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A Chemically-triggered Transition from Conflict to Cooperation in Burying Beetles

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34 **Although interspecific competition has long been recognized as a major**
35 **driver of trait divergence and adaptive evolution¹⁻³, relatively little effort**
36 **has focused on how it influences the evolution of intraspecific cooperation⁴⁻**
37 **⁶. Here we identify the mechanism by which the perceived pressure of**
38 **interspecific competition influences the transition from intraspecific**
39 **conflict to cooperation in a facultative cooperatively breeding species, the**
40 **Asian burying beetle *Nicrophorus nepalensis*. In their natural environment**
41 **in central Taiwan, *N. nepalensis* are typically aggressive to conspecifics and**
42 **only cooperate with others of their own species at critical carcass resources**
43 **in the presence of blowflies, their primary competitors⁷. We demonstrate**
44 **that beetles form larger groups and are more cooperative in carcass**
45 **preparation in warmer environments where the pressure of interspecific**
46 **competition with blowflies is highest⁸. To test the hypothesis that the**
47 **presence of blowflies promotes beetle cooperation and to identify the**
48 **mechanism by which this occurs, we manipulated blowfly larvae on**
49 **carcasses in the lab. We not only found that beetles are more cooperative at**
50 **carcasses when blowfly maggots have begun to digest the tissue, but that**
51 **this social cooperation appears to be triggered by a single chemical cue—**
52 **dimethyl disulfide (DMDS)—emitted from carcasses consumed by blowflies**
53 **but not from control carcasses lacking blowflies. Our results provide**
54 **experimental evidence that interspecific competition promotes the**
55 **transition from intraspecific conflict to cooperation in *N. nepalensis* via a**
56 **surprisingly simple social chemical cue that is a reliable indicator of**
57 **interspecific competition. This finding helps bridge the gap between the**
58 **proximate and ultimate factors regulating the transition between**
59 **cooperation and conflict and moves toward a more comprehensive**
60 **understanding of the evolution of mechanisms governing intraspecific**
61 **variation in social behaviour.**

62

63 Burying beetles (*Nicrophorus spp.*) use small vertebrate carcasses as their sole
64 resource for reproduction and often face intense intra- and interspecific
65 competition for access to these precious but limiting resources⁹⁻¹¹. Previous work
66 has suggested that the key benefit of cooperation in the Asian burying beetle *N.*

67 *nepalensis* is that cooperative carcass preparation—including carcass cleaning,
68 shaping, and burial, as well as the elimination of competing species⁹⁻¹²—enables
69 beetles to outcompete their primary competitor, blowflies (family Calliphoridae),
70 particularly in warmer environments where blowflies are most abundant. By
71 experimentally manipulating burying beetle group size along an elevational
72 gradient, we showed that in cooler environments where the pressure of
73 interspecific competition is low, beetles in large groups are more aggressive
74 toward same-sex conspecifics and often engage in intense and even lethal fights
75 that result in a single individual monopolizing the carcass and having a higher
76 probability of breeding successfully than those in large groups⁸. In contrast, in
77 warmer environments where blowflies are more common, burying beetles
78 cooperate with conspecifics to more quickly bury carcasses and escape blowfly
79 competition⁷, ultimately gaining greater reproductive success⁸. Although the
80 presence of blowflies at carcasses appears to facilitate a shift from competitive to
81 cooperative behaviour in *N. nepalensis*, it remains unclear what drives this
82 transition in beetle social behaviour and how individuals know to reduce conflict
83 and tolerate conspecifics.

84

85 To determine how ecology influences inter- and intraspecific social interactions
86 in natural burying beetle populations, we first quantified beetle social behaviour
87 and dynamics by video recording their breeding behaviours at 25 sites along two
88 elevational gradients in eastern and western Taiwan, each spanning more than
89 1000 m in elevation. We calculated the time that beetles spend on cooperative

90 carcass preparation (hereafter cooperative investment) both in terms of total
91 investment (i.e. the cumulative time of the social group) and on a per capita basis
92 for large (groups larger than the median size) and small groups (groups smaller
93 than the median size), as well as in cool ($<14.5^{\circ}\text{C}$) and warm environments
94 ($>14.5^{\circ}\text{C}$). We found that group size peaked at moderate temperatures ($\chi^2_1 =$
95 $5.52, P = 0.019, n = 245$; Fig. 1a) and that per capita cooperative investment along
96 the temperature gradient varied with group size (group size \times temperature
97 interaction, $\chi^2_1 = 11.20, P = 0.001, n = 89$). Specifically, per capita cooperative
98 investment increased with daily minimum temperature in large groups ($\chi^2_1 =$
99 $5.39, P = 0.02, n = 33$), but not in small groups ($\chi^2_1 = 0.05, P = 0.83, n = 56$; Fig
100 1b). Similarly, total cooperative investment increased with daily minimum
101 temperature in large groups ($\chi^2_1 = 4.88, P = 0.03, n = 33$), but not in small groups
102 ($\chi^2_1 = 0.24, P = 0.60, n = 56$; Fig. 1c). In contrast, per capita social conflict along
103 the temperature gradient, measured as the number of intraspecific conflict
104 events for each individual, varied with group size (mean group size \times
105 temperature interaction, $\chi^2_1 = 6.64, P < 0.01, n = 82$, Fig. 2b), such that conflict
106 increased with group size in cool environments ($\chi^2_1 = 11.24, P < 0.001, n = 40$;
107 Fig. 1d), but not in warm environments ($\chi^2_1 = 1.59, P = 0.2, n = 42$; Fig. 1d).

108

109 To confirm that these patterns of social conflict and cooperation were the result
110 of changes in social behaviour and not simply changes in activity associated with
111 differences in ambient temperature, we further separated cooperative
112 investment into (1) time spent simply walking on the carcass and (2) more

113 complex carcass-preparation behaviours, which are presumably more costly—
114 including maggot and rotten tissue removal, as well as carcass dragging,
115 depilation, and burial. We found that time spent on more complex carcass
116 preparation behaviours increased with increasing daily minimum temperature in
117 large groups ($\chi^2_1 = 5.39, P = 0.02, n = 33$; Fig. 2a), but not in small groups ($\chi^2_1 =$
118 $0.17, P = 0.68, n = 56$; Fig. 2a). However, there was no significant relationship
119 between walking time and daily minimum temperature in large ($\chi^2_1 = 0.24, P =$
120 $0.60, n = 33$; Fig. 2b) or small groups ($\chi^2_1 = 0.79, P = 0.37, n = 56$; Fig. 2b),
121 suggesting that the increase in total cooperative investment in warmer
122 environments was not simply the result of increased activity at warmer
123 temperatures.

124

125 Our field results demonstrate that *N. nepalensis* exhibits remarkably flexible
126 social behaviours along elevational and thermal gradients: beetles are normally
127 asocial and aggressive towards conspecifics in cooler environments but become
128 social and cooperate with conspecifics in warmer environments where the
129 competition for critical resources with other species is intense⁷. However, to
130 demonstrate experimentally that blowfly competition for carcasses drives the
131 transition from intraspecific competition to intraspecific cooperation, we
132 performed a series of laboratory experiments to directly manipulate the
133 presence or absence of blowflies at carcasses.

134

135 Our first experiment introduced blowfly competition to burying beetles by
136 exposing carcasses to adult blowflies in an incubator at 26°C for two days,
137 conditions that match those in the field and are optimal for blowflies to lay eggs
138 and for their maggots to partially consume the carcass. We then allowed six
139 beetles (three males and three females) to breed on the carcass. We found that
140 more beetles cooperated ($t = 5.26, P < 0.001$; Fig. 3a), and that each individual
141 beetle spent significantly more time cooperating, in the blowfly treatment than in
142 the control treatment containing carcasses but no blowflies ($t = 3.27, P = 0.002$;
143 Fig. 3b). As a consequence, the total cooperative investment was higher in the
144 blowfly treatment than in the control treatment ($t = 5.37, P < 0.001$; Fig. 3c).
145 Although there was no difference in per capita social conflict between the blowfly
146 and control treatments ($t = -0.33, P = 0.75$; Fig. 3d), after controlling for total
147 investment time by dividing per capita social conflict by the total cooperative
148 investment, the adjusted per capita number of social conflicts per unit time was
149 significantly lower in the blowfly treatment than in the control treatment ($t = -$
150 $2.58, P = 0.013$; Fig. S1). Thus, social conflict in burying beetles was lower and
151 cooperation higher when blowflies were present on carcasses.

152

153 What is the mechanism driving the transition from intraspecific competition to
154 intraspecific cooperation? Since blowfly species are diurnal but *N. nepalensis* is
155 nocturnal, it is unlikely that the physical presence of blowflies influences *N.*
156 *nepalensis* behaviour. Previous studies have demonstrated that sulfur-containing
157 volatile organic compounds (S-VOCs) emitted from decomposing carcasses

158 attract burying beetles to this key resource^{13,14}. Because GC-MS analysis showed
159 that dimethyl disulfide (DMDS) appeared earlier and was more abundant in the
160 blowfly treatment than in the control (Fig. 4a), we hypothesized that DMDS is the
161 key infochemical¹⁵—indicating not only the presence of a decaying carcass but
162 also the degree of interspecific competition at that carcass—that mediates the
163 transition between cooperative and competitive strategies in *N. nepalensis*.

164

165 To experimentally test this hypothesis, we injected DMDS into the body cavity of
166 mouse carcasses. We found that more individuals cooperated ($t = -3.76$, $P <$
167 0.001 ; Fig. 4b), and that each individual spent more time cooperating, in DMDS
168 treated carcasses relative to controls ($t = -2.55$, $P = 0.014$; Fig. 4c). Thus, there
169 was a higher total cooperative investment in the DMDS treatment than in the
170 control ($t = -3.8$, $P < 0.001$; Fig. 4d). These results were similar to those observed
171 in the blowfly treatment from the initial experiment. The only difference between
172 the DMDS and blowfly treatments was that there was marginally more social
173 conflict in the DMDS treatment than in the hexane control ($t = -1.97$, $P = 0.054$;
174 Fig. 4e), whereas this trend—while in the same direction—was not significant in
175 the blowfly treatment ($t = -0.33$, $P = 0.75$), presumably because there were no
176 real competitors that beetles need to remove in the DMDS treatment.

177

178 Our study shows that burying beetles transition from competitive to more
179 cooperative interactions as the pressure of interspecific competition increases.

180 Accumulating empirical evidence from other animals suggests that social conflict
181 in cooperative societies is often lower in adverse environments with strong
182 interspecific competition⁵. This pattern of reduced social conflict under strong
183 interspecific competition has largely been explained by the fact that the cost of
184 engaging in competitive interactions increases under adverse conditions¹⁶. Yet,
185 there is little empirical evidence demonstrating that social animals increase their
186 investment in cooperation under the threat of interspecific competition. One
187 exception comes from cooperatively breeding superb fairy-wrens (*Malurus*
188 *cyaneus*) who cooperate more in nest defence when exposed to a greater threat
189 of interspecific brood parasitism¹⁷. However, it remains unclear how intraspecific
190 conflict in fairy-wrens is influenced by the threat of interspecific competition.
191 Our study helps fill this knowledge gap by showing that cooperative carcass
192 preparation to reduce blowfly competition in warmer environments is critical for
193 predicting both the cooperative and competitive interactions among individuals
194 of the same species.

195

196 Furthermore, we show that the conditional cooperative and competitive
197 strategies^{18,19} used by *N. nepalensis* to maximize their utility of carcasses are
198 mediated by a surprisingly simple chemical mechanism. DMDS is produced
199 during the decomposition process and acts as an indicator of the level of
200 competition from blowflies. Although interspecific competition has long been
201 recognized as a major ecological force that drives adaptive evolution¹⁻³, relatively
202 little effort has focused on how it influences intraspecific cooperation⁴⁻⁶. Our

203 discovery of a novel social chemical cue provides unambiguous evidence that
204 interspecific competition has shaped social evolution in *N. nepalensis*. DMS acts
205 as a kairomone because it is produced by heterospecifics (i.e. blowfly digestion),
206 but benefits the receiver¹⁵, and not as a pheromone produced by conspecifics^{20,21}.
207 Pheromones are often used for kin discrimination, and studying the olfactory
208 sensory system and its genes have greatly advanced our understandings of the
209 role that chemically-driven kin recognition has played in social evolution,
210 especially in ants^{22,23}. Here we demonstrate that interspecific chemical
211 communication is also important to insect social evolution. Ultimately, by
212 showing that chemically-mediated interspecific competition is a key driver of
213 intraspecific cooperation and of social evolution more generally, our work
214 demonstrates the value of integrating ultimate and proximate levels to study the
215 evolution of cooperation²⁴.

216

217 **Methods**

218 **Field Study.** The field study was conducted in Taiwan from 2012 to 2015 along
219 elevational gradients composed primarily of uncultivated forest in Nantou county
220 (spanning 1688 m to 2650 m above sea level) and Hualien county (spanning
221 1193 m to 2720 m above sea level). A variety of social behaviours, including per
222 capita social conflict and investment in cooperative carcass preparation (i.e.
223 cooperative investment), were scored on the first night of video observation
224 (from 19:00 to 05:00) using the Observer[®] XT 14 (Noldus). To quantify total
225 cooperative investment, we estimated the cumulative time that each beetle spent
226 depilating rat hair, cleaning rat carcasses by removing maggots, or dragging

227 carcasses during carcass burial and preparation. We measured per capita
228 cooperative investment as the total cooperative investment divided by the mean
229 group size, defined as the maximum number of beetles that stayed on or under
230 carcasses averaged over three time periods (22:30 to 22:40; 01:30 to 01:40 and
231 04:30 to 04:40) during each video observation. Investment in cooperation was
232 quantified as the duration of cumulative time sampled for a 10 mins observation
233 period in each hour (i.e. 100 mins for each breeding experiment). In total, there
234 were 89 breeding experiments (resulting in 8900 mins of video recordings) from
235 which we were able to quantify total cooperative investment. Aggressive
236 interactions were defined as social conflict if a beetle attacked, wrestled, chased,
237 or escaped from another same-sexed individual (see below for definitions of each
238 behaviour). We measured total social conflict as the total number of aggressive
239 interactions over the 240 mins observation period. We measured per capita
240 social conflict as the total number of aggressive interactions divided by the mean
241 group size for each observation period. Conflict was quantified as the total
242 number of aggressive interactions sampled for two 120 mins observation periods
243 (from 19:30 to 21:30 and from 23:30 to 1:30). In total, there were 82 breeding
244 experiments (resulting in 19,680 mins of video recordings) from which we were
245 able to quantify conflict behaviour. We determined the mean group size on the
246 first night of each beetle's arrival in 245 breeding experiments (resulting in 7350
247 mins of video recordings).

248

249 **Collection and maintenance.** Lab experiments were carried out using *N.*
250 *nepalensis* individuals from laboratory-reared strains that originated from
251 Meifeng, Nantou County, Taiwan (24°5' N, 121°10'). Burying beetles were
252 collected using hanging pitfall traps baited with 100 g rotten chicken breasts.
253 Collected beetles were randomly paired and supplied with frozen and re-thawed
254 75 ± 5 g dead rats (*Rattus norvegicus*) in 23 × 15.5 × 16 cm plastic boxes filled
255 with 10 cm moist peat for reproduction. The emerged beetles were housed
256 individually in 7.3 × 7.3 × 3.5 cm plastic boxes filled with 2 cm moist peat and fed
257 with dead superworms (*Zophobas morio*) once a week. All individuals were kept
258 in environmental chambers at 13.2 ~ 19.7 °C (to resemble the natural daily
259 temperature fluctuation in their natural habitat) on a 14 L:10 D photoperiod.
260 Experimental beetles were between 40 and 80 days of age, which is their optimal
261 age for reproduction (individuals can live for over three months in the
262 laboratory).

263

264 **Experimental design and procedure.** For each experimental replicate, three
265 unrelated males and three unrelated females were randomly chosen from
266 different families to avoid relatedness affecting their behaviours. Each individual
267 was weighed to the nearest 0.1 mg and marked with a Uni POSCA paint marker
268 on the elytra and coated with Scorch® Super GlueGel for individual identification
269 in videos. The marking and weighing of beetles was done 2 hrs prior to beginning
270 an experiment to ensure that all beetles would return to normal activity levels.
271 All six marked beetles were placed into the experimental boxes in random order

272 at the beginning of each experiment. Experimental boxes consisted of a smaller
273 plastic container (23 × 15.5 × 13.5 cm filled with 13.5 cm moist peat) located
274 inside a larger plastic container (45 × 34.5 × 25 cm filled with 13.5 cm moist
275 peat). A 4 cm high iron net with 2 cm² mesh was placed around the small
276 container to prevent beetles moving carcasses outside the field of view of the
277 digital cameras, but beetles could still move freely between the inner and outer
278 areas. A digital camera was fitted on the top of a 25 × 20 × 55 cm acrylic box,
279 which was fixed on the cap of the large container. To equalize the temperature of
280 the experimental apparatus, boxes were filled with moist peat and put into the
281 environmental chambers one day before the experiments began.

282 The blowfly treatment was conducted by exposing a 75 ± 5 g rat thawed
283 carcass to blowflies, oriental latrine flies (*Chrysomya megacephala*), in 32 × 32 ×
284 32 fly cages for 50 hrs before the start of each experiment. Fly cages contained
285 oriental latrine flies that had emerged from 10 g pupa and been kept in
286 environmental chambers at 26°C on a 14 L:10 D photoperiod. Except for maggot-
287 digested carcasses, all other carcasses in the same weight range were thawed at
288 4°C for 24 hrs before experiments began. Carcasses used in all treatments were
289 moved into the environmental chambers 8 hrs prior to the start of experiments
290 to equalize their temperatures. The hexane control and DMDS treatment used
291 thawed-only carcasses injected with 2 ml hexane or 0.01 M DMDS solution,
292 respectively, into abdominal cavities through the anus using 3 ml Terumo®
293 Syringes and needles 1 hr prior to the start of the experiment. The thawed-only
294 carcasses served as controls. The carcasses in controls and all treatments were

295 moved into the experimental boxes and put on the surface of peat in smaller
296 containers 1 hr before experiments began. Behavioural videos were recorded
297 either from 7 PM until the day and time at which a carcass was completely buried
298 into peat or for 72 hrs if the beetles did not completely bury the carcass (under
299 natural conditions, a carcass would be completely consumed by blowflies if
300 beetles did not completely bury it within 72 hrs). In total, 1020 hrs of videos
301 were analyzed from 23 blowfly control replicates, 23 blowfly treatment
302 replicates, 32 hexane control replicates, and 24 DMDS replicates. Social conflict
303 and cooperative investment behaviours were recorded in the first 10 hrs (7 PM
304 to 5 AM) of each experimental treatment using The Observer[®] XT 14 (Noldus).

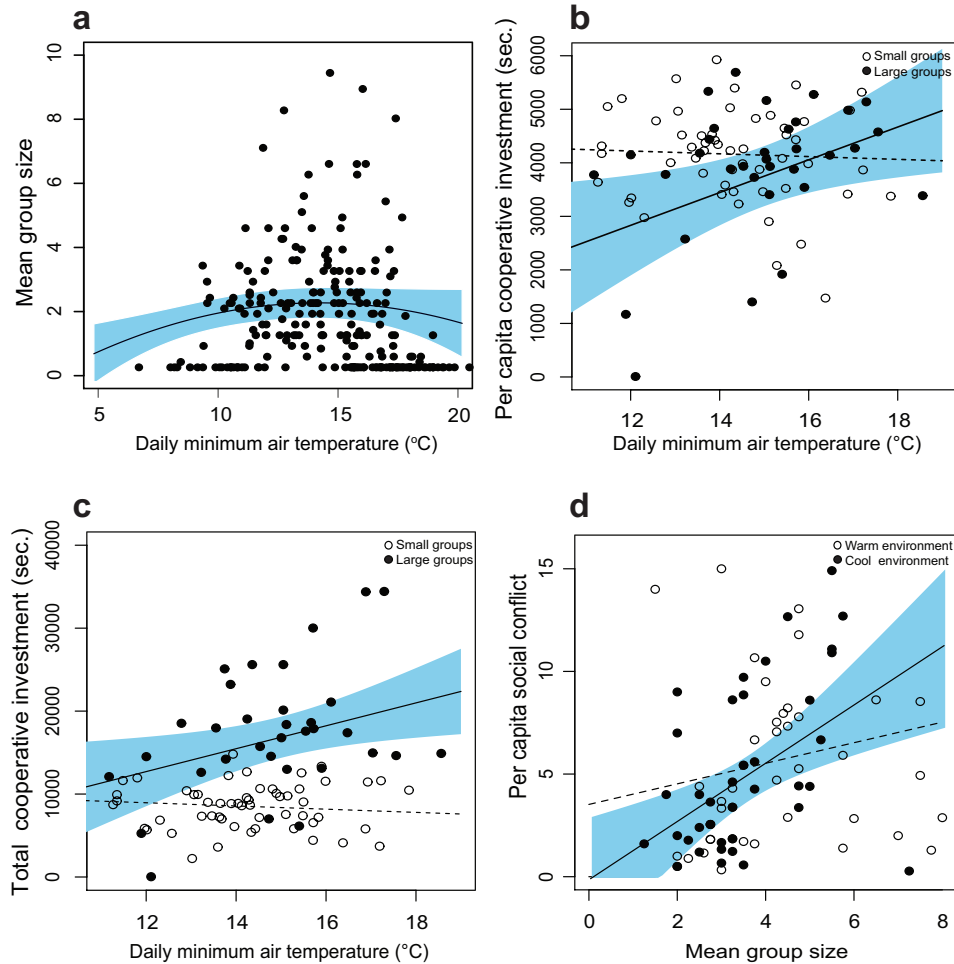
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306 **Gas chromatography-mass spectrometry (GC-MS) analysis.** The composition
307 of volatile organic compounds (VOCs) emitted by carcasses was determined from
308 two control and two blowfly treated carcasses prepared using the same
309 procedure described previously. The prepared carcasses were put on the peat
310 surface in glass vacuum desiccators (15 cm diameter × 22 cm tall) filled with 5
311 cm of moist peat. The stopcock and ground-glass rim of the desiccator lid were
312 greased with a thin layer of petroleum jelly to prevent the leakage of emitted
313 VOCs, as well as contamination from the atmosphere. The VOCs were sampled
314 using solid-phase micro-extraction (SPME)²⁵. The SPME holder with CAR/PDMS
315 fiber (Supelco, previously desorbed for 5 mins in GC injection port heated to
316 200°C) was inserted through the hole of the stopcock into the atmosphere
317 surrounding the rat carcass. Immediately after exposing the fiber for 15 mins, the

318 sample was GC-MS-analyzed using a 6890N Network Gas Chromatograph
319 (Agilent Technologies) equipped with a HP-5ms column (Agilent J&W) and a
320 5975 Mass Selective Detector (Agilent Technologies). The GC oven was operated
321 at an initial temperature 40°C for 1 min and then ramped up at a rate 10°C per
322 min to 250°C (with a 10 mins hold). The temperatures of the GC inlet and
323 detector were set to 200°C and 260°C, respectively. The SPME samples were GC
324 analysed split-less. Helium (1 ml per min) was used as a carrier gas. Since the GC-
325 MS results showed DMDS was the major VOC emitted by the blowfly-treated
326 carcasses, DMDS was injected into carcasses in the further experiments. Two
327 DMDS-injected carcasses (also prepared using the same procedure described
328 previously) were used in GC-MS analyses (following the procedure described
329 above) to determine the composition of the VOCs they emitted.

330

331 **Statistical analyses.** Multivariate analyses were performed using generalized
332 linear models (GLMs) to determine statistical significance for differences
333 between controls and blowfly treatments or hexane controls and DMDS
334 treatments in mean group size, total and per capita cooperative investment, and
335 total and per capita social conflict. All statistical analyses were performed in R
336 using the packages stats, lme4, car, multcomp (<http://cran.r-project.org/>), and
337 glmmADMB (<http://glmmadmb.r-forge.r-project.org/>).



338

339 **Figure 1 | Changes in *N. nepalensis* group size and social behaviours during**

340 **carcass preparation along a temperature gradient.** The relationship between

341 daily minimum air temperature and **(a)** mean group size, **(b)** per capita

342 cooperative investment, **(c)** total cooperative investment in large (closed circles)

343 and small groups (open circles). Group size peaked at moderate temperatures,

344 whereas per capita and total cooperative investment increased with daily

345 minimum temperature in large but not small groups. Solid lines denote predicted

346 relationships from GLMs, whereas dashed lines denote non-significant

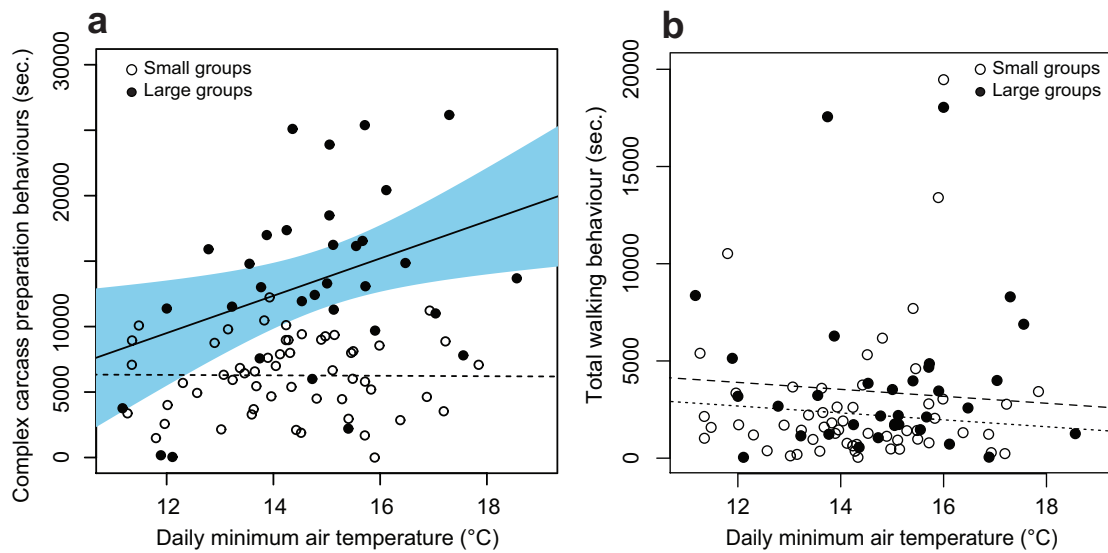
347 relationships. **(d)** Per capita social conflict increased with group size in cool

348 environments (closed circles), but not in warm environments (open circles).

349 Lines represent least-squared means (solid lines denote significant relationships

350 and dotted lines non-significant relationships), and blue shaded areas represent

351 95% confidence intervals expected from GLMMs.

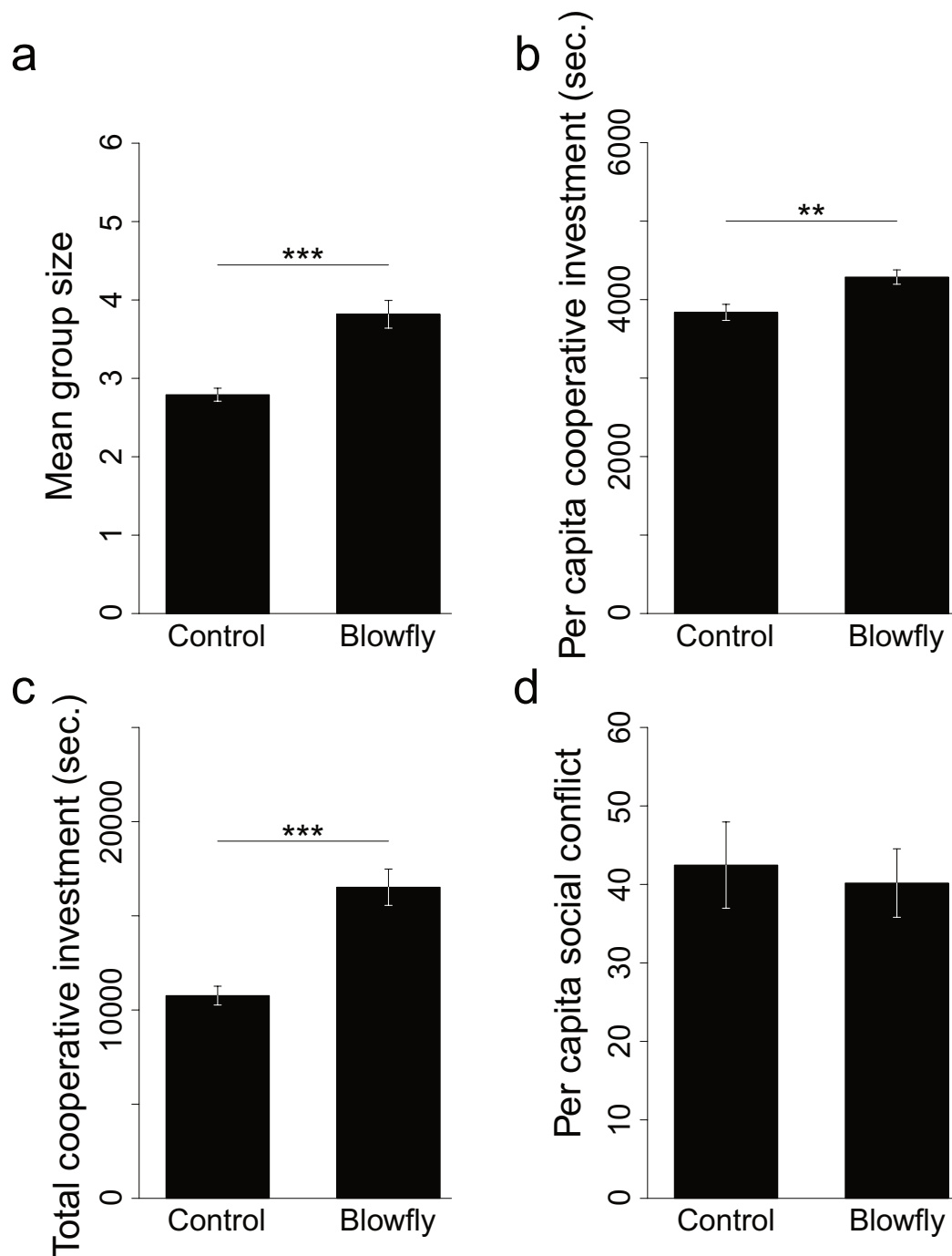


352

353 **Figure 2 | Complex carcass preparation and simple walking behaviours**

354 **during cooperative carcass preparation along the temperature gradient.**

355 The time that beetles spent on **(a)** complex carcass preparation behaviours and
356 **(b)** walking on the carcass in relation to daily minimum air temperature in large
357 and small groups. Compared to small groups (open circles), large groups (closed
358 circles) spent more time on complex carcass preparation but not on walking as
359 daily minimum air temperature increased, suggesting that the increase in total
360 cooperative investment in warmer environments was not simply the result of
361 increased activity at warmer temperatures. Lines represent least-squared means
362 (solid lines denote significant relationships and dotted lines non-significant
363 relationships), and the blue shaded area represent 95% confidence intervals
364 expected from GLMMs.



365

366

Figure 3 | *N. nepalensis* social behaviours in control and blowfly treatments.

367

(a) Mean group size, **(b)** per capita cooperative investment, **(c)** total cooperative

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investment, and **(d)** per capita social conflict of burying beetles on carcasses.

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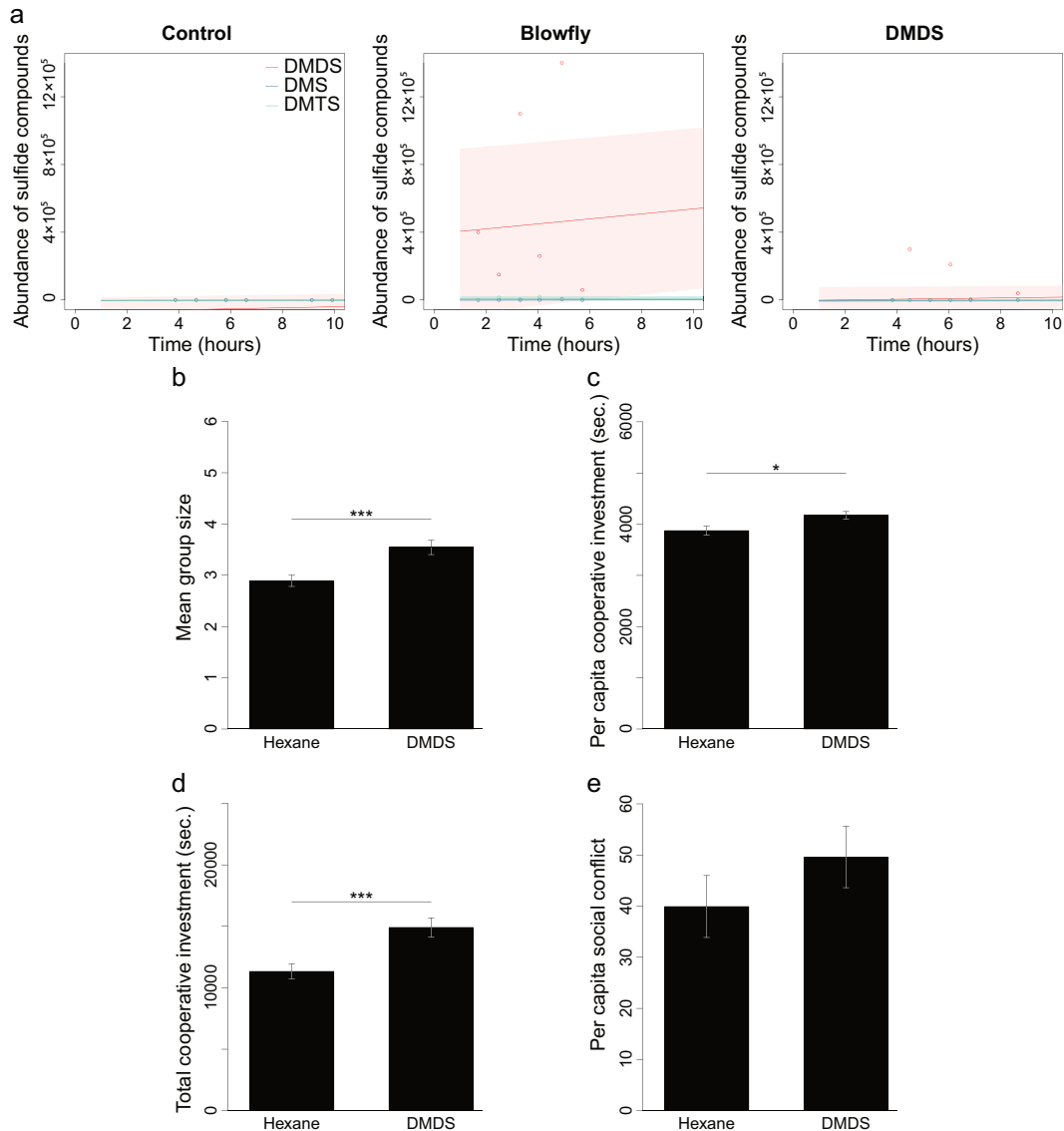
Beetles formed larger groups and had greater per capital and total cooperative

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investment in carcass preparation in the presence of blowflies than in control

371

treatments where blowflies were absent. ** $P \leq 0.01$; *** $P \leq 0.001$.



372

373 **Figure 4 | Results of gas chromatography-mass spectrometry (GC-MS)**

374 **analyses and *N. nepalensis* social behaviours in hexane and DMDS**

375 **treatments. (a)** GC-MS analyses showed an abundance of sulfide compounds,

376 including dimethyl sulfide (DMS), dimethyl disulfide (DMDS) and dimethyl

377 trisulfide (DMTS) in control, blowfly, and DMDS treatments during the first 10

378 hrs. DMDS was the major sulfide compound emitted by maggot-digested

379 carcasses. Shaded areas represent 95% confidence intervals expected from

380 GLMMs. **(b)** Mean group sizes, **(c)** per capita cooperative investment, **(d)** total

381 cooperative investment, and **(e)** per capita social conflict of burying beetles on

382 carcasses in DMDS and hexane control treatments. Beetles formed larger groups

383 and had greater per capital and total cooperative investment on carcasses in the

384 DMDS treatment compared to the hexane control treatment. * $P \leq 0.05$; *** $P \leq$

385 0.001.

386 **Author contributions:**

387 S.-F.S. conceived the idea for the study. B.-F.C., M.L., D.R.R. and S.-F.S. design the
388 experiments. B.-F.C., M.L., S.-J.S. performed field experiment. B.-F.C. and J.-N.L.
389 performed lab behavior experiments. B.-F.C. and Y.-H.L. did the GC-MS analysis.
390 B.-F.C., M.L., D.R.R. and S.-F.S. analyzed the data and wrote the paper.

391

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399 **Reference:**

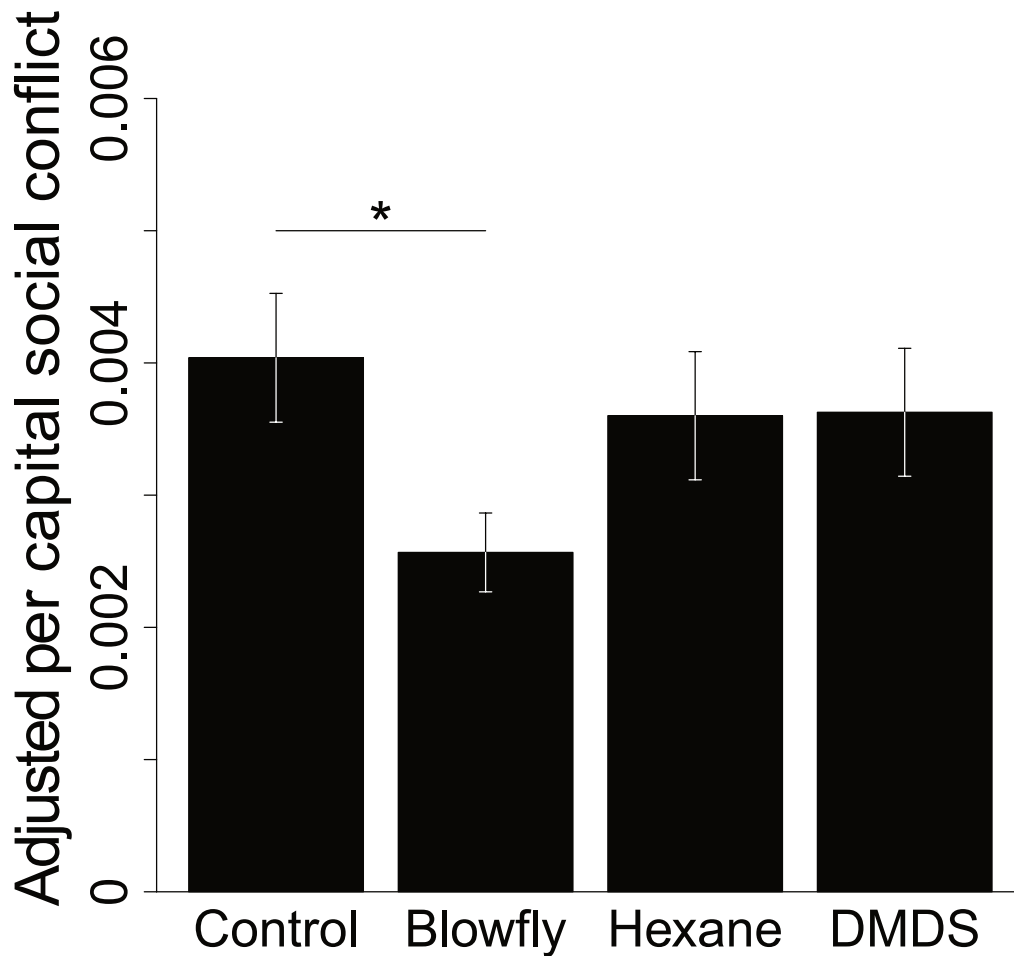
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465 **Figure S1 | Adjusted per capita social conflict in different experimental**
466 **treatments.** Adjusted per capita social conflict (i.e. per capita social conflict
467 divided by the total cooperative investment time) was lower in the blowfly than
468 control treatments. There was no difference in adjusted per capita social conflict
469 between the DMDS and hexane control treatments. * $P < 0.05$.