How does hunger affect convergence on prey patches in a social forager?

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ABSTRACT

Internal state, in this case hunger, is known to influence both the organisation of animal groups and the social foraging interactions that occur within them. In this study we investigated the effects of hunger upon the time taken to locate and converge upon hidden simulated prey patches in a socially foraging fish, the threespine stickleback (*Gasterosteus aculeatus*). We predicted that groups of food-deprived fish would find and recruit to prey patches faster than recently fed groups, reasoning that they might search more rapidly and be more attentive to inadvertent social information produced by other foragers. Instead we saw no difference between the two groups in the time taken to find the patches and found that in fact, once prey patches had been discovered, it was the recently fed fish that converged on them most rapidly. This finding is likely due to the fact that recently fed fish tend to organise themselves into fewer but larger subgroups, which arrived at the food patch together. Hunger has a significant impact upon the social organisation of the fish shoals, and it appears that this has a stronger effect upon the rate at which they converged upon the food patches than does internal state itself.

INTRODUCTION

Social foragers can both search for food directly and monitor the behaviour of group mates, using social information to identify those that have located resources (Beauchamp 2013). If they can gain a share of the resource from the finder then they are expected to try to join them. Indeed, access to socially transmitted information about the distribution of resources might be one of the key benefits of grouping with others for some species (Krause & Ruxton 2002; Beauchamp 2013; Ward & Webster 2016).

Factors such as internal state should affect sensitivity to social cues in group foragers. For example, hungry animals might be expected to be more likely to respond to groupmates that have found food. Such an effect has been seen within flocks of house sparrows (*Passer domesticus*), where individuals with lower energy reserves scrounged more during their first feed of the day (Lendvai et al. 2004; 2006). In zebra finches (*Taeniopygia guttata*), individuals with higher basal metabolic rates tended to scrounge more frequently compared to those with lower basal metabolic rates (Mathot et al. 2009). Hunger can also affect the organisation of groups, including overall group size and the spacing and density of individuals with the group. For example, herring (*Clupea havengus*) maintained on lower rations formed less dense and less polarised schools than they did when daily food rations were greater (Robinson & Pitcher 1989). Food-deprived threespine sticklebacks (*Gasterosteus aculeatus*) spent less time shoaling with the larger of two conspecific groups than did recently fed fish (Krause 1993a), while hungry killifish (*Fundulus diaphanous*) spent more time alone compared to recently fed individuals (Hensor et al. 2003). Hansen et al. (2015a) revealed that hungrier rainbowfish (*Melanotaenia duboulayi*) maintained greater shoaling distances from their groupmates when shoaling. Both of these factors (an individual's sensitivity to social cues and the organisation of the group) can potentially combine to affect both how likely an individual is to be exposed to social information, and also how likely they are to respond to it. Given this, we might predict that social foraging dynamics will differ between food-deprived and recently fed groups of foragers.

In this study we tested this prediction, investigated how hunger affected social foraging behaviour in groups of foraging threespine sticklebacks. Groups of fifteen fish were allowed to explore an arena containing a hidden simulated prey patch. The simulated prey patch was designed so that the fish could not see the prey stimulus until they entered it, but that when a fish that had entered attempted to feed on the prey stimulus its behaviour would be visible to others outside the patch, generating social information that they could detect and respond to. We compared the social organisation and foraging behaviour of groups that had been fed recently and groups that had been deprived of food prior to testing. Based upon previous studies (Hensor et al. 2003; Hansen et al. 2015a) we predicted that in our study food-deprived fish would form smaller units than recently fed fish. We also predicted that the food-deprived fish would locate the hidden food stimulus sooner. This prediction was supported by work showing that hungry fish travel faster, venture further into open areas and explore more widely than do satiated fish (Hansen et al. 2015b). Furthermore, we reasoned that the greater number of separate subunits anticipated in the food-deprived treatment should increase rate at which one or more of the fish encountered the prey patch during the observation period compared to the recently fed treatment, where fewer subunits were expected to form (Pitcher et al. 1982). Finally, we predicted that fish within food-deprived groups, would converge on the food patch more rapidly upon prey patches once they had been discovered.

METHODS

Sticklebacks were collected from the Kinnessburn, St Andrews, UK (56.349°N, 2.7885°S) in October and November 2015 using hand nets. All fish were non-reproductive young-of the-year, and measured 28-32 mm in body length. They were not sexed. They were kept in groups of 25-35 in 90l tanks at a temperature of 8°C. The tanks contained external filters, sand substrate and artificial plants. The fish were fed frozen bloodworm daily at 4pm, prior to being tested. The light: dark regime was 12: 12 hours. Fish were held under these conditions for 4 weeks.

In total, 450 fish were tested, in 30 groups of 15. Of these, 20 groups were used in the main experiment, 10 in each treatment, and a further 10 groups were used in a control condition, described below, with five groups in each treatment. Seven days before being tested, each group of 15 was taken from one of the holding tanks and placed within its own 45l aquarium. Holding conditions were otherwise as described above. Half of the fish were tested in the food-deprived treatment, and were not fed for 72h immediately prior to testing. The other half were tested in the recently-fed treatment. These were fed 24h prior to the trial. Within groups fish were drawn from the same holding tank in order to standardise familiarity, which has been shown to affect social foraging in this species (Atton et al. 2014), but were otherwise randomly allocated to groups. After testing, the fish were placed in different stock tanks and played no further part in this study.

Testing arena and procedure

Experiments took place in a white plastic arena (70x70cm) with 45° sloping sides to minimise wall-following (top of arena: 82 x 82cm, base of arena: 70 x 70cm). The water depth and temperature in the arena were 4.5cm and 8°C. The arena was held within a larger pool (145cm diameter, 30cm tall). In the centre of the arena floor was a square ‘prey patch’ (outer edge: 13x13cm, inner edge: 7.5x7.5cm, 1cm tall) made out of white stone tiles. A red laser pointer (Zeadio ZLR-BO3) attached to a tripod and held 90cm above the right side of the arena was used to provide a prey stimulus, a red dot of light, in the centre of the prey patch. Sticklebacks readily attack red objects and stimuli (Smith et al. 2004). The enclosure-like structure of the prey patch prevented fish from seeing the red laser point until they had entered it. Fish that were outside it however were able to see others as they attacked it (Webster & Laland 2012). Another tripod held a Canon HG10 camera centred 145cm directly above the arena. The whole experimental arena was held within a white plastic shelter measuring 2x2.5m and 1.8m tall which served both to minimise variation illumination and prevent external disturbance. On each wall of the shelter, four lights (linkable LED strip lights, 605lm and 55cm long) were held in pairs 35cm and 75cm above the arena on the walls of the enclosure that surrounded arena. The laser control was accessible via a hatch on the side of the wall and the camera was activated by remote control.

Trials lasted 90min. Each replicate group of 15 fish was placed within the experimental arena and were allowed to acclimate and move freely for 30min. Following this the camera was activated and the fish were filmed for another 30min period. Next, for 20 of the 30 groups (10 recently fed and 10 food-deprived), the laser was switched on, providing the prey stimulus and the trial was filmed for a third 30min period. For the remaining 10 groups (five recently fed and five food-deprived) the laser was left switched off. These trials acted as controls, allowing us to test whether foraging-like behaviour directed towards the laser was indeed the stimulus to which others in the group were attracted.

From each trial we extracted data on shoaling during the middle 30 minute block of the trial, and discovery and recruitment to the prey patch during the final 30 minute block. A prey patch discovery occurred when a fish first entered the prey patch after the laser stimulus has been switched on and began attacking the red point of light. Typically after this occurred, other fish orientated towards and then approached and entered the prey patch too. We refer to these recruitment events as waves. All groups registered at least one wave of recruitment, and the majority registered three. Some groups registered more than this but because sample sizes were low we restrict our analyses to a maximum of three waves per group. If, after all the fish had left the patch following a wave, a fish entered the prey patch again and was joined by others we considered this a new wave. Data were extracted and analysed as follows.

Group size

Group size was recorded at one minute intervals for 30mins after the initial 30min settling phase and prior to the laser stimulus being switched on. All fish within 2 body lengths (approximately 6cm) of one another were deemed to be shoaling (Atton et al. 2012; 2014; Webster et al. 2013). We recorded the number of fish in the largest subgroup and the total number of separate elements (subgroups or lone individuals that were isolated from other fish by more than two body lengths). Provisional inspection of these data when plotted revealed no trends towards changes in group size or number over time (largest subgroup: R^2=0.05 and 0.04 and number of elements=0.03 and 0.02 for the 10 recently fed and 10 food-deprived groups respectively in the experimental treatment). We therefore reduced the data by calculating rolling averages of the largest subgroup size and the total number of separate elements for every five minute block. These were each analysed using a repeated measures GLM with treatment (food-deprived or recently fed) as a categorical covariate.

Time to first locate prey patch

For each of the first three recruitment waves we recorded the absolute time at which the first fish entered the patch and attacked the stimulus after the laser stimulus was switched on. Discovery times were compared between food-deprived and recently fed treatment groups using Cox regressions. A separate regression was performed for each recruitment wave.

Recruitment waves

For each of the first three recruitment waves we compared the number of fish that recruited to the patch using a repeated measures GLM with treatment (food-deprived or recently fed) as a categorical covariate.

We also recorded the rate at which recruitment occurred. For each group we subtracted the arrival time of each subsequent fish to recruit from that of the first fish to enter the patch. These data were then compared using Cox regressions, with one regression performed for each wave.

RESULTS

Overview

In the control groups, although some individual fish did enter the prey patch, they performed no foraging-like behaviours and we saw no recruitment waves to the patch at all. Based on this we concluded that the foraging behaviour of the fish directed towards the laser in the experimental groups was indeed the stimulus to which fish were responding when recruiting. Data from these control trials was not used in the analyses presented below. In the experimental treatment groups we recorded at least one recruitment wave in each group, two waves in nine of the recently fed and seven of the food-deprived groups and three waves in seven groups from each treatment. Prior to the laser being switch on there were no recruitment waves to the prey patch in either treatment among the experimental groups.

Group sizes

The size of the largest subgroup did not change over time (Wilks' λ= 0.55, $F_{(5, 14)}$=2.29, P=0.11), but was larger for fish in the recently fed treatment that it was in the food-deprived treatment ($F_{(1, 18)}$=40.82, P=<0.001, Figure 1a). These was no interaction effect between time and treatment

(Wilks' λ= 0.93, $F_{(5, 14)}$=0.19, P=0.96). While the number of separate elements did not change over time (Wilks' λ= 0.66, $F_{(5, 14)}$=1.43, P=0.27), fewer were seen in the recently fed compared the food-deprived treatment groups ($F_{(1, 18)}$=51.83, P<0.001, Figure 1b). Again, no interaction effect was seen (Wilks' λ= 0.88, $F_{(5, 14)}$=0.36, P=0.86).

Time to first locate patch

Absolute times to first locate the patch (first wave) and times of the onset second and third waves of patch visits did not vary between the two treatments (Wald X^2= 1.82, df=1, P=0.17; Wald X^2= 0.05, df=1, P=0.81 and Wald X^2= 0.04, df=1, P=0.84, Figure 2).

Recruitment waves

In each of the three waves we saw variation between groups in the time taken to recruit to the patch. In the first two waves, but not the third, we also saw an effect of treatment, with fish in the recently fed treatment groups recruiting faster (first wave: treatment, Wald X^2= 5.42, df=1, P=0.002, group, Wald X^2= 133.63, df=18, P<0.001; second wave: treatment, Wald X^2= 7.76, df=1, P=0.005, group, Wald X^2= 46.21, df=3, P<0.001; third wave: treatment, Wald X^2= 0.74, df=1, P=0.39, group, Wald X^2= 65.52, df=1s, P<0.001, Figure 3).

The numbers of fish in each wave fell from first to third (Wilks' λ= 0.36, $F_{(2, 11)}$=15.19, P<0.001, Figure 4). While we saw no difference between the two treatments ($F_{(1, 18)}$=2.10, P=0.16), there was an interaction effect between time and treatment, with fewer food-deprived fish recruiting in the second wave (Wilks' λ= 0.71, $F_{(2, 11)}$=3.45, P=0.05).

DISCUSSION

In both treatments, fish recruited rapidly to the prey patch after one of their group had entered it and begun to attack the prey stimulus, with the majority of the group typically arriving within 30 seconds of the first fish beginning to perform feeding-like behaviour. In the control treatment, in which the prey stimulus was absent, fish that entered the prey patch did not perform feeding behaviour, and no recruitment of other fish was observed. Feeding behaviour has been shown to be attractive to conspecifics in other socially foraging species, such as spice finches (*Lonchura punctulata*) (Coolen et al. 2001). These cues are mostly likely an unintended by-product of foraging behaviour, rather than an active signal (Dall et al. 2005).

Contrary to our predictions, we saw no difference in the time taken for the fish in the food-deprived and recently fed groups to locate the simulated prey patch. Furthermore, when it came to recruiting to the patch after one group member had entered it and begun attacking the prey stimulus it was members of the recently fed, and not the food deprived groups that converged most rapidly. This was the case for the first two recruitment waves, but not for the third, where no difference between treatments was apparent. This unexpected finding might be explained by the sizes of shoals formed by the fish- recently fed fish consistently formed fewer, larger subunits compared to those seen in the food-deprived groups. The greater number of recruits to the prey patch by fish in the recently fed treatment groups might therefore result from the tendency of fish that are already grouping to follow one another arrive at the patch together. This effect can be seen in the survival plots in Figure 3, which show distinctly staggered arrival times for fish in the food-deprived treatment groups compared to the recently fed groups. Such a pattern was seen in an earlier study of social foraging behaviour by Atton et al. (2012), who dubbed it an 'untransmitted social effect'. An experimental design in which the hunger levels of the group members can be varied but group size held constant is needed to fully understand this process. It is not clear how this might be achieved, but training the animals to expect a particular food distribution, discussed below, might be effective. Holding animals at high densities or testing them under heightened predation risk (which promotes grouping in many species) could also achieve this effect.

Earlier studies have also found that food-deprived fish tend to form smaller groups, or that they maintain greater distances between one another when shoaling (e.g. Krause 1993a; Hansen et al. 2015a). This may function to minimise competition, allowing individuals enough time to consume an item of food before others are able to join them and attempt to steal it while satiated animals might prioritise safety in numbers over minimising competition (Ward & Webster 2016). Interestingly, the group sizes formed by foragers may represent some expectation of the pattern of distribution of the food in the environment. Previous experience of dispersed or clustered food has been shown to affect the grouping and searching behaviour of foragers (Ryer & Olla 1995). Whether or not hunger interacts with previous experience to shape grouping behaviour is unclear and warrants further exploration. It seems plausible that animals experienced in foraging for discreet patches of contestable prey might group with others, allowing them to use social information to find food, and that this effect might be stronger in hunger-motivated than in recently-fed foragers. (Prior to the commencement of our experiments, the fish were fed for several weeks in their stock tanks with food being haphazardly spread throughout their tanks during feeding). On the other hand, if foragers are able to easily detect and rapidly close upon others that have located food then they may not need to group closely in order to obtain these benefits.

In both treatments we saw that the number of fish that recruited to the prey patch fell between the first and third wave. This may reflect a habituation response, with the lack of reinforcement, in the form of food, leading some fish to become less likely to visit during later waves. This reduction in recruits occurred faster in the food-deprived treatment. Potentially, hungry individuals may invest more time in gathering social information, and perhaps are better able to discriminate between genuine foraging behaviour performed by group mates and behaviour that looks similar but which yields no prey. This is speculative however, and more work is needed to test these ideas.

Our experiment compared groups where all fish were in a similar state- all hungry or all recently fed. Under natural conditions we might expect to see variation within groups, as well as between them. In mixed state groups, hungry individuals have been shown to move towards the leading edge of the group, where prey encounter rates might be expected to be higher (Krause et al. 1992; Krause 1993b), while in other experiments hungrier individuals have been shown to scrounge more (Lendvai et al. 2004; 2006). Studies that take into account the social structure of groups, by quantifying association networks have used this information to capture the rate and order in which information about prey resource distribution spreads between group members (Aplin et al. 2012; Atton et al. 2013; 2014; Webster et al. 2013; Boogert et al. 2014; Hasenjager & Dugatkin 2016). A similar approach could be applied to study the effects of variation in hunger within groups on associations and other interactions the consequences of these for social foraging.

To summarise, we have shown here that groups of food-deprived sticklebacks did not find hidden (simulated) food patches sooner than recently fed groups, and that once prey patches had been discovered, it was the recently fed fish that converged on the patch most rapidly. This finding is most likely due to the fact that recently fed fish tend to organise themselves into fewer but larger subgroups, which arrive at the food patch together. Internal state affected the social organisation of the fish shoals, and it appears that this had a stronger effect upon recruitment than did hunger itself.

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FIGURE LEGENDS

Figure 1. (a) The number of fish in the largest element (or subgroup) and (b) the number of separate elements (subgroups separated by two or more body lengths) during the second 30 minute phase of the trial. Data shows means +/- 95% confidence intervals. The lines show values point sampled at one minute intervals and the points show the rolling averages for each five minute block of the observation period. The rolling averages were used in the statistical analyses presented in the main text. Black points and lines show data for the recently fed treatment and grey points and lines for the food-deprived treatment.

Figure 2. Survival plots from the Cox regression showing the time for the first fish in each replicate group to locate the prey patch in each of three waves. Black lines show data for the recently fed treatment and grey lines for the food-deprived treatment. Sample sizes are first wave, n=10, 10, second wave n= 9, 7 and third wave n=7, 7 for the recently fed and food - deprived treatment respectively.

Figure 3. Survival plots from the Cox regression showing the time the time taken for the fish in each replicate group to recruit to the prey patch after the first fish had entered it and begun attacking the prey stimulus in each of three waves. Black lines show data for the recently fed treatment and grey lines for the food-deprived treatment. Sample sizes are first wave, n=10, 10, second wave n= 9, 7 and third wave n=7, 7 for the recently fed and food -deprived treatment respectively.

Figure 4. The number of fish that recruited to the prey patch in each replicate group (mean +/- 95% confidence interval). Black points show data for the recently fed treatment and grey points for the food-deprived treatment. Sample sizes are first wave, n=10, 10, second wave n= 9, 7 and third wave n=7, 7 for the recently fed and food -deprived treatment respectively.

Figure 1.

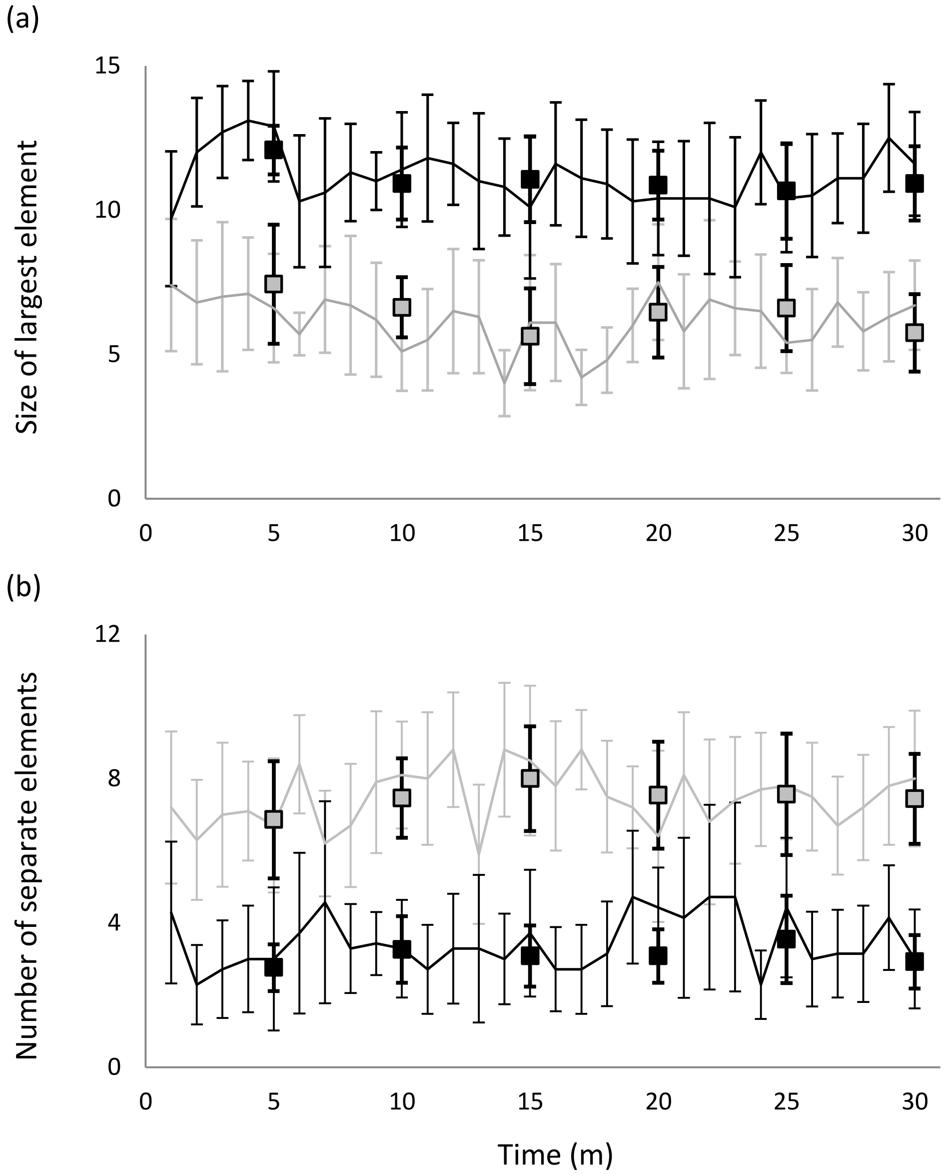

(a)
Size of largest element
0
5
10
15
0
5
10
15
20
25
30
(b)
Number of separate elements
0
4
8
12
0
5
10
15
20
25
30
Time (m)

Figure 2.

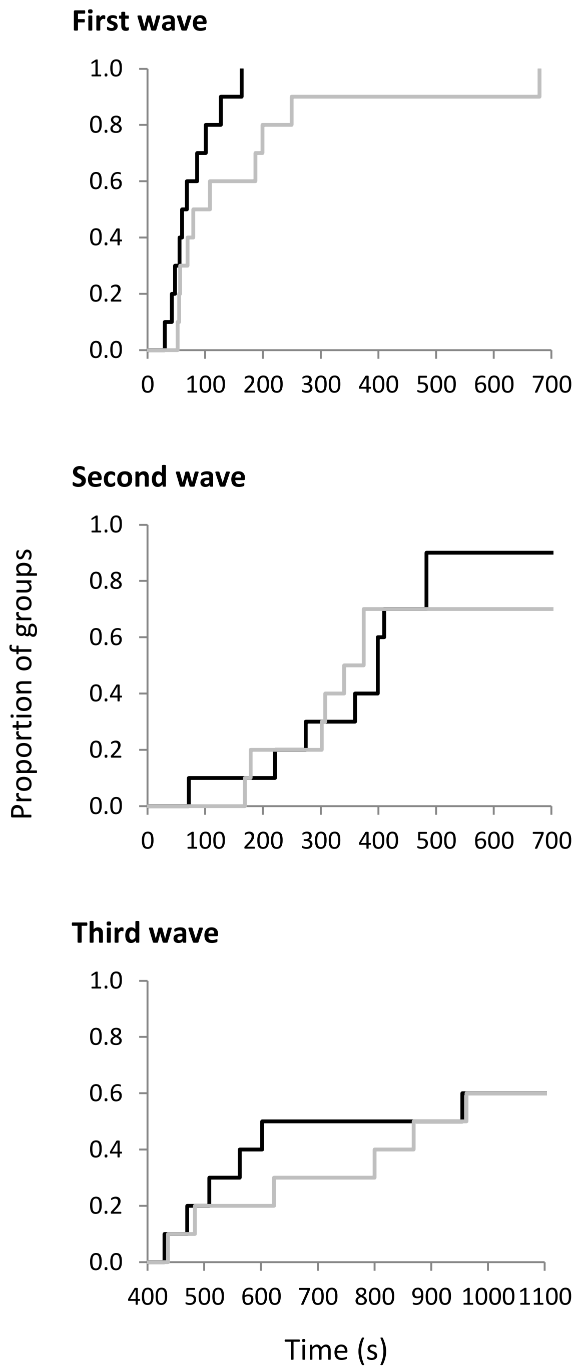
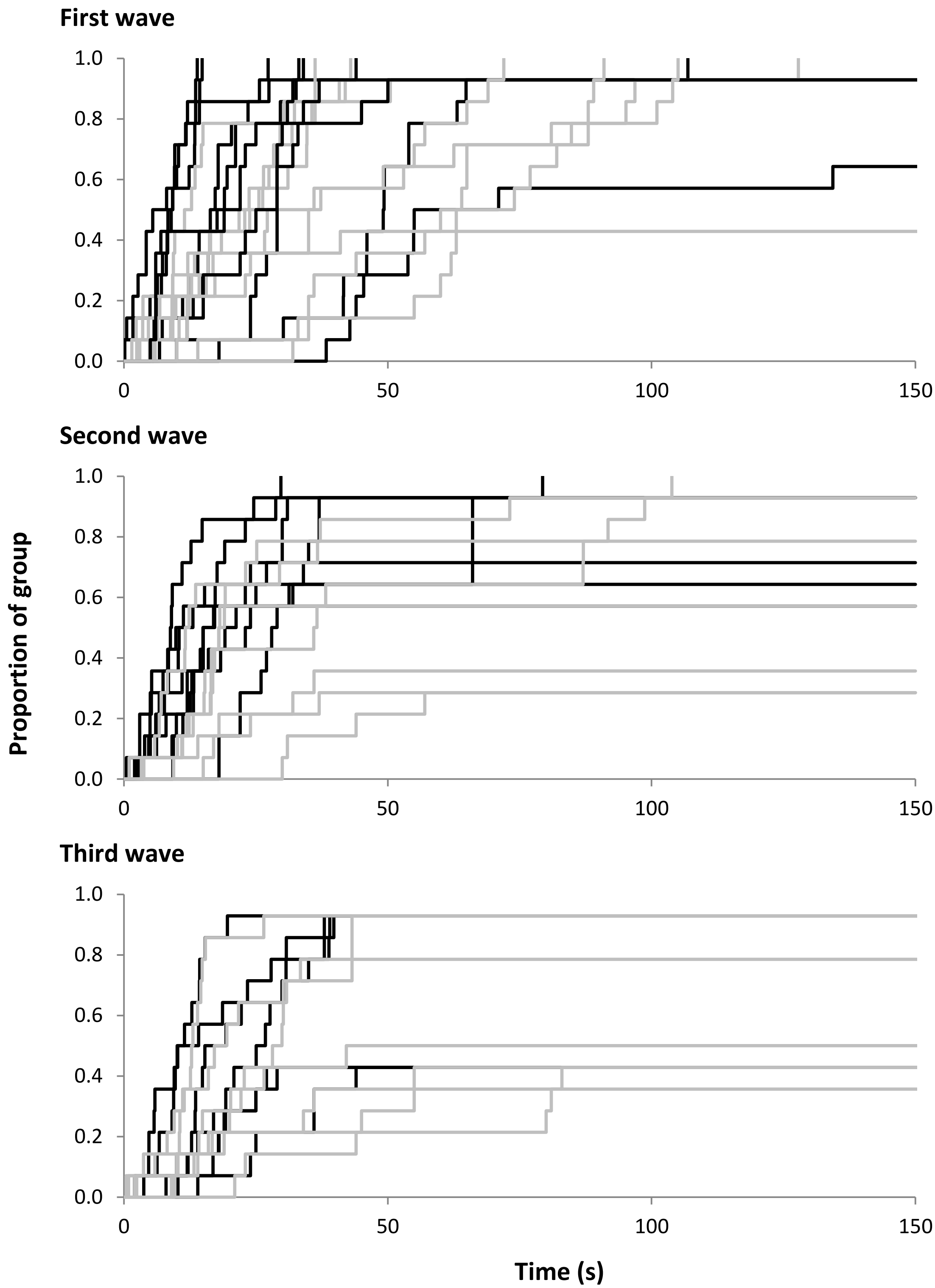

First wave
1.0
0.8
0.6
0.4
0.2
0.0
0 100 200 300 400 500 600 700
Second wave
Proportion of groups
1.0
0.8
0.6
0.4
0.2
0.0
0 100 200 300 400 500 600 700
Third wave
1.0
0.8
0.6
0.4
0.2
0.0
400 500 600 700 800 900 1000 1100
Time (s)

Figure 3.



First wave
Second wave
Third wave
Proportion of group
Time (s)
1.0
0.8
0.6
0.4
0.2
0.0
0
50
100
150

Figure 4.