

1 Dynamic networks of fighting and mating in a wild cricket population

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10

11 **Abstract**

12

13 Reproductive success is often highly skewed in animal populations. Yet the
14 processes leading to this are not always clear. Similarly, connections in animal social
15 networks are often non-randomly distributed, with some individuals with many
16 connections and others with few, yet whether there are simple explanations for this
17 pattern has not been determined. Numerous social interactions involve dyads
18 embedded within a wider network. As a result, it may be possible to model which
19 individuals accumulate social interaction through a more general understanding of
20 the social network's structure, and how this structure changes over time. We
21 analysed fighting and mating interactions across the breeding season in a population
22 of wild field crickets under surveillance from a network of video cameras. We fitted
23 stochastic actor-oriented models to determine the dynamic process by which
24 networks of cricket fighting and mating interactions form, and how they co-influence
25 each other. We found crickets tended to fight those in close spatial proximity to them,
26 and those possessing a mutual connection in the fighting network, and heavier
27 crickets fought more often. We also found that crickets who mate with many others
28 tended to fight less in the following time period. This demonstrates that a mixture of
29 spatial constraints, characteristics of individuals and characteristics of the immediate
30 social environment are key for determining social interactions. The mating interaction

31 network required very few parameters to understand its growth and so structure; only
32 homophily by mating success was required to simulate the skew of mating
33 interactions seen in this population. This demonstrates that relatively simple, but
34 dynamic processes can give highly skewed distributions of mating success.

35

36 **Key words:** dynamic analysis, *Gryllus*, individual-based model, reproductive skew,
37 social network analysis

38

39 **Introduction**

40

41 Organisms engage in social interactions when they mate, fight, cooperate and
42 compete for resources with conspecifics (Frank 2007). Interactions such as these
43 influence an individual's fitness and allow it to influence the fitness of others
44 (Formica et al. 2012; Royle et al. 2012; Wey et al. 2013). Social interactions can
45 therefore play a key role in ecological and evolutionary processes. Furthermore,
46 these interactions are temporally dynamic, as individuals change interactions
47 partners over time (Blonder and Dornhaus 2011; Blonder et al. 2012). This may
48 influence the rate at which individuals encounter potential mates or competitors, the
49 rate of opportunities for pathogen and information transmission, and the
50 opportunities for different social strategies (Pinter-Wollman et al. 2013). How
51 individuals accumulate social interactions is therefore key for several aspects of their
52 fitness.

53 Reproductive skew in wild populations is typically substantial, with many
54 individuals achieving no or little success, while some individuals are highly
55 successful (Keller & Reeve 1994; Clutton-Brock *et al.* 1997; Engh 2002; Frentiu &
56 Chenoweth 2008; Ryder *et al.* 2009; Rodríguez-Muñoz *et al.* 2010; Thompson *et al.*
57 2011). This indicates a skew in social interactions, with some individuals having
58 many mating connections, while most having very few or none. In fact such a skew is
59 common across all sorts of social networks, where most individuals have few
60 connections, while a small number of others are very well connected (Croft et al.
61 2008; Krause et al. 2014). Since both a network of social interactions and a set of
62 mating interactions in a population arise from many dyadic interactions accumulating
63 over time, this raises the possibility that similar processes give strong skews in
64 mating success and social network connections. Not mutually exclusively, it is also

65 possible that the accumulation of interactions in one context influences the
66 interactions in the other context, so for example a high number of interactions in a
67 grooming network leads to many connections in a mating network.

68 Networks with properties similar to real-world networks can be simulated by
69 dynamic network growth models with few rules (Newman 2002; Ilany and Akçay
70 2016), indicating that a network's structure can be directly depend on the dynamic
71 processes that form it. Similarly, simple rules that individuals follow in relation to the
72 movement of fellow group members can result in the apparently complex patterns
73 displayed in murmurations of starlings or synchronised swimming in shoals of fish
74 (Sumpter 2006; Rosenthal et al. 2015). Understanding individual-level decisions
75 about interactions with other population members may therefore allow us to explain
76 the structure and properties of whole groups, including the spread of mating
77 interactions within a population.

78 To investigate these topics, we use dynamic social network analysis to
79 explore how fighting interactions accumulate over time within the lifetimes of
80 individually marked wild adult field crickets (*Gryllus campestris*) to give highly non-
81 random social networks. We then looked at how networks of mating interactions co-
82 change over time alongside the fighting networks, and how these two networks
83 dynamically influence each other. We therefore assessed what processes
84 underpinned the formation of these two networks, and so what could explain the
85 skew in connections apparent in each (Figs. 1 & 2), as well as how they influence
86 each other.

87

88 **Methods**

89

90 **Study site**

91 The study site is located in a meadow in Northern Spain, see www.wildcrickets.org
92 and Rodríguez-Muñoz *et al.* (2010; 2018) for further information. We used data
93 collected in 2013 for this analysis. In the early spring we located each burrow and
94 marked it with a unique identifier. In late April, just before adults start to emerge, we
95 set out 124 cameras at random at burrows with an active juvenile cricket (nymph).
96 This allowed us to record the exact moment of emergence for those adults, and all
97 subsequent behaviour at the burrows. We directly monitored burrows that were
98 without cameras daily or every other day and recorded the life stage and identity of

99 the individual using the burrow. As nymphs only very rarely move among burrows,
100 when there was an untagged adult at a burrow where on the previous days there had
101 been a nymph, we could infer the emergence date for that adult. This allowed us to
102 record accurate emergence dates for the vast majority of the population. Adults mate
103 with members of the opposite sex, fight individuals of typically the same sex and hide
104 from predators at these burrows, so by monitoring the burrows directly we capture
105 the vast majority of relevant cricket behaviour. If we did not observe a cricket's
106 death, we estimated it as the day after it was last observed. A few days (mean \pm
107 standard deviation = 3.76 ± 2.81) after a cricket emerged as an adult, we trapped it
108 (using a custom-built trap, see www.wordpress.com/crickettrapping for more details),
109 and transported it to a laboratory adjacent to the field site. Here we weighed it and
110 fixed a water-proof vinyl tag to its pronotum using cyanoacrylate glue. This allows the
111 identification of individuals, and as far as we are aware does not affect their natural
112 behaviour. After tagging the crickets, we released them back to the burrow they were
113 trapped from, which we kept blocked in the meantime to prevent other animals,
114 including other crickets, from usurping the burrow. We moved cameras away from
115 burrows that hosted no cricket activity for two days to nearby ones where cricket
116 activity had been directly observed or which showed signs of activity. As the season
117 progresses there become more cameras than live adult crickets. This gives us very
118 good information on behaviours over individuals' entire adult lifetimes. In the centre
119 of the meadow there is a weather station that takes measurements of rain fall and
120 intensity of solar radiation every ten minutes (Vantage Pro 2, Davis instruments,
121 California).

122

123 Study organism

124 *G. campestris* is univoltine and adults are active in the months April – July following
125 overwintering as nymphs in burrows they dig themselves. Once sexually mature,
126 males start calling to attract mates, and both sexes move among burrows to search
127 for mating partners. When encountering a member of the same sex at a burrow they
128 will typically fight, with the loser leaving the burrow (Alexander 1961). While many
129 male and female *G. campestris* achieve very low fitness, small males that sing
130 frequently, and larger, long lived, and more promiscuous individuals of both sexes
131 achieve higher lifetime reproductive success (Rodríguez-Muñoz et al. 2010). In *G.*

132 *campestris*, reproductive success is strongly influenced by mating success
133 (Rodríguez-Muñoz et al. 2010), although post-copulatory processes may have some
134 influence (Bretman and Tregenza 2005; Bretman et al. 2009, 2011). Hence the use
135 of accumulation of mating interactions as a proxy for the accumulation of fitness is
136 reasonable.

137

138 Modelling dynamic networks with SAOMs

139 We used stochastic actor-orientated models (SAOMs) to model the dynamic
140 networks of mating and fighting interactions in our population of field crickets and
141 therefore 1) determine processes that lead to the skew in connections in each and 2)
142 determine how the networks influence each other. SAOMs allow the modelling of the
143 change in individuals' social interactions and behaviours over time, as influenced by
144 individual or dyadic (depending on some aspect of the existing relationship between
145 two individuals) effects and properties of the existing network structure (Steglich et
146 al. 2006; Burk et al. 2007; Snijders et al. 2010). SAOMs can also be used to study
147 transmission dynamics (e.g. Pasquaretta et al. 2016; Silk et al. 2017), and the effect
148 of environmental factors on social interactions (e.g. Ilany et al. 2015). These models
149 are therefore useful for testing a range of hypotheses of interaction in behavioural
150 and evolutionary ecology (Fisher et al. 2017). We implemented our SAOMs in the R
151 package "RSiena" (Ripley et al. 2015).

152

153 Network construction

154 Initially we were interested in the fighting behaviour of individual crickets. We judged
155 two crickets to have fought if there was any kind of aggressive interaction between
156 them, which can be unidirectional. These fights typically occur immediately after a
157 cricket arrives at a burrow at which there is already a member of the same sex. The
158 loser will then leave the burrow. These fights are assumed to be over potential
159 mating partners (Alexander 1961) or to provide access to the safety of a burrow. We
160 split the season into nine eight-day time-periods, which gives a manageable number
161 of time steps but also allows enough time for interactions to occur to prevent each
162 time-period having a low frequency of interactions. To avoid exceptionally sparse
163 networks we removed crickets ($n = 58$) who only fought a single other individual in a
164 single time-period, leaving networks of 108 individuals. For each time-period we

165 created a network, linking individuals if they fought at least once in that time-period
166 (hence the networks were binary). If an individual was not alive during a time-period
167 we entered “structural zeroes” for all its potential interactions. These indicate that
168 interactions with that individual could not have taken place, preventing the lack of
169 interaction from informing parameter estimates (Ripley et al. 2015).

170 For the mating network, we linked crickets in a network if they mated at least
171 once in the eight-day period, similar to the fighting network (again a binary network).
172 We added structural zeroes for all potential interactions between individuals of the
173 same sex, as such interactions in that network were impossible. This was input into a
174 SAOM alongside the networks of fighting behaviour, as we expected them to
175 influence each other. We limited both networks to crickets who mated or fought more
176 than one other cricket or mated or fought in more than one time-period, giving
177 networks of 113 crickets, a slightly larger subset of the population than used
178 previously, again to prevent exceptionally sparse networks. For both networks, if an
179 individual was not alive during a time-period we entered structural zeroes for all its
180 potential interactions.

181

182 Network analysis

183 Unless otherwise stated, we used the same method and rationale as outlined in
184 Fisher *et al.* (2017) and that article’s supplementary materials. We initially had nine
185 eight-day time-periods. However, in the first two and last two time-periods there were
186 not enough social interactions to investigate the processes that influence their
187 change, so we did not use them, leaving the middle five time-periods (spanning
188 20/5/2013-28/6/2013). Terms are considered significant at the 95% if the absolute
189 value of “estimate / standard error” was > 2 (Burk et al. 2007; Ripley et al. 2015).
190 Below we explain the modelling process for each of the networks.

191 For the fighting network we used a forcing model (model type 2), where one
192 individual dictates whether a tie is created or dissolved (Ripley et al. 2015), as for
193 fighting a cricket can simply attack another or leave the area when they both meet.
194 The initial SAOM for fighting behaviour contained rate parameters for each time-
195 period and the effects of “density” (the tendency for individuals to be connected to all
196 others in the network, typically negative as networks are generally sparse) and
197 “triadic closure” (the tendency for individuals to form connections with those they

198 share a mutual connection with, typically positive as individuals interact with those
199 they share a mutual connection with). We tested this for satisfactory goodness-of-fit
200 (GOF) with three network statistics: degree distribution (the frequencies of the
201 different numbers of unique connections possessed by crickets in the networks),
202 geodesic distribution (the frequencies of the different shortest path lengths in the
203 networks) and the triad census (the frequencies of each set of three crickets that
204 possessed 0, 1, 2 or 3 links among them, c.f. Ilany et al. 2015). These are chosen as
205 they are commonly calculated network statistics, but their values are not defined by
206 any of the parameters in the model (Ripley et al. 2015). The observed network
207 statistics were not different from the network statistics of the set of networks
208 generated by the model fitting process ($p = 0.281, 0.399$ & 0.994 for the GOF tests
209 for degree distribution, geodesic distribution and the triad census respectively),
210 indicating a satisfactory fit had been achieved. We therefore began adding terms of
211 interest. After adding a term, we ran the model until it achieved convergence, and
212 assessed the GOF. If the GOF had worsened we removed the newly-added term(s)
213 before continuing, otherwise it/they were retained.

214 First, we added the individual covariate of sex, and two parameters, one for
215 sex affecting the number of interactions an individual has, and one for interactions
216 occurring depending on the sex of both individuals. The former term models the
217 tendency for members of one sex to fight more often than members of the other sex,
218 which we expect to have little effect based on previous results (Fisher et al.
219 2016a,b). The latter term models the tendency for crickets to predominantly fight
220 members of the same sex as themselves, which we expected to be a strong effect
221 as fights between males and females are exceptionally rare. We next added a
222 changing dyadic covariate of distance, which was the Euclidean distance between
223 each pair of crickets at the start of the time-period. This models the extent to which
224 crickets nearer each other are more likely to interact than those further away. As a
225 SAOM models the transitions between networks, rather than the structure of the
226 networks themselves, we entered four instead of five measures of distance for the
227 four transitions. We then added the constant covariate of individual mass (g), and its
228 effect on the number of connections and individual acquired, and the interaction
229 between the mass of each individual and its potential associates. We expected
230 heavier crickets to fight more often (Dixon and Cade 1986), and crickets to avoid
231 fighting much heavier individuals (Arnott and Elwood 2009). We next added two

232 effects for weather: the total amount of rainfall (cm) and the intensity of solar
233 radiation (Watts/m^2) in each time-period. These were predicted to increase and
234 decrease the frequency of social interactions respectively, as they have concurrent
235 effects on movement around burrows (Fisher et al. 2015). Each individual is scored
236 as being exposed to the same amount of rainfall and solar radiation in each time-
237 period. Each term did not worsen the GOF of the model (not shown) and so were
238 retained. This is the final model for the fighting network dynamics.

239

240 Mating and fighting networks

241 To simultaneously analyse mating and fighting we entered the five mating networks
242 alongside the five fighting networks into a SAOM. We used a unilateral initiative and
243 reciprocal confirmation model (model type 3; Ripley *et al.* 2015), since for mating,
244 both crickets need to be receptive for it to occur. This model initially includes the
245 effects of density and triadic closure for both networks. We removed the effect of
246 triadic closure from the mating network, as it is impossible in this network (as the
247 third interaction in the triad would have to be a same-sex mating). Once this model
248 converged, we began adding terms. The GOF for the mating network was not initially
249 satisfactory ($p = 0.019, 0.041$ & 0.008 for the GOF tests for degree distribution,
250 geodesic distribution and the triad census respectively) so we added the effect of
251 “degree assortativity” for the mating network. If significant and positive, this effect
252 indicates that individuals with many associations preferentially interact with other
253 individuals with many associations. This possibly represents mutual mate choice,
254 something we have found inferential evidence for previously (Fisher et al. 2016a).
255 This model converged, and achieved satisfactory GOF ($p = 0.413, 0.612$ & 1.00 for
256 the GOF tests for degree distribution, geodesic distribution and the triad census
257 respectively), so we began adding terms of interest.

258 We first added the changing dyadic covariate of distance for both networks,
259 calculated in the same way as previously of the fighting network. We next added the
260 effect of mass for both networks, and the interaction between the mass of two
261 potential associates for the mating network. The latter effect was not added for the
262 fighting network in this two-network model, as the prior results indicated it was not
263 important (Table 1), and we wished to avoid over-parameterising the model. We
264 expected mass to be positively related to mating interactions, but for the interaction
265 to not be important, as individuals of all sizes may prefer larger, presumably more

266 fecund individuals (e.g. Aquiloni & Gherardi 2008; Baldauf *et al.* 2009). We also
267 added the effects of rainfall and solar radiation for the mating network. These were
268 not added for the fighting network as previous results indicated they were not
269 important (Table 1).

270 We then added terms relating to the co-evolution between the networks. The
271 first of these was the effect of “across-network popularity”, where the number of an
272 individual’s connections in one network influences its number of connections in the
273 other network. We actually added two effects here, one for the mating-networks’
274 effect on the fighting networks, and then the effect in the opposite direction. We
275 expect this to be positive, as individuals engaging in many fights are assumed to be
276 doing so to gain access to many mating partners, while individuals mating with many
277 partners presumably are also encountering many rivals to fight with. We finally
278 added the “mutual partner” effect, from the fighting network to the mating network.
279 This models the possibility that two individuals that fight are then more likely to share
280 a mutual connection in the mating network. We have previously found that two males
281 who fight are also typically in sperm competition (Fisher *et al.* 2016a) so we expect
282 this effect to be positive. This was our final model.

283

284 **Results**

285

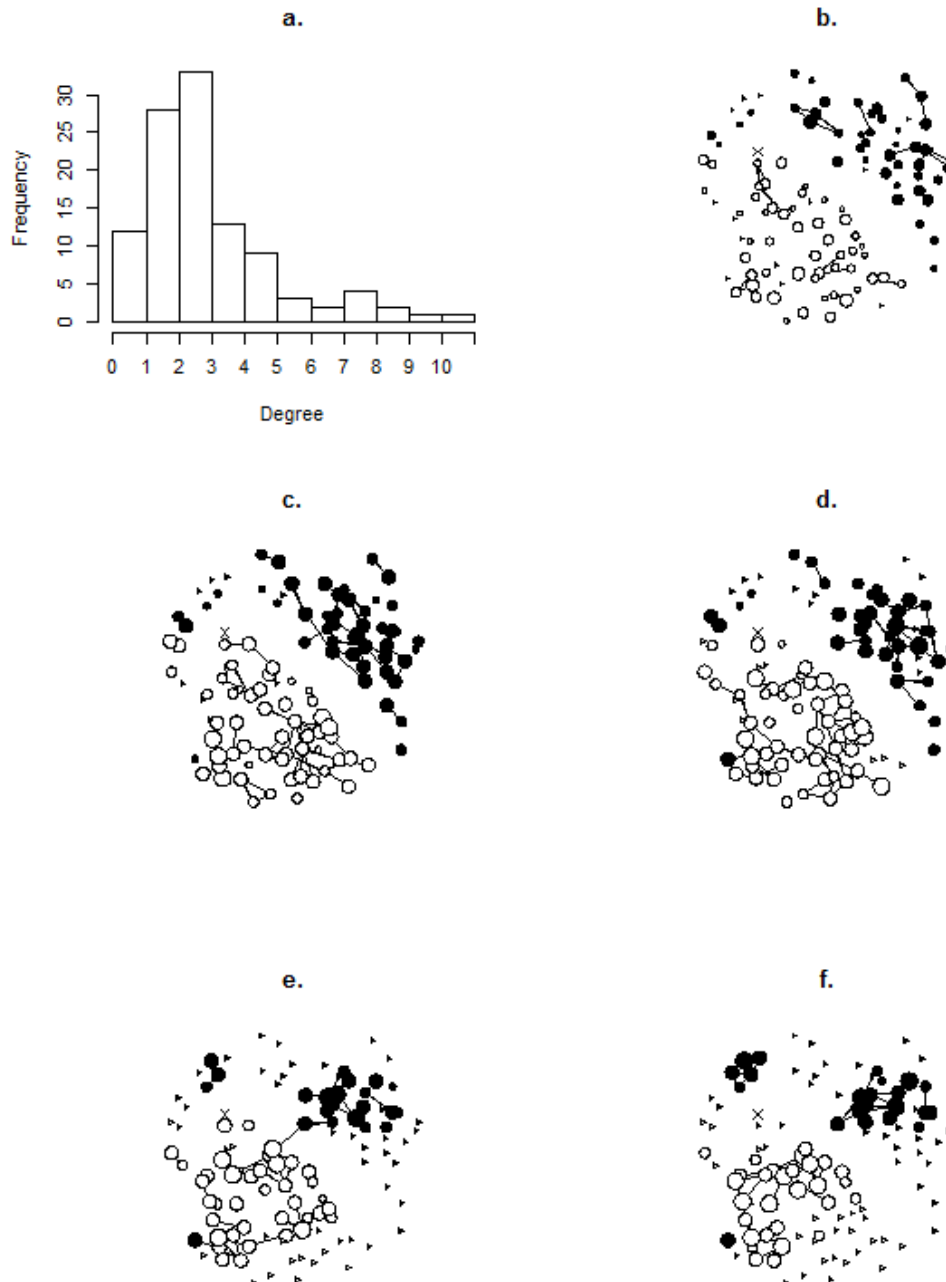
286 Fighting network

287 From the final model of fighting we found significant effects of density, triadic closure,
288 the spatial distance between two individuals, an individual’s mass and both the main
289 effect of sex and the interaction between the sexes of two potential associates
290 (Table 1). The density effect was strongly negative, indicating that crickets tend not
291 to be connected to all other crickets, and so the network is relatively sparse, like
292 most social networks (Snijders *et al.* 2010). Triadic closure was positive, indicating
293 that the presence of a mutual connection increased the chances of two crickets
294 fighting. This was true even when accounting for the effect of distance between
295 individuals, which negatively influenced their tendency to have interactions. The sex
296 effect was negative, indicating that males fought fewer other individuals than
297 females, while the interaction between the sex of one cricket and the sex of another
298 was strongly positive, indicating fights are predominantly intra-sex. Heavier crickets
299 fought more other crickets, again as predicted, but individuals did not avoid fighting

300 those of greatly different weight to them (the interaction between the mass of an
301 individual and the mass of its potential fighting partner was not important). The
302 weather variables did not influence the fighting network.

303

304



305 Figure 1. The degree distribution of the fighting network (a.), and a network plot for
306 each of the five time-periods (b-f.). For the degree distribution all five time periods
307 are aggregated to give the frequencies of the total number of different crickets an

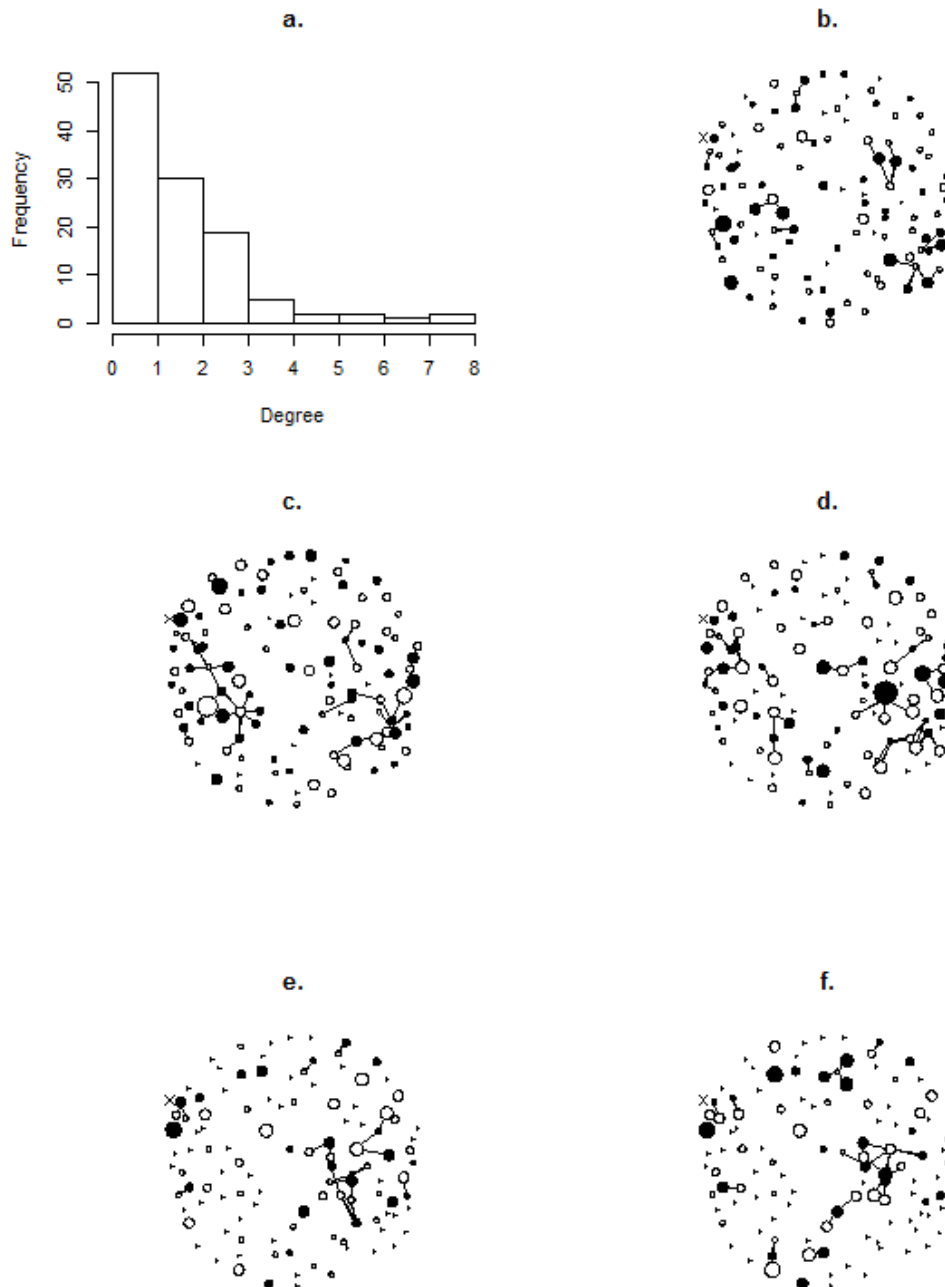
308 individual fought in 40 days. For the network plots, males are filled circles, and
309 females open circles. The size of the circular nodes indicates the activity level of the
310 individual (from 1-4) with individuals who were not alive during the time-period
311 plotted as a small triangle. The position of an individual is the same in each plot,
312 using a Fruchterman-Reingold algorithm (Fruchterman and Reingold 1991) based on
313 an aggregation of all five time-periods. For illustrative purposes, the “X” indicates a
314 female who fought two other individuals and recorded 3 leaves events (and so an
315 activity level of 2) in the 1st time-period, 1 fight and 4 leaves (activity = 2) in the 2nd
316 time-period, 0 fights and 9 leaves (activity = 3) in the 3rd time-period, 0 fights and 12
317 leaves (activity = 3) in the 4th time-period, and was dead for the 5th time-period.
318 Networks plotted using the R package “network” (Butts 2008).

319

320 Mating and fighting networks

321 In the SAOM for the mating and fighting networks, all the significant effects from the
322 previous analysis of the fighting network were in the same direction as before,
323 although the effects of sex, distance and mass were not significant (Table 3). This
324 possibly indicates a lack of power in this analysis. The effect of across network
325 popularity from the mating network to the fighting network was significantly negative,
326 indicating that individuals who mate with many others fight fewer other crickets in the
327 next time-period.

328 For the mating network, the density effect was strongly negative as for the
329 fighting network, again indicating the mating network is sparse much like other social
330 networks. The effect of degree assortativity was positive, indicating that promiscuous
331 males mated with promiscuous females. Otherwise no effects were significant, but
332 since there is a lack of power in this analysis we will mention the following effects
333 that were close to significance ($|\text{estimate} / \text{standard error}| > 1$). Increasing distance
334 decreased the likelihood of mating interactions, while rainfall increased their
335 likelihood. The mutual partner effect was positive, suggesting that crickets who are
336 connected in the fighting network tend to be more likely to share a mutual connection
337 in the mating network. Neither the main effect of mass nor the interaction between
338 mass of the male and female were important, nor was the effect of solar radiation
339 and the effect of popularity in the fighting network.



340

341

342 Figure 2. The degree distribution of the mating network (a.), and a network plot for
343 each of the five time-periods (b-f.). For the degree distribution all five time points are
344 aggregated to give the frequencies of the total number of different crickets an
345 individual mated with over 40 days. For the network plots, males are filled circles,
346 females open circles. The size of the circular nodes indicates the degree in the
347 fighting network of that individual in that time-period. Individuals who were not alive
348 in the time-period are plotted as small triangles. The position of an individual is the

349 same in each plot, using a Fruchterman-Reingold algorithm (Fruchterman and
 350 Reingold 1991) based on an aggregation of all five time-periods. For illustrative
 351 purposes, the “X” indicates a male that had no matings and a single fight in the first
 352 time-period, 1 mating and 3 fights in the 2nd time-period, no matings and 1 fight in the
 353 3rd time-period, 2 matings and 2 fights in the 4th time-period, and 1 mating and no
 354 fights in the 5th time-period. Networks plotted using the R package “network” (Butts
 355 2008).

357 Table 1. Results for the SAOM for the fighting network. Shown are the effect
 358 estimates, standard errors, convergence scores and the t-statistics (estimate /
 359 standard error). Effects are considered significant at the 95% level when the
 360 absolute t-statistic is greater than two. Such effects (aside from the rate parameters)
 361 are highlighted in bold. Rate parameters in a SAOM with only one dependent
 362 network are calculated rather than estimated, so convergence scores are not given
 363 here.

Effect name	Estimate	Standard error	Convergence	t-statistic
<i>Rate of change (period 1)</i>	3.300	1.130	NA	2.921
<i>Rate of change (period 2)</i>	2.169	0.373	NA	5.811
<i>Rate of change (period 3)</i>	1.040	0.191	NA	5.456
<i>Rate of change (period 4)</i>	1.913	0.456	NA	4.200
Density	-4.519	0.355	0.057	-12.739
Triadic closure	0.861	0.217	0.024	3.959
Distance	-0.159	0.018	-0.075	-8.790
Sex	-0.414	0.183	-0.031	-2.262
Sex ego x Sex alter	6.398	1.144	0.059	5.595
Mass	1.991	0.892	-0.003	2.232
<i>Mass ego x mass alter</i>	-5.214	5.466	-0.005	-0.954
<i>Rainfall</i>	0.007	0.013	0.058	0.592
<i>Solar radiation</i>	< 0.001	< 0.001	-0.025	1.500

Maximum Convergence ratio = 0.118

364
 365
 366

367

368 Table 2. Results for the mating and fighting network SAOM used for the third (and to
 369 a lesser extent the first) question. Effects are considered significant at the 95% level
 370 when the absolute t-statistic is greater than two. Such effects (aside from the rate
 371 parameters) are highlighted in bold. The four rate-of-change parameters for the
 372 fighting network were fixed rather than freely estimated, hence their statistics other
 373 than the estimate are not provided (see Table 1).

<i>Fighting network effects</i>	<i>Estimate</i>	<i>Standard error</i>	<i>Convergence</i>	<i>t-statistic</i>
<i>Rate of change (period 1)</i>	3.300	NA	NA	NA
<i>Rate of change (period 2)</i>	2.169	NA	NA	NA
<i>Rate of change (period 3)</i>	1.040	NA	NA	NA
<i>Rate of change (period 4)</i>	1.913	NA	NA	NA
<i>Density</i>	-2.004	0.170	-0.067	-11.795
<i>Triadic closure</i>	0.862	0.221	-0.026	3.907
<i>Distance</i>	-0.005	0.016	0.072	-0.313
<i>Sex</i>	-0.129	0.135	0.030	-0.955
<i>Sex ego x Sex alter</i>	3.270	0.577	-0.076	5.672
<i>Mass</i>	0.997	0.714	0.056	1.396
<i>Popularity in mating network</i>	-0.637	0.291	0.027	-2.185

<i>Mating network effects</i>	<i>Estimate</i>	<i>Standard error</i>	<i>Convergence</i>	<i>t-statistic</i>
<i>Rate of change (period 1)</i>	5.306	1.490	0.015	3.558
<i>Rate of change (period 2)</i>	3.829	1.018	-0.009	3.761
<i>Rate of change (period 3)</i>	3.280	0.894	0.013	3.669
<i>Rate of change (period 4)</i>	3.664	1.657	0.007	2.212
<i>Density</i>	-1.605	0.118	-0.002	-13.609
<i>Degree assortativity</i>	0.158	0.066	-0.004	2.411
<i>Distance</i>	-0.019	0.017	0.004	-1.139
<i>Mass</i>	-0.610	0.715	-0.033	-0.853
<i>Mass ego x Mass alter</i>	-1.704	4.520	-0.019	-0.377

<i>Rainfall</i>	0.011	0.007	-0.028	1.454
<i>Solar radiation</i>	< 0.001	< 0.001	0.001	0.343
<i>Popularity in fighting network</i>	-0.026	0.185	-0.033	-0.138
<i>Mutual partner</i>	1.143	0.838	-0.009	1.364
Maximum Convergence Ratio = 0.146				

374

375 **Discussion**

376

377 Overall, using two SAOMs we could recapture the skew in social interactions that
378 occurs in both the fighting and mating networks. This demonstrates that individual
379 mass, physical distances and the presence of mutual connections with males and
380 females all influence the accumulation of fighting interactions in wild crickets, and
381 lead to a skew in social interactions that is common to the vast majority of social
382 networks. We were also able to recapture the skew in interactions in the mating
383 network. This demonstrated that a relatively simple process, the assortment of
384 individuals by their existing number of connections, can lead to the kind of skew in
385 mating success that is very commonly observed in nature. Furthermore, we identified
386 how the mating interaction network influences the fighting interaction network. This
387 shows how social interactions in one context can influence the accumulation of
388 interactions in another context. We now deal with each of our results in more detail.

389

390 Interactions in the fighting network

391 We found that males fought fewer different individuals than females (see also: Fisher
392 et al. 2016b). This does not necessarily mean that females are more aggressive; in
393 this species, while both sexes engage in active mate searching (Hissmann 1990),
394 typically it is females that move between burrows, while males sit and sing to attract
395 them. Females are therefore more likely to encounter several different females as
396 they are moving among burrows, and so be involved in an aggressive interaction
397 with them. Males may engage in repeated fights with the same individuals, especially
398 if they are calling from nearby burrows. Fighting amongst males does not decrease
399 the intensity of sperm competition between them (Fisher et al. 2016a), and since
400 fights have inevitable energetic costs and carry the risk of injury, male fights may not
401 bring sufficient sexually selected benefits to drive combat with many different rivals.

402 The effect of spatial distance was negative, as expected. In many species
403 individuals will associate more with those close to them, so controlling for spatial
404 proximity when attempting to detect genuinely socially driven associations is
405 important (Whitehead and James 2015). However, the relationship is likely to be
406 bidirectional for many species, with space-use influencing who you interact with and
407 animals moving based on the results or potential consequences of social interactions
408 (Cantor et al. 2012; Webber and Vander Wal 2018). This makes simply “controlling”
409 for space use problematic when space use itself may be an expression of social
410 behaviour.

411 Heavier crickets fought more different individuals. This may suggest that
412 fighting is a condition dependent strategy (Luttbeg and Sih 2010) or that heavier
413 individuals employ a different social strategy that involves attempting to dominate
414 their rivals (Hack 1997; Brown et al. 2006). The interaction between the mass of an
415 individual and its potential associates was however not important. This may reflect
416 how we only modelled the occurrence of fights, not who won. It may well be that
417 crickets of different sizes will encounter each other at a burrow and interact
418 aggressively, and then the size difference influences the outcome.

419 Finally, we found no link between the weather variables and frequency of
420 fighting behaviour. We consider it unlikely that rain and solar radiation do not
421 influence cricket social interactions, as crickets’ activity levels on a given day are
422 influenced by the amount of rain and solar radiation (Fisher et al. 2015). Instead, we
423 suspect that the eight-day periods we selected were too coarse a scale to detect
424 these fine-scale behavioural responses. Ilany *et al.* (2015) found that wetter years
425 lead to more sparse spotted hyena (*Crocuta crocuta*) social networks using a SAOM,
426 so relationships between environmental and network characteristics can be detected
427 with this approach in some systems.

428

429 Interactions in the mating network

430 After adding the term of degree assortativity, we were successful in simulating the
431 mating network, including a highly skewed pattern of mating success. Reproductive
432 skew is ubiquitous in natural populations (Keller & Reeve 1994; Clutton-Brock *et al.*
433 1997; Engh 2002; Frentiu & Chenoweth 2008; Ryder *et al.* 2009; Rodríguez-Muñoz
434 *et al.* 2010; Thompson *et al.* 2011) and helps provide the variation in fitness
435 necessary for adaptation. It would be very interesting to know to what extent other

436 mating systems can be modelled in this manner, and whether the processes of
437 degree assortativity is as important in other mating systems as it is in the crickets.

438 Lifetime reproductive success is correlated with number of mating partners in
439 this species (Rodríguez-Muñoz et al. 2010). Therefore, assortment by promiscuity
440 may indicate mutual mate choice or assortment by “quality” (Aquiloni and Gherardi
441 2008; Baldauf et al. 2009), which could increase the variance in reproductive
442 success in the population if high-fecundity individuals pair. However, as males with
443 many mating partners mate with more promiscuous females, they face increased
444 sperm competition for each ovum of females they mate with. This will reduce the
445 variance in reproductive success among-males (Sih et al. 2009). Both the main
446 effect of mass and the interaction between the mass of an individual and the mass of
447 its potential mating partners was not related to links in the mating network,
448 suggesting mating partner choice is not based on mass. Instead, chemical cues such
449 as cuticular hydrocarbons are likely to be important in mediating partner choice
450 between closely related species (Tyler et al. 2015), so may play a role here.

451 Only degree assortativity was needed to get a satisfactory GOF for the mating
452 network, perhaps suggesting that the mating system is quite simple and beyond
453 these few terms only stochasticity plays an additional role in determining its
454 structure. This would be troubling given the amount of effort that is devoted to
455 understanding patterns of mate choice and sexual selection in the wild. However,
456 there is the potential for a lot of different behavioural processes to be contained
457 within the effect of degree assortativity, such as the trait(s) crickets are using for
458 mate choice and the processes that generate variation in these traits that cannot be
459 exploited by “cheats” who do not signal honestly. Additionally, we have only
460 modelled the choice of mating partners, not the frequency of mating with a particular
461 partner in an eight-day period, as we used binary networks. Therefore, there is likely
462 variation in preference among mating partners that we are ignoring, which could
463 influence fitness as frequency of copulation is likely related to share of paternity
464 (Parker 1970; Simmons 1987).

465 We found that spatial distance did not significantly influence the mating
466 network. This surprising result could stem from a number of sources. A lack of power
467 as suggested earlier may have prevented us from detecting a biologically important
468 effect. Alternatively, this may reflect the fact that there are many crickets near each
469 other that do not mate. In general, if the choice of mates for an individual in a

470 population is not limited to its immediate neighbours, simple models for population-
471 level processes such as partner choice or sexual disease transmission that do not
472 explicitly account for spatial constraints may be more accurate than thought
473 (Patterson et al. 2008). The weather variables were also not important, but we
474 hesitate to make conclusions about this since it may stem from looking at too coarse
475 a scale as suggested above for the fighting network.

476 Individuals with more mating partners tended to have fewer fighting partners
477 at the next time step. This seems to contrast with previous results that the
478 involvement in fighting and sperm competition is positively correlated (Fisher et al.
479 2016a). However, these results are compatible if we consider the dynamic nature of
480 the new result. Crickets over their lifetimes may show positive correlations between
481 involvement in different types of competition, perhaps due to links to “quality” or
482 differences in lifespan, but at any given time they may not be able to do both (perhaps
483 due to energetic constraints), creating a negative relationship between adjacent time
484 steps. Furthermore, crickets that shared a mutual connection in the mating network
485 were more likely to fight. This seems a direct response to the threat of sperm
486 competition, as we have found previously (Fisher et al. 2016a). Crickets have flexible
487 mating systems where they are involved in pre- and post-copulatory competition
488 (Buzatto et al. 2014), so they are adapted to both physical contests and sperm
489 competition. In other systems, where males can monopolise access to females
490 through physical domination, we would not expect to see such a pattern.

491

492 Conclusions

493 We have analysed how networks of fighting and mating interactions between crickets
494 accumulate over time, and therefore arrived at a holistic understanding of how these
495 networks come to be structured. By demonstrating that various individual and
496 network-based factors influence social interactions, we have helped link social
497 network analysis to existing theory on dominance interactions and sexual selection
498 theory. These factors, along with stochastic processes, produced networks with a
499 skewed degree distribution that mirrors the observed skew in social interactions and
500 reproductive success in the population, suggesting these a network approach is an
501 appropriate way to model these systems. We hope this stimulates others to use
502 approaches such as this to gain more complete understanding of complex animal
503 social systems.

504

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509

510 **Author contributions**

511 All authors conceived of the research questions, contributed to study design and
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513 and conducted the data analysis. All authors approved of the final manuscript for
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515

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520

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