Animal Behaviour 83 (2012) 1469–1476

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Individual sociability and choosiness between shoal types

Julien Cote [a,b,c,*], Sean Fogarty [c], Andrew Sih [c]

[a] CNRS, EDB (Laboratoire Evolution et Diversité Biologique), UMR 5174, Toulouse, France
[b] Université de Toulouse UPS, Laboratoire Evolution et Diversité Biologique, Toulouse, France
[c] Department of Environmental Science and Policy, University of California, Davis, U.S.A

ARTICLE INFO

Article history:
Received 19 September 2011
Initial acceptance 13 December 2011
Final acceptance 5 March 2012
Available online 14 April 2012
MS. number: 11-00745R

Keywords:
behavioural syndrome
density
Gambusia affinis
group size
mosquitofish
schooling
sociality

In social species, individual and group fitness and social dynamics in groups often depend on group size and on the group's social composition (e.g. the mix of personality types within groups). In turn, the size and social composition of groups is an emergent outcome of the grouping tendencies of individuals. While grouping behaviour has often been studied at a species level, within-species variation in grouping tendency has rarely been studied. We examined the role of personality type in shoaling preferences in a social fish, the western mosquitofish, *Gambusia affinis*. After scoring individuals for their social personality types (sociability), we gave individuals the choice to associate with shoals that differed in size and in the average sociability of individuals in the shoal. Shoal preferences depended on both the individual's sociability and on shoal size and composition in sociability types, and on the interaction between the individual's sociability and shoal size and composition. On average, fish preferred large to small shoals and groups made up of social individuals to groups made of asocial individuals at least when shoal size was small. Individual sociability types were linked to the time individuals spent far from any shoal and to consistent differences in choosiness about social contexts. Asocial individuals shoaled less and swam more between shoals than social ones, but preferred large shoals during the short time that they shoaled. These results can help explain patterns of group size and composition and individual and population-level personality-dependent dispersal.

In many taxa, individuals form more or less cohesive groups (swarms, herds, flocks, shoals or schools; Pulliam & Caraco 1984; Krause & Ruxton 2002). Individuals benefit from living in social groups through social information that aids in food localization, reduced predation risk (confusion/dilution/vigilance effects) or higher success in finding mates (Godin et al. 1988; Pitcher & Parrish 1993; Krause & Ruxton 2002). However, social groups also impose costs on individuals including stronger competition (e.g. for food, mates), increased disease transmission and predator attraction (Cote & Poulin 1995; Krause & Godin 1995). Group size can thus have major impacts on individual fitness and group dynamics. Importantly, group size is not a random property, but is instead an emergent outcome of the grouping tendencies of individuals in the population. Larger groups form if individuals generally exhibit stronger grouping tendencies. A key individual trait that can influence grouping tendencies is the individual's personality type (aka behavioural types), where some individuals are consistently more bold, aggressive or sociable than others (Dall et al. 2004; Sih et al. 2004; Bell 2006; Reale et al. 2007, 2010; Sih & Bell 2008). For example, by definition, more sociable individuals should be more likely to join groups than asocial ones. Or, because being in a social group can reduce predation risk, more cautious individuals might exhibit a stronger preference for being in a group (Budaev 1997; Ward et al. 2004; Leblond & Reebs 2006).

Beyond group size, another key group property is the mix of personality types in the group, which can also influence the behaviour and fitness of each individual in the group (e.g. Magnhagen & Bunnefeld 2009). For example, the aggressiveness and sociability of group members can change the cohesion of a group and in turn its efficiency as protection against predators. Similar patterns can be expected for the average activity, boldness or exploratory behaviour of a group. Furthermore, the benefits of group size or of the group's social composition can depend on the personality of the focal individual. For example, interactions between the individual's personality, the group's mix of personality types and group size can change the balance between food localization and competition within a group, a major driver of social grouping.

Given that the benefits of being in a group depend on group size, the group's mix of personalities and the personality type of each individual, a key issue that has rarely been studied is to understand how an individual's personality type affects its group size

* Correspondence: J. Cote, CNRS, EDB (Laboratoire Evolution et Diversité Biologique), UMR 5174, 118 route de Narbonne, 31062 Toulouse Cedex 9, France.
E-mail address: julien.cote@univ-tlse3.fr (J. Cote).

0003-3472/$38.00
doi:10.1016/j.anbehav.2012.03.019

preference or its preference for groups with a particular mix of personality types (e.g. Saltz 2011).

We studied the role of personality type in shoaling preferences in a social fish, the western mosquitofish, *Gambusia affinis*. In many fish species, individuals shoal for at least part of their life (Pitcher & Parrish 1993). Shoaling fish often prefer to group with larger shoals made of similar, healthy or familiar individuals (Pitcher & Parrish 1993; Hoare et al. 2000; Krause et al. 2000a, b; Ward et al. 2002; Lee-Jenkins & Godin 2010). Individual personality types differ, however, in their shoaling tendencies. Bold fish are expected to shoal less or to adopt positions at the exterior or at the front of shoals where predation risk is higher (Budaev 1997; Ward et al. 2004; Leblond & Reebs 2006). Bold individuals that are more risk prone in order to forage more have higher foraging rates (Biro & Stamps 2008) and are thought to adopt a producer strategy in a social group (Kurvers et al. 2010). In three-spined sticklebacks, *Gasterosteus aculeatus*, bold individuals indeed exhibit a weaker tendency (relative to shy ones) to shoal, and are more likely to adopt a producer strategy (while shy individuals are scroungers), and thus are more likely to lead shoal movements where shy individuals follow bold ones (Ward et al. 2004). The mix of personality types in a shoal also influences outcomes, including the distribution and intensity of social interactions (Pike et al. 2008), the foraging success of all shoal members (Dyer et al. 2009) and even dispersal from the group (Cote et al. 2011). While the above-cited studies showed individual variation in shoaling tendency and the role of personality types in this variation, it is less well known how shoal composition in personality types affects individual shoal preferences in interaction with the individual's own personality type (Harcourt et al. 2009).

In western mosquitofish, we have repeatedly found strong and consistent individual differences in shoaling tendency (Cote et al. 2010b, 2011). In this species, we term an individual's shoaling tendency its sociability (individual variation in attraction to others; Budaev 1997; Cote & Clobert 2007; Reale et al. 2007; Rodriguez-Prieto et al. 2010). In contrast to some other species, mosquitofish that are bolder in a novel environment tend to shoal more and not less (higher sociability). Moreover, individual dispersal behaviour is negatively related to individual and population sociability levels (Cote et al. 2010b, 2011). We studied how individual choosiness for shoals of different size and composition in sociability types depends on individual sociability type. Two well-established ideas that we tested are that, on average, individuals in highly social species generally prefer to join larger shoals, and that in particular more sociable individuals prefer to join larger shoals. More novel hypotheses that we tested are that shoal choice also depends on the mix of personality types in the shoal, and, furthermore, that shoal choice might depend on an interaction between the individual's personality and the group's size or composition.

Finally, we examined the intuitively reasonable, yet rarely quantified possibility that individuals are consistent not just in their social preferences, but also in the strength of their choosiness (Sih & Bell 2008); that is, some individuals are consistently choosier than others about their social groups. The notion that individuals with different personalities might differ in their social group choices leads to the possibility of individual social specialization, which has been mentioned in several review articles (Bergmüller & Taborsky 2010; Krause et al. 2010; Reale et al. 2010), but rarely quantified (Bergmüller et al. 2010).

We first measured individual sociability level (attraction to a large shoal), a behaviour that has been shown to be consistent over time. Using some of these fish, we created small and large shoals made of only social or only asocial individuals. Then, using the remaining fish, we looked at the relationship between individual preferences for these different shoal types and the focal individual's own sociability type. We predicted that (1) for higher safety, fish should generally prefer larger shoals over smaller shoals, and shoals made of social individuals over those made of asocial fish, (2) asocial fish should consistently shoal less regardless of the shoal's size or mean personality type and (3) asocial fish should be consistently less choosy than more sociable fish about shoal size or social composition.

METHODS

Six hundred mosquitofish (ca. one-third males, two-thirds females) were transported from the Sacramento-Yolo Mosquito and Vector Control District to the Center for Aquatic Biology and Aquaculture (CABA), University of California, Davis, U.S.A. in March 2010. At the Sacramento-Yolo Mosquito and Vector Control District, we captured fish with fish nets from a large rearing pool and brought them to CABA in coolers provided with bubblers. Fish were held in groups of 60 in 80-litre glass aquaria with recirculating pumps and filters on a natural photoperiod (for late April, 14:10 h light:dark) at 22 °C and fed Tetramin flakes ad libitum. Mosquitofish were acclimated to these conditions for >1 month prior to behavioural observations, which were carried out in April 2010.

To give focal fish a choice between 'stimulus shoals' that differed in their group properties, we first created 16 stimulus shoals of two different sizes composed of fish of two different sociability types (see below). Then, over a 1-week period, we assayed 80 fish (block 1) for their sociability (using six other shoals, see below) and then for their shoal preferences. The following week, we repeated these assays with 80 additional fish (block 2). Only females were used for this experiment to remove variation from sexual interactions.

Measuring Sociability

Following methods from our previous studies (Cote et al. 2010b, 2011), we assayed individual sociability by taking individuals out of their home tanks and placing them individually in 5.7-litre plastic tubs, with 2.5 litres of well-water, and a 12 cm piece of 5 cm diameter PVC pipe that served as a refuge. This takes focal individuals away from their familiar groups where their attraction to the group may depend on a history of social interactions (which differs for different individuals) and instead places each individual in a standardized situation. One day later, we recorded the amount of time spent near a shoal of conspecifics in a standardized assay (Ward et al. 2004; Cote et al. 2010b, 2011). The experimental arena was an aquarium (25 × 50 cm and 30 cm high filled to a depth of 13.6 cm with 17 litres of well-water) divided into three compartments (two small and one large centre compartment) using two transparent glass partitions 12.5 cm away from each side wall. One compartment held a stimulus shoal, while the other was left empty. The partitions allowed visual but not physical or olfactory interaction between the shoal and the focal individual. We used six predetermined stimulus shoals each comprising 14 randomly chosen mosquitofish (seven females, seven males). Although we did not assay or control for the personality types of the individuals in these shoals, using a relatively large shoal size ensured that shoals were all similar in average personality type. One of six predetermined stimulus shoals was introduced to one of the small compartments of each of six aquaria 1 h before experiments began while the other small compartment was left empty as a control. After 1 h, the focal fish was introduced into the centre of the larger compartment and allowed to acclimate for 10 min. Previous work showed that after 10 min of acclimation, fish no longer showed signs of stress (e.g. constant swimming along the sides of the tank) associated with being moved, and that behaviour was stable over the next 10 min (e.g. sociability scores for the 5 min after