



The effect of group size and tutor-to-observer ratio on socially learned antipredator responses in woodfrog tadpoles



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ARTICLE INFO

Article history:

Received 14 November 2014
Initial acceptance 19 January 2015
Final acceptance 28 January 2015
Available online 9 April 2015
MS. number: A14-00927R

Keywords:

antipredator behaviour
group living
information transfer
learned predator recognition
Lythobates sylvaticus
optimal group size
social learning
tutor-to-observer ratio
woodfrog

It is well established that living in a social group provides animals with considerable antipredator benefits, including the ability to socially learn the identity of unknown predators by observing the actions of others. There has been considerable interest in understanding optimal group size, but surprisingly, little work has focused on understanding how different group composition (i.e. group size and tutor-to-observer ratio) influences the acquisition of information about predators. Here, we manipulated the composition of woodfrog, *Lythobates sylvaticus*, tadpole groups and found that the ratio of tutors to observers, but not group size, influenced the intensity of learned predator recognition. This finding is in line with theoretical models of the spread of information in social groups but contrasts with some empirical work on information transfer in fish shoals. We suggest that such a discrepancy could arise from the degree to which different animals rely on coordinated group evasion behaviour to avoid capture.

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Living in social groups reflects a fine balance whereby individuals gain considerable benefits while concurrently paying costs (Krause & Ruxton, 2002). Faster food finding, the ability to exhibit group evasion behaviours and the reduced cost of finding potential mates are balanced against increased competition for food and mates, and an increased likelihood of disease and parasite exposure among other things (Coates, 1980; Couzin, Krause, Franks, & Levin, 2005; Griffin, 2004; Poulin, 1991). A key advantage of group living is the ability to learn information from knowledgeable conspecifics (Galef & Laland, 2005; Wakano, Aoki, & Feldman, 2004). Brown and Laland (2003) defined social learning as any incidence in which individuals acquire new information about their environment via observation of, or interaction with, other animals or their products. Individuals learn information about the location and profitability of food patches (Lachland, Crook, & Laland, 1998; Reader & Laland, 2003). They learn characteristics of high-quality mates (Dugatkin, 1992; White & Galef, 2000) and the identity

and threat level of unknown predators (Crane & Ferrari, 2013; Griffin & Evans, 2003; Mathis, Chivers, & Smith, 1996). Indeed, when prey watch conspecifics respond strongly to predator cues, they learn that the predator represents a high threat, whereas if they observe conspecifics showing a weak response, they learn that the predator represents a mild threat (Ferrari, Trowell, Brown, & Chivers, 2005).

For any particular individual, the relative costs and benefits of living in a group will vary based on group size, and will most likely not be the same for all individuals in the group (Brown, 1982; Creel & Creel, 1995). An increase in group size, for example, could cause greater dilution of risk and provide prey with an earlier detection of nearby threats (Mathis & Chivers, 2003). However, larger groups could be attacked more frequently than smaller groups. This means that for any individual, the cost/benefit trade-off associated with being in groups of different size should be variable, taking into account how important dilution and group evasion are to avoid predators compared to how much competition reduces foraging gains or how likely an individual is to be exposed to a disease.

Few studies have specifically addressed how group dynamics (defined here as group size and ratio of tutors to observers) influences social learning of predators. Following the logistic

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contagion model (Lefebvre & Giraldeau, 1994), we predicted that with a greater proportion of individuals that know the identity of a predator, the easier it should be for individuals to acquire information by observing the actions of others. In accordance with this model, Ferrari and Chivers (2008) showed that a high tutor-to-observer ratio facilitated greater learning of predators by boreal chorus frog tadpoles, *Pseudacris maculata*. In stark contrast, Vilhunen, Hirvonen, and Laakkonen (2005) showed that social learning in Arctic charr, *Salvelinus alpinus*, only occurred when there was a smaller proportion of experienced tutors to naïve tutors. These contradictory results could be explained if we consider how group size influences antipredator behaviour. Ferrari and Chivers (2008) used groups of seven, whereas Vilhunen et al. (2005) used groups of 20. As group size increases, each individual in the group has a reduced chance of being captured, and consequently should show a weaker response to the predator. This fact could make it very difficult for the observers to learn the identity of predators from large groups of informed tutors.

Both Ferrari and Chivers (2008) and Vilhunen et al. (2005) kept group size constant in their studies and hence only manipulated tutor-to-observer ratio. However, another study on fish (damselfish: Manassa, McCormick, Dixon, Ferrari, & Chivers, 2014) kept tutor numbers constant while manipulating the number of observers, effectively manipulating both group size and tutor-to-observer ratio concurrently. This study showed effective social learning of predators, but failed to find any effect of group composition (group size or tutor-to-observer ratio). To gain a full understanding of the effects of group composition on transmission of social information, we need studies that manipulate both group size and the ratio of tutors to observers. Here, we do just this, using a well-characterized model of social learning in amphibians (Chivers & Ferrari, 2014; Ferrari, Messier, & Chivers, 2007) in which woodfrog, *Lithobates sylvaticus*, tadpoles act as our prey species and tiger salamanders, *Ambystoma tigrinum*, act as our predators. We examined social learning under three different group compositions (i.e. with a tutor-to-observer ratio of 2:2, 8:2 and 8:8).

The antipredator response of tadpoles is to reduce activity (Chivers & Mirza, 2001), and hence it is likely this reduction in tutor activity that is used by observers to learn to recognize the predator. The greater the reduction in activity by the tutors, the greater the learning we should see in the observers. Chivers and Ferrari (2014) demonstrated that tutors that were fed restricted diets had much higher activity levels than those fed ad libitum food resources. Their high activity made them more conspicuous to nearby conspecifics, and hence their overall greater reduction in activity caused them to be much more efficient as tutors. Our predictions about the importance of group size and tutor-to-observer ratio need to consider both the absolute and proportional reduction in activity as factors important in facilitating learning. For example, if the proportional change in activity is the key driver of the intensity of learned recognition, then we would expect tadpoles in the 2:2 group to show the same learning as those in the 8:8 group, while tadpoles in the 8:2 group should learn to respond to the predator with a stronger response. In the first two groups, a total of 50% of tadpoles would be responding whereas in the latter group a total of 80% of tadpoles would be responding (i.e. reducing their movement). If it is not the proportional reduction in activity but rather the absolute reduction in activity that facilitates stronger learning, then the 2:2 group should show reduced learning compared to the 8:2 or 8:8 groups. Finally, if it is both the proportional and absolute reduction in activity combined that is important, then we predicted that the 8:2 group would show the strongest learned responses, the 2:2 group the weakest response and the 8:8 group an intermediate response.

METHODS

Ethical Note

All work reported here was conducted in accordance with the University of Saskatchewan Animal Care protocol number 20060014. We conducted all of the procedures outdoors, allowing animals to experience natural conditions (temperature, sun exposure, photoperiod, etc.). Approximately 3 weeks prior to starting the experiment, we filled a 1900-litre tub with well water and seeded it with aquatic plants (sedges, slough grasses) and plankton from a local pond. This procedure ensured that the water that would be used in our experiment contained natural pond odours, but lacked any cues from potential predators. This water was used as the water source for the entire experiment.

We prepared the predator odours from four adult tiger salamanders (range 11–14 cm snout–vent length). These salamanders were originally caught in a Saskatchewan pond and were held in captivity for 4 years for use as cue donors in numerous experiments. Salamanders were fed a diet of earthworms for 2 weeks prior to odour collection. Odours were obtained by soaking individual salamanders in 1.5 litres of well water for 24 h and then freezing the water until needed. We randomly mixed the odour from two salamanders for use in each trial.

We used dip-nets to collect larval woodfrogs (Gosner stage 25; Gosner, 1960) from several ponds in south-central Alberta for use in our experiments. All ponds were within 1 km of each other. Our previous work has established that naïve tadpoles collected from these ponds do not show antipredator responses to salamander odour, but they can be trained to recognize them (Chivers & Ferrari, 2014; Ferrari & Chivers, 2009). The tadpoles were held in large pools for 2 days prior to the start of the experiment. They fed on algae present in the pool and were supplemented with alfalfa pellets and Tetramin flakes. To condition tutor tadpoles to recognize salamanders as predators (see phase 1 below), we needed to prepare an alarm cue solution from crushed tadpoles. We could not anaesthetize the tadpoles prior to crushing them because we did not want to contaminate the alarm cue solution with anaesthetics. However, as noted by Chivers and Ferrari (2014), the entire body of the tadpoles are completely crushed into a paste by the mortar and pestle in less than 1 s and hence represent a humane method of euthanasia. At the end of the experiment the tadpoles were returned to their natal pond.

Experimental Protocol

Our experiment followed a well-established protocol to test for social learning (Chivers & Ferrari, 2014; Ferrari & Chivers, 2008; Ferrari et al., 2007). This protocol consisted of a three-step process. Initially, we conditioned groups of tadpoles to recognize salamander odour as a threat (predator-experienced tutors) and had another group undergo a control protocol (predator-naïve tutors). In the second phase, these naïve and experienced tutors were then paired with naïve observer tadpoles and exposed to predator odour. Observers that are paired with the naïve tutors should not learn to recognize the predator as dangerous while those that are paired with experienced tutors should learn the salamander as dangerous. During this conditioning phase, we manipulated both group size and ratio of tutors to observers. The third step tested observer tadpoles alone for learned recognition of the salamander cues. Here, we exposed observer tadpoles from phase 2 to either salamander odour or a control of pond water. Our experiment can be summarized as a $2 \times 3 \times 2$ factorial design, where we had two types of tutors (naïve and experienced) that were maintained under three group compositions (tutor-to-observer ratios of 2:2, 8:2

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