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

Won Lee [1] , Eilene Yang [1] , James P Curley [Corresp. 1, 2, 3]

1 Department of Psychology, Columbia University, New York, New York, United States

2 Center for Integrative Animal Behavior, Columbia University, New York, New York, United States

3 Department of Psychology, University of Texas at Austin, Austin, Texas, United States

Corresponding Author: James P Curley
Email address: curley@utexas.edu

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.

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

3 Won Lee[1], Eilene Yang[1] & James P Curley[1,2,3]

4 1 Department of Psychology, Columbia University, New York, NY, USA

5 2 Center for Integrative Animal Behavior, Columbia University, New York, NY, USA

6 3 Department of Psychology, The University of Texas at Austin, Austin, TX, USA

8 Corresponding author:

9 James P Curley[1,2,3]

11 Email address: curley@utexas.edu

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.

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 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). We further

150   confirmed stability of each social hierarchy through observation of stabilization of Glicko ratings

151   (Fig. S2) after Day 5 of group housing as well as at least three days before and after the day of

152   foraging behavior video recording. During to 1440-minute observation/video window, we coded

153   the identities of those animals that drank or ate at the particular hopper (left/right side of a

154   vivarium) during each minute bin. These data provided a measure of the number of minutes

155   engaged in and the circadian rhythmicity of feeding and drinking behavior for each animal across

156   a single dark/light cycle of a 24-hour period. However, as it is possible that individuals may spend

157   different amount of time eating or drinking per visit dependent on their rank or the day we further

158   selected 603 eating and drinking visits (1.2% of eating bouts, 2.1% of drinking bouts, 3.3% of total

159   visits) across all groups for duration analysis. We sampled data probabilistically with the

160   representation of each animal in the duration dataset being weighted according to their frequency

161   of eating and drinking.

162   Inter-rater reliability: Each video was coded by 2-3 observers from a pool of 11 trained coders.

163   Observers showed a high degree of inter-rater reliability (unweighted Cohen's kappa = 0.805,

164   p<0.001) (Jacob Cohen, 1960; Lombard, Snyder-Duch & Bracken, 2002; Gamer, Lemon & Singh,

165   2012).

166

167   **Statistical analysis**

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

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

170   foraging and agonistic behaviors are described.

171   Analysis of agonistic behavior data

172   With agonistic interaction data, we tested the linearity and stability of each social hierarchy by

173   calculating Landau's h-value and triangle transitivity (*ttri*), and directional consistency (DC) and

174   associated p-values derived from 10,000 Monte-Carlo randomizations (De Vries, 1995; McDonald

175   & Shizuka, 2012) using the compete R package (Curley, 2016a) as well as by verifying the

176   stabilization of individual Glicko ratings. Values and associated significance tests were determined

177   for observational data up to the end of each day and over all observations. Individual ranks were

178   determined through calculation of Glicko Ratings using the R package PlayerRatings (Stephenson

179   & Sonas, 2012). In the Glicko Rating system (Glickman, 1999; Williamson, Lee & Curley, 2016),

180   animals are initially assigned with 2,200 points then gain or lose points based on the number of

181   wins and losses relative to the difference in ratings between themselves and their opponent (see

182   Williamson et al. (2016) for a more detailed description of the calculations). After each contest in

183   each group the Glicko ratings of all animals in that group was continuously updated. Based on our

184   behavioral observation of social hierarchy dynamics, we further categorized individuals into three

185   social status groups using Glicko ratings. An alpha male holds the highest Glicko rating (social

186   rank 1) in the hierarchy. Males in the subdominant social group are those with Glicko ratings

187   higher than or equal to initial points, 2,200 but not the highest rating. The remainder of the males

188   in the hierarchy that hold Glicko ratings lower than 2,200 are in the subordinate social group. The

189   despotism of each alpha male was calculated using the compete R package (Curley, 2016a) by

190   determining the proportion of all wins by alpha to all agonistic interaction (see (Williamson, Lee

191   & Curley, 2016) for details) that occurred in each group up to the day of video recording.

192   Associations between body weight measured on Day 1 of group housing and social rank were

193   tested for each hierarchy using Spearman Rank correlation tests.

194   Analysis of frequency and bout duration data of eating and drinking

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

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

197   MCMCglmm R package (Hadfield, 2010). MCMC is a reliable method to fit data with non-

198   Gaussian distribution and is particularly powerful for accounting for overdispersion of Poisson

199   distributed data (Hadfield, 2010). As our eating and drinking frequency data follows Poisson

200   distribution with overdispersion, we adopted MCMC method for statistical analysis. We specified

201   a Poisson family for the dependent variables of eating and drinking frequency of each individual

202   (count data) and Gaussian family for duration of eating and drinking (continuous data). A default

203   uninformative inverse gamma prior in the MCMCglmm library was used. We fitted all models

204   with cohort ID as random slopes and intercepts in each model. We tested the effect of following

205   fixed factors on eating and drinking frequency in each model with 1,000,000 iterations, 5,000 burn-

206   in, and a thinning interval of 100; (i) the individual Glicko rank and despotism of each group on

207   Day 1 and up to the day of eating/drinking video recording, (ii) individuals' social status group

208   (alpha, subdominant, subordinate), (iii) dark/light phase and whether the hierarchies have been

209   established (Day 1 vs. Stable) and an interaction between them. We then tested whether social

210   status group as a fixed factor had effects on the following dependent variables in each model with

211   1,000,000 iterations, 5,000 burn-in, and a thinning interval of 20; (i) the percentage of visits made

212   by individuals in the light phase to total visits (visits in light cycle/total visits in dark/light

213   cycles*100), (ii) the maximum period of quiescence / inactivity of eating and drinking. With eating

214   and drinking bout duration data, we tested if the bout duration of eating and drinking were

215   associated with the following fixed factors with 10,000,000 interactions, 100,000 burn-in, and a

216   thinning interval of 50; (i) the individual Glicko social rank on the day, (ii) despotism of each

217   group, and (iii) whether the hierarchies were stabilized. In all models, we confirmed that

218 convergence of the chains was attained by visually inspecting the MCMCglmm object plots,

219 setting thinning intervals so that autocorrelation between samples were less than 0.10, and using a

220 Gelman-Rubin test in the coda R package (Plummer et al., 2016). We tested the interactions among

221 fixed effects and only included the interaction effects if the model with interaction terms yielded

222 the lowest deviance information criterion (DIC). All interaction terms among fixed variables were

223 tested and only selected when the model with interaction terms had significantly lowest DIC

224 values. A two-tailed exact binomial test was used to test whether each mouse showed a location

225 preference (right versus left) between the two food/water hoppers.

226 Association patterns in foraging behavior and aggressive behavior

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

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

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

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

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

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

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

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

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

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

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

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

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

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

241   association strength of agonistic interactions.

242

243   **Results**

244   **Social hierarchy characteristics**

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

246   (IQR) = [0.67-0.81], all p<0.001; *ttri* = 0.87 [0.83-0.93], all p<0.001; DC = 0.86 [0.84 – 0.92], all

247   p<0.001). All 11 cohorts videoed after Day 6 had formed a stable linear hierarchy by the day of

248   video recording (h' = 0.71 [0.64 – 0.80], all p<0.05; ttri 0.91 [0.88 – 0.97] all p<0.05; DC = 0.91

249   [0.88 – 0.93] all p<0.001, stabilized individual Glicko ratings shown in Fig. S2). We were able to

250   identify the final rank of all animals in each hierarchy using the Glicko ratings method as well as

251   identify individual ranks on the day of eating/drinking video recording. For the 11 cohorts videoed

252   on day 6 or later, individual ranks on the day of video recording correlated highly with final rank

253   at the end of group housing indicating high stability (rhos = 0.92 [0.88-0.95], all p<0.01). In 9/11

254   groups the alpha male on the day of video recording was the same alpha male at the end of group

255   housing. Although in the other two groups the final alpha male was ranked 2 and 3 respectively

256   on the days of video recording, these two alpha males maintained their alpha status for at least 13

257   days after the day of video recording (Cohort A and E in Fig. S2). In the other two groups the final

258   alpha male was ranked 2 and 3 respectively on the days of video recording. In the 5 groups recorded

259   on day 1, 3/5 males remained the alpha male throughout the study and the other two males became

260   2nd and 3rd ranked in their respective groups (Fig. S2). The degree of alpha male despotism during

261   the whole housing period varied across groups (0.56 [0.38-0.63]). For social groups videoed after

262   Day 6, alpha-male despotism ranged between 0.36-0.85 with a median and IQR of 0.50 [0.42-

263   0.61] on the day of feeding/drinking video recording. Across all cohorts, initial body weight did

264   not predict social rank (Spearman's rank correlation tests, all cohorts p>0.68).

265

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

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

268   housing, eating frequency did not have linear relationship with social rank (determined by

269   individual Glicko ratings based on agonistic behavioral data collected on Day 1) (fixed effect

270   mean= -0.022, 95% Bayesian credibility interval (BCI)= [-0.047, 0.006], pMCMC=0.099, **Fig.**

271   **1a**) or despotism (0.037 [-0.015, 0.087], pMCMC=0.099). Mice with more dominant social

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

273   individuals from groups with higher despotism drank water more frequently (0.032 [0.007,

274   0.054], pMCMC=0.012). In established stable social hierarchies, more dominant individuals ate

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

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

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

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

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

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

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

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

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

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

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

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

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

288   drinking: -0.749 [-1.151, -0.356], pMCMC<0.001; **Fig. S3a**) and subordinate groups (eating: -

289   0.483 [-0.788, -0.150], pMCMC=0.004; drinking: -0.984 [-1.318, -0.606], pMCMC<0.001).

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

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

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

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

294   pMCMC=0.024; **Fig. S3b**) and subordinate males (eating: -0.350 [-0.541, -0.170],

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

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

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

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

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

300   (eating: pMCMC=0.106; drinking: pMCMC=0.913; **Fig. S4**), but the bout duration of eating and

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

302   [3.486 – 20.856], pMCMC=0.009; drinking: 2.922s [0.730 – 4.986], pMCMC=0.005. The

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

304   [17.3s-50.9s] after Day 5. The average bout duration of drinking across all ranks was 4.7s [3.2s-

305   6.4s] on Day 1 and 7.4s [4.5s-9.9s] after Day 5). This finding suggests that the observed increase

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

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

308

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

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

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

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

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

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

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

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

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

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

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

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

321 19% of sub-dominants, 13% of subordinates) ate and drank more during the light phase

322 compared to the dark phase (**Fig. S5a**). Subdominant males had a higher proportion of foraging

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

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

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

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

327 drinking bouts over 24 hours (**Fig. S5b**), it is clear that subordinates show the most pronounced

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

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

330 compared to after hierarchy stabilization.

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

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

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

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

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

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

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

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

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

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

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

342

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

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

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

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

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

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

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

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

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

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

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

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

355   males did (**Fig. S6**). It is clear that animals do not grossly avoid the alpha males simply by

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

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

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

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

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

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

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

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

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

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

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

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

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

369

370   **Discussion**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

416 individuals in the social hierarchy drink water more frequently, as predicted from our previous

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

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

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

420 1989). Using the visible burrow system of housing 4 males and 4 female rats in a large arena, the

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

453   2005; Pannozzo et al., 2007). This finding also suggests that mice living in social hierarchies are

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

455   on specific social experiences.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

479

480   **Conclusions**

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

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

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

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

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

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

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

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

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

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

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

492 hierarchies.

493

494 **Data accessibility**

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

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

497

498 **Acknowledgments**

499 We thank Dr. Rae Silver and Dr. Frances Champagne for advice and suggestions in writing the

500 manuscript and Curley Lab students for help with behavioral observations.

501

References

Adams DB. 1976. The Relation of Scent-Marking, Olfactory Investigation, and Specific Postures
  in the Isolation-Induced Fighting of Rats. *Behaviour* 56:286–297. DOI:
  10.1163/156853976X00064.

Alanärä A., Burns MD., Metcalfe NB. 2001. Intraspecific resource partitioning in brown trout:
  the temporal distribution of foraging is determined by social rank. *Journal of Animal
  Ecology* 70:980–986. DOI: 10.1046/j.0021-8790.2001.00550.x.

Banks EM., Wood-Gush DG., Hughes BO., Mankovich NJ. 1979. Social rank and priority of
  access to resources in domestic fowl. *Behavioural Processes* 4:197–209. DOI:
  10.1016/0376-6357(79)90001-9.

Barroso FG., Alados CL., Boza J. 2000. Social hierarchy in the domestic goat: effect on food
  habits and production. *Applied Animal Behaviour Science* 69:35–53. DOI:
  10.1016/S0168-1591(00)00113-1.

Becker C., Zeau B., Rivat C., Blugeot A., Hamon M., Benoliel J-J. 2007. Repeated social defeat-
  induced depression-like behavioral and biological alterations in rats: involvement of
  cholecystokinin. *Molecular Psychiatry* 13:1079–1092. DOI: 10.1038/sj.mp.4002097.

Bhatnagar S., Vining C., Iyer V., Kinni V. 2006. Changes in Hypothalamic-Pituitary-Adrenal
  Function, Body Temperature, Body Weight and Food Intake with Repeated Social Stress
  Exposure in Rats. *Journal of Neuroendocrinology* 18:13–24. DOI: 10.1111/j.1365-
  2826.2005.01375.x.

Biro PA., Stamps JA. 2010. Do consistent individual differences in metabolic rate promote
  consistent individual differences in behavior? *Trends in Ecology & Evolution* 25:653–
  659. DOI: 10.1016/j.tree.2010.08.003.

525 Blanchard RJ., Blanchard DC. 1989. Antipredator defensive behaviors in a visible burrow

526   system. *Journal of Comparative Psychology* 103:70–82. DOI: 10.1037/0735-

527   7036.103.1.70.

528 Bonanni R., Cafazzo S., Fantini C., Pontier D., Natoli E. 2007. Feeding-order in an urban feral

529   domestic cat colony: relationship to dominance rank, sex and age. *Animal Behaviour*

530   74:1369–1379. DOI: 10.1016/j.anbehav.2007.02.029.

531 Bürkner P-C. 2018. *brms: Bayesian Regression Models using Stan*.

532 Chase ID. 1982. Dynamics of hierarchy formation: the sequential development of dominance

533   relationships. *Behaviour* 80:218–239.

534 Christian DP. 1980. Vegetative Cover, Water Resources, and Microdistributional Patterns in a

535   Desert Rodent Community. *Journal of Animal Ecology* 49:807–816. DOI: 10.2307/4228.

536 Chuang J-C., Perello M., Sakata I., Osborne-Lawrence S., Savitt JM., Lutter M., Zigman JM.

537   2011. Ghrelin mediates stress-induced food-reward behavior in mice. *The Journal of*

538   *Clinical Investigation* 121:2684–2692. DOI: 10.1172/JCI57660.

539 Curley JP. 2016a. *compete: Organizing and Analyzing Social Dominance Hierarchy Data*.

540 Curley JP. 2016b. Temporal pairwise-correlation analysis provides empirical support for

541   attention hierarchies in mice. *Biology Letters* 12:20160192. DOI:

542   10.1098/rsbl.2016.0192.

543 De Vries H. 1995. An improved test of linearity in dominance hierarchies containing unknown or

544   tied relationships. *Animal Behaviour* 50:1375–1389.

545 Deaner RO., Khera AV., Platt ML. 2005. Monkeys Pay Per View: Adaptive Valuation of Social

546   Images by Rhesus Macaques. *Current Biology* 15:543–548. DOI:

547   10.1016/j.cub.2005.01.044.

548 Desjardins JK., Hofmann HA., Fernald RD. 2012. Social Context Influences Aggressive and

549   Courtship Behavior in a Cichlid Fish. *PLoS One; San Francisco* 7:e32781. DOI:

550   http://dx.doi.org.ezproxy.cul.columbia.edu/10.1371/journal.pone.0032781.

551 Desjardins C., Maruniak JA., Bronson FH. 1973. Social rank in house mice: differentiation

552   revealed by ultraviolet visualization of urinary marking patterns. *Science (New York,*

553   *N.Y.)* 182:939–941.

554 Deutsch JC., Lee PC. 1991. Dominance and feeding competition in captive rhesus monkeys.

555   *International Journal of Primatology* 12:615–628. DOI: 10.1007/BF02547673.

556 Drews C. 1993. The concept and definition of dominance in animal behaviour. *Behaviour*

557   125:283–313.

558 Drickamer LC. 1995. Rates of urine excretion by house mouse (Mus domesticus): Differences by

559   age, sex, social status, and reproductive condition. *Journal of Chemical Ecology*

560   21:1481–1493. DOI: 10.1007/BF02035147.

561 Ekman JB., Lilliendahl K. 1993. Using priority to food access: fattening strategies in dominance-

562   structured willow tit (Parus montanus) flocks. *Behavioral Ecology* 4:232–238. DOI:

563   10.1093/beheco/4.3.232.

564 Farr L., Andrews RV. 1978. Rank-associated differences in metabolic rates and locomotor

565   activity of dominant and subordinate Peromyscus maniculatus. *Comparative*

566   *Biochemistry and Physiology Part A: Physiology* 61:401–406. DOI: 10.1016/0300-

567   9629(78)90054-3.

568 Foster MT., Solomon MB., Huhman KL., Bartness TJ. 2006. Social defeat increases food intake,

569   body mass, and adiposity in Syrian hamsters. *American Journal of Physiology-*

570   *Regulatory, Integrative and Comparative Physiology* 290:R1284–R1293. DOI:

571   10.1152/ajpregu.00437.2005.

572 Gamer M., Lemon J., Singh IFP. 2012. *irr: Various Coefficients of Interrater Reliability and*

573   *Agreement*.

574 Glickman ME. 1999. Parameter estimation in large dynamic paired comparison experiments.

575   *Journal of the Royal Statistical Society: Series C (Applied Statistics)* 48:377–394.

576 Godde S., Humbert L., Côté SD., Réale D., Whitehead H. 2013. Correcting for the impact of

577   gregariousness in social network analyses. *Animal Behaviour* 85:553–558. DOI:

578   10.1016/j.anbehav.2012.12.010.

579 Gosling LM., Roberts SC., Thornton EA., Andrew MJ. 2000. Life history costs of olfactory

580   status signalling in mice. *Behavioral Ecology and Sociobiology* 48:328–332.

581 Gunawardane K., Krarup Hansen T., Sandahl Christiansen J., Lunde Jorgensen JO. 2000.

582   Normal Physiology of Growth Hormone in Adults. In: De Groot LJ, Chrousos G, Dungan

583   K, Feingold KR, Grossman A, Hershman JM, Koch C, Korbonits M, McLachlan R, New

584   M, Purnell J, Rebar R, Singer F, Vinik A eds. *Endotext*. South Dartmouth (MA):

585   MDText.com, Inc.,.

586 Hadfield JD. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The

587   MCMCglmm R Package | Hadfield | Journal of Statistical Software. DOI:

588   10.18637/jss.v033.i02.

589 Haller J. 1995. Biochemical background for an analysis of cost-benefit interrelations in

590   aggression. *Neuroscience & Biobehavioral Reviews* 19:599–604. DOI: 10.1016/0149-

591   7634(95)00053-4.

592   Herberholz J., McCurdy C., Edwards DH. 2007. Direct Benefits of Social Dominance in Juvenile

593   Crayfish. *The Biological Bulletin* 213:21–27. DOI: 10.2307/25066615.

594   Hogstad O. 1987. It Is Expensive to Be Dominant. *The Auk* 104:333–336.

595   Hou XH., Hyun M., Taranda J., Huang KW., Todd E., Feng D., Atwater E., Croney D., Zeidel

596   ML., Osten P., Sabatini BL. 2016. Central control circuit for context-dependent

597   micturition. *Cell* 167:73-86.e12. DOI: 10.1016/j.cell.2016.08.073.

598   Hurst JL., Beynon RJ. 2004. Scent wars: the chemobiology of competitive signalling in mice.

599   *Bioessays* 26:1288–1298.

600   Jacob Cohen 1960. A Coefficient of Agreement for Nominal Scales. *Educational and*

601   *Psychological Measurement* 20:37–46. DOI: 10.1177/001316446002000104.

602   Jones RB., Nowell NW. 1973. Aversive and aggression-promoting properties of urine from

603   dominant and subordinate male mice. *Animal Learning & Behavior* 1:207–210. DOI:

604   10.3758/BF03199075.

605   King AJ., Clark FE., Cowlishaw G. 2011. The dining etiquette of desert baboons: the roles of

606   social bonds, kinship, and dominance in co-feeding networks. *American Journal of*

607   *Primatology* 73:768–774. DOI: 10.1002/ajp.20918.

608   Lee W., Khan A., Curley JP. 2017. Major urinary protein levels are associated with social status

609   and context in mouse social hierarchies. *Proc. R. Soc. B* 284:20171570. DOI:

610   10.1098/rspb.2017.1570.

611   Lombard M., Snyder-Duch J., Bracken CC. 2002. Content Analysis in Mass Communication:

612   Assessment and Reporting of Intercoder Reliability. *Human Communication Research*

613   28:587–604. DOI: 10.1111/j.1468-2958.2002.tb00826.x.

614   Maruska KP., Fernald RD. 2010. Behavioral and physiological plasticity: rapid changes during

615   social ascent in an African cichlid fish. *Hormones and behavior* 58:230–240.

616   McDonald DB., Shizuka D. 2012. Comparative transitive and temporal orderliness in dominance

617   networks. *Behavioral Ecology*:ars192.

618   McEwen BS., Karatsoreos IN. 2015. Sleep Deprivation and Circadian Disruption: Stress,

619   Allostasis, and Allostatic Load. *Sleep Medicine Clinics* 10:1–10. DOI:

620   10.1016/j.jsmc.2014.11.007.

621   Meerlo P., Overkamp GJF., Daan S., Hoofdakker RH van den., Koolhaas JM. 1996. Changes in

622   Behaviour and Body Weight Following a Single or Double Social Defeat in Rats. *Stress*

623   1:21–32. DOI: 10.3109/10253899609001093.

624   Melhorn SJ., Krause EG., Scott KA., Mooney MR., Johnson JD., Woods SC., Sakai RR. 2010.

625   Meal patterns and hypothalamic NPY expression during chronic social stress and

626   recovery. *American Journal of Physiology - Regulatory, Integrative and Comparative*

627   *Physiology* 299:R813–R822. DOI: 10.1152/ajpregu.00820.2009.

628   Moles A., Bartolomucci A., Garbugino L., Conti R., Caprioli A., Coccurello R., Rizzi R., Ciani

629   B., D'Amato FR. 2006. Psychosocial stress affects energy balance in mice: Modulation

630   by social status. *Psychoneuroendocrinology* 31:623–633. DOI:

631   10.1016/j.psyneuen.2006.01.004.

632   Montero D., Lalumera G., Izquierdo MS., Caballero MJ., Saroglia M., Tort L. 2009.

633   Establishment of dominance relationships in gilthead sea bream Sparus aurata juveniles

634   during feeding: effects on feeding behaviour, feed utilization and fish health. *Journal of*

635   *Fish Biology* 74:790–805. DOI: 10.1111/j.1095-8649.2008.02161.x.

636 Naud A., Chailleux E., Kestens Y., Bret C., Desjardins D., Petit O., Ngoubangoye B., Sueur C.

637   2016. Relations between Spatial Distribution, Social Affiliations and Dominance

638   Hierarchy in a Semi-Free Mandrill Population. *Frontiers in Psychology* 7. DOI:

639   10.3389/fpsyg.2016.00612.

640 Nelson AC., Cunningham CB., Ruff JS., Potts WK. 2015. Protein pheromone expression levels

641   predict and respond to the formation of social dominance networks. *Journal of*

642   *Evolutionary Biology* 28:1213–1224. DOI: 10.1111/jeb.12643.

643 Noaín D., Pérez-Millán MI., Bello EP., Luque GM., Cordero RC., Gelman DM., Peper M.,

644   Tornadu IG., Low MJ., Becú-Villalobos D., others 2013. Central dopamine D2 receptors

645   regulate growth-hormone-dependent body growth and pheromone signaling to

646   conspecific males. *The Journal of Neuroscience* 33:5834–5842.

647 Olofsson J. 1999. Competition for Total Mixed Diets Fed for Ad Libitum Intake Using One or

648   Four Cows per Feeding Station. *Journal of Dairy Science* 82:69–79. DOI:

649   10.3168/jds.S0022-0302(99)75210-0.

650 Pannozzo PL., Phillips KA., Haas ME., Mintz EM. 2007. Social Monitoring Reflects Dominance

651   Relationships in a Small Captive Group of Brown Capuchin Monkeys (Cebus apella).

652   *Ethology* 113:881–888. DOI: 10.1111/j.1439-0310.2007.01392.x.

653 Plummer M., Best N., Cowles K., Vines K., Sarkar D., Bates D., Almond R., details AM coda

654   author. 2016. *coda: Output Analysis and Diagnostics for MCMC.*

655 R Core Team. 2017. *R: A language and environment for statistical computing.* Vienna, Austria:

656   R Foundation for Statistical Computing.

657 Ramsey KM., Yoshino J., Brace CS., Abrassart D., Kobayashi Y., Marcheva B., Hong H-K.,

658   Chong JL., Buhr ED., Lee C., Takahashi JS., Imai S., Bass J. 2009. Circadian Clock

659   Feedback Cycle Through NAMPT-Mediated NAD+ Biosynthesis. *Science* 324:651–654.

660   DOI: 10.1126/science.1171641.

661 Razgour O., Korine C., Saltz D. 2011. Does interspecific competition drive patterns of habitat

662   use in desert bat communities? *Oecologia* 167:493–502. DOI: 10.1007/s00442-011-1995-

663   z.

664 Robbins MM. 2008. Feeding Competition and Agonistic Relationships Among Bwindi

665   <Emphasis Type="Italic">Gorilla beringei</Emphasis>. *International Journal of*

666   *Primatology* 29:999. DOI: 10.1007/s10764-008-9275-4.

667 Sagazio A., Shohreh R., Salvatori R. 2011. Effects of GH deficiency and GH replacement on

668   inter-male aggressiveness in mice. *Growth Hormone & IGF Research* 21:76–80.

669 Saito C. 1996. Dominance and feeding success in female Japanese macaques,Macaca fuscata:

670   effects of food patch size and inter-patch distance. *Animal Behaviour* 51:967–980. DOI:

671   10.1006/anbe.1996.0100.

672 Sapolsky RM. 1993. The physiology of dominance in stable versus unstable social hierarchies.

673   In: Mason WA, Mendoza SP eds. *Primate social conflict*. Albany, NY, US: State

674   University of New York Press, 171–204.

675 Sloman KA., Gilmour KM., Taylor AC., Metcalfe NB. 2000. Physiological effects of dominance

676   hierarchies within groups of brown trout, Salmo trutta, held under simulated natural

677   conditions. *Fish Physiology and Biochemistry* 22:11–20. DOI:

678   10.1023/A:1007837400713.

679 So N., Franks B., Lim S., Curley JP. 2015. A social network approach reveals associations

680   between mouse social dominance and brain gene expression. *PLoS ONE* 10:e0134509.

681   DOI: 10.1371/journal.pone.0134509.

682   Stephenson A., Sonas J. 2012. *PlayerRatings: Dynamic updating methods for player ratings*

683   *estimation*.

684   Sterck EHM., Steenbeek R. 1997. Female Dominance Relationships and Food Competition in

685   the Sympatric Thomas Langur and Long-Tailed Macaque. *Behaviour* 134:749–774. DOI:

686   10.1163/156853997X00052.

687   Stricklin WR., Gonyou HW. 1981. Dominance and eating behavior of beef cattle fed from a

688   single stall. *Applied Animal Ethology* 7:135–140. DOI: 10.1016/0304-3762(81)90091-2.

689   Vogel ER. 2005. Rank differences in energy intake rates in white-faced capuchin monkeys,

690   Cebus capucinus: the effects of contest competition. *Behavioral Ecology and*

691   *Sociobiology* 58:333–344. DOI: 10.1007/s00265-005-0960-4.

692   Whitehead H. 2008. *Analyzing animal societies : quantitative methods for vertebrate social*

693   *analysis*. Chicago: University of Chicago Press.

694   Whitten PL. 1983. Diet and dominance among female vervet monkeys (Cercopithecus aethiops).

695   *American Journal of Primatology* 5:139–159. DOI: 10.1002/ajp.1350050205.

696   Williamson CM., Franks B., Curley JP. 2016. Mouse social network dynamics and community

697   structure are associated with plasticity-related brain gene expression. *Frontiers in*

698   *Behavioral Neuroscience*:152. DOI: 10.3389/fnbeh.2016.00152.

699   Williamson CM., Klein IS., Lee W., Curley JP. 2018. Immediate early gene activation

700   throughout the brain is associated with dynamic changes in social context.

701   *bioRxiv*:275495. DOI: 10.1101/275495.

702   Williamson CM., Lee W., Curley JP. 2016. Temporal dynamics of social hierarchy formation

703   and maintenance in male mice. *Animal Behaviour* 115:259–272. DOI:

704   10.1016/j.anbehav.2016.03.004.

705   Williamson CM., Romeo RD., Curley JP. 2017. Dynamic changes in social dominance and

706   mPOA GnRH expression in male mice following social opportunity. *Hormones and*

707   *Behavior* 87:80–88. DOI: 10.1016/j.yhbeh.2016.11.001.

708   Wood SK., Walker HE., Valentino RJ., Bhatnagar S. 2010. Individual differences in reactivity to

709   social stress predict susceptibility and resilience to a depressive phenotype: role of

710   corticotropin-releasing factor. *Endocrinology* 151:1795–1805.

711   Xie L., Kang H., Xu Q., Chen MJ., Liao Y., Thiyagarajan M., O'Donnell J., Christensen DJ.,

712   Nicholson C., Iliff JJ., Takano T., Deane R., Nedergaard M. 2013. Sleep Drives

713   Metabolite Clearance from the Adult Brain. *Science* 342:373–377. DOI:

714   10.1126/science.1241224.

715

Figure 1

Frequency of bouts of (a) Eating and (b) drinking on the day of video recording across social ranks on the first day of group housing (Day 1) and after social hierarchies were established (Stable).

Social ranks were determined by individual Glicko ratings based on agonistic behavioral data collected until the day of the video recording. Boxplots show median (horizontal bars), interquartile ranges (boxes) and 95% confidence intervals (whiskers).
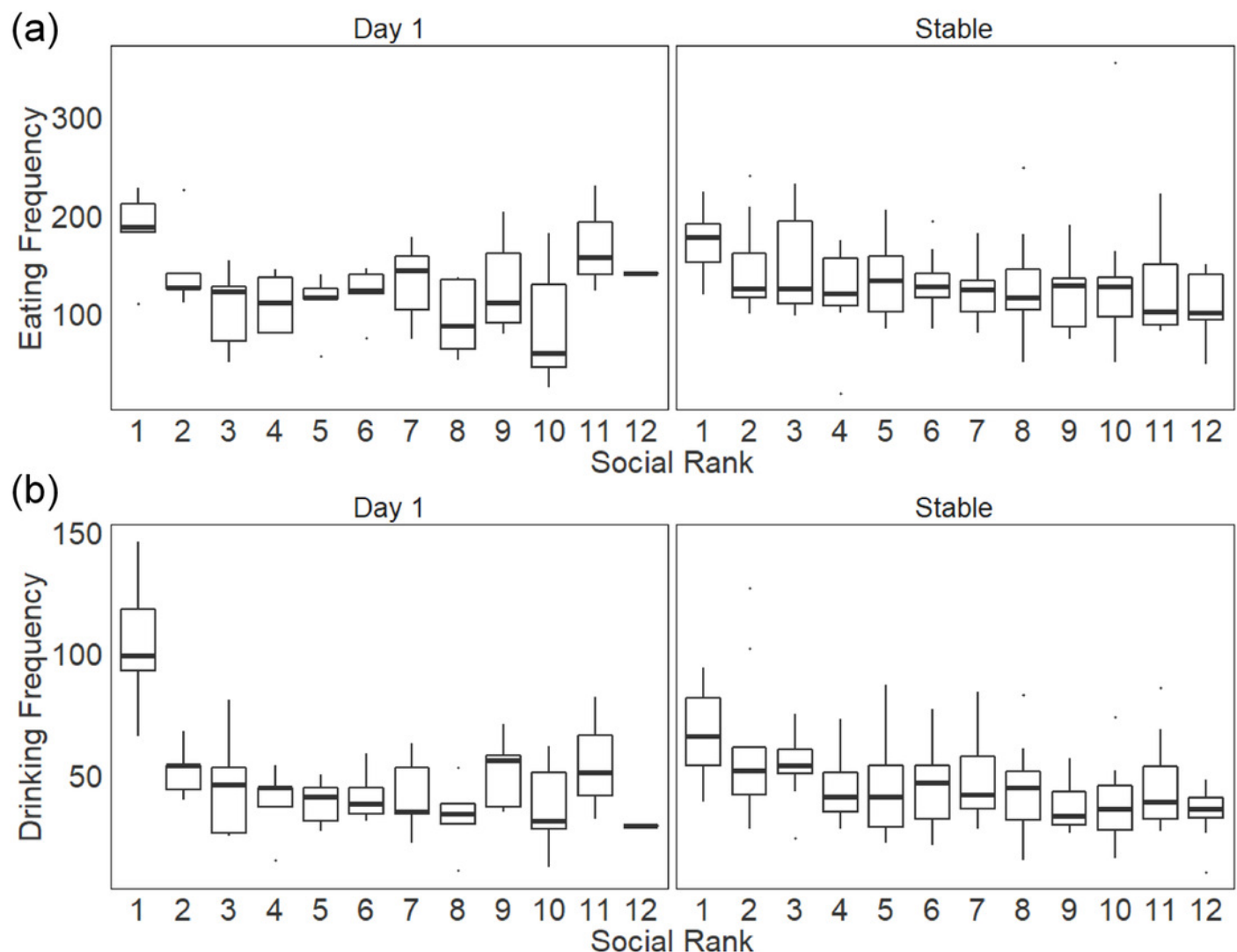
Figure 2

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.

(a, c)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). Mice eat and drink more frequently in the dark cycle both on Day 1 and after the hierarchies are established. (b, d)There was a significant interaction effect between dark/light phases and stability of hierarchies on eating and drinking frequency. Boxplots show median (horizontal bars), IQR (boxes) and 95% CI (whiskers).
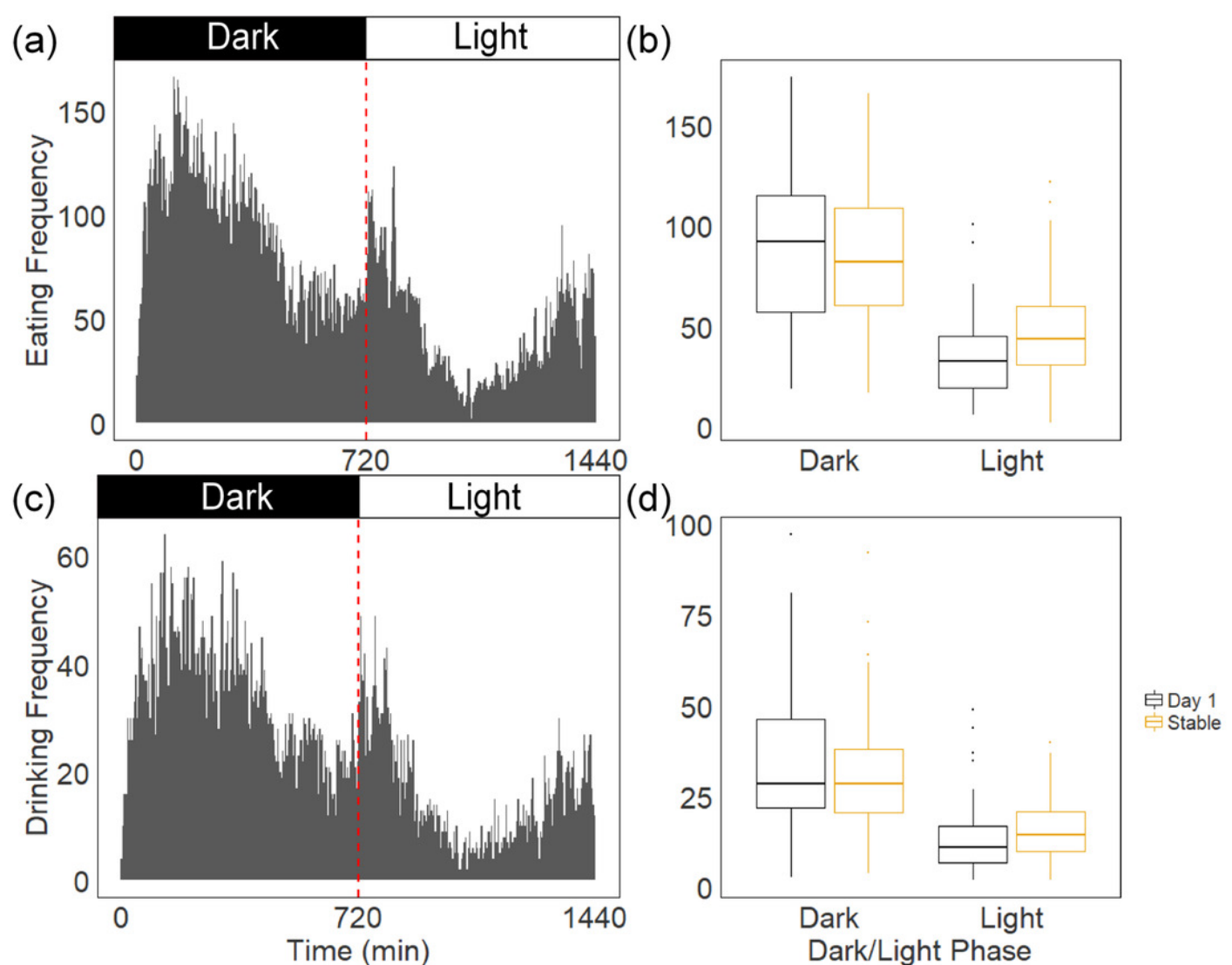
Figure 3

The effect of social status on maximum length of inactivity (quiescence) in eating and drinking by social status group (a) on Day 1 and (b) in stabilized hierarchies.

Boxplots show median (horizontal bars), IQR (boxes) and 95% CI (whiskers). Raw data points of each group are also shown on the right side of each box plot. Significant differences between groups are shown; *pMCMC<0.05, **pMCMC<0.01, ***pMCMC<0.001.
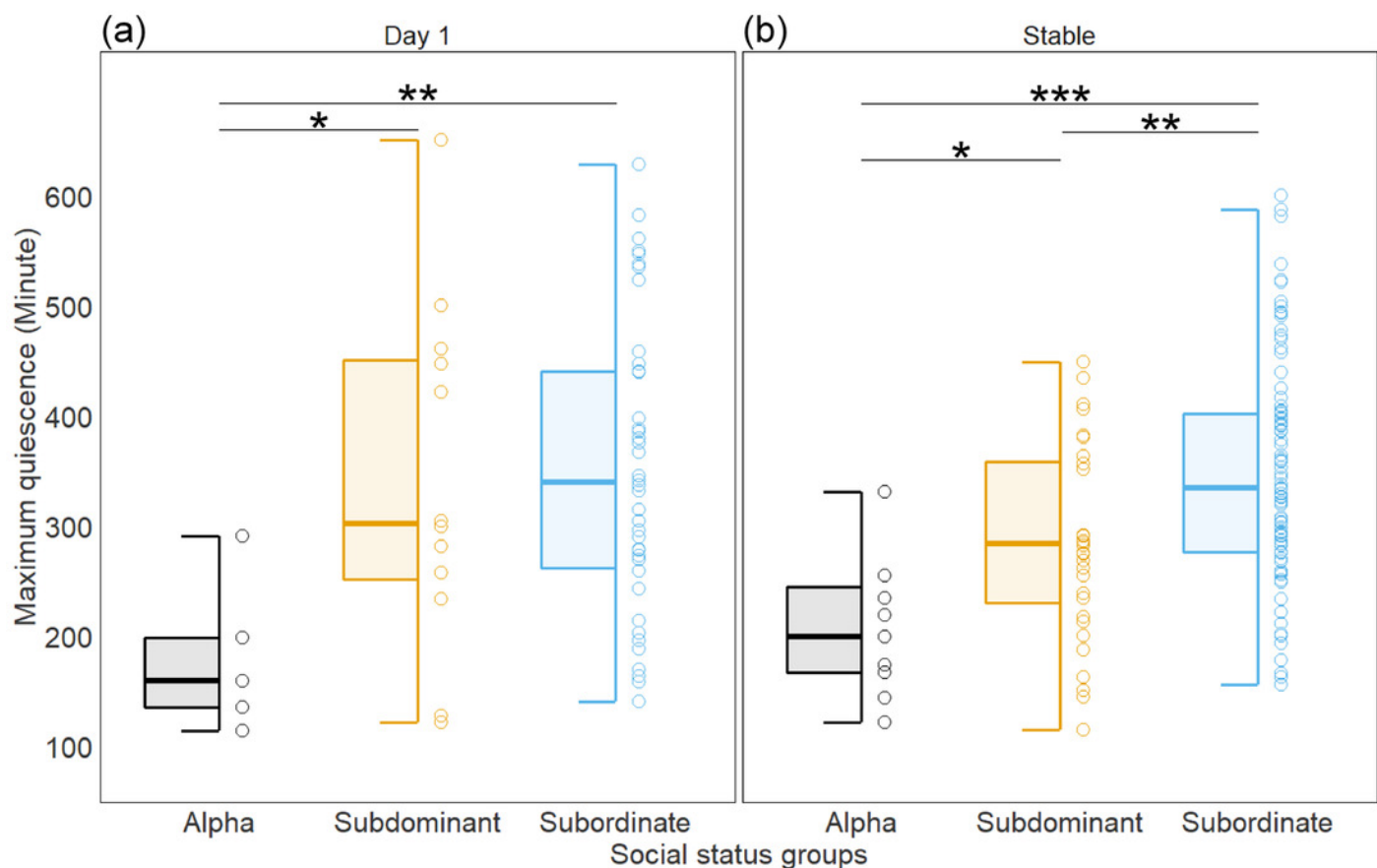
Figure 4

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. Boxplots show median (horizontal bars), IQR (boxes) and 95% CI (whiskers). 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.