations in birds;
570 Investing in costly and energy-consuming behaviour towards individuals situated immediately
571 adjacent to them in the hierarchy, and low-cost behaviour by higher-order species when the
572 rank difference is high (Parker, 1974; Wright et al., 2019). Moreover, the study for the first
573 time also sheds light on the impact of seasonality in exhibiting dominant interactions, which
574 lacks in previous studies. Supporting one of our assumptions on aggressive interaction in

575 spring, during the breeding phase, increased levels of hormones such as androgen, estrogen,
576 and testosterone makes the species territorially aggressive in order to protect resources, mating
577 partner, nest, and the chicks (Harding, 1981; Balthazart, 1983; Canoine & Gwinner, 2002).
578 Hence regardless of the availability of food in the surrounding, the tendency to be aggressive
579 between closely positioned species in the hierarchy remains the similar in comparison to
580 winter. Overall, ‘close competitor’ strategy is seen in mixed-species aggregation regardless of
581 the season. The effect of seasonality, however, can be seen in the case of cooperative interaction
582 which is restricted intra-specifically in spring. This could be the consequence of the formation
583 breeding pairs and territoriality in spring, besides increased food availability (Hinde, 1956).
584 Moreover, the lack of any type of interaction by lower-ranking species towards higher-ranking
585 species in spring (rank diff: >0.55 to 7), unlike in winter, might also indicate the indirect effect
586 of seasonality. Hence, more studies must be conducted in spring in order to confirm whether
587 avoidance of any type of interaction by lower-ranking species towards higher-ranking species
588 is in order to prevent the risk of injuries, unlike in winter where the species are forced to interact
589 under the circumstance of poor food availability.

590 **5. Conclusion**

591 The dominance hierarchy correlates with the body size as suggested by many studies in the
592 past (French & Smith, 2005; Miller et al., 2017; Francis et al., 2018; Moreno-Opo et al., 2020).
593 The group size is larger in the winter season and comparatively higher for gauze ball feeders
594 due to the critical conditions in winter and high nutrient and fat content in the gauze ball
595 feeders. Therefore, winter season is the crucial period, during which supplementary food at the
596 feeder need to be provisioned and monitored actively. However, the feeding tendency of the
597 participating birds is affected by dominance ranks and shows a general positive linear trend
598 with dominance rank. Feeding tendency is not only limited by rank but it is also a function of
599 species’ diet and its interaction with season. There is a strong interplay between diet and season,
600 which shows that although granivores are from the higher rank, they show increased tendency
601 to feed only in spring and not in winter. On the other hand, the season does not have an effect
602 on omnivores and primary granivores, in general (however, some of the omnivores showed
603 species specific variations). As the feeder does not comprise of the insectivorous diet, and that
604 the insectivores fall under the lowest rank in the hierarchy, they have the least feeding tendency.
605 Overall, these results suggest that besides the rank, diet and season has a huge impact especially
606 on granivores and insectivores. Therefore, the food supply and contents of the supplementary
607 food at the feeders needs to be adjusted and managed based on the season and the community

608 composition of birds in the vicinity. We also conclude that mixed species aggregations at the
609 feeder exhibit close competitor strategy in both the season, which has not been tested before.
610 Here the species competing from closely position ranks are aggressive in order to constantly
611 establish dominance due to the similarity in body size. While the species with high-rank
612 differences use agonistic interaction and hence minimize the risk and maximize the benefit as
613 the ranks are well established due to the difference in body size. Further, the retention of the
614 close competitor strategy in spring regardless of the abundance in food supply is expected due
615 to the phenological and hormonal changes in birds with the season. Although the strategic
616 interaction of dominance shows ‘close competitor’ strategy with no effect of season, as a result
617 of harsh conditions in winter, the subordinate species show cooperative interactions
618 preferentially towards higher-ranking species. Additonally, this interaction is expressed only
619 interspecifically in spring as a result of increased food abundance and mate formation.
620 Moreover, the lack of any type of interaction by subordinates towards the dominant species
621 suggest that seasonality has an indirect effect on strategic interactions on subordinate species
622 in mixed-species aggregation.

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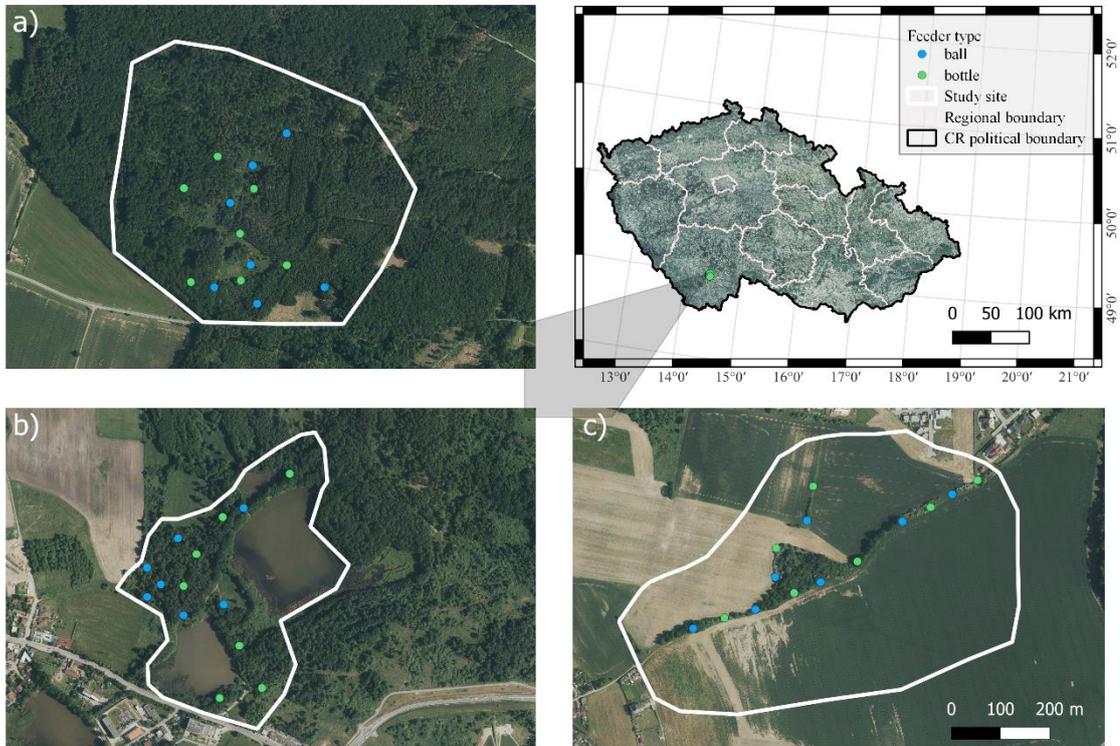
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799

800 **Appendix**

801 1. Vegetation map of the study sites located in České Budějovice, Czech Republic (Figure
802 1).



803

804 Figure 1: Map of all the three study sites where a, b, and c refer to Branišovský les,
805 Mladohaklovský Rybník, and U Švába respectively which are located in České Budějovice,
806 South Bohemia, Czech Republic. The inset map is the orthophoto map of Czech Republic
807 which is the WMS view service sourced from the Czech Office for Surveying, Mapping
808 and Cadastre (https://geoportal.cuzk.cz/WMS_ORTOFOTO_PUB/WMSservice.aspx).
809 Blue and green points represent gauze ball feeder and bottle feeder, respectively.

810

811

2. Experimental sites located in České Budějovice, Czech Republic (Figure 2).

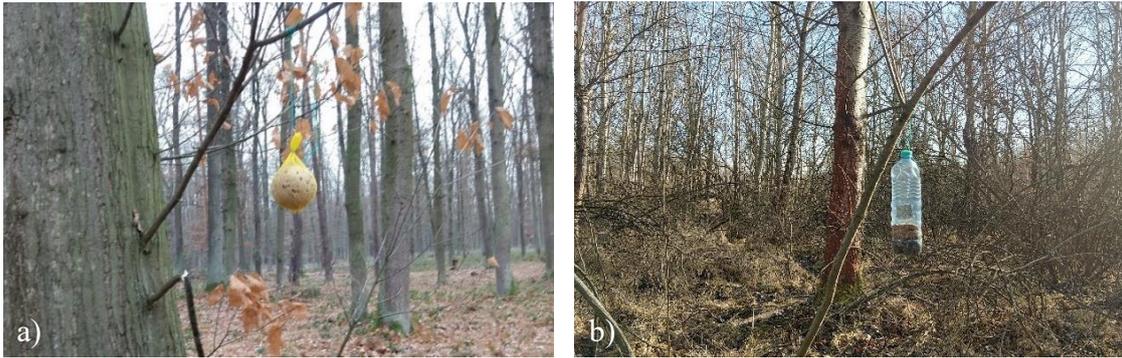


812

813 Figure 2: a) Branišovský les (48.979N, 14.418E) represents a mixed forest predominated
814 by oak (*Quercus sp.*), spruce (*Picea abies*) and pine (*Pinus sylvaticus*), b) Mladohaklovský
815 rybník (48.993N, 14.437E) represents forest with mixed stands of aspen (*Populus tremula*)
816 and birch (*Betula sp.*) with willow shrubs (*Salix sp.*), and c) U Švába (48.967N, 14.444E)
817 is a line of vegetation with a draw stand of shrubs and trees between crop fields with the
818 predominating elder (*Sambucus niger*), blackthorn (*Prunus spinosa*), aspen and oak. The
819 crop fields surrounding this line of vegetation were sown with barley (*Hordeum vulgare*)
820 and rapeseed (*Brassica napus*) or left ploughed.

821

822 3. Two types of feeders used in the study (Figure 3)



823

824 Figure 3: Images of two types of feeders installed in the field site, namely: a) Gauze ball
825 feeder and b) Bottle feeder

826

827
828

4. Table 1 contains list of the total number of recordings per season, tree density and understorey density for each feeder

Site	Feeder identity	Feeder type	Recordings in spring	Recordings in winter	Tree density	Understorey density
1	1	bottle	5	5	0.127	0.216
1	9	bottle	5	5	0.080	0.124
1	10	ball	5	6	0.054	0.204
1	11	bottle	6	5	0.076	0.267
1	12	ball	6	6	0.070	0.318
1	13	bottle	5	5	0.245	0.108
1	14	ball	5	5	0.067	0.213
1	15	bottle	5	5	0.105	0.089
1	16	ball	5	5	0.045	0.188
1	17	bottle	5	5	0.064	0.166
1	18	ball	6	6	0.041	0.576
1	19	bottle	5	5	0.064	0.363
1	20	ball	5	7	0.003	0.560
1	21	ball	5	5	0.003	0.159
2	1	ball	5	5	0.207	0.264
2	3	ball	5	5	0.118	0.172
2	4	bottle	5	5	0.216	0.236
2	5	ball	5	5	0.169	0.204
2	7	ball	5	5	0.102	0.283
2	10	bottle	6	5	0.080	0.201

2	11	ball	5	5	0.099	0.102
2	12	bottle	5	5	0.124	0.140
2	15	ball	5	5	0.185	0.325
2	17	bottle	5	5	0.076	0.207
2	18	ball	5	5	0.229	0.115
2	19	bottle	6	5	0.172	0.207
2	20	bottle	5	5	0.255	0.076
2	21	bottle	6	5	0.095	0.060
3	1	bottle	5	5	0.041	0.073
3	2	ball	5	5	0.013	0.006
3	3	bottle	5	5	0.048	0.118
3	4	ball	5	5	0.006	0.207
3	7	bottle	5	5	0.019	0.172
3	8	ball	5	5	0.035	0.137
3	9	bottle	5	5	0.045	0.057
3	10	ball	5	5	0.073	0.041
3	11	bottle	5	5	0.019	0.051
3	12	ball	5	5	0.029	0.076
3	13	bottle	5	5	0.035	0.134
3	14	ball	5	5	0.025	0.188
3	16	ball	5	5	0.006	0.029
3	19	bottle	5	5	0.000	0.016

829 Table 1: List of total number recordings from each feeder for respective seasons, sites and
830 feeder type. Study site 1, 2 and 3 is Branišovský les, Mladohaklovský rybník and U Švába.

831 The table also represents the understorey density and tree storey density within 10m radius
832 of each feeder type
833

834 4. Table 2 below represents the probability to win suggesting the steepness of the
 835 hierarchy. It is calculated based on the elo scores generated through winner and loser
 836 dyadic interaction data using the ‘plot_hierarchy_shape’ function from aniDom
 837 package

Rank difference	Probability to win	CI (upper)	CI (lower)
1	0.833333	0.948952	0.717715
2	0.666667	0.793345	0.539988
3	0.933333	1	0.835594
4	0.958333	1	0.896711
5	1	1	0.975
6	1	1	0.944444
7	0.913043	0.993536	0.832551
8	1	1	0.833333
9	1	1	0.833333
10	1	1	0.5
11	1	1	0.75

838