Consequences of variation in predator attack for the evolution of the selfish herd

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25   **Abstract**

26   There is a strong body of evidence that patterns of collective behaviour in

27   grouping animals are governed by interactions between small numbers of

28   individuals within the group. These findings contrast with study of the 'selfish

29   herd', where increasingly complex individual-level movement rules have been

30   proposed to explain the rapid increase in aggregation observed when prey

31   groups are startled by or detect a predator. While individuals using simple rules

32   take into account the position of only a few neighbours, those using complex

33   rules incorporate multiple neighbours, and their relative distance, to determine

34   their movement direction. Here, we simulate the evolution of selfish herd

35   behaviour to assess the conditions under which simple and complex movement

36   rules might evolve, explicitly testing predictions arising from previous work. We

37   find that complex rules outperform simple ones under a range of predator attack

38   strategies, but that simple rules can fix in populations particularly when they are

39   already in the majority, suggesting strong positive frequency dependence in rule

40   success. In addition, we explore whether a movement rule derived from studies

41   of collective behaviour (where individuals use the position of 7 neighbours to

42   determine movement direction) performs as successfully as more complex rules,

43   finding again positive frequency dependence in rule success, and a particular

44   role for predator attack strategy (from within or outside the group).

45

Introduction

Aggregation into groups is a widely observed natural-history trait, both taxonomically and across different biomes. An understanding of the selective pressures underlying animal grouping behaviours has been a dominant feature throughout the study of behavioural ecology (all four editions of the seminal textbook 'An Introduction to Behavioural Ecology' devote a whole chapter to the phenomenon; e.g. Davies et al. 2012). Aggregation often considered to arise as a response to predation (Krause and Ruxton 2002; Wood and Ackland 2007), as it carries with it a number of anti-predator benefits, including increased vigilance (e.g. Roberts 1996), dilution (reduced chance of being the individual attacked; Foster and Treherne 1981), encounter-dilution (reduced encounter rate; Turner and Pitcher 1986) and confusion effects (cognitive limitations reducing success; Miller 1922; Krakauer 1995), which act to reduce individual risk to each group member.

Individuals within groups also benefit from the mechanisms outlined by the selfish herd hypothesis (Hamilton 1971), where individuals reduce their own risk of predation at the expense of others in the group, effectively seeking cover within the group and placing other group members at increased risk. Work on selfish herds focuses primarily on the behavioural strategies ('movement rules') of individuals that generate aggregations, to explain the oft-observed phenomenon of facultative or increased aggregation in response perceived threat (Hamilton 1971; Foster and Treherne 1981; Krause and Tegeder 1994; Watt et al. 1997; Spieler and Linsenmair 1999; Viscido and Wethey 2002).

71   Perceived threat can also increase synchrony within groups (Bode et al. 2010).

72   The synchronous behaviour of large aggregations has been the focus of

73   significant research effort, in an attempt to understand how large-scale collective

74   behaviour can be brought about through interactions between individuals.

75   Theoretical (e.g. Huth and Wissel 1992; Huth and Wissel 1994; Couzin and

76   Krause 2003; Giardina 2008; Hildenbrandt et al. 2010; Bode et al. 2011a) and

77   empirical (e.g. Buhl et al. 2006; Ballerini et al. 2008a; Katz et al. 2011) evidence

78   suggests that patterns of collective behaviour in grouping animals are governed

79   by interactions between small numbers of individuals within the group. For

80   starling flocks, for example, each individual interacts with 6 or 7 neighbours on

81   average (Ballerini et al. 2008a); models incorporating interactions over similar

82   topological distances confirm collective behaviour as an emergent property of

83   the system (Hildenbrandt et al. 2010; Bode et al. 2011a; Bialek et al. 2012). Pair-

84   wise interactions in fish shoals effectively capture spatial patterns in groups of

85   up to 30 individuals (Katz et al. 2011), and locust swarms are coordinated by

86   only by short-range local interactions within a range of 13.5cm (Buhl et al. 2006).

87

88   This focus on generating large scale patterns from interactions with small

89   numbers of neighbours contrasts sharply with the study of selfish herd

90   behaviour, where research has focused on identifying movement rules that

91   result from complex interactions between increasingly large numbers of

92   neighbours (Morton et al. 1994; Viscido et al. 2002; Reluga and Viscido 2005).

93   Evolutionary simulations of selfish herds suggest that populations become

94   dominated by individuals that account for the position of much larger numbers

95   of neighbours (Reluga and Viscido 2005), but empirical evidence for selfish herd

96   movement rules is limited. Sticklebacks move towards a neighbour that can be

97   reached more quickly, rather than one that is geographically closer (Krause and

98   Tegeder 1994), and seals' movement is consistent with attraction towards a

99   single neighbour (using simple rules) rather than multiple neighbours (De Vos

100   and O'Riain 2012). In contrast, sheep movement patterns in response to threat

101   from a sheepdog are consistent with the idea that they are moving towards the

102   group centre (King et al. 2012).

103

104   A key difference between these two areas of work is that while collective

105   behaviour represents a stable level of aggregation, the selfish herd is a process of

106   (increasing) aggregation levels. However, theoretical research on the selfish herd

107   focuses primarily on the point at which stable aggregations have formed, but

108   recent work suggests that timing of predator attacks in relation to the point at

109   which prey first detect the predator and initiate anti-predator behaviour is

110   crucial in determining the success of movement rules, and that simpler rules,

111   accounting for fewer neighbours, might evolve under a range of biologically-

112   plausible conditions (Morrell and James 2008; Morrell et al. 2011a). While it is of

113   course feasible that the different situations of movement synchronisation and

114   increasing aggregation use different methods of processing information, the

115   discrepancy in research activity is worthy of further investigation.

116

117   In our previous work, we found that simpler mutant aggregation strategies

118   (rules) experienced a reduced share of the risk in populations of more complex

119   rules, when predators attacked during the process of aggregation (Morrell et al.

120   2011a), and in populations that are of lower density (Morrell et al. 2011b) and

121   larger size (Morrell & James 2008). More complex rules are more effective at

122   reducing risk in larger and denser populations (Morrell & James 2008, Morrell et

123   al. 2011b) and when predators attack later in the movement sequence (Morrell

124   et al. 2011a). Complex rules are also more effective at moving individuals from

125   the periphery of a group to the centre (Morrell et al. 2011b), where they will be

126   protected from predators that attack from outside the group (for a discussion of

127   predator attack strategies, see Morrell and Romey 2008; Morrell et al. 2011a and

128   2011b). We use the terms 'simple' and 'complex' rules to reflect the terminology

129   used in previous papers in this field. There has been no investigation into

130   whether these rules are cognitively 'simple' or 'complex' for animals, and this

131   may differ between species (discussed in Morrell and James 2008; Morrell et al.

132   2011a; 2011b). Essentially more complex rules appear to require individuals to

133   obtain a greater amount of information from their environment in order to apply

134   them.

135

136   Our previous work (Morrell & James 2008, Morrell et al. 2011a, b) provides a

137   series of predictions, based on reduction of individual risk in a group, as to when

138   mutant individuals using simpler rules should be able to invade a population of

139   more complex rules. Here, we explicitly test those predictions in an evolutionary

140   simulation model, to explore whether the reduction in risk translates into

141   fixation in a population over evolutionary time. Our first aim, therefore, is to test

142   the following predictions arising from previous work:

143   1. Predators that attack from the periphery favour the evolution of complex

144   movement rules in prey

145   2. When predators attack early in the movement sequence (i.e. shortly after

146   they are detected, and when individuals have had little time to move in

147   response to detecting the predator), simple strategies are favoured, while

148   predators that attack later favour the evolution of more complex

149   strategies.

150   3. Variation in attack timing (i.e. when predators can attack both quickly and

151   more slowly after prey initiate aggregation) should favour the

152   maintenance of mixtures of strategies within the population (following

153   from prediction 2).

154   4. Simple rules are favoured in large, low-density populations, while

155   complex rules are favoured in small, compact populations.

156 Our second aim (which could be considered a special case of the more general

157 aim 1) is derived from the substantial body of work on collective behaviour (e.g.

158 Couzin and Krause 2003; Ballerini et al. 2008a; Giardina 2008; Hildenbrandt et

159 al. 2010; Buhl et al. 2011; Katz et al. 2011; Bode et al. 2011a; Bialek et al. 2012),

160 and is to specifically assess whether a rule whereby individuals move towards 7

161 neighbours might perform as effectively as more complex rules in reducing

162 individual risk. This leads to the prediction that:

163   5. A rule whereby individuals account for the position of 7 neighbours (i.e. a

164   relatively small number) is as likely to evolve as a more complex rule

165   whereby individuals account for the position of up to 20 individuals (the

166   "Local Crowded Horizon" rule; Viscido et al. 2002, table 1).

167

168 **Materials and Methods**

169   We used an agent-based modelling framework used in previous work on selfish

170   herd behaviour (James et al. 2004; Morrell and James 2008; Morrell et al. 2011b;

171   Morrell et al. 2011a) as the basis for our evolutionary simulation. In each

172   generation of the model, N point-like agents representing the prey individuals

173   are randomly placed (following a uniform random distribution) into a circular

174   arena of radius R m, giving a prey density $d = N/\pi R^2$. We assume that the habitat

175   is homogeneous and provides no areas of cover that could be used to reduce

176   predation risk: in accordance with (Hamilton 1971), cover is provided by

177   position relative to other individuals only, and prey receive no directional

178   information regarding predatory threat (Hamilton 1971; Morton et al. 1994;

179   Viscido et al. 2002; James et al. 2004; Morrell and James 2008; Morrell et al.

180   2011b; Morrell et al. 2011a). We consider $N = 20$ and $d = 4$ as our 'baseline'

181   parameter values, and explore the independent effects of increasing group size

182   ($N = 50$) and increasing density ($d = 10$).

183

184   Each prey is allocated a movement rule, selected from those previous proposed.

185   We consider 4 movement rules here, following previous work on the topic.

186   Firstly, we consider the 3 rules investigated by Morrell et al. (2011a) and Morrell

187   et al. (2011b): nearest neighbour (*NN*), 3 nearest neighbours (*3NN*) and local

188   crowded horizon (*LCH*). These rules are described in table 1. To investigate

189   whether rules that account for 7 neighbours are competitive against those that

190   account for more (prediction 4), we also include a 7 nearest neighbour rule

191   (*7NN*) in our investigations. Although previous work has considered 'random

192   movement' as a potential rule, we do not include it here as it is well established

193   that all other rules are beneficial in relation to random movement (Morton et al.

194   1994; Viscido et al. 2002; Morrell and James 2008). In each generation, N_p

195   individuals are allocated a 'population' movement rule, and N_m are allocated a

196   'mutant' movement rule ($N_m + N_p = N$). We explore 2 different starting

197   combinations: a single mutant in a population using a different rule ($N_m = 1$, $N_p =$

198   N-1), and a situation where both rules begin at equal frequencies ($N_m = N_p =$

199    $N/2$). These two scenarios represent two possible events: a mutant rule arising

200   by chance in an existing group, and a situation where two groups, using different

201   rules, meet. Throughout, we refer to the 'simpler rule' as the one that requires

202   information about the position fewer neighbours, and the 'more complex rule' as

203   one that require information about more neighbours (table 1).

204

205   As in previous work, the start of the simulation (timestep $t = 0$) represents the

206   point in time at which the prey first detect the predator and movement begins.

207   We assume that all individuals detect the predator simultaneously and begin

208   moving, following Hamilton (1971), Morton et al (1994), Viscido et al. (2002)

209   and Morrell and James (2008). The end of the simulation occurs at time T, which

210   is the point at which the predator attacks the prey. In each timestep t (t=0.1 s),

211   each prey individual identifies its target location, dependent on its allocated

212   movement rule and moves at a speed of 0.15 m s^{-1} towards the target location

213   (representing the movement speed of a three-spined stickleback, following

214   James et al. 2004). All individuals move simultaneously, and update their target

215   location in each timestep. At time T ($T > 0$) the predator appears, and attacks the

216   closest prey item. T takes either fixed values ($T = 20, 50$ and 100 are used here)

217   or is randomly drawn from a uniform distribution between 0 and T_{max} ($T_{max} = 50$,

218   100).

219

220   We investigate two predation strategies P: the predator may appear within the

221   group (following Hamilton 1971) or may appear outside the group (empirical

222   evidence for these strategies is reviewed in Morrell and Romey (2008) and

223   discussed in Morrell and James (2008) and Morrell et al. (2011a, 2011b) in the

224   context of the selfish herd). If the predator appears within the group, we

225   calculate the mean group centre from the x and y coordinates of the prey at T,

226   and the maximum distance of all prey from the mean group centre. The predator

227   is placed at random within the circle described by these two parameters,

228   following a uniform distribution. Predators attacking from outside the group

229   appear at the edge of the circular arena (distance R from the arena centre), at a

230   location determined by an angle drawn from a random uniform distribution.

231

232   Once the predator location has been determined, the predator attacks the closest

233   prey item. We assume that an attack always occurs, and that all attacks result in

234   successful predation. The movement rule of the predated individual is recorded.

235   For simplicity, we assume that only one individual is predated, and that

236   individual is replaced in the next generation. To determine the movement rule of

237   the replacement individual, we calculate the proportion of surviving individuals

238   using each rule. If a random number drawn from a uniform distribution between

239   0 and 1 is less than N_m/N, the replacement individual follows the mutant

240   movement rule; otherwise it follows the population movement rule. N_m and N_p

241   are updated in each generation for a total of 5000 generations, or until the

242   population fixes at a single movement rule (N_m or $N_p = N$). This final movement

243   rule is recorded, or, if a mixture of movement rules still remains (N_m and $N_p > 0$),

244 this fact is recorded. For each combination of movement rules, and for each set of

245 parameter values (see below), we ran 1000 replicates to give a final output of the

246 number of replicates ending in each of the three possible outcomes: mutant rule

247 fixes, population rule fixes, and mixture of rules remains. We standardised the

248 starting positions of both prey and predators for each combination of movement

249 rules and set of parameter values (Morrell et al. 2008), such that each set of 1000

250 replicates x 5000 generations was run with the same set of initial positions for

251 both predators and prey.

252

253 We compare the frequency at which each rule becomes fixed against random

254 expectation i.e. the proportion of simulations in which a rule is expected to fix if

255 predation is independent of movement rule (i.e. through drift). The probability of

256 such a 'neutral' mutant rule becoming fixed is equal to its frequency in the

257 population at the start of the simulation (i.e. N_m/N, Kimura 1962). Statistical

258 comparisons between model output and the expected frequency were made

259 using binomial tests (R v2.12.2, R Development Core Team 2011), corrected for

260 multiple testing (180 tests were run) using a Bonferroni correction. These

261 results are displayed on the figures. We found essentially similar results to those

262 represented here when we re-ran the model with different combinations of

263 parameter values caused by different discretization of strategy-space, so can be

264 relatively confident our results are robust in this regard. Our key findings are

265 summarised in table 2.

266

267 In contrast to previous work (Hamilton 1971; Morton et al. 1994; Viscido et al.

268 2002; James et al. 2004; Morrell and James 2008; Morrell et al. 2011b; Morrell et

269 al. 2011a) we do not explicitly calculate the Domain of Danger (DOD; Hamilton

270 1971) or limited DOD (LDOD; James et al. 2004) for each individual. This is

271 implicitly captured in our assumption that predators target the nearest

272 individual, as the DOD describes the space around each individual that is closer

273 to it than to any other individual. Thus, when a predator attacks the closest

274 individual, it is by definition within the DOD of that individual.

275

276 **Results**

277 ***(a) Invasion success and predator attack strategy***

278 Firstly, we investigated the effect of predator attack strategy (from within the

279 group or from outside it, prediction 1) and fixed attack time T of 20, 50 and 100

280 timesteps (equivalent to 2, 5 and 10 s, prediction 2) on the proportion of

281 simulations ending with the fixation of each rule. We find that in general,

282 complex populations (groups where the field strategy is complex) are highly

283 stable against invasion by a single simpler mutant (figure 1a, d and g), with only

284 occasional instances of 3NN mutants becoming fixed in LCH populations (figure

285 1g). Otherwise, successful invasions by simpler rules are consistent with random

286 expectation, or worse. When both rules begin at equal frequencies (figure 1b, e

287 and h), the complex rule is likely to outcompete the simpler one and reach

288 fixation more often than expected by chance. The exception to this is at short

289 attack times when predators attack from within the group, when NN strategies

290 can reach fixation against LCH (figure 1e) at a rate consistent with chance, and

291 3NN reaches fixation at the expense of LCH (figure 1h). Logically, this is sensible:

292 in a short period of time, an individual moving towards a dense but more distant

293 area of a group makes little immediate progress towards a near neighbour

294   (remaining isolated for longer), while an individual moving directly to that

295   neighbour reduces its risk rapidly (Morrell and James 2008).

296

297   More complex mutants can successfully reach fixation more often than expected

298   by chance in simpler populations (groups where the field strategy is simple)

299   (figure 1c, f and i), but they do not dominate the results, suggesting that simple

300   populations can be stable against single, more complex mutants. This is

301   particularly true when predators attack from the inside, when attack times are

302   shorter, and when the difference in rule complexity is smaller (i.e. NN v 3NN and

303   3NN v LCH, but less for NN v LCH). At fixed attack times, as expected, we see very

304   few situations where a mixture of rules is maintained in the population: the only

305   instance of this occurring is seen in figure 3h, at $T = 100$ and when predators

306   attack from within the group (see table 2 for a summary).

307

308   *(b) Fixed versus variable attack timing*

309   Next, we investigate the effect of variable attack timing (where attack timing is

310   drawn from a uniform distribution between 0 and T_{max}) on the fixation of rules

311   (prediction 3). As we previously (figure 1) showed that mixtures might be

312   favoured particularly when groups start with equal frequencies of the two rules,

313   we explore this starting combination here. We find no evidence to suggest that

314   mixtures of rules are maintained in the population when attack time T is variable

315   (i.e. drawn from a random uniform distribution) for any pairwise combination of

316   movement rules at any of the three group size and density parameters we tested

317   (figure 2).

318

(c) Effects of population size and density

We did, however find that population size and density influenced the success of different rules (prediction 4, figure 2). Increasing the size of the population (comparing the left hand column of figure 2 where N = 20 to the central column where N = 50) favours simpler rules at short attack times, for NN v LCH (at the shortest attack time T = 20) and 3NN v LCH (at attack times T = 20, T = 50 and both variable timings, but not at T = 100, where LCH is favoured by increasing population size). Simple rules are not favoured by increasing population size for NN v 3NN where 3NN is increasing favoured as group size increases (figure 2b), or for NN v LCH, where LCH remains superior at attack times other than T = 20. Increasing the density of the population (right hand column of figure 2) slightly favours the fixation of more complex rules across all rule combinations.

(d) Effectiveness of 7NN

Both 7NN and LCH populations are generally stable against mutants using the alternative rule (prediction 5, figure 3). In LCH populations, 7NN may come to dominate in a small proportion of replicates, especially when predators attack from within the group (figure 3a-c). 7NN populations, on the other hand, are stable except when predators attack from outside the group, when LCH can invade a small proportion of the time (figure 3g-i). Increasing density reduces slightly population stability for both rules (figure 3c and i), but increasing population size benefits only LCH mutants. When the rules begin at equal ratios (figure 3d-f), 7NN fixes in a larger proportion of replicates when predators attack from within the group, while LCH fixes in the majority of simulations when predators attack from outside the group. This is particularly true at increased

344   population sizes (figure 3e) and differences are less marked in denser groups

345   (figure 3f).

346

347   **Discussion**

348   A key motivation for our study was a growing apparent incongruity in the

349   literature. On one hand, much of the theoretical literature on behaviours

350   underlying the selfish herd, including our results here, suggests that cognitively

351   more complex behavioural rules generally outperform simpler rules (Viscido et

352   al. 2002; Reluga and Viscido 2005; Morrell and James 2008; Morrell et al. 2011a).

353   On the other hand, empirically based works suggest that in most taxa studied the

354   behaviours that appear to underlie the formation and especially maintenance of

355   groups appear to be relatively simple, involving responsiveness to only a small

356   number of neighbouring individuals (Couzin and Krause 2003; Ballerini et al.

357   2008b; Ballerini et al. 2008a; Hildenbrandt et al. 2010; Katz et al. 2011; Bode et

358   al. 2011a; Bialek et al. 2012). Here we have been able to offer pointers towards a

359   resolution of this incongruity. In particular we show that the performance of

360   individuals with particular behaviours within a group is strongly positively

361   frequency dependent. Thus under a wide range of the situations explored in this

362   study we find that a mutant with a more complex movement rule can fail to

363   invade a population with a simpler rule, even in circumstances where the

364   complex rule would be evolutionarily stable to reinvasion by the simpler one if it

365   did reach numerical dominance in the population. Hence, if it is the case the

366   simple aggregation-linked movement rules are a common evolutionary

367   intermediate stage in the development of more complex rules, then this strong

15

368   positive frequency dependence may mean that initial flourishing of simple rules

369   stops subsequent evolutionary spread of complex rules.

370

371   Although the idea that complex aggregation rules evolve from simpler ones is

372   highly plausible (Reluga and Viscido 2005), our results point to the considerable

373   benefit this field would gain from increasing our understanding of the evolution

374   the cognitive underpinning of such rules to test this conjecture. Little is known

375   about the relative costs of the different rules in relation to their apparent

376   complexity. Complex rules may carry cognitive costs associated with, for

377   example, information gathering either before or during a predation event, and

378   we suggest there is an urgent need for empirical investigation of the costs and

379   benefits of different movement rules, and for an evaluation of the effects of these

380   costs on the potential for different rules to evolve in nature.

381

382   Despite the pattern of strong positive frequency dependence in rule success, we

383   do find evidence that changing conditions (predator attack strategy, attack

384   timing and population size and density) shift the balance of rule success (Morrell

385   et al. 2011b; Morrell et al. 2011a). In line with our predictions we find some

386   evidence that peripheral attack strategies are more likely to favour the evolution

387   of complex rules (prediction 1, figure 1), and that those complex rules are more

388   likely to be favoured at later attack times (prediction 2, figure 1). We find no

389   evidence, however, that variation in attack timing supports the coexistence of

390   rules within a population (prediction 3, figure 2). We find that increased

391   population size and lower population density may sometimes improve the

392   success of simple rules, although this is not always the case (prediction 4, figure

393   2).

394

395   With respect to our prediction that 7NN and LCH are similarly successful, we find

396   partial support. The positive frequency dependence pattern is particularly strong

397   here, with successful invasions of single mutants occurring at low frequencies

398   under the majority of parameters assessed here. However, we see a particular

399   effect of predator attack strategy here in the equal ratios scenario: LCH

400   outperforms 7NN when predators attack from outside the group, while 7NN

401   succeeds when predators attack from within the group. This likely arises because

402   the more complex a rule is, the more effective it is in allowing individuals to

403   reach the centre of the group (Morrell et al. 2011b), where they are protected

404   from peripheral predators, while simpler rules allow for rapid reduction in

405   individual risk when predators attack from within the group (Morrell & James

406   2008, Morrell et al. 2011a). Thus, 7NN (as the simpler of the two) is favoured

407   when predators attack from within the group, and LCH (as the more complex)

408   when predators attack from outside.

409

410   Notice that our consideration of the relative fitness of different strategies

411   considers only within-group differences in expected fitness – and not between-

412   group heterogeneity in predation risk. This is because a key assumption of the

413   selfish herd hypothesis is that there is no group-level variation in predation risk

414   (Hamilton 1971). Our simulations assumed that predators always attack and

415   attacks are always successful, thus any benefits that one individual in a group

416   gains from cover seeking through the selfish herd comes at the expense of

417   increasing predation risk felt by one or more group-mates. This greatly simplifies

418   the scenarios that need to be explored in evaluating the likely evolutionary

419   trajectory of different behavioural rules. Specifically the per-capita average

420   predation risk of individuals in a group is independent of the distribution of

421   strategies played by individuals within that group, and so in considering whether

422   one strategy will prevail evolutionary, we need only consider the comparison of

423   strategies within a group without the added complicity of differential

424   performance of groups with different strategy mixes. Most importantly, if a

425   complex rule rose to numerical dominance within one group, we would not

426   expect this to allow that group to flourish differentially with respect to groups

427   using a simpler rule.

428

429   Our work also points to other ways in which the behaviours underlying group

430   formation through selfish herd effects might usefully be explored. In common

431   with all previous works we consider situationally-unresponsive rules (Hamilton

432   1971; Morton et al. 1994; Viscido et al. 2002; James et al. 2004; Reluga and

433   Viscido 2005; Morrell and James 2008; Morrell et al. 2011b; Morrell et al. 2011a).

434   That is, a given individual employs the same rule regardless of the situation it

435   finds itself in. However, it is easy to imagine that individuals could modify the

436   rule they use to drive their behaviour according to any number of factors:

437   including the size of the group they are in, population density, their position

438   relative to the group centre, time since the predator was first detected,

439   information transfer through the group (Bode et al. 2011b) and behaviours

440   observed in other individuals. As a simple example, an individual might utilise

441   one rule if it perceives that it is one of the first individuals to detect a predator,

442 and another rule if it perceives that it is one of the later-responders. It would be

443 interesting to explore whether a suite of simple situationally-responsive rules

444 can outperform a single more complex but situationally-unresponsive rule.

445

446 Another interesting issue worthy of further exploration is the ecological

447 robustness of rules. Different taxa will experience differences in the intensity and

448 nature of variation in predation scenarios encountered, but strict uniformity of

449 encounter of the type considered in most of our and previous theoretical

450 situations will not be the norm. That is, in the context of the scenario explored

451 here, a given individual may (over its lifetime) experience variation in the

452 number of individuals with which it might potentially form an aggregation, the

453 initial spatial density of those individuals, the time interval between first

454 detection of the predator and completed attack, and the position of the predator

455 relative to prey individuals at the point of first detection. One possible way to

456 cope with such environmental variability would be to have situationally-

457 responsive rules of the type discussed above, and (for example) behave

458 differently when in a low-conspecific-density situation to a high-density one.

459 However, it may be that sometimes conspecific density (in this case) is difficult

460 for individuals to evaluate, and individuals do best of have a "robust" behavioural

461 rule which performs well when evaluated across the frequency distribution of

462 different environmental circumstances likely to be encountered by individuals.

463 Hence, another exciting avenue for the exploration of behavioural rules

464 underlying selfish herd aggregation behaviours is how environmental variation

465 in the types of predator-prey encounters experienced selects for either

466 situationally-responsive strategies of the type discussed above, or robust

467 strategies that would not be evolutionarily stable in a uniform environment of

468 one fixed type of predator-prey encounter but which offer good performance

469 when evaluated over a frequency distribution of different encounter types.

470

471 One last avenue worthy of exploration is error-tolerance. In common with

472 previous works, our evolutionary simulations assume that individuals utilising a

473 particular rule can gather all the information on conspecifics needed for the

474 implementation of that rule without error. This is likely to be a simplification of

475 reality, and it would be interesting to explore how the introduction of different

476 plausible error structures influences the relative performance of different rule

477 types. For example, it may be that errors in the evaluation of another individual

478 increase with increasing distance of that individual from the focal individual. If

479 errors are common and essentially independent when evaluating information on

480 different individuals this may select for more complex rules that obtain

481 stochastic cancellation of such errors (the "many wrongs principle" – discussed

482 in the literature on in group navigation decisions e.g. Simons 2004; Hancock et al.

483 2006; Biro et al. 2006; Codling et al. 2007; Faria et al. 2009). Additionally, errors

484 may be influenced by environmental factors such as ambient light levels. This

485 may offer the opportunity for empirical testing of theoretical predictions about

486 how behavioural rules might be expected to change in response to increased

487 error rates in information gathering (say as induced experimentally by lowering

488 ambient light levels).

489

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492   based, Steve Moss assisted with additional programming, and Dick James

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494

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601   aggregating strategies in an individual-based model. P R Soc B 274:1637–
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603

604

Figure legends:

606 **Figure 1**: Number of simulations resulting in fixation for the simpler (white

607 shading), more complex (grey shading), or neither (black shading) rule, for 3

608 scenarios (columns) and three movement rule combinations (rows). Each

609 column represents a different invasion scenario: a simple rule invading a more

610 complex population (left hand column, a, d and g), a more complex rule invading

611 a simple population (right hand column, c, f and i), and a situation where both

612 rules begin at equal frequencies (central column, b, e and h). Each row

613 represents a different pairwise combination of movement rules: NN v 3NN (top

614 row, a-c), NN v LCH (middle row, d-f) and 3NN v LCH (bottom row, g-i). In each

615 case the simpler rule is specified first (see table 1). The horizontal dashed line

616 represents the expected proportion of simulations in which the simpler rule

617 would be expected to fix if predation were random with respect to movement

618 rule, ** indicates significant deviation from random expectation at $p < 0.001$, NS

619 indicates no significant deviation from random expectation. Each panel shows

620 the outcome for 3 different fixed attack times (20, 50 and 100 timesteps) when

621 the predator attacks from within the group (left of the thick vertical line) and

622 from outside the group (right of the thick vertical line). Other parameters: N =

623 20, d = 4.

624

625 **Figure 2**: Number of simulations resulting in fixation for the simpler (white

626 shading), more complex (grey shading), or neither (black shading) rule, for three

627 movement rule combinations and when predators attack from within the group.

628 Each panel shows both fixed (left of the thick vertical line) and variable (right of

629   the thick vertical line) attack timings for populations of N = 20 (left column, a, c,

630   e) and N = 50 (right column (b, d, f). Three combinations of rules are shown, both

631   begin at equal frequencies in the population: top row: NN v 3NN, middle row: NN

632   v LCH, bottom row: 3NN v LCH. Results are shown at three different population

633   size/density combinations: left column: N=20, d=4 (baseline), middle column:

634   N=50, d=4 (increased population size) and right column: N=20, d=10 (increased

635   population density). The horizontal dashed line represents the expected

636   proportion of simulations in which the simpler rule would be expected to fix if

637   predation were random with respect to movement rule, ** indicates significant

638   deviation from random expectation at $p < 0.001$, NS indicates no significant

639   deviation from random expectation.

640

641   **Figure 3**: Number of simulations resulting in fixation for the 7NN (white

642   shading), LCH (grey shading), or neither rule (black shading) for pairwise

643   contests between 7NN and LCH, for 3 invasion scenarios (rows) and three

644   population size and density combinations (columns). The left column shows data

645   for N=20, d=4 (a, d, g). In the middle column group size is increased to N=50

646   while keeping d=4, and in the right column density is increased to d=10 while

647   keeping N=20. The top row shows a 7NN mutant against and LCH population,

648   while the middle row shows the results from equal starting frequencies, and the

649   bottom row shows an LCH mutant in a 7NN population. Each panel shows both

650   fixed and variable attack times (x-axis) and predators that attack from inside

651   (left hand columns) and outside (right hand columns) the group (separated by

652   the thick vertical line). The horizontal dashed line represents the expected

653   proportion of simulations in which the simpler rule would be expected to fix if

654   predation were random with respect to movement rule, * indicates significant

655   deviation from random expectation at $p < 0.05$, ** at $p < 0.001$ and NS indicates

656   no significant deviation from random expectation.

657

658

659   **Tables and Figures**

660   **Table 1**: Movement rules

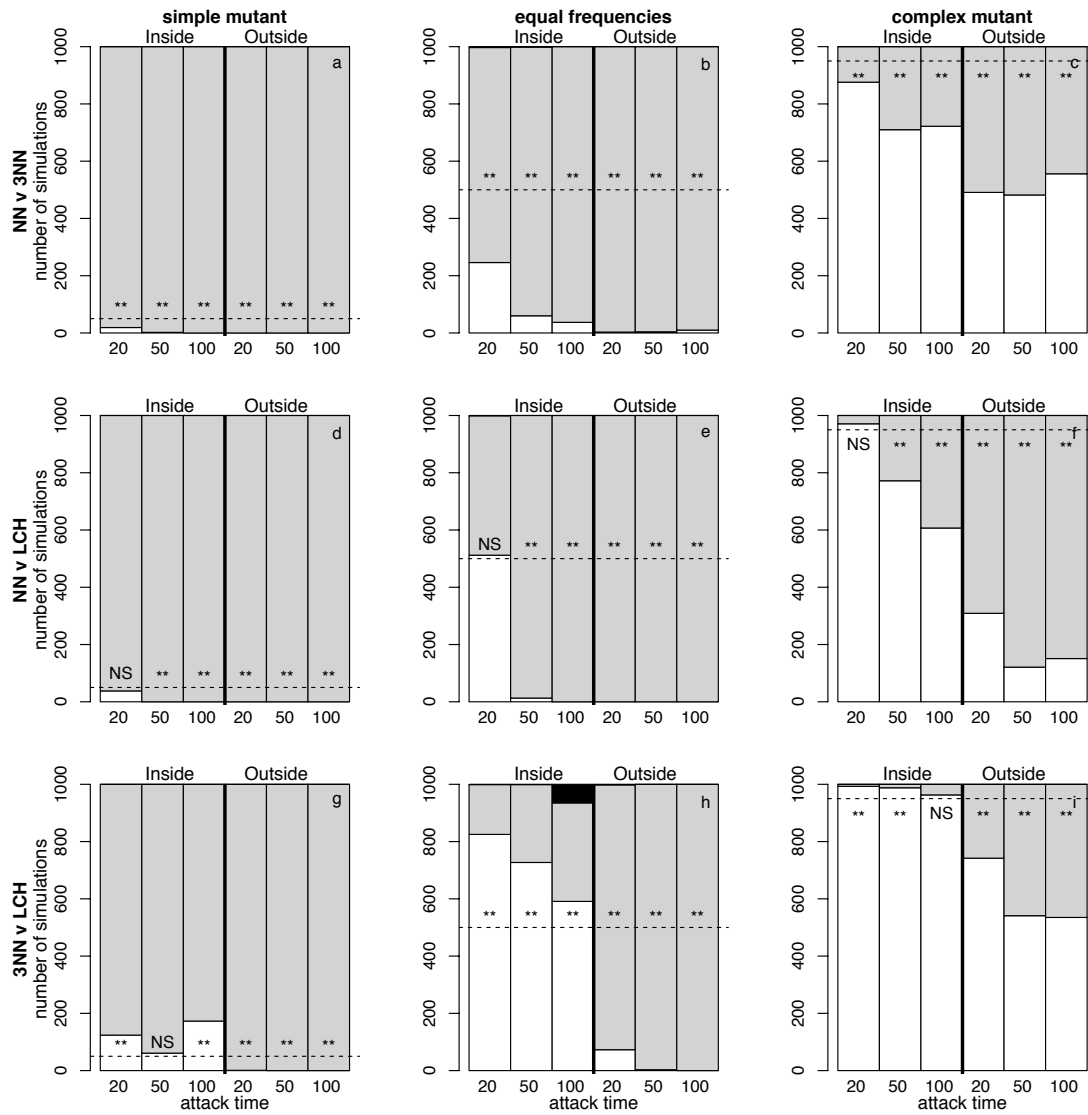| Rule	Description
NN	Each prey individual moves directly towards its closest neighbour (Hamilton 1971). This is the simplest rule we consider, and is used in testing predictions 1-4.
3NN	Each individual moves towards the average location of its three closest neighbours (Morton *et al.* 1994).
7NN	Each individual moves towards the average location of its seven closest neighbours (Morton *et al.* 1994). This rule is used to test prediction 5 only.
LCH	Each individual takes into account the location of up to 20 closest neighbours, although closer individuals have a stronger influence on movement direction, described by the perception function $f(x) = \dfrac{1}{1 + kx}$ where k=0.375 and x is the distance from the focal individual to each neighbour. Individuals thus move towards the densest areas of the group (Viscido *et al.* 2002). This is the most complex rule we consider.

661

662

663   **Table 2:** Summary of predictions and results

664   (Please see the additional document for this table, which is formatted as

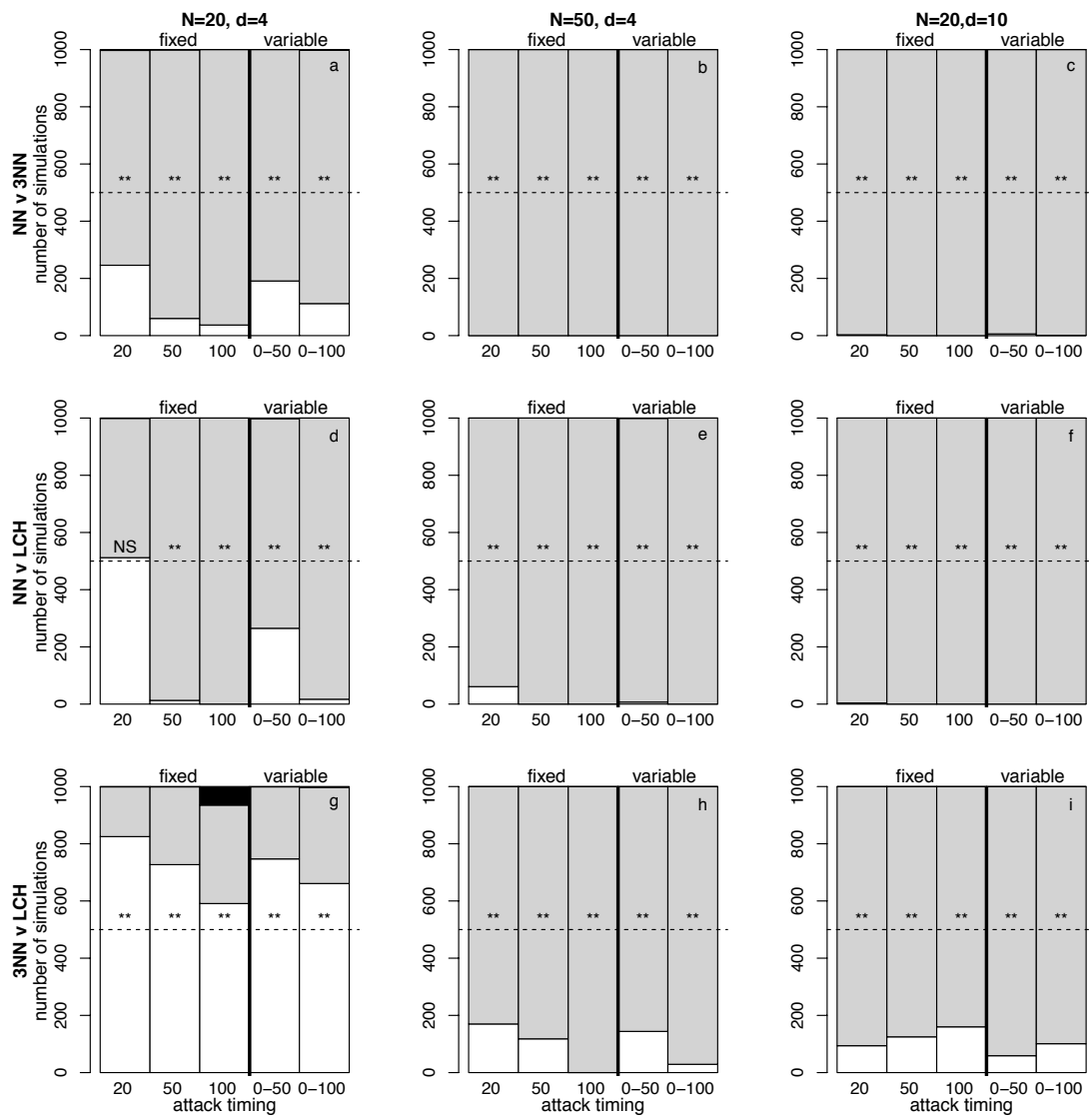665   landscape)

666

667   Figure 1

668

669

670

Figure 2

Figure 3