Foraging dynamics are associated with social status and context in mouse social hierarchies

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Living in social hierarchies requires individuals to adapt their behavior and physiology. We have previously shown that male mice living in groups of 12 form linear and stable hierarchies with alpha males producing the highest daily level of major urinary proteins and urine. These findings suggest that maintaining alpha status in a social group requires higher food and water intake to generate energetic resources and produce more urine. To investigate whether social status affects eating and drinking behaviors, we measured the frequency of these behaviors in each individual mouse living in a social hierarchy with non-stop video recording for 24 hours following the initiation of group housing and after social ranks were stabilized. We show alpha males eat and drink most frequently among all individuals in the hierarchy and had reduced quiescence of foraging both at the start of social housing and after hierarchies were established. Subdominants displayed a similar pattern of behavior following hierarchy formation relative to subordinates. The association strength of foraging behavior was negatively associated with that of agonistic behavior corrected for gregariousness (HWIG), suggesting animals modify foraging behavior to avoid others they engaged with aggressively. Overall, this study provides evidence that animals with different social status adapt their eating and drinking behaviors according to their physiological needs and current social environment.

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12 **Abstract**

13 Living in social hierarchies requires individuals to adapt their behavior and physiology. We have

14 previously shown that male mice living in groups of 12 form linear and stable hierarchies with

15 alpha males producing the highest daily level of major urinary proteins and urine. These findings

16 suggest that maintaining alpha status in a social group requires higher food and water intake to

17 generate energetic resources and produce more urine. To investigate whether social status affects

18 eating and drinking behaviors, we measured the frequency of these behaviors in each individual

19 mouse living in a social hierarchy with non-stop video recording for 24 hours following the

20 initiation of group housing and after social ranks were stabilized. We show alpha males eat and

21 drink most frequently among all individuals in the hierarchy and had reduced quiescence of

22 foraging both at the start of social housing and after hierarchies were established. Subdominants

23 displayed a similar pattern of behavior following hierarchy formation relative to subordinates.

24 The association strength of foraging behavior was negatively associated with that of agonistic

25 behavior corrected for gregariousness (HWIG), suggesting animals modify foraging behavior to

26 avoid others they engaged with aggressively. Overall, this study provides evidence that animals

27 with different social status adapt their eating and drinking behaviors according to their

28 physiological needs and current social environment.

29

30 **Introduction**

31 Social dominance hierarchies emerge as animals measure the competitive ability of others

32 through social interactions and individuals learn to consistently yield towards relatively

33 dominant individuals (Chase, 1982; Drews, 1993). One of the universal characteristics of

34 dominance hierarchies observed across species in the wild or housed in a laboratory is that

35   resources such as space, food and mating partners are unevenly distributed with preferential

36   access being skewed towards more dominant individuals (Banks et al., 1979). Variation in

37   feeding behavior has been observed as a function of social status. In particular, more dominant

38   individuals typically have increased access to food resources as reported in cats (Bonanni et al.,

39   2007), fish (Sloman et al., 2000; Alanärä, Burns & Metcalfe, 2001; Montero et al., 2009),

40   crayfish (Herberholz, McCurdy & Edwards, 2007), domestic fowl (Banks et al., 1979), willow

41   tits (Ekman & Lilliendahl, 1993), deer mice (Farr & Andrews, 1978), rats (Blanchard &

42   Blanchard, 1989; Melhorn et al., 2010), goats (Barroso, Alados & Boza, 2000), dairy cows

43   (Olofsson, 1999), and non-human primates (Whitten, 1983; Deutsch & Lee, 1991; Saito, 1996;

44   Sterck & Steenbeek, 1997; Vogel, 2005; Robbins, 2008), although some studies do not show this

45   pattern (Stricklin & Gonyou, 1981; Moles et al., 2006). This monopolization of resources comes

46   about in part because in many hierarchies dominant animals must increase food intake to meet

47   the metabolic demands associated with acquiring and maintain dominance via asserting physical

48   aggression or producing chemical signals (Hogstad, 1987; Gosling et al., 2000; Hurst & Beynon,

49   2004; Biro & Stamps, 2010; Nelson et al., 2015). Further, dominant animals may need to invest

50   more in feeding due to having a lower caloric efficiency (Moles et al., 2006) and a higher oxygen

51   consumption rate (Hogstad, 1987). Conversely, subordinate animals may also experience shifts

52   in feeding and metabolism due to experiencing social stress. For instance, chronically socially

53   defeated mice have been found to both increase (Bhatnagar et al., 2006; Foster et al., 2006;

54   Chuang et al., 2011) and decrease (Meerlo et al., 1996; Becker et al., 2007) food intake when

55   experiencing chronic social stress.

56   Competition for water occurs in some species when water is an in-demand resource (Christian,

57   1980; Razgour, Korine & Saltz, 2011), but may also be a key feature of living in a social

58 hierarchy even when water resources are not scarce. Indeed, dominant male rats living in social

59 groups have a significantly higher frequency of drinking water when even when it was given *ad*

60 *libitum* (Blanchard & Blanchard, 1989). Further, in species where dominants scent-mark to

61 attract females or mark their territories, dominant individuals may be physiologically required to

62 intake more water than subordinates. Notably, dominant rats and mice scent-mark more

63 frequently than subordinates (Hurst & Beynon, 2004) and typically have empty bladders

64 (Desjardins, Maruniak & Bronson, 1973). Moreover, Desjardins et al. (Desjardins, Maruniak &

65 Bronson, 1973) demonstrated that dominant mice flush intravenously injected radioactive

66 molecules via urination significantly faster than subordinates. Conversely, subordinate rats and

67 mice inhibit scent-marking behavior and show a decrease in daily urination volume (Desjardins,

68 Maruniak & Bronson, 1973; Drickamer, 1995; Wood et al., 2010; Nelson et al., 2015; Hou et al.,

69 2016; Lee, Khan & Curley, 2017). Taken together, these findings suggest that dominant rats and

70 mice must increase their water intake relative to subordinate individuals.

71 Living in a social hierarchy also forces animals to adapt their behavioral patterns to maximize

72 their fitness by paying attention to more dominant individuals. In primates, fish and mice,

73 subordinate animals may monitor dominant animals or animals with whom they have had

74 frequent aggressive interactions and inhibit their own social behavior accordingly (Deaner,

75 Khera & Platt, 2005; Pannozzo et al., 2007; Desjardins, Hofmann & Fernald, 2012; Curley,

76 2016b). Since eating and drinking are essential activities for survival regardless of social status

77 in groups, subordinate animals cannot completely inhibit their foraging behavior but rather may

78 need to adjust these behaviors to avoid conflict with dominants. For example, desert baboon

79 dominant males have stronger co-feeding relationships with other dominants than with

80 subordinates males (King, Clark & Cowlishaw, 2011). In semi-free ranging Mandrills,

81 individuals tend to visit feeding zones at the same time more often when they are distant in the

82 social hierarchy rather than close in ranks (Naud et al., 2016). In brown trout, subordinates

83 temporally segregate their feeding time to avoid conflict with dominant males by choosing to

84 visit food sources during less desirable times of the day (Alanärä, Burns & Metcalfe, 2001).

85 Clearly dominant and subordinate animals adjust the timing of their feeding and drinking

86 dependent upon their relative relationship to other individuals in their groups.

87 Previously, we have demonstrated that groups of 12 male outbred CD-1 male mice living in a

88 complex housing system rapidly form stable and linear social hierarchies (So et al., 2015;

89 Williamson, Lee & Curley, 2016; Curley, 2016b; Williamson, Romeo & Curley, 2017; Lee,

90 Khan & Curley, 2017). Each male maintains a unique social rank and adjusts their social

91 behavior flexibly and appropriately according to social context (Curley, 2016b; Williamson,

92 Romeo & Curley, 2017; Williamson et al., 2018). Further, we recently reported that more

93 dominant males produce and excrete higher levels of major urinary proteins (MUPs) and a higher

94 volume of urine than subordinates (Lee, Khan & Curley, 2017). These findings pose several

95 questions regarding the feeding and drinking patterns of differently ranked mice that face

96 different physiological needs. In the current study, we addressed three specific questions

97 regarding the foraging behavior of mice living in a social hierarchy: (i) *Do more dominant males*

98 *eat or drink more frequently than subordinate males to account for their increased energetic*

99 *demands? (ii) Do individuals choose feeding sites away from alpha males to avoid conflict? (iii)*

100 *Do individuals adjust their eating and drinking times to avoid encountering more dominant*

101 *males or males from whom they have received frequent aggression?*

102

103

104   **Methods**

105   **Subjects and housing**

106   Animals: In this study, we observed agonistic, eating and drinking behaviors of a total of 156 male

107   outbred CD-1 mice aged 9-12 weeks. 7-week old mice were obtained from Charles River

108   Laboratories (Wilmington, MA, USA) and housed in groups of 3 for 2 weeks in standard sized

109   cages with ad libitum standard chow and water. All mice were individually marked by dying their

110   fur with nontoxic animal markers (Stoelting Co., Wood Dale, IL, USA). The 156 mice were

111   assigned into 13 distinct groups of 12 males. These social groups were part of several different

112   ongoing studies in our laboratory with the aim of analyzing blood and brain tissue post-mortem.

113   The purpose of this study was to assess how feeding and drinking behavior varies with social status

114   across hierarchy formation. Therefore, we acquired 24-hour observations of feeding and drinking

115   behavior for each of the social groups (described below). Animals were undisturbed throughout

116   the experiment.

117   Housing: On the day of group-housing 12 mice were weighed and placed into custom-built vivaria

118   **Fig. S1**; 150 × 80 cm and 220 cm high; Mid-Atlantic, Hagerstown, MD, USA). The vivarium was

119   constructed as previously described (So et al., 2015; Williamson, Lee & Curley, 2016), and

120   consisted of an upper level with multiple shelves covered in pine bedding (36,000 cm^2 = 3 floor ×

121   150 cm × 80 cm) and a lower level with 5 nest boxes filled with pine bedding (2,295 cm^2 = 5 cages

122   × 27 cm × 17 cm) connected by tubes. The total surface of a vivarium is approximately 62,295

123   cm^2, providing 5191 cm^2 per mouse. Standard chow and water were provided ad libitum from two

124   locations on the top shelf of the vivarium. All animals either had no previous experience with any

125   other animal in the group or had been previously housed with only one other male in the social

126   group. Subjects were housed with constant temperature (22–23°C) and humidity (30-50%) and a

127   12/12 light/dark cycle with white light (light cycle) on at 2400 hours and red lights (dark cycle) on

128   at 1200 hours. We observed if any animal exhibited a sign of pain or injury every day. All

129   procedures were conducted with approval from the Columbia University Institutional Animal Care

130   and Use Committee (IACUC protocols: AC-AAAP5405, AC-AAAG0054).

131

132   **Data collection: Agonistic behavior, eating, and drinking**

133   Agonistic behavior data collection: Animals were housed in groups for up to 27 days (range 10-

134   28 days, mean= 18.31 days). An average of 1.70 hours of daily behavior observations were

135   undertaken on each group to determine the social hierarchy. Observations always occurred in the

136   dark phase of the light cycle. Trained observers recorded all occurrences of fighting, chasing,

137   mounting, subordinate posture and induced-flee behaviors and the identity of the dominant and

138   subordinate individuals in each interaction (for ethogram, see **Table S1**). Data were collected using

139   handheld android devices and directly uploaded to a timestamped Google Drive.

140   Video data collection: On 16 unique days we mounted two GoPro cameras directly in front of the

141   food and water hoppers on the left and right sides of each vivarium and continuously recorded

142   eating and drinking for 24 hours. We collected data on first day of group housing (Day 1) from

143   five cohorts, recording from the time that animals were put into the vivarium. Eating and drinking

144   in stable social hierarchies (Stable) were recorded from 11 separate cohorts between days 6 and

145   22. By sampling across a range of days we were able to assess if the time since group formation

146   also affected feeding and drinking behavior. A total of 3 cohorts were videoed for feeding and

147   drinking behavior on both Day 1 and post Day 6 (Stable). We controlled for this using cohort-ID

148   as a random effect in all models where appropriate. We have previously demonstrated that all

149   hierarchies become stable from Day 4 or 5 onwards (Williamson, Lee & Curley, 2016). During to

150   1440-minute observation/video window, we coded the identities of those animals that drank or ate

151   at the particular hopper (left/right side of a vivarium) during each minute bin. These data provided

152   a measure of the number of minutes engaged in and the circadian rhythmicity of feeding and

153   drinking behavior for each animal across a single dark/light cycle of a 24-hour period. However,

154   as it is possible that individuals may spend different amount of time eating or drinking per visit

155   dependent on their rank or the day we further selected 603 eating and drinking visits (1.2% of

156   eating bouts, 2.1% of drinking bouts, 3.3% of total visits) across all groups for duration analysis.

157   We sampled data probabilistically with the representation of each animal in the duration dataset

158   being weighted according to their frequency of eating and drinking.

159   <u>Inter-rater reliability:</u> Each video was coded by 2-3 coders from a pool of 11 trained coders. Coders

160   showed a high degree of inter-coder reliability (unweighted Cohen's kappa = 0.805, p<0.001)

161   (Jacob Cohen, 1960; Lombard, Snyder-Duch & Bracken, 2002; Gamer, Lemon & Singh, 2012).

162

163   **Statistical analysis**

164   All statistical analyses were undertaken in R v. 3.4.3 (R Core Team, 2017). The statistical analysis

165   for agonistic behavior, eating and drinking frequency and duration, and social network analysis of

166   foraging and agonistic behaviors are described.

167   <u>Analysis of agonistic behavior data</u>

168   With agonistic interaction data, we tested the linearity of each social hierarchy by calculating

169   Landau's h-value and triangle transitivity and associated p-values derived from 10,000 Monte-

170   Carlo randomizations (De Vries, 1995; McDonald & Shizuka, 2012) using the compete R package

171   (Curley, 2016a). Values and associated significance tests were determined for observational data

172   up to the end of each day and over all observations. Individual ranks were determined through

173   calculation of Glicko Ratings using the R package PlayerRatings (Stephenson & Sonas, 2012). In

174   the Glicko Rating system (Glickman, 1999; Williamson, Lee & Curley, 2016), animals are initially

175   assigned with 2,200 points then gain or lose points based on the number of wins and losses relative

176   to the difference in ratings between themselves and their opponent (see Williamson et al. (2016)

177   for a more detailed description of the calculations). After each contest in each group the Glicko

178   ratings of all animals in that group was continuously updated. Based on our behavioral observation

179   of social hierarchy dynamics, we further categorized individuals into three social status groups

180   using Glicko ratings. An alpha male holds the highest Glicko rating (social rank 1) in the hierarchy.

181   Males in the subdominant social group are those with Glicko ratings higher than or equal to initial

182   points, 2,200 but not the highest rating. The remainder of the males in the hierarchy that hold

183   Glicko ratings lower than 2,200 are in the subordinate social group. The despotism of each alpha

184   male was calculated using the compete R package (Curley, 2016a) by determining the proportion

185   of all wins by alpha to all agonistic interaction (see (Williamson, Lee & Curley, 2016) for details)

186   that occurred in each group up to the day of video recording. Associations between body weight

187   measured on Day 1 of group housing and social rank were tested for each hierarchy using

188   Spearman Rank correlation tests.

189   <u>Analysis of frequency and bout duration data of eating and drinking</u>

190   We analyzed the data on frequency and duration of eating and drinking with generalized linear

191   mixed effects models with a Bayesian Markov chain Monte Carlo (MCMC) sampling using the

192   MCMCglmm R package (Hadfield, 2010). We specified a Poisson family for the dependent

193   variables of eating and drinking frequency of each individual (count data) and Gaussian family for

194   duration of eating and drinking (continuous data). A default uninformative inverse gamma prior

195   in the MCMCglmm library was used. We fitted all models with cohort ID as random slopes and

196   intercepts in each model. We tested the effect of following fixed factors on eating and drinking

197   frequency in each model with 1,000,000 iterations, 5,000 burn-in, and a thinning interval of 100;

198   (i) the individual Glicko rank and despotism of each group on Day 1 and up to the day of

199   eating/drinking video recording, (ii) individuals' social status group (alpha, subdominant,

200   subordinate), (iii) dark/light phase and whether the hierarchies have been established (Day 1 vs.

201   Stable) and an interaction between them. We then tested whether social status group as a fixed

202   factor had effects on the following dependent variables in each model with 1,000,000 iterations,

203   5,000 burn-in, and a thinning interval of 20; (i) the percentage of visits made by individuals in the

204   light phase to total visits (visits in light cycle/total visits in dark/light cycles*100), (ii) the

205   maximum period of quiescence / inactivity of eating and drinking. With eating and drinking bout

206   duration data, we tested if the bout duration of eating and drinking were associated with the

207   following fixed factors with 10,000,000 interactions, 100,000 burn-in, and a thinning interval of

208   50; (i) the individual Glicko social rank on the day, (ii) despotism of each group, and (iii) whether

209   the hierarchies were stabilized. In all models, we confirmed that convergence of the chains was

210   attained by visually inspecting the MCMCglmm object plots, setting thinning intervals so that

211   autocorrelation between samples were less than 0.10, and using a Gelman-Rubin test in the coda

212   R package (Plummer et al., 2016). We tested the interactions among fixed effects and only included

213   the interaction effects if the model with interaction terms yielded the lowest deviance information

214   criterion (DIC). All interaction terms among fixed variables were tested and only selected when

215   the model with interaction terms had significantly lowest DIC values. A two-tailed exact binomial

216   test was used to test whether each mouse showed a location preference (right versus left) between

217   the two food/water hoppers.

218   <u>Association patterns in foraging behavior and aggressive behavior</u>

219 Within stable (post Day 6) cohorts we measured the association strength of foraging behavior by

220 calculating the simple ratio association index (SRI) for each of 726 dyads (total number of dyadic

221 relationships in the 11 stable cohorts of 12 individuals in each group) (Whitehead, 2008). Briefly,

222 we placed two separate food and water dispensers on the opposite sides of vivaria. For a dyad with

223 mouse A and mouse B, their simple ratio association index is calculated by $SRI = \frac{x}{x + yAB + yA + yB}$

224 where x = total number of minute bins where A and B were foraging (eating or drinking) at the

225 identical dispenser location, yA = total number of minute bins with only A identified, yB = total

226 number of minute bins with only B identified, yAB = total number of minute bins where A and B

227 are identified from different locations. As mice differ in their tendency to associate aggressively

228 (gregariousness) across social ranks, we calculated HWIG (half-weight index corrected for

229 individual gregariousness) as described in (Godde et al., 2013) as a measure of the association

230 strength of agonistic behavior. As the SRI of foraging behavior followed a zero-inflated beta

231 distribution, we used the brms package (Bürkner, 2018) to fit models accordingly. We tested

232 whether the SRI of foraging is affected by types of relationship (alpha-other, other-other) and the

233 association strength of agonistic interactions.

234

235 **Results**

236 **Social hierarchy characteristics**

237 All cohorts formed a linear hierarchy over the housing period (h' mean = 0.78, interquartile range

238 (IQR) = [0.67-0.81], all p<0.001; $ttri$ = 0.87 [0.83-0.93], all p<0.001). All 11 cohorts videoed after

239 Day 6 had formed a stable linear hierarchy by the day of video recording (all h' p<0.05). We were

240 able to identify the final rank of all animals in each hierarchy using the Glicko ratings method as

241 well as identify individual ranks on the day of eating/drinking video recording. For the 11 cohorts

242   videoed on day 6 or later, individual ranks on the day of video recording correlated highly with

243   final rank at the end of group housing indicating high stability (rhos = 0.92 [0.88-0.95], all p<0.01).

244   In 9/11 groups the alpha male on the day of video recording was the same alpha male at the end

245   of group housing. In the other two groups the final alpha male was ranked 2 and 3 respectively on

246   the days of video recording. In the 5 groups recorded on day 1, 3/5 males remained the alpha male

247   throughout the study and the other two males became 2nd and 3rd ranked in their respective groups.

248   The degree of alpha male despotism during the whole housing period varied across groups (0.56

249   [0.38-0.63]). For social groups videoed after Day 6, alpha-male despotism ranged between 0.36-

250   0.85 with a median and IQR of 0.50 [0.42-0.61] on the day of feeding/drinking video recording.

251   Across all cohorts, initial body weight did not predict social rank (Spearman's rank correlation

252   tests, all cohorts p>0.68).

253

254   **Associations between individual social rank, group despotism and foraging frequency**

255   For those groups in which we observed eating and drinking frequency on Day 1 of group

256   housing, eating frequency did not have linear relationship with social rank (fixed effect mean= -

257   0.022, 95% Bayesian credibility interval (BCI)= [-0.047, 0.006], pMCMC=0.099, **Fig. 1a**) or

258   despotism (0.037 [-0.015, 0.087], pMCMC=0.099). Mice with more dominant social status drank

259   significantly more frequently (-0.049 [-0.084, -0.018], pMCMC=0.001, **Fig. 1b**) and individuals

260   from groups with higher despotism drank water more frequently (0.032 [0.007, 0.054],

261   pMCMC=0.012). In established stable social hierarchies, more dominant individuals ate and

262   drank more frequently than subordinate animals did (eating: -0.031 [-0.046, -0.016],

263   pMCMC<0.001; drinking: -0.045 [-0.061, -0.028], pMCMC<0.001, **Fig. 1**). Despotism did not

264   have an effect either on eating and drinking frequency in stable groups (eating: pMCMC=0.521,

265   drinking: pMCMC=0.433). This effect was consistent across all days sampled in stable

266   hierarchies from Day 6 to Day 22 as there was no significant effect of day on eating and drinking

267   frequencies post Day 6 (eating: pMCMC=0.720; drinking: pMCMC= 0.498). Mice also did not

268   differ in eating and drinking frequency between Day 1 and the days after the hierarchies were

269   stabilized (eating: pMCMC=0.381; drinking: pMCMC=0.276).

270   We further examined differences in eating and drinking frequency among three social status

271   groups: alpha (Glicko rank 1, the highest Glicko rating), subdominant (other males with Glicko

272   ratings higher than their initial starting point) and subordinate (males with Glicko ratings less

273   than their initial starting point) (see **Table S2**). On Day 1, alpha males ate and drank significantly

274   more frequently compared to subdominant (eating: -0.444 [-0.808, -0.090], pMCMC=0.015;

275   drinking: -0.749 [-1.151, -0.356], pMCMC<0.001; **Fig. S2a**) and subordinate groups (eating: -

276   0.483 [-0.788, -0.150], pMCMC=0.004; drinking: -0.984 [-1.318, -0.606], pMCMC<0.001).

277   Subdominant males did not differ in both eating and drinking frequency from subordinate males

278   (eating: pMCMC=0.741; drinking: -0.235 [-0.498, 0.0316], pMCMC=0.083). Once hierarchies

279   were established, alpha males still showed higher frequency of eating and drinking than

280   subdominant (eating: -0.244 [-0.456, -0.047], pMCMC=0.021; drinking: -0.252 [-0.467, -0.029],

281   pMCMC=0.024; **Fig. S2b**) and subordinate males (eating: -0.350 [-0.541, -0.170],

282   pMCMC<0.001; drinking: -0.494 [-0.696, -0.298], pMCMC<0.001), but the effect sizes were

283   diminished compared to Day 1. Notably, subdominant males drank significantly more frequently

284   than subordinate males did (-0.243 [-0.373, -0.108], pMCMC<0.001) but did not eat more

285   frequently than subordinate males did (-0.106 [-0.231, 0.018], pMCMC=0.100).

286   There were no significant differences in average eating or drinking bout duration across all ranks

287   (eating: pMCMC=0.106; drinking: pMCMC=0.913; **Fig. S3**), but the bout duration of eating and

288 drinking was shorter on Day 1 compared to after the hierarchies stabilized (eating: 11.943s

289 [3.486 – 20.856], pMCMC=0.009; drinking: 2.922s [0.730 – 4.986], pMCMC=0.005. The

290 average bout duration of eating across all ranks was 16.8s [6.4s-28.8s] on Day 1 and 25.1s

291 [17.3s-50.9s] after Day 5. The average bout duration of drinking across all ranks was 4.7s [3.2s-

292 6.4s] on Day 1 and 7.4s [4.5s-9.9s] after Day 5). This finding suggests that the observed increase

293 in the frequency of eating and drinking in alpha males translates to significant increases in total

294 food and water consumed compared to subdominant and subordinate males.

295

296 **Variation in eating and drinking frequency during dark and light phases**

297 Mice were housed under a 12:12 hours dark/light cycle and eating and drinking behavioral data

298 were collected beginning with the onset of the dark cycle for 24 hours. Animals of all ranks ate

299 and drank significantly more frequently during the dark phase compared to the light phase both

300 on Day 1 and after the hierarchies achieved stability (eating: -1.033 [-1.120, -0.870],

301 pMCMC<0.001; drinking: -1.047 [-1.244, -0.852], pMCMC<0.001; **Fig. 2**). There was however

302 significant interaction effects of dark/light phase and the stability of hierarchies (Day 1 vs.

303 Stable) in both eating and drinking frequency (eating: 0.399 [0.199, 0.586], pMCMC<0.001;

304 drinking: 0.400 [0.173, 0.634], pMCMC<0.001; **Fig. 2**). Mice ate and drank more frequently

305 during the light phase once hierarchies stabilized compared to Day 1.

306 At the individual level, only 5% of mice on Day 1 (0% of alpha males, 8% of sub-dominant

307 mice, 5% of subordinate mice) and 14% of mice in established hierarchies (0% of alpha males,

308 19% of sub-dominants, 13% of subordinates) ate and drank more during the light phase

309 compared to the dark phase (**Fig. S4a**). Subdominant males had a higher proportion of foraging

310 bouts in the light phase compared to subordinates on Day 1 (-8.13 [-16.09, -0.18],

311   pMCMC=0.045) and after the hierarchies were stabilized (subordinate: -5.90 [-10.90, -1.01],

312   pMCMC=0.020). Alpha males did not differ significantly from either subdominants or

313   subordinates (all pMCMC>0.062). When examining the relative frequency of eating and

314   drinking bouts over 24 hours (**Fig. S4b**), it is clear that subordinates show the most pronounced

315   morning peak of foraging and alpha males are more likely to eat consistently evenly throughout

316   the dark phase. Further, these differences are most pronounced on Day 1 of hierarchy formation

317   compared to after hierarchy stabilization.

318   We also analyzed the longest duration of inactivity in eating/drinking behavior for each mouse

319   (**Fig. 3**). For 82% (158 out of 192 mice) of all individuals, the longest quiescent period occurred

320   during the light phase. 16% (30 mice) had their longest quiescent period across dark and light

321   phases. Only 2% of all mice (4 mice) had their longest inactive period during the dark phase. On

322   both Day 1 and after hierarchies were established, alpha males had significantly shorter quiescent

323   periods in eating/drinking than both subdominant (Day 1: 159.8 [35.2, 285.5], pMCMC=0.013;

324   Stable: 79.4 [13.5,146.8], pMCMC=0.020) and subordinate mice (Day 1: 167.9 [55.0, 277.6],

325   pMCMC=0.004; Stable: 141.9 [81.6, 203.5], pMCMC<0.001). On Day 1, subdominants did not

326   differ from subordinates in the duration of the longest quiescent periods (8.5 [-68.4, 86.2],

327   pMCMC=0.823) while having a significantly shorter quiescent period than subordinates after the

328   hierarchies were established (62.3 [22.6, 101.1], pMCMC=0.002).

329

330   **Location preference and patterns of social association while foraging**

331   In each vivarium, mice could eat and drink from one of two hoppers. One was placed in the top

332   right of the vivarium and the other in the top left. We used a binomial test to see if mice showed

333   a location preference between the two dispensers. Out of 60 mice observed on Day 1, 45 mice

334   showed significant preferences for one particular food/water location; 7 animals preferred the left

335   food hopper and 38 animals preferred the right one. Among the 5 cohorts observed on Day 1, the

336   alpha males from three cohorts showed a significant location preference. 18 of the 27 non-alpha

337   males in those three cohorts preferred the same location that the alphas preferred, and 9 males

338   chose to visit the other location more often. For the 11 cohorts we observed after the social

339   hierarchies were stabilized, 96 out of 132 mice showed a location preference (left: 36, right: 60

340   mice). The alpha males of 7 stable cohorts significantly preferred one specific location, and 42

341   out of 60 non-alpha males in those 7 cohorts preferred the same location as their respective alpha

342   males did (**Fig. S5**). It is clear that animals do not grossly avoid the alpha males simply by

343   preferring food/water locations that are non-preferred by the alphas.

344   Whether animals avoid associating with the alpha male in their groups while eating or drinking

345   was more completely addressed by comparing the mean difference of association indices of

346   eating and drinking behaviors at feeding/drinking locations between alpha-other and other-other

347   relationships. Overall, associations were very low and individuals associated with the alpha male

348   at a similar rate as they did with other males (0.07 [-0.01, 0.25]; **Fig. 4a**). Next, we tested

349   whether the association strength of foraging behavior is related to the association strength of

350   agonistic interactions. Since individuals vary in their tendency to associate in agonistic

351   interactions with others, we used HWIG, a measure of the association strength of a dyadic

352   relationship corrected for the gregariousness of both individuals (Godde et al., 2013). There was

353   a significant moderate relationship between the association indices of foraging and the HWIG of

354   agonistic interaction (-0.16 [-0.27, -0.04]; **Fig. 4b**), suggesting that while eating or drinking

355   animals avoid others that they had associated frequently with in aggressive interactions.

356

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Discussion

357

358 In this study we demonstrate that alpha male mice in social hierarchies eat and drink more than

359 animals of all other ranks. Once hierarchies are stable, subdominant males also drink more

360 frequently than subordinate males. Animals of all ranks visit the food and water dispensers more

361 often during the dark phase than the light phase, though once the hierarchy is stabilized,

362 individuals increase the proportion of eating and drinking that occurs during the light phase.

363 Subordinate animals show the most pronounced temporal patterning of feeding and drinking

364 behavior with longer periods of inactivity of foraging behavior than dominant males and sharper

365 peaks in relative activity at the onset of the dark phase. Alpha males tend to eat and drink

366 consistently throughout the day. By analyzing the association strength of foraging behavior and

367 agonistic behavior, we also show that animals avoid eating or drinking with others that they have

368 exchanged aggressive interactions with rather than avoiding alpha males specifically. These

369 findings extend our previous findings where we observed alpha males living in social hierarchies

370 produce significantly more MUPs and urine daily suggesting that the increased food and water

371 intake is required to meet these metabolic demands (Lee, Khan & Curley, 2017). Overall, this

372 study supports the hypothesis that individuals living in a large group adapt their eating and

373 drinking behaviors in response to physiological needs and concurrent social dynamics.

374 Alpha males ate more frequently than other animals on the day of hierarchy formation (Day 1)

375 and on all days measured after hierarchies were established. Although we were not able to

376 directly measure the amount of food and water each mouse consumed, we show that the

377 durations of individual eating and drinking bouts across light phases is not different across social

378 ranks, suggesting that the frequency of eating and drinking is a reliable measure of the amount of

379 food and water each animal consumed. Dominant animals in a social hierarchy, especially the

380   alpha male of a group, initiate and engage in a significantly higher number of aggressive

381   interactions than relatively subordinate individuals (Sapolsky, 1993; Maruska & Fernald, 2010;

382   Williamson, Franks & Curley, 2016; Williamson, Lee & Curley, 2016) requiring high amounts

383   of metabolic energy (Haller, 1995). Moreover, Moles et al. (Moles et al., 2006) found that even

384   when dominant and subordinate male mice do not engage in physical aggression because they

385   are only allowed to exchange sensory communication via perforated barriers, dominant males

386   had a lower caloric efficiency than subordinates. This is likely because dominant animals

387   constantly signal their dominance to either females or male competitors requiring significant

388   metabolic energy investment (Desjardins, Maruniak & Bronson, 1973; Hurst & Beynon, 2004).

389   Using the same group housing environment we used in this study, we previously showed males

390   with a higher social rank invest more in producing MUPs (Lee, Khan & Curley, 2017). Taken

391   together, we suggest that maintaining dominant status in social hierarchies is energetically costly

392   and animals consume more food to meet these demands. One possible common underlying

393   mechanism linking the increased production of MUPs and feeding may be the relationship

394   between ghrelin and growth hormone (GH). Although the regulation of food intake and energy

395   balance is regulated by multiple neuropeptides, ghrelin directly promotes both food intake and

396   GH release (Gunawardane et al., 2000). In rodents, GH directly stimulates the liver to produce

397   MUPs (Sagazio, Shohreh & Salvatori, 2011; Noaín et al., 2013). Therefore, ghrelin may be

398   elevated as animals perceive their social status as dominant, thus increasing food intake as well

399   as MUP production, though this remains to be tested in future studies.

400   To our knowledge, this is the first time that the drinking frequency of all mice living in large

401   social housing has been recorded with non-stop recording for a full light/dark cycle while

402   evaluating all individuals' social status. We confirmed our hypothesis that more dominant

403   individuals in the social hierarchy drink water more frequency, as predicted from our previous

404   finding that individuals with higher social ranks produced a higher volume of urine daily (Lee,

405   Khan & Curley, 2017). Our finding that alpha males visit the water most frequently is also

406   consistent with a previous study conducted using rats living in groups (Blanchard & Blanchard,

407   1989). Using the visible burrow system of housing 4 males and 4 female rats in a large arena, the

408   alpha male in each group drank water significantly more often than the other 3 males.

409   Interestingly, we show that alpha males drink most frequently even at the onset of social housing

410   and this could suggest either that individual drinking behavior correlates with competitive ability

411   or that mice are highly capable of recognizing current social context and quickly adapt their non-

412   social behavior and physiology. We also found that subdominant individuals drank more

413   frequently than subordinates. While alpha males in hierarchies increase their drinking frequency

414   to match increased urination volume (Lee, Khan & Curley, 2017), non-alpha males require less

415   water as they inhibit scent-marking behavior. Previous studies have shown that subordinate rats

416   and mice limit their scent-mark to the edge of housing (Desjardins, Maruniak & Bronson, 1973;

417   Adams, 1976; Hou et al., 2016) to avoid conflict with dominants (Jones & Nowell, 1973). This

418   inhibition of urination could be more accentuated in subordinate males than subdominants, thus

419   subdominants show higher drinking frequency than subordinates. It is also possible that

420   subdominants may be primed to take-over alpha status and already increase their water intake in

421   readiness (Williamson, Romeo & Curley, 2017; Williamson et al., 2018).

422   Another possible explanation for the finding that subordinate mice eat and drink less frequently

423   is that they experience higher levels of social stress leading to appetite loss (Meerlo et al., 1996;

424   Becker et al., 2007). We have previously found that subordinate mice have elevated

425   corticosterone levels than alpha males only in groups with highly despotic males, suggesting that

426   differences in social stress may not account for differences in feeding behavior. Further, social

427   stress may also be related to increase rather than decrease in food intake (Bhatnagar et al., 2006;

428   Foster et al., 2006; Chuang et al., 2011) suggesting that a complex relationship between stress

429   and appetite exist in mice. Another alternative hypothesis is that subordinates avoid foraging

430   when the alpha male is actively foraging to decrease their risk of attack. However, we found that

431   foraging associations between non-alpha and alpha males were not different from those between

432   two non-alpha males suggesting that individuals did not actively avoid the alpha male

433   specifically. Consistent with this interpretation, we found that although many individuals had a

434   location preference for foraging, location preference was unrelated to the alpha male's location

435   preference in their hierarchy. Significantly, however, we did find that mice associate less

436   strongly while foraging with any individuals that they had being in aggressive interactions with.

437   Although we do not know the mechanism through which this behavioral pattern is achieved, it is

438   possible that it occurs via individuals socially monitoring those other individuals that direct

439   aggressive behavior towards them (Alanärä, Burns & Metcalfe, 2001; Deaner, Khera & Platt,

440   2005; Pannozzo et al., 2007). This finding also suggests that mice living in social hierarchies are

441   socially competent being able to recognize each mouse and flexibly adjust their behavior based

442   on specific social experiences.

443   We also show that mice visit food and water dispensers more frequently during the dark phase

444   compared to the light phase of the light cycle. This is consistent with previous findings that mice

445   are more active and intake more food during the 'active' dark phase (Ramsey et al., 2009;

446   Melhorn et al., 2010). Interestingly in the light phase, mice in stable hierarchies ate and drank

447   more frequently compared to mice in the initial phases of group housing. This suggests that as

448   groups become familiar with each other, individuals adjust the circadian patterning of foraging

449   behavior. We investigated whether these shifts in temporal dynamics were different between

450   ranks but found no difference in the proportion of time spent foraging in the light versus dark

451   phases between dominant, subdominant or subordinate mice. This finding is in contrast to some

452   other species such as fish and rats where it has been shown that subordinate individuals do

453   temporally segregate their foraging from more dominant individuals (Alanärä, Burns &

454   Metcalfe, 2001; Melhorn et al., 2010). For example, subordinate, but not dominant, rats in the

455   visible burrow system have been found to increase their meal frequency during the light phase

456   and decrease during the dark phase in established hierarchies (Melhorn et al., 2010). We did

457   however identify that the longest period of inactivity between foraging bouts was significantly

458   shorter for alpha males (mean 198 minutes) than for other males (mean 336 minutes). For the

459   vast majority of individuals, the longest period of inactivity occurs during the light phase and is

460   likely when individuals are engaged in sleep. These results suggest the possibility that dominant

461   alpha males have significantly reduced sleep, though further studies are necessary to test how

462   social status modulates the type, length and quality of sleep. Since sleep has restorative functions

463   such as the removal of toxins from the brain and boosting the immune system (Xie et al., 2013;

464   McEwen & Karatsoreos, 2015), shortened sleep pattern of alpha males may add a higher

465   allostatic load to dominants on top of their increased metabolic needs.

466

467   **Conclusions**

468   In this study we demonstrate how individual social status associates with feeding and drinking

469   behavior in social hierarchies of male mice. In combination with our lab's previous findings

470   showing the dramatic increase in MUP production and daily urination volume by alpha males,

471   we propose that maintaining alpha status in social groups is metabolically expensive and requires

472 dominant male mice to consume more food and increase water intake. This dynamically changes

473 their temporal patterning of foraging behavior and may influence the behavioral patterns of other

474 individuals in their social group. Additionally, we also show that outbred CD-1 mice are able to

475 flexibly adapt their foraging behavior based on past agonistic interactions suggesting a degree of

476 social competence. We believe these current results lay a basis for future studies examining the

477 neurobiological and physiological mechanisms connecting perception of social status and critical

478 physiological adaptions that occur during the establishment and maintenance of social

479 hierarchies.

480

481 **Ethics**

482 All experiments were conducted with approval from the Columbia University Institutional

483 Animal Care and Use Committee (IACUC Protocols: AC-AAAP5405, AC-AAAG0054).

484

485 **Data accessibility**

486 All raw data and code used in this paper are publicly available at Github

487 (https://github.com/jalapic/foraging)

488

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492

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706

Figure 1

(a) Eating and (b) drinking frequency across social ranks on the first day of group housing (Day 1) and after social hierarchies were established (Stable).
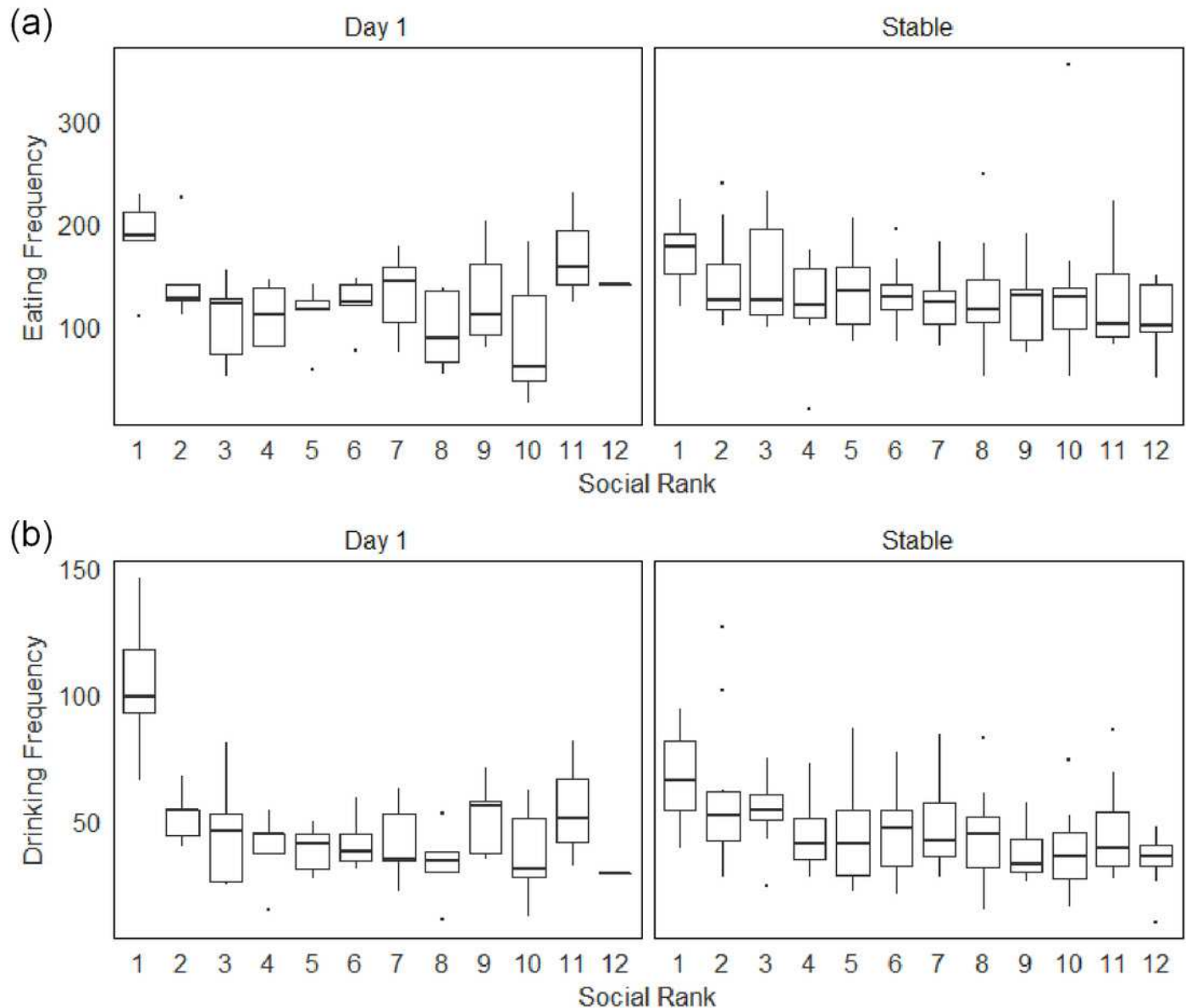
Figure 2

Total frequency of eating and drinking in 24 hours of all individuals observed on Day 1 of hierarchy formation and after stable hierarchies were established.

The first half of observation period was in dark cycle (minute 0 to 720) and the rest half was in light cycle (721 to 1440).
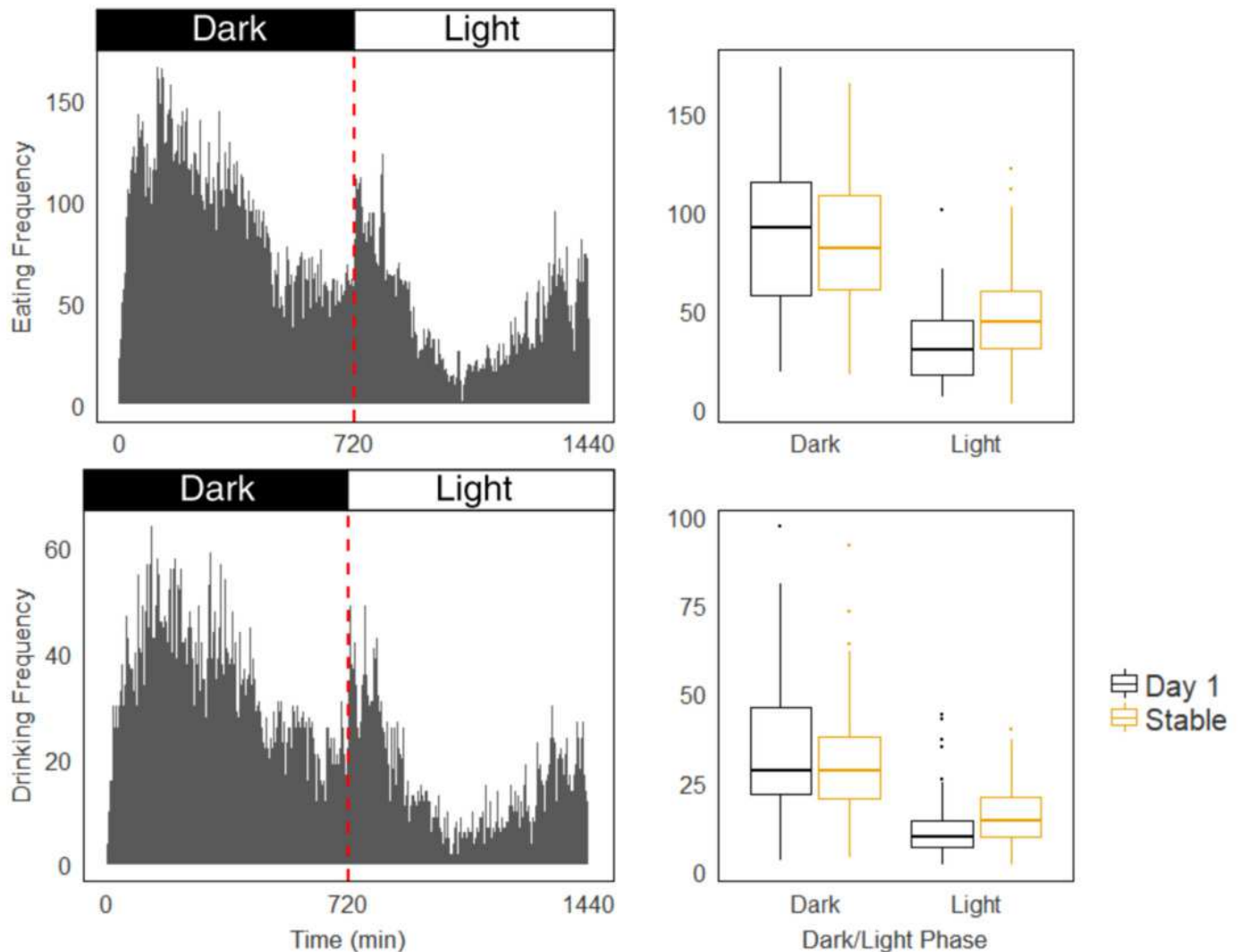
Figure 3

The effect of social status on maximum length of inactivity in eating/drinking by social status group on Day 1 and in stabilized hierarchies
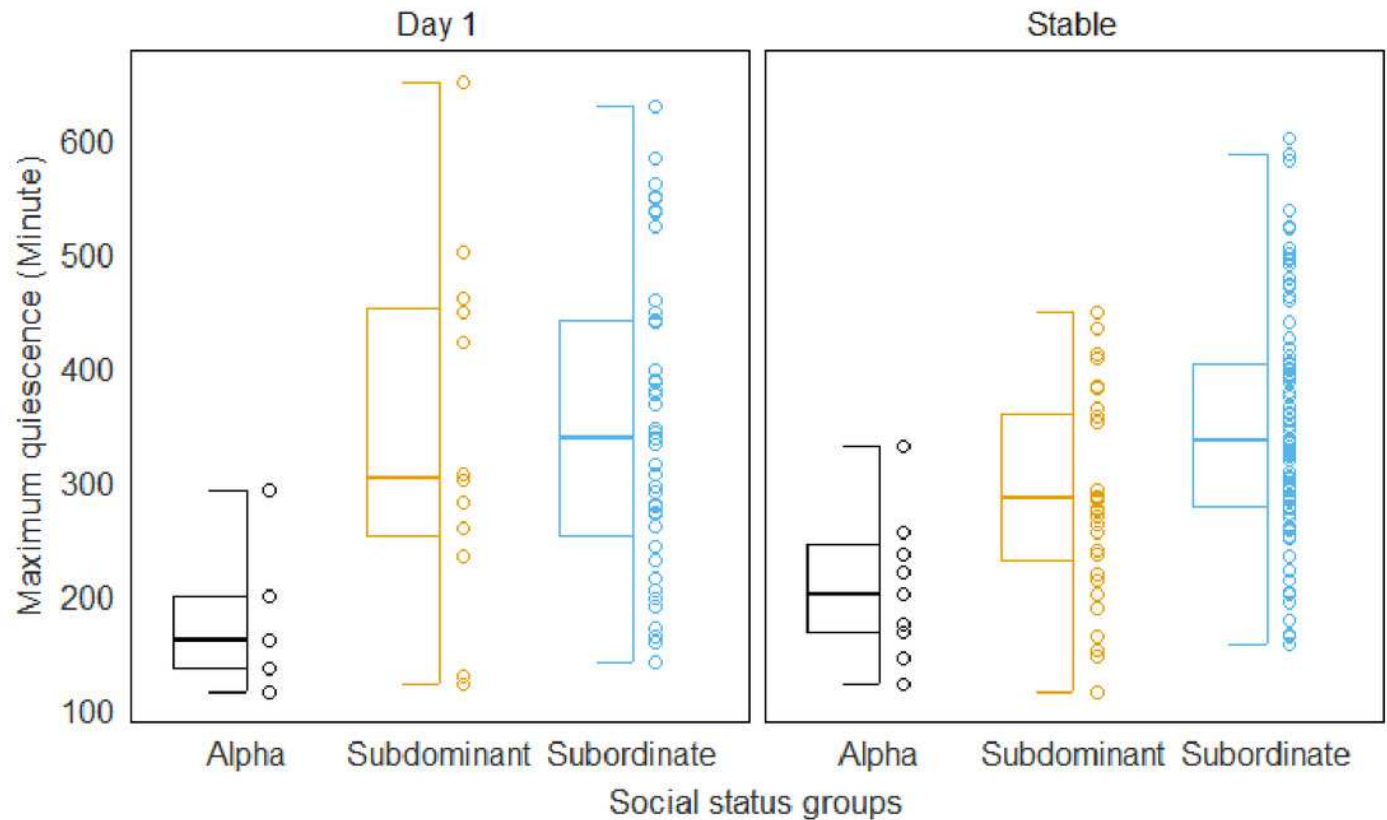
Figure 4

Association indices of dyadic relationships in eating and drinking behavior.

(a) Foraging association indices are not different between those of alpha-other and other-other relationships. Raw data points are also shown on the right side of each box plot. (b) The association strength of foraging behavior is negatively associated with the half-weight index corrected for individual gregariousness (HWIG) of agonistic interactions. The red line indicates the fitted trend line.