

1 Title: Japanese macaques depend not only on neighbours but also on more distant members for  
2 group cohesion

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**Abstract**

A well-known behavioural model for group aggregation is that an individual depends on a few neighbouring individuals to adjust its movement, such as departure (repulsion) from and approach (attraction) to neighbours. However, an individual may rely not only on a few closest neighbours, but also on more distant individuals, in a group of stable membership. We measured temporal changes in the local density of individuals around a focal individual and changes in distance to other focal individuals in a group of wild Japanese macaques to determine whether the macaques depended only on a few neighbours or also on more distant individuals for adjustments in cohesiveness. We used simultaneous focal animal sampling, with two observers recording the individuals' locations using a global positioning system (GPS), over three seasons. Numbers of individuals within 20 m from an animal tended to increase after 10 min when there were a small number of individuals around the animal. However, the number tended to decrease when there was a larger number of individuals. It remained similar when there were an intermediate number of individuals. The two focal animals tended to separate after 10 min when the interindividual distance was short. However, they tended to move closer when far apart. They remained a similar distance apart when they were at an intermediate distance. Contact calls, which are suggested to function as locating group members and keeping cohesiveness, were emitted more frequently when the distance between the two focal animals was very large in two seasons. However, the rate of contact calls was not influenced by the number of individuals within 20 m from an animal. These results suggest that individual Japanese macaques do not only rely on a few closest neighbours, but also on more distant group members. Japanese macaques may know the general whereabouts of the whole group, and when they stay at the periphery of the group, they may emit contact calls frequently and move towards the central zone so as not to become separated from the group.

## 50 **Introduction**

51 Many social animals exhibit cohesive aggregation, such as insect swarming, fish  
52 schooling, bird flocking, and mammalian herding (Cavagna et al. 2010; Schellinck & White  
53 2011). While maintaining a close distance to others is favourable for predation avoidance  
54 (Hamilton 1971), it is unfavourable for foraging because of competition among group members  
55 (e.g., Wrangham, 1980). The cost of grouping may be mediated by adjusting an individual's  
56 proximity to other group members (Aureli et al. 2008), raising the question of how animals  
57 adjust proximity and cohere as a group.

58 Theoretical studies have proposed models of individual movement strategies explaining  
59 collective group motion in which an animal monitors the locations and movements of a few  
60 closest neighbours and adjusts its movements to those of those neighbours. For example, when  
61 an individual is too close to its neighbour, it travels in the opposite direction (repulsion) and  
62 when an individual is far from its neighbour, it moves towards the neighbour (attraction)  
63 (Schellinck & White 2011).

64 Such models provide simple mechanisms of collective movement, which require an  
65 animal to know the locations of other animals within a close distance, but not those of all  
66 members of the group. However, some other behavioural processes may be at work during  
67 collective movement in social animals that form small groups with stable memberships and  
68 have high cognitive ability, such as primates (Aureli et al. 2008; Shimooka 2003) and dolphins  
69 (Karczmarski et al. 2005). One possible behavioural process is that an individual relies not only  
70 on a few close neighbours, but also on individuals more distant in location and/or movement of  
71 the whole group. To examine this, we observed adjustments of proximity among Japanese  
72 macaques (*Macaca fuscata*) in the wild.

73 Japanese macaques form female philopatric groups. Females reside in the natal group,

74 whereas males emigrate out of the group at adolescence (Yamagiwa & Hill 1998). There is a  
75 linear dominance hierarchy, based on kin relationships, between resident females (Hill &  
76 Okayasu 1995), and the groups are relatively cohesive with stable membership. The group's  
77 habitat and activities vary seasonally (Tsuji et al. 2006). It has been suggested that the  
78 frequently emitted contact call, or "coo call" (Green 1975), is an important means of  
79 maintaining group cohesiveness (Koda & Sugiura 2010; Suzuki & Sugiura 2011).

80 Japanese macaques are known to change their behaviour, such as monitoring other  
81 individuals, depending on the proximity to nearby members (Suzuki & Sugiura 2011). Thus, it  
82 is likely that they rely on the neighbours for the adjustment of proximity, however, it is possible  
83 that Japanese macaques also may rely on more distant animals. Although the data on proximity  
84 to distant animals is quite limited, they may locate approximate position of the whole group  
85 (Wada & Matsuzawa 1986).

86 As the first aim of this study, we examined a basic assumption that Japanese macaques  
87 adjust proximity to group members. If they do, proximity to group members is expected to  
88 increase when they are far apart and *vice versa*. In particular, we predicted that 1) the number of  
89 individuals within 20 m of an animal would increase and/or 2) distance to the other focal female  
90 would decrease (both indicating increased proximity to group members), if an animal is far  
91 apart from group members and *vice versa*.

92 Our second aim is to examine whether Japanese macaques rely on the neighbour  
93 individuals and/or more distant individuals for their adjustment of proximity. If they adjust  
94 proximity relying only on neighbours, change (i.e., increase and decrease) in proximity to group  
95 members is expected to be accounted for by initial state of proximity to the neighbours. In this  
96 case, we predicted that 1) variance in change in number of individuals within 20 m and 2)  
97 variance in change in distance to the other focal individual would largely be accounted for by

98 the initial number of individuals within 20 m. Alternatively, they may rely not only on  
99 neighbours but also on more distant individuals. In this case, we predicted that variances in  
100 these two response variables would be accounted for both by the initial number of individuals  
101 within 20 m and also by the initial distance to the other focal animal.

102 We also examined the rate of contact calls with the same analytical design to explore the  
103 possibility that macaques change behaviour related to group aggregation depending not only on  
104 close neighbours but also on more distant animals.

105 We propose that macaques rely on both close neighbours and more distant animals and  
106 that they know the location of the whole group and adjust their movements based on such  
107 information. In addition, we discuss possible mechanisms and functions of adjustment of  
108 proximity.

109

## 110 **Methods**

### 111 *Subjects*

112 We studied the A group of wild Japanese macaques on Kinkazan Island, northern Japan  
113 (38.30°N, 141.56°E; elevation 0–445 m ASL). Members of the A group have been identified  
114 individually since 1983 and are used to human observers (Sato 1988). No natural predator of  
115 these monkeys exists on the island and hunting is forbidden by law and religion. During the  
116 study period, the subject group included 31–39 individuals: 17 adult females ( $\geq 5$  years old),  
117 5–13 adult males ( $\geq 5$  years old), 2–5 juvenile females (1–4 years old), 2–4 juvenile males (1–4  
118 years old), and 5–8 infants ( $< 1$  year old). The macaques' range covered approximately 3 km<sup>2</sup>  
119 during the study period. Details of the subjects and their habitat have been described elsewhere  
120 (Tsuji et al. 2006; Tsuji & Takatsuki 2004; Tsuji & Takatsuki 2012).

121 We collected data during three seasons: autumn (16 October to 8 November, 2003),

122 winter (10–22 February, 2004), and summer (6–23 July, 2004). Observation was conducted in  
123 6:30–16:40 in autumn, 7:15–16:55 in winter, and 6:15–18:30 in summer. Data were collected  
124 almost equally during these hours. We chose 10, 9, and 7 females of varying dominance ranks  
125 as the subjects in the autumn, winter, and summer, respectively. Seven of the animals were  
126 observed during all three study periods. The mean observation times per individual were  
127  $33.1 \pm 5.0$ ,  $31.9 \pm 3.5$ , and  $29.1 \pm 1.3$  h in the autumn, winter, and summer, respectively. We  
128 observed 30 of 45 possible pairs in autumn, 29 of 36 possible pairs in winter, and all 21 possible  
129 pairs in summer. The mean observation times per pair were  $7.3 \pm 0.1$  (mean  $\pm$  SE),  $9.3 \pm 0.1$ , and  
130  $4.4 \pm 0.1$  h in the autumn, winter, and summer, respectively.

131

### 132 *Data Collection*

133 Two observers followed each anoestrous focal adult female using the focal animal  
134 sampling method. We excluded oestrous females from the study because they tended to stay on  
135 the periphery of the group to mate with low-ranking or non-troop males (Hayakawa 2007).

136 Each observation session lasted 4 h, during which we recorded the number of coo calls  
137 (Green 1975; Sugiura 2007b) emitted by each focal animal per minute. We recorded the number  
138 of individuals within 20 m of each focal animal in 5-min intervals by instantaneous sampling.  
139 We excluded infants  $< 1$  year of age because they were usually dependent on other individuals.  
140 We excluded data when visibility was  $< 20$  m.

141 We measured location, time, and the positional dilution of precision (PDOP, a  
142 measurement of position accuracy) using a GPS receiver (IPS-5100; Sony, Tokyo, Japan or  
143 GPS Pathfinder Pocket; Trimble, Sunnyvale, CA, USA). We recorded GPS data every 1 s on a  
144 handheld computer (200LX or iPAQ h2210; Hewlett-Packard, Tokyo, Japan). We typically  
145 remained within a horizontal distance of 10 m from the focal animal and considered the position

146 of the observer to be that of the focal animal. We excluded GPS data recorded when the focal  
147 animal was out of view or was  $> 15$  m away for  $> 1$  min.

148

#### 149 *Analysis*

150 We used two measures of proximity, covering different ranges of distance. One is  
151 proximity to group members at close range (0–20 m). We measured the number of individuals  
152 within 20 m from the focal adult female (i.e., the density of individuals around an animal) and  
153 its change after 10 min. Another is proximity to a group member over a longer distance ( $\geq 40$  m).  
154 We measured the distance to the other focal individual observed simultaneously with GPS (i.e.,  
155 the distance between two random adult females in a group) and its change after 10 min.

156 We converted location data into rectangular coordinates using universal traverse mercator  
157 (UTM) projection. To remove large location errors, we used only measurements with a PDOP  
158 smaller (better) than 6.5 with a three-dimensional fix (D'Eon & Delparte 2005). We chose the  
159 location data with the smallest PDOP within a window of -15 to +15 s from the sampling time.  
160 On occasion, three observers simultaneously followed a focal animal. In these cases, we used  
161 the distance between each pair combination (e.g., A-B, A-C, B-C) as independent data.

162 We examined three response variables as behavioural correlates of adjustment of  
163 proximity: 1) change in number of individuals, 2) change in distance between two focal animals,  
164 and 3) contact call (coo call) rate. We tested whether the variance in each of these three response  
165 variables was influenced by two explanatory variables: 1) initial number of individuals within  
166 20 m from a focal animal and 2) initial distance to the other focal animal.

167 Changes in numbers of individuals and in distance to the other focal animal were sampled  
168 in 15-min intervals (at a minimum). Call rate was sampled in 5-min intervals (at a minimum).

169 The sampling interval was extended by 5 min (i.e., 20, 25, 30 min) if loss of the focal animal,  
170 loss of the number of individuals around the focal animal, or unreliable GPS positions occurred.

171 We performed all analyses separately in each of the three seasons, because the  
172 cohesiveness of the group varied largely with season (Sugiura et al. 2011). Our main interest  
173 was to examine whether the adjustment of proximity occurs in each season, as opposed to being  
174 due to merely seasonal variation in proximities among group members. Thus, we conducted  
175 analysis in each season to simplify the design of statistical analyses. Interindividual distances  
176 were extremely large (0–1225 m) and subgrouping occurred during the summer (Sugiura et al.  
177 2011). We divided the distances into three categories of non-subgrouping, subgrouping, and  
178 unknown, following a previous study (Sugiura et al. 2011). We used data categorised as  
179 non-subgrouping and subgrouping separately in the present analysis. Our main objective was to  
180 examine the adjustment of proximity in normal grouping (i.e., non-subgrouping). However,  
181 behavioural differences between grouping and subgrouping were also of interest, because the  
182 differences may reveal characteristics of grouping. Thus, we also analysed the behaviour during  
183 subgrouping.

184 We used data when the initial distance to the other focal individual was  $\geq 40$  m. Two  
185 explanatory variables, initial number of individuals within 20 m of the focal animal and initial  
186 distance, correlated weakly with each other, when we included all the data. However, this  
187 correlation disappeared, excluding the data where the distance to the other focal animal was  
188  $< 40$  m. Our main objective was to examine which of the explanatory variables accounted for  
189 response variables; thus, we excluded data where the effects of the two factors were difficult to  
190 separate. This procedure tends to exclude instances where the group spread was small.

191 The change in number of individuals was calculated as (number of individuals after  
192 10 min) – (initial number of individual). Thus, a positive value indicates that the local density of



193 individuals around the focal animal increased (increase in proximity), whereas a negative value  
194 indicates a decrease in the local density of individuals (decrease in proximity). The change in  
195 distance was calculated as (initial distance) – (distance after 10 min). Thus, a positive value  
196 indicates approach (increase in proximity), whereas a negative value indicates greater  
197 separation (decrease in proximity). Call rate was the number of coo calls made by the focal  
198 animal from 0 to +1 min, where we measured the number of individuals around the focal animal  
199 at 0 min.

200 To analyse changes in numbers of individuals and in distance, two explanatory variables  
201 (initial numbers near the focal animal and distance to the other focal animal) were treated as  
202 continuous variables. To analyse contact call rate, we treated one explanatory variable (distance  
203 to the other focal animal) as a discrete variable to describe the general trend in coo call rate at  
204 different interindividual distances, because our exploratory analyses revealed that the rate of  
205 coo calls did not change linearly with the initial distance, but increased especially at long  
206 distances.

207 Statistical analyses were conducted using generalised linear mixed models and the SAS  
208 software (ver. 9.2; SAS Institute, Cary, NC). We used a normal distribution to analyse changes  
209 in numbers of individuals and changes in distances, and a generalised Poisson distribution to  
210 analyse coo call rates. Analyses of changes in numbers of individuals and rates of coo calls were  
211 performed on an individual basis. For the analysis, we treated the focal individuals as a random  
212 factor. Analysis of changes in distance was performed on a pair basis, because this response  
213 variable was derived from the positions of the two focal animals. For this, we used two  
214 explanatory variables; 1) initial number of individuals around the focal animals as an average of  
215 the numbers of individuals around the two focal animals, and 2) initial distance between the two  
216 focal animals. We treated the focal pair as a random factor. *Post hoc* pairwise comparisons

217 were conducted for the analyses of coo call rate, using the Bonferroni correction.

218

## 219 **Results**

### 220 *Changes in numbers of individuals at a close distance*

221 We examined the changes in the number of individuals within 20 m from the focal animal  
222 after 10 min (Fig. 1). A positive value indicated that the number of individuals increased  
223 (increase in proximity), a negative value indicated that it decreased (decrease in proximity), and  
224 a value of zero indicated that it remained the same. Changes in number of individuals were  
225 influenced negatively by the initial number of individuals in each of the three seasons during  
226 non-subgrouping; that is, when the number of individuals around the focal animal was small,  
227 the number of individuals tended to increase after 10 min (Fig. 1, autumn,  $F_{1,9} = 21.9$ ,  $p = 0.001$ ;  
228 winter,  $F_{1,8} = 23.0$ ,  $p = 0.001$ ; summer  $F_{1,6} = 43.1$ ,  $p = 0.0006$ ). The same tendency was  
229 observed during subgrouping in the summer, where each of the two focal individuals was in a  
230 separate subgroup ( $F_{1,6} = 56.7$ ,  $p = 0.0003$ ).

231 By contrast, the changes in the numbers of individuals were not affected by the initial  
232 distance to the other focal animal in any season, including in subgrouping in the summer  
233 (autumn,  $F_{1,9} = 0.08$ ,  $p = 0.79$ ; winter,  $F_{1,8} = 0.76$ ,  $p = 0.41$ ; summer, non-subgrouping,  $F_{1,6} =$   
234  $4.97$ ,  $p = 0.06$ ; summer, subgrouping,  $F_{1,6} = 1.48$ ,  $p = 0.27$ ).

235

### 236 *Changes in Distance*

237 We examined changes in distance after 10 min between two individuals (Fig. 2). A  
238 positive value indicated that the distance decreased (increase in proximity to the other focal  
239 individual), a negative value indicated that it increased (decrease in proximity), and a value of  
240 zero indicated that it remained the same. Changes in distance were influenced positively by the

241 initial distance during non-subgrouping. When the distance to the other focal animal was larger,  
 242 they tended to come closer after 10 min (Fig. 2A–C, autumn,  $F_{1,24} = 28.2$ ,  $p < 0.0001$ ; winter,  
 243  $F_{1,28} = 52.6$ ,  $p < 0.0001$ ; summer, non-subgrouping,  $F_{1,18} = 10.8$ ,  $p = 0.004$ ). This tendency was  
 244 not observed during subgrouping in the summer (Fig. 2D,  $F_{1,13} = 2.0$ ,  $p = 0.18$ ).

245 In contrast, variance in changes in distance were not accounted for by the initial number  
 246 of individuals around the focal animal in any season, including in subgrouping in the summer  
 247 (autumn,  $F_{1,21} = 1.99$ ,  $p = 0.17$ ; winter,  $F_{1,28} = 1.18$ ,  $p = 0.29$ ; summer, non-subgrouping,  $F_{1,18} =$   
 248  $1.09$ ,  $p = 0.31$ ; summer, subgrouping,  $F_{1,11} = 3.32$ ,  $p = 0.10$ ).

249

#### 250 *Rate of Contact Calls*

251 We examined whether the contact call rates of focal animals varied based on the distance  
 252 from another focal animal and on the number of individuals around the focal animal. In the  
 253 autumn, the effect of distance apart was significant but that of the number of individuals was not  
 254 (Fig. 3A, distance,  $F_{4,41} = 2.66$ ,  $p = 0.046$ ; number of individual,  $F_{1,9} = 0.18$ ,  $p = 0.68$ ). Pairwise  
 255 comparisons revealed no significant difference between any pair. However, call rates tended to  
 256 be higher with an interindividual distance of 90–230 m, versus those of 40–50 m ( $p = 0.06$ ).

257 Also in the winter, the effect of distance apart was significant but that of the number of  
 258 individuals was not (Fig. 3B, distance,  $F_{7,63} = 3.60$ ,  $p = 0.003$ ; number of individual,  $F_{1,8} =$   
 259  $0.0001$ ,  $p = 0.99$ ). Pairwise comparisons revealed that call rates were significantly higher for  
 260 interindividual distances of 120–270 m, compared to distances of 40–50 m and 60–70 m ( $p <$   
 261  $0.05$ ).

262 In the summer, none of the effects was significant during non-subgrouping (distance,  
 263  $F_{11,72} = 0.74$ ,  $p = 0.70$ ; number of individual,  $F_{1,6} = 1.53$ ,  $p = 0.26$ ) or subgrouping (distance,  
 264  $F_{8,45} = 0.24$ ,  $p = 0.98$ ; number of individual,  $F_{1,6} = 0.61$ ,  $p = 0.43$ ).

265

266 **Discussion**

267

268 *Adjustment of Proximity to Close Neighbours*

269 In our observations, the number of individuals within 20 m of the focal individual tended  
270 to increase after a short period of time when there was a small number of individuals around her  
271 and tended to decrease when there was a larger number of individuals in each of three seasons,  
272 including when the two focal animals were in different subgroups. In contrast, the change in  
273 number of individuals was not accounted for by the distance to the other focal individual.

274 These results suggest that Japanese macaques adjust their proximity to group members  
275 relying on the local density of group members within a close distance. Japanese macaques  
276 increased the number of neighbours, i.e., increased proximity, when they were far apart and *vice*  
277 *versa*. This adjustment appears to be a negative feedback of local density that may stabilize it. In  
278 this sense, this adjustment may be similar to attraction—repulsion movement toward the  
279 neighbours, and may be a common mechanism of aggregation with those of other animals, such  
280 as fish school (Aoki 1982) and bird flocks (Lukeman et al. 2010).

281 The mean number of individuals within 20 m of a focal animal (when the distance to the  
282 other focal animal was  $\geq 40$  m) was 3.1 in autumn, 2.0 in winter, 1.4 in non-subgrouping in  
283 summer, and 1.3 in subgrouping in summer. Thus, the local density of individuals around focal  
284 animals was high in autumn, middle in winter and low in summer. Although the density of  
285 animals differed among seasons, adjustment of proximity to neighbours was constantly  
286 observed in each of the three seasons.

287 The mean visibility in the subject group's habitat is ca. 30–50 m (Koda et al. 2008); thus,  
288 Japanese macaques are likely to keep sight of group members within a close distance, ca. 20 m. It

289 has been suggested that they monitor group members visually and adjust their movements to  
290 keep cohesiveness with other group members (Koda & Sugiura 2010; Suzuki & Sugiura 2011).  
291 Such adjustment continued even when the group was split into subgroups in the summer. This is  
292 consistent with the view that the group is split into two (or a few) subunits that move  
293 collectively with group members.

294

#### 295 *Adjustment of Proximity to Distant Individuals*

296 The distance to the other focal animal also tended to decrease after a short period of time  
297 when the distance was longer and tended to increase when the distance was shorter in each of  
298 three seasons, except in subgrouping in the summer. This change of distance, however, was not  
299 accounted for by the numbers of individuals within 20 m from the focal animals.

300 These results suggest that Japanese macaques adjust their proximity to group members at  
301 relatively far distances. Focal pairs of macaques tended to separate after a short period of time  
302 when they were close together and tended to move closer when they were farther apart. This  
303 indicates that individual Japanese macaques move to cohere with group members at relatively  
304 far distances. This adjustment may also be a negative feedback of distance to far individuals,  
305 which may stabilize the proximity to distant group members.

306 The mean distance between the two focal individuals (when the distance was  $\geq 40$  m)  
307 was 58.2 m in autumn, 72.0 m in winter, 85.1 m in non-subgrouping in summer, and 365.8 m in  
308 subgrouping in summer. Thus, the distance between two individuals was short in autumn,  
309 middle in winter and long in summer. Although the distance differed among seasons,  
310 adjustment of proximity to distant individuals was constantly observed in each of the three  
311 seasons, except in subgrouping in summer.

312 Such movement was not accounted by the local density of group members within a close

313 distance. Because the distance to the other focal animal and the number of individuals within 20  
314 m was not correlated, they might not be able to know the distance to the other focal animal from  
315 the local density of animals around them. These changes were observed even when the distance  
316 to the other focal animal was more than 40 m. Considering visibility in the habitat, it seems  
317 unlikely that a focal individual directly monitored the position and movement of the other focal  
318 individual. This tendency, however, disappeared when the two animals were in separate  
319 subgroups. On such occasions, Japanese macaques lost the location of the other subgroup and  
320 their movements became independent of each other.

321         However, it is possible that Japanese macaques depend only on nearby individuals but  
322 not distant members. An alternative explanation is that Japanese macaques monitor more subtle  
323 information from the nearby individuals, which enable them to adjust proximity to distant  
324 individuals. A possible cue is temporal change of proximity of nearby group members, which  
325 may reflect group cohesiveness. However, change in local density of individuals in 10 min  
326 (average change in number of individuals within 20 m from the two focal animals from 0 to +10  
327 min) did not explain the variance in change in distance between two focal individuals (Sugiura  
328 et. al., unpublished data). There are several possible cues from nearby individuals, e.g., timing  
329 and amount of change in proximity, activity of nearby individuals and social relationships to  
330 nearby individuals. In the present study, we could not record these detailed information of  
331 neighbour individuals in a natural setting. Continuous observation of nearby individuals, such  
332 as video recording would be applicable to further examinations.

333         In addition, we analyzed the change in distance on a pair basis, and used the numbers of  
334 nearby group members of the two focal individuals (average number) as an explanatory  
335 variable. However, an individual can know its own nearby members but not that of the other  
336 distant focal animal. Thus, the average number of nearby group members is a relatively rough

337 approximation and it might have reduced the effect of nearby group members on the change of  
338 distance. This limitation can be improved if we can analyze this effect on an individual basis,  
339 e.g., discriminating one of the two animals that is more responsible for the change of distance.

340

#### 341 *Contact Calls at Different Proximity*

342 Our results show that the coo call rate increased, especially for the longest distance class,  
343 in the autumn and winter. The coo call rate, however, was not influenced by the number of  
344 individuals within 20 m in any season. When the distance between two animals fell in the  
345 largest distance class, one or both focal animal(s) was likely to stay at the periphery of the  
346 spread group. Thus, the macaques seemed to emit contact calls frequently in the peripheral zone  
347 to contact group members. Therefore, Japanese macaques are apparently aware of which group  
348 zone they are in.

349 Such use of the contact call seems quite reasonable, considering the function of coo calls.  
350 The coo calls of Japanese macaques have been suggested to maintain group cohesiveness (Itani  
351 1963; Mitani 1986) and are often emitted by individuals that may be likely to become separated  
352 from the group (Koda & Sugiura 2010; Suzuki & Sugiura 2011). Similar usage of contact calls  
353 are found in other species of primates. Chacma baboons (*Papio cynocephalus*) emit contact  
354 calls more frequently when they were separated from the group (Rendall et al. 2000).  
355 White-faced capuchin monkeys (*Cebus capucinus*) emit contact calls more often at the  
356 peripheral zone of the group and the calls are likely to relate to group movement (Boinski &  
357 Campbell 1995).

358 Coo calls are, however, often elicited by the other's coo calls as vocal response (Sugiura  
359 2007a). Thus, increase of coo call rate might have caused by the increase of coo calls of the  
360 other individuals. Because we did not record the vocalization from the other individuals, in this

361 study, we can not examine the effect of other's call. Further observation should be needed,  
362 recording the rate of calls from other individuals and discriminating between spontaneous call  
363 (i.e., without preceding calls of the other individual) and response call (i.e., with preceding calls  
364 of the other individual).

365 We failed to detect difference in call rate in summer. The mean coo call rate per minute  
366 (when the distance to the other focal animal was  $\geq 40$  m) was 0.36 in autumn, 0.22 in winter,  
367 0.54 in non-subgrouping in summer, and 0.44 in subgrouping in summer. In summer, subject  
368 females produced coo calls frequently, probably because the group dispersed and they needed  
369 vocal contact most in this season. In this season, they may emit coo calls so frequently at any  
370 distance that they do not emit additional coo calls when they stayed far from the other focal  
371 animals.

372

### 373 *Possible Mechanisms of Adjustment of Proximity to Distant Individuals*

374 Japanese macaques may somehow locate the general whereabouts of the entire group.  
375 Assuming that macaques are aware of their proximity to their group's central zone, individual  
376 movement from the peripheral zone towards the central zone may explain the more rapid  
377 approach from greater interindividual distances apart.

378 One possible mechanism for knowing the general location of the entire group is  
379 monitoring the movements of nearby group members. It appears difficult for an individual to  
380 see all of the group members directly, because it spreads over a wider area than one can see in  
381 the forest. In such conditions, movements of nearby group members may help to know the  
382 general location of the entire group. For example, if an individual remembers that most group  
383 members passed ahead of it, it ascertains that it is in a peripheral position in the group. Such a  
384 mechanism is plausible, considering their cognitive abilities (Roberts 2002) and that Japanese



385 macaques usually travel straight to food sources (Maruhashi et al. 1998). Another possible  
386 mechanism is vocal communication. Audible range of contact calls is usually wider than visible  
387 range in forest, and contact calls from group members appears to help an individuals to locate  
388 the whole group. If they locate the general whereabouts of the entire group, they may change  
389 behaviour in relation to their own spatial position, e.g., central – peripheral zone of the group  
390 (Janson 1990; Robinson 1981). Further examination of behavioural changes in relation to  
391 relative position of the group is necessary, such as monitoring behaviour of group members  
392 (Kazahari & Agetsuma 2010; Suzuki 2011) and contact calls (Boinski & Campbell 1995;  
393 Rendall et al. 2000; this study).

394 Another possible mechanism for knowing the location of the group is that group  
395 members share knowledge of food resources and aggregate at a food patch (Ramos-Fernandez  
396 et al. 2006). If we assume that each individual accurately knows information of food resources  
397 and knows where group members go next, they can aggregate at such places without locating  
398 the whole group. However, it is unlikely that group members share the prior knowledge of food  
399 resources to such degree that they can forecast the other members' destinations. Aggregating at  
400 a food patch may help them to cohere, but monitoring the position of the group should be  
401 needed.

402 In addition, Japanese macaques do not always aggregate at a large food patch, especially  
403 in lean seasons. In the subject group, they feed on clumped food such as fruiting trees for about  
404 80 % of feeding time in autumn (Sugiura et al. 2011), where aggregating at such food patches  
405 may be possible. However, they feed on scattered food such as herb for about 85% and 63% of  
406 feeding time in winter and in summer, respectively (Sugiura et al. 2011), where they feed alone  
407 or with a few members. In such ecological condition, aggregating at a food patch would be  
408 difficult. In spite of these drastic changes of food availability, we observed a significant effect of

409 initial distance of the focal pair on the change in distance between them, in different seasons.  
410 Thus, aggregating at a food patch alone can not account for group cohesion, although this  
411 should also help them to cohere.

412 In this study, the subjects did not engage in a particular activity, but did in various ones  
413 when we sampled their movements. The proportion of activities also varied in different seasons.  
414 In spite of this variation, the adjustment of distance between two distant animals was constantly  
415 observed in each of the three seasons. Thus, it is unlikely that adjustment of proximity is derived  
416 from a particular situation, such as aggregating at food patches. In autumn, the proportions of  
417 activities of subject animals were 17.0 % in grooming, 12.4 % in resting, 54.2 % in foraging,  
418 15.7 % in moving and 0.7 % in agonistic interaction. In winter, the proportions were 11.1 % in  
419 grooming, 6.4 % in resting, 72.7 % in foraging, 9.4 % in moving and 0.3 % in agonistic  
420 interaction. In summer, the proportions were 11.1 % in grooming, 21.5 % in resting, 32.9 % in  
421 foraging, 34.4 % in moving and 0.3 % in agonistic interaction.

422

#### 423 *Possible Function of Adjustment of Proximity to Distant Individuals*

424 A major cost of grouping is feeding competition with group members (van Schaik & van  
425 Noordwijk 1986), but adjusting proximity to group members can mediate the feeding  
426 competition. Adjusting proximity not only to members in close proximity but also to more  
427 distant members should bring more flexible group cohesion and foraging tactics. If we assume  
428 that Japanese macaques keep a particular distance to a few neighbours, they should need to  
429 synchronize their arrival and leave of a food patch with their neighbours. Such adjustment of  
430 proximity to neighbours should be a firm means for cohesion but are likely to affect feeding  
431 competition.

432 Actually, however, Japanese macaques seem to flexibly change their proximity and group

433 cohesiveness. They change their proximity to group members depending on the quality of food  
434 (Sugiura et al. 2011). In addition, they do not always synchronize their foraging (Agetsuma  
435 1995) or timing of leave from food patches (Kazahari & Agetsuma 2010). Japanese macaques  
436 appear to adjust proximity to distant members, probably by locating approximate position of the  
437 whole group. This may bring them more freedom of positioning themselves and thus, freedom  
438 of food choice with lesser competition and/or better feeding efficiency. Predation free condition  
439 in this study should contribute to such flexible adjustment of proximity. Lack of predation may  
440 reduce the necessity of their keeping cohesiveness with nearby individuals, and made the  
441 adjustment proximity to distant individuals more detectable.

442         The present study suggests that Japanese macaques adjust their proximity to group  
443 members, relying not only on neighbouring group members, but also on more distant animals.  
444 Although adjustment of proximity to neighbours have been reported in a variety of species,  
445 adjustment of proximity to distant group members may be unique to group living animals that  
446 form a relatively small group with stable memberships, like Japanese macaques. However, it is  
447 still possible that Japanese macaques rely only on the information from nearby group members,  
448 and it accounts for the change in distance between two distant individuals. Further examination  
449 of the influence of nearby group members on the change of distance should be necessary, such  
450 as their activities, movements and coo calls. Examination from another view point would also  
451 possible. If they relay also on the distant group members, they should know the location of the  
452 whole group and adjust their movements based on such information. Examination of this  
453 possibility would also help to elucidate our hypothesis and to understand the mechanism of  
454 group cohesion in Japanese macaques and other group living animals.

455

456

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463

464 **Figure Legends**

465

466 **Figure 1.** Initial numbers of individuals within 20 m from the focal individual ( $x$  axis) and  
467 changes in the number of individuals after 10 min ( $y$  axis), in the autumn (A), the winter (B),  
468 non-subgrouping in the summer (C), and subgrouping in the summer (D). A positive value  
469 indicates that the number of individuals increased, a negative value indicates that it decreased,  
470 and a value of zero indicates that it remained the same. A line represents the linear estimate by a  
471 generalised linear model, where the initial distance is the mean. Size of marks vary with the  
472 sample size (see legends in the figure), because multiple samples are plotted at the same point.

473

474 **Figure 2.** Initial distance between two individuals ( $x$  axis) and changes in distance apart after  
475 10 min ( $y$  axis) in the autumn (A), the winter (B), non-subgrouping in the summer (C), and  
476 subgrouping in the summer (D). A positive value indicates that the distance apart became  
477 shorter, a negative value indicates that it became greater, and a value of zero indicates that it  
478 remained the same. A line represents the linear estimate by a generalised linear model, where  
479 the initial number is the mean.

480

481 **Figure 3.** Initial distance between two individuals ( $x$  axis) and mean coo-call rates during the  
482 following 1 min ( $y$  axis) in the autumn (A), the winter (B), non-subgrouping in the summer (C),  
483 and subgrouping in the summer (D). Error bars show 95% confidence intervals of means.  
484 Classes connected with bold lines showed a significant difference in *post hoc* pairwise  
485 comparisons ( $P < 0.05$ , panel B), and those connected with dashed lines showed a  
486 near-significant difference ( $P = 0.06$ , panel A).

487

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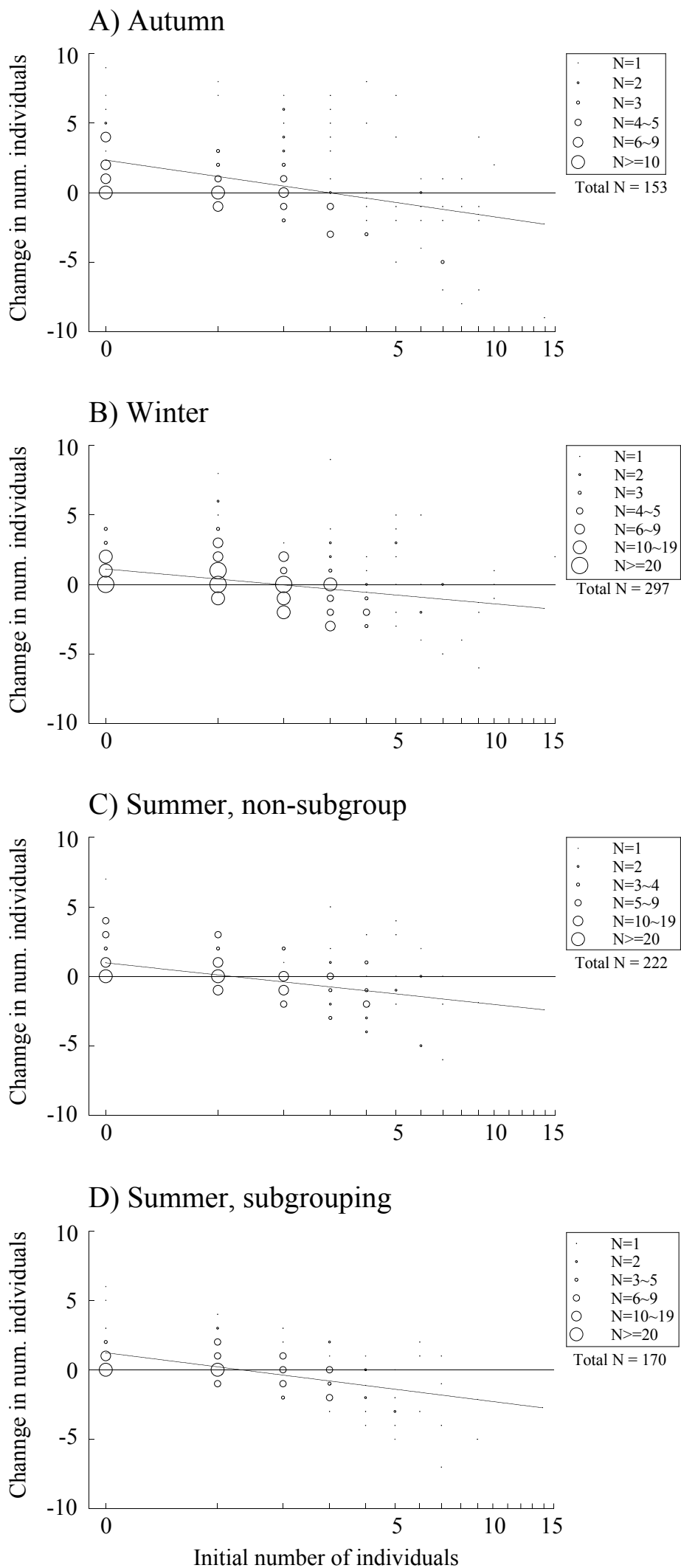


Fig. 1

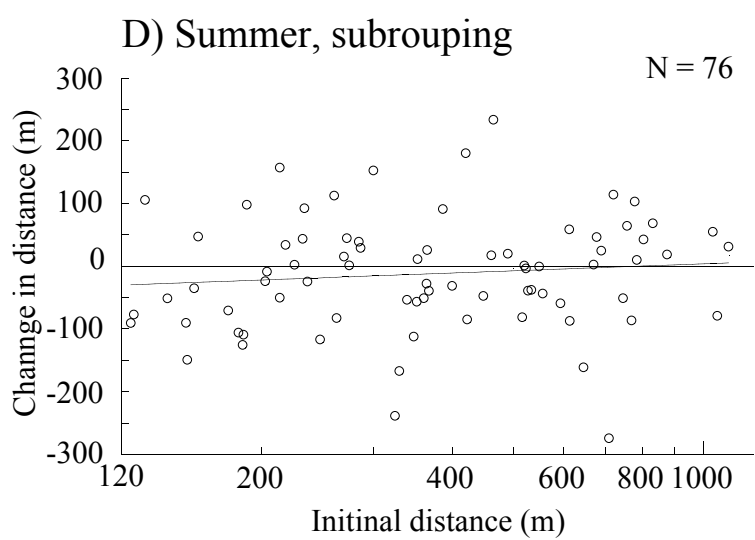
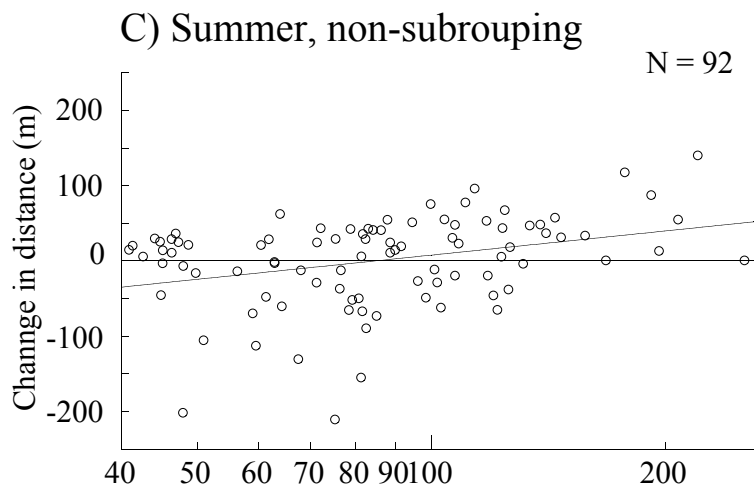
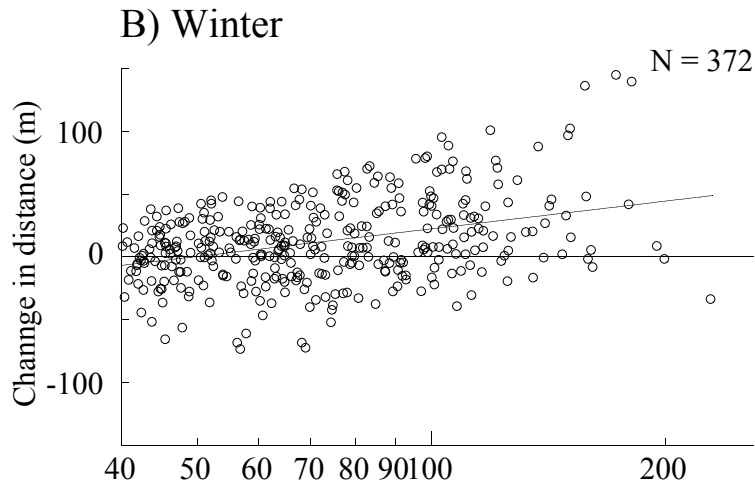
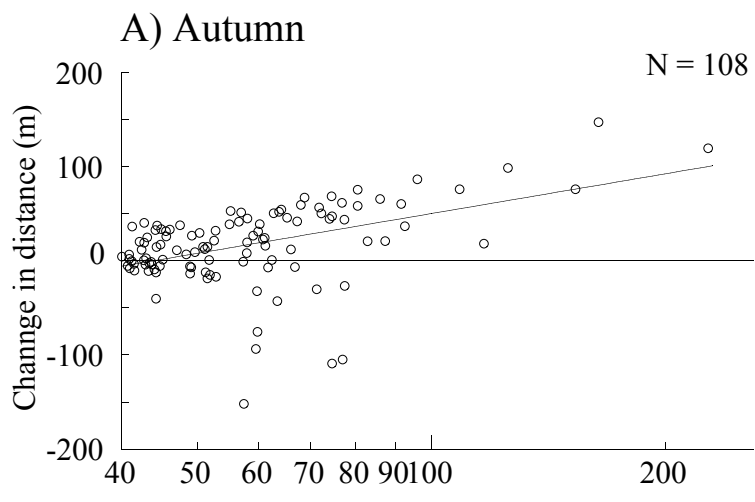


Fig. 2

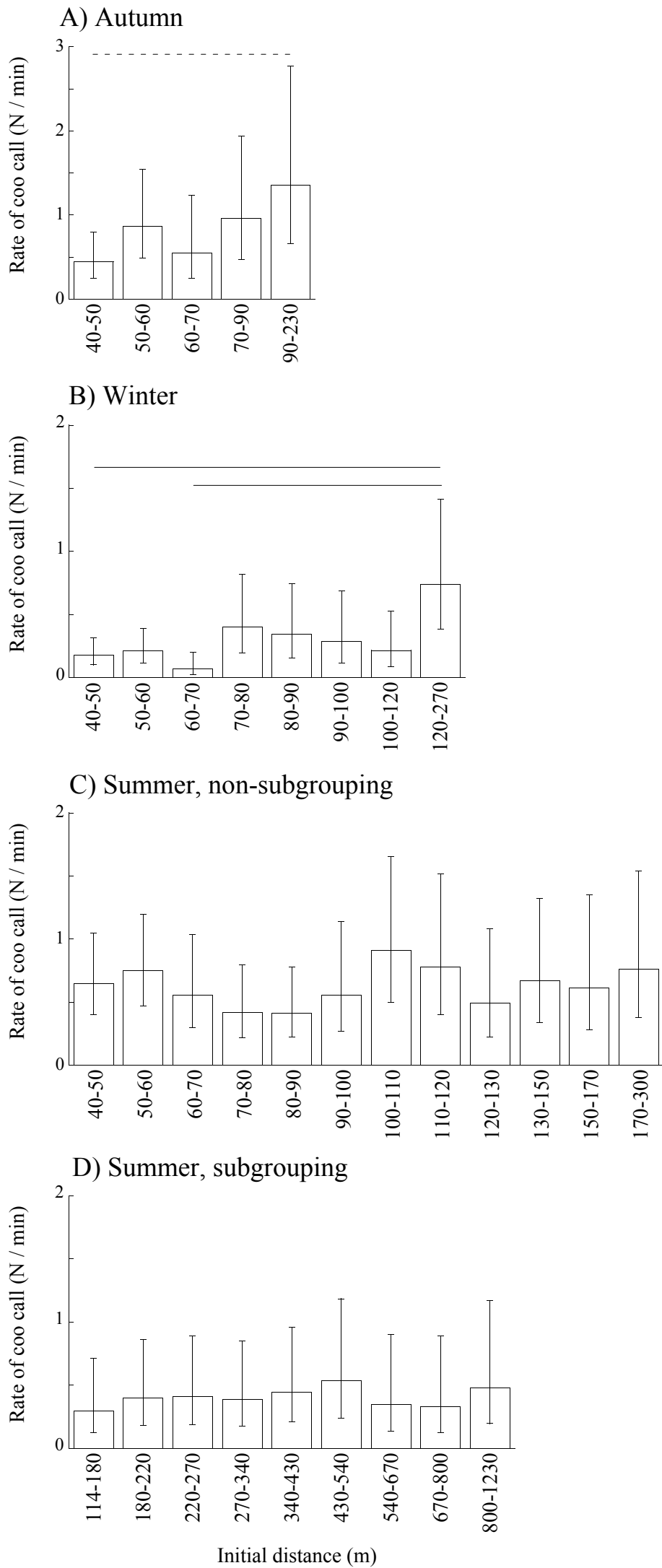


Fig. 3