Available online at www.sciencedirect.com

ScienceDirect

Prior association reduces kleptoparasitic prey competition in shoals of three-spined sticklebacks

MICHAEL M. WEBSTER & PAUL J. B. HART

Department of Biology, University of Leicester

Familiarity within groups of animals is thought to consolidate social dominance hierarchies and reduce the frequency of contests over prey. For many species in nature, however, group composition is affected by dynamic fission–fusion events, and it is likely that not all individuals within a group will be familiar with each other at any given time. This means that the advantages of associating with familiar conspecifics may not be available to all individuals within a group. We investigated this effect by constructing shoals of three-spined sticklebacks, *Gasterosteus aculeatus*, that contained two familiar fish and four further individuals that were unfamiliar both to each other and to the familiar pair. We observed that, per capita, familiar pair members engaged in fewer kleptoparasitic prey contests with each other than they did with unfamiliar members and than unfamiliar members did with each other. We saw no differences in the mean proportion of prey consumed by familiar and unfamiliar individuals, nor any differences in tendency to initiate contests over prey. Our findings suggest that there are indirect benefits to be gained from foraging with familiar individuals and we discuss them in the context of adaptive trade-offs and social network theory.

Social foragers bear lower per capita vigilance and predation risk costs and stand to gain from potentially higher prey detection rates compared to those foraging alone, but are often compelled to compete among themselves more vigorously for prey to maximize their share of it. If individuals are able to discriminate between groupmates with whom they have recently interacted, and subsequently to modify their own behaviours towards them, then they should be better able to balance these costs and benefits (Barnard & Burk 1979; Krause & Ruxton 2002).

This effect is termed familiar recognition and has been widely studied in shoaling fish (Griffiths 2003; Ward & Hart 2003; Griffiths & Ward 2006). Rates of agonistic prey competition are lower and dominance hierarchies more stable in groups composed of familiar members than in groups where individuals are unfamiliar with each other (Höjesjö et al. 1998; Utne-Palm & Hart 2000;

Seppa et al. 2001). Furthermore, familiar shoals may forage more efficiently (Swaney et al. 2001), transfer information and innovative behaviours more rapidly among members (Laland & Williams 1997; Lachlan et al. 1998), and benefit from lower predation risk through greater shoal cohesion (Chivers et al. 1995).

Numerous laboratory studies have revealed that in a variety of fish species, individuals preferentially associate with familiar over unfamiliar conspecifics (reviewed in Griffiths 2003). In nature, most free-ranging fish shoals are open in structure with their composition changing subject to fission–fusion processes. They tend to be highly sorted by such factors as species, phenotype and parasite load (Krause et al. 1996; Hoare et al. 2000), but evidence for familiarity as an important shoal-structuring mechanism remains equivocal. Klimley & Holloway (1999) described a high level of shoal fidelity in pelagic yellowfin tuna, *Thunnus albacares*, while Griffiths & Magurran (1997a) and Ward et al. (2002) described stable association preferences between individuals in channel-bound populations of guppies, *Poecilia reticulata*, and three-spined sticklebacks, *Gasterosteus aculeatus*, respectively. Conversely, studies of yellow perch, *Perca flavescens* (Helfman 1984),

Correspondence and present address: M. M. Webster, Department of Biology, University of St Andrews, St Andrews, Fife KY16 9TS, U.K. (email: mike.m.webster@g.mail.com). P. J. B. Hart is at the Department of Biology, Adrian Building, University of Leicester, Leicester LE1 7RH, U.K.

banded killifish, *Fundulus diaphanous* (Hoare et al. 2000), guppies (Godin et al. 2003) and red-bellied piranha, *Pygocentrus nattereri* (Magurran & Queiroz 2003) reported no evidence for shoal fidelity or association preferences for familiar individuals.

This apparent difference may be attributed to the fact that while these shoaling preferences are seen to arise over several days or weeks in the laboratory (e.g. Griffiths & Magurran 1997b; Croft et al. 2004a), the composition of free-ranging shoals often changes over a period of seconds to hours in nature, as individuals leave and join groups under the influence of temporally dynamic predation, foraging or sexual pressures (Hoare et al. 2000; Croft et al. 2003a). Despite this instability, research in a range of social vertebrate species suggests that even where overall group fidelity is low, small groups of individuals may still persistently associate with one another, giving rise to social association networks (Muller & Thalmann 2000; Lusseau 2003; Lusseau & Newman 2004; Vonhof et al. 2004; Croft et al. 2004b; Cross et al. 2004, 2005). These individuals may still benefit from the advantages of associating with familiar conspecifics, even when group composition is constantly changing around them.

Our aim in this study was to investigate whether familiar fish within an otherwise unfamiliar shoal could benefit from the effects of reduced prey competition and associated agonistic behaviours previously seen in studies where all individuals were equally familiar to one another. We created experimental shoals, embedding familiar pairs of three-spined sticklebacks into groups of unfamiliar conspecifics. We predicted that during foraging trials, members of familiar pairs would contest prey with each other to a lesser extent and consume a greater share of the prey resource than their unfamiliar conspecifics.

METHODS

Fish Collection and Housing

We collected 120 subadult three-spined sticklebacks (27−30 mm standard length) from a 500-m stretch of Stonton Brook, Leicestershire, U.K. in March 2005. They were captured with dip nets and were transported in four 40-litre containers by road for 40 min to the laboratory. There they were distributed equally between 12 chemically and visually isolated holding tanks (40 × 25 cm and 25 cm high, water depth 20 cm, fine sand substrate 1 cm deep, flow-through rate approximately 0.1 litres/min). The water temperature and light:dark regimes were held at 11°C and 12:12 h, respectively, over the duration of the study. Two days after capture these fish were tagged, as described below. The fish were held in these tanks for a further 30 days before the experiments. They were fed frozen chironomid larvae once per day.

Tagging Procedure

To be able to recognize individuals within experimental groups we gave each fish a fluorescing Visible Implant Elastomer (VIE) tag (Northwest Marine Technology Inc.,

Shaw Island, Washington, U.S.A.), which has been used to identify individual small fish in other behavioural experiments (Croft et al. 2003b; Ward et al. 2004a). The fish were first cooled in iced water for several minutes instead of being anaesthetized, as anaesthesia can cause high levels of stress and mortality in small fish (personal observation). A tag (ca. 3 × 0.4 mm) was implanted, with a 0.4-mm-diameter needle, into the dorsal surface of each fish.

In half the trials we placed a single yellow tag in front of the first dorsal spine in familiar fish or behind the third dorsal spine in unfamiliar fish. In the other half of the trials these positions were swapped, to control for any effects of tag positioning. Immediately after tagging, fish were transferred to aerated water at 11°C to recover. These tags had no obvious adverse effects upon the health or behaviour of the fish. They were retained and remained visible when fish were viewed side on for the duration of the study.

Experimental Groups

The fish were deprived of food for 24 h to increase feeding motivation. We then created 20 experimental groups of six fish per group. One pair of fish was taken from each of the first four holding tanks and placed into its own chemically and visually isolated holding tank. These pairs of fish had been housed together for 32 days previously; we termed these individuals familiar. To each familiar pair we added four fish from the remaining eight holding tanks. No two of these were drawn from the same holding tank, and these fish had previously been held separately both from each other and from the familiar pair. We termed these individuals unfamiliar. Thus we created 20 experimental groups comprising six individuals, two of whom were familiar to each other, but unfamiliar to the other four members, who were also unfamiliar to one another. Each experimental group was held together for 1 h before the trial was conducted.

Experimental Procedure

Trials took place in an experimental tank (40 × 25 cm and 25 cm high, water depth 20 cm, fine sand substrate 1 cm deep), the sides and rear of which were covered with nontransparent screening to minimize outside disturbance. Observations were made via a slit in an opaque screen to remove observer effects. One side of the tank contained a row of five equally spaced 5-mm holes at the waterline. These served as prey introduction points, through which we introduced prey items over the course of a trial via a 5-cm³ syringe in 2 cm³ of water. Sections of chironomid larvae 5 mm long were used as prey. These were introduced sequentially, as described below.

Before a trial the experimental group was placed in the experimental tank and allowed to settle for 5 min. Individual prey items were introduced through the prey introduction points, and 10 s was allowed to elapse between the ingestion of one prey item and the introduction of the next. We introduced prey items through a different point each time, in a randomly predetermined order. A total of

18 prey were offered; fish of the size used in this study have been seen to consume up to 10 5-mm chironomid sections within 5 min (personal observation), so competition for prey should persist even when an individual has consumed its expected share of three prey items. We recorded the number of prey items consumed by familiar and unfamiliar fish, the number of contested prey items, and the identity, i.e. familiar pair member or unfamiliar shoalmate, of the individual that first engaged the prey, the individual that contested it, and the individual that ultimately consumed it.

Kleptoparasitic prey contests occurred when an individual attempted to obtain a prey item from the jaws of the fish that had originally captured it. This behaviour had two components, the pursuit of the initial captor by the challenger, followed by the seizure of the prey by the challenger, resulting in either the retention and ingestion of the prey by the captor or it being yielded to the challenger. The prey items used in this study were of sufficient size to require a period of handling before ingestion, thus providing the opportunity for kleptoparasitism to occur.

Ethical Note

No fish died during the study and after the trials the fish were retained in the laboratory as breeding stock. Three-spined sticklebacks are extremely common at the location from which they were collected, and the removal of 120 individuals for use in this study is unlikely to have had any negative ecological consequences. No licence was required for the study.

Statistical Analyses

We determined the mean proportion of the prey supply consumed by familiar and unfamiliar individuals within each group and compared these data with a Wilcoxon signed-ranks test.

We calculated the mean rate of prey contests per prey item per individual. We produced three classifications of interactions. (1) Prey contests that occurred between members of familiar pairs: for each member of the familiar pair there was one other familiar individual with which it could interact. (2) Prey contests that occurred between members of familiar pairs and unfamiliar fish, where the familiar pair member initiated the contest: for each member of the familiar pair there were four unfamiliar individuals with which it could interact. (3) Prey contests that occurred between unfamiliar fish, where the contest was not initiated by a member of a familiar pair: for each unfamiliar fish there were five unfamiliar individuals with which it could interact, since the members of the familiar pair were unfamiliar to the other four fish. We standardized contest rates within each interaction by dividing the number of contests within each classification by the number of competitors with which an individual could have interacted. We used a Friedman test to compare the standardized proportion of contests that occurred within each classification per group, and performed post hoc

analyses using equal-groups paired comparisons as described by Langley (1979).

Finally, we looked at contests that occurred between familiar and unfamiliar individuals. We compared the proportion of these contests that were initiated by familiar and unfamiliar individuals. We then compared the proportion of contests won by familiar and unfamiliar individuals both when they had initiated and when they had received the contest challenge. Again we used Wilcoxon signed-ranks tests for these analyses. Statistical tests are two tailed.

RESULTS

Prey Share

The mean proportions of the prey supply consumed by unfamiliar individuals and members of familiar pairs did not differ significantly from each other (Wilcoxon signed-ranks test: $Z = -0.676$, $N = 20$, $P = 0.499$; Fig. 1).

Contest Rate

The mean number of prey contests per trial $\pm$ SE was 6.95 ± 0.94 ($N = 20$). Within experimental groups the contest rate between members of familiar pairs was significantly lower than those between unfamiliar individuals and between members of familiar pairs and unfamiliar individuals (Friedman test: $\chi^2_{2,20} = 19.452$, $P < 0.001$; Fig. 2). To control for effects of satiation that may have caused fish to stop competing for prey and biased our results, we compared the number of contests that occurred for the first nine prey items against the number occurring for the second nine, finding no differences (Wilcoxon signed-ranks test: $Z = -0.169$, $N = 20$, $P = 0.866$).

Contest Victories

Familiar and unfamiliar fish were equally likely to initiate contests (Wilcoxon signed-ranks test: $Z = -0.506$, $N = 20$, $P = 0.613$), and were equally likely to be victorious, both when they initiated ($Z = -0.241$,
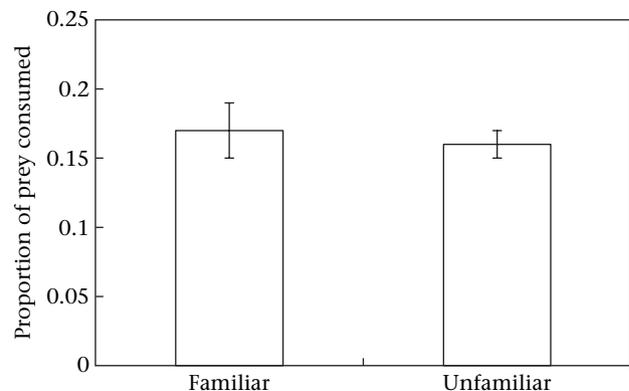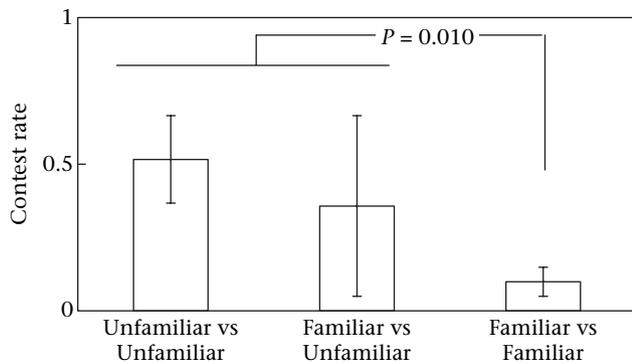

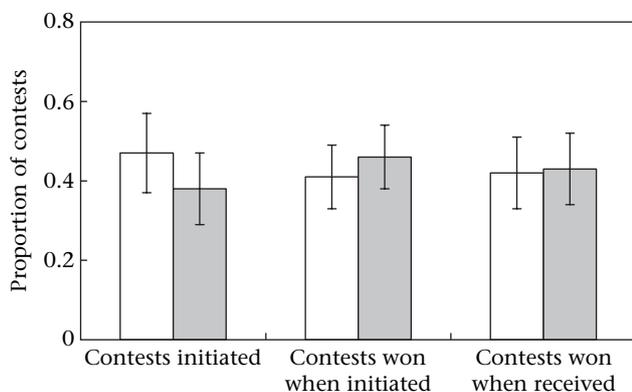**Figure 1.** Mean proportion of the prey supply consumed by members of familiar pairs and unfamiliar fish $\pm$ SE.

Figure 2. The mean ± SE proportion of prey contests per individual per shoal between familiar and unfamiliar individuals. Within each shoal an unfamiliar fish could potentially interact with five other unfamiliar fish, whereas a member of a familiar shoal could interact with four unfamiliar fish and with one familiar fish, and the proportional contest rates have been adjusted to account for this. Prey contests occurring between unfamiliar fish that were initiated by a member of a familiar pair were considered separately from contests between unfamiliar fish that were not initiated by a member of a familiar pair to show the difference in per capita contest rates between familiar and unfamiliar individuals and members of familiar pairs.

$N = 20$, $P = 0.810$) and when they received ($Z = -0.188$, $N = 20$, $P = 0.851$) the contest challenge (Fig. 3).

DISCUSSION

Members of familiar pairs engaged in fewer kleptoparasitic prey contests with each other than they did with unfamiliar fish, and than did unfamiliar individuals with each other. Neither familiar pair members nor unfamiliar individuals differed in their likelihood of initiating contests, however, which suggests that the lower contest rate between pair members was due to a nonrandom allocation of competitive effort by these individuals rather than a general tendency to engage in fewer contests per se.

Familiar and unfamiliar fish did not differ in terms of the proportion of the prey supply that they consumed. We consider it unlikely that this is due to sample size effects ($N = 20$ experimental groups). Although individual fish

Figure 3. Mean proportions of contests initiated and of contest victories ± SE for members of familiar pairs (□) and unfamiliar fish (▧).

that are otherwise phenotypically similar can differ consistently in their competitive ability (Metcalfe & Thomson 1995; Ward et al. 2004a; Webster & Hart 2006), the fish used in our study were selected randomly, and variation in competitive ability should have been spread equally between treatments, but instead variation in the proportion of the prey supply consumed was relatively low (Fig. 1). Our results suggest that discriminating between familiar and unfamiliar individuals in the context of prey competition may instead bring indirect benefits. Prey competition is costly, using up time that could otherwise be spent engaging in other behaviours, and increasing the risk of predation through reducing the vigilance or increasing the conspicuousness of competing individuals (Jakobsson et al. 1995; Slotow & Paxinos 1997). Given this, a strategy that reduces prey contest rates while preserving the benefits of group foraging is likely to be of adaptive value.

The mechanism facilitating recognition of familiar individuals upon which this effect depends remains unclear, and may vary according to species, habitat stability, population density and other factors. A system of learned recognition may operate, whereby individuals recognize, or can quickly gauge, the hierarchical standing of their opponent allowing them to concede contests with known superior competitors, in which they are more likely to lose out on the contested resource anyway, or rapidly escalate contests with subordinates, where they are more likely to win, without the need for protracted interaction (Barnard & Burk 1979). Learned recognition may account for the differences in contest rates observed in our study between familiar individuals and between familiar and unfamiliar individuals; when individuals face unfamiliar but phenotypically similar competitors, the outcome of a contest may not be so readily predictable and the value to both parties of pursuing a contest is therefore potentially greater. This, however, is a fairly complex mechanism, placing substantial cognitive demands upon the individual, and with several associated costs. First, prolonged interaction over a substantial period may be required for identities to be learned (Griffiths 2003) and second there is an upper limit on the number of individual identities that can be learned and recalled (Griffiths & Magurran 1997a). In nature these demands may be irreconcilable with the temporally dynamic structure of free-ranging shoals, and the potentially very high number of conspecifics with which an individual may associate on a day-to-day basis (Ward et al. 2002).

Winner and loser effects, allowing individuals to assess their chances of winning or losing contests based, respectively, upon their past victories or losses (Hollis et al. 1995) liberates them from the cognitive constraints of learning separate identities, but this mechanism alone cannot explain how familiar individuals are differentiated from unfamiliar ones. A general assortative mechanism, recently shown to operate in shoaling fish by Ward et al. (2004b, 2005) is one of self-referent matching of chemical cues pertaining to recent prey and habitat use. Again, this mechanism does not assume the capacity for individual recognition. It represents an inexpensive means of assessing group composition and stability, one that can be easily

overridden, and useful future work could consider the roles of these different mechanisms in free-ranging populations, and the conditions under which each or either is used.

In groups where animals leave and join at different rates over time, the ability to discriminate between familiar and unfamiliar individuals brings another benefit, one analogous to heterogeneous advantage. This is a phenomenon much studied in a kin-selective context, whereby individual fitness is higher in groups where genetic diversity is greater (Griffiths & Armstrong 2001; Greenberg et al. 2002). In this case, however, we consider diversity in levels of familiarity. In fish, familiar groups have been shown to forage and disseminate foraging-related information among themselves more efficiently than groups of unfamiliar individuals (Laland & Williams 1997; Lachlan et al. 1998). Furthermore, unfamiliar outsiders exploit this effect, by identifying and preferentially associating with familiar groups to enhance their own foraging rates through local enhancement and social facilitation (Ward & Hart 2005). By discriminating between their longer established, and more foraging-efficient, group members and any relative newcomers that may be usurping the successes of the group, and allocating competitive effort accordingly, individuals may better balance the costs of prey competition with conspecifics exploiting a common resource with the benefits of kleptoparasitizing the efforts of others.

Our study provides evidence that individuals interact differently with familiar conspecifics and may benefit from doing so even where overall group fidelity is low, an important assumption in social network theory (Croft et al. 2004b). Useful future work that considers the mechanisms by which these behaviours operate and the environmental pressures that affect them will enhance our knowledge of social network structure, and give us further insight into the evolution of sociality.

Acknowledgments

References

Barnard, C. J. & Burk, T. 1979. Dominance hierarchies and the evolution of individual recognition. *Journal of Theoretical Biology*, **81**, 65–73.

Chivers, D. P., Brown, G. E. & Smith, R. J. F. 1995. Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): implications for antipredator behaviour. *Canadian Journal of Zoology*, **73**, 955–960.

Croft, D. P., Arrowsmith, B. J., Bielby, J., Skinner, K., White, E., Couzin, I. D., Magurran, A. E., Ramnarine, I. & Krause, J. 2003a. Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*. *Oikos*, **100**, 429–438.

Croft, D. P., Albanese, B., Arrowsmith, B. J., Botham, M., Webster, M. M. & Krause, J. 2003b. Sex-biased movement in the guppy (*Poecilia reticulata*). *Oecologia*, **137**, 62–68.

Croft, D. P., Arrowsmith, B. J., Webster, M. M. & Krause, J. 2004a. Intra-sexual preferences for familiar fish in male guppies. *Journal of Fish Biology*, **64**, 279–283.

Croft, D. P., Krause, J. & James, R. 2004b. Social networks in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society of London, Series B*, **271**, 516–519.

Cross, P. C., Lloyd-Smith, J. O., Bowers, J. A., Hay, C. T., Hofmeyr, M. & Getz, W. M. 2004. Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger National Park. *Annales Zoologici Fennici*, **41**, 879–892.

Cross, P. C., Lloyd-Smith, J. O. & Getz, W. M. 2005. Disentangling association patterns in fission–fusion societies using African buffalo as an example. *Animal Behaviour*, **69**, 499–506.

Godin, J.-G. J., Alfieri, M. S., Hoare, D. J. & Sadowski, J. A. 2003. Conspecific familiarity and shoaling preferences in a wild guppy population. *Canadian Journal of Zoology*, **81**, 1899–1904.

Greenberg, L. A., Hernnas, B., Bronmark, D., Dahl, J., Eklov, A. & Olsen, K. H. 2002. Effects of kinship on growth and movements of brown trout in field enclosures. *Ecology of Freshwater Fish*, **11**, 251–259.

Griffiths, S. W. 2003. Learned recognition of conspecifics by fishes. *Fish and Fisheries*, **4**, 256–268.

Griffiths, S. W. & Armstrong, J. D. 2001. The benefits of genetic diversity outweigh those of kin association in a territorial animal. *Proceedings of the Royal Society of London, Series B*, **268**, 1293–1296.

Griffiths, S. W. & Magurran, A. E. 1997a. Schooling preferences for familiar fish vary with group size in a wild guppy population. *Proceedings of the Royal Society of London, Series, B*, **264**, 547–551.

Griffiths, S. W. & Magurran, A. E. 1997b. Familiarity in schooling fish: how long does it take to acquire? *Animal Behaviour*, **53**, 945–949.

Griffiths, S. W. & Ward, A. J. W. 2006. Learned recognition of conspecifics. In: *Fish Learning and Behaviour* (Ed. by C. Brown, K. Laland & J. Krause), pp. 139–157. Oxford: Blackwell.

Helfman, G. S. 1984. School fidelity in fishes: the yellow perch pattern. *Animal Behaviour*, **32**, 663–672.

Hoare, D. J., Ruxton, G. D., Godin, J. G. J. & Krause, J. 2000. The social organisation of free-ranging fish shoals. *Oikos*, **89**, 546–554.

Höjesjö, J., Johnsson, J. I., Petersson, E. & Jarvi, T. 1998. The importance of being familiar: individual recognition and social behavior in sea trout (*Salmo trutta*). *Behavioral Ecology*, **9**, 445–451.

Hollis, K. L., Dumas, M. J., Singh, P. & Fackelman, P. 1995. Pavlovian conditioning of aggressive behaviour in blue gourami fish (*Trichogaster trichopterus*): winners stay winners and losers stay losers. *Journal of Comparative Psychology*, **109**, 123–133.

Jakobsson, S., Brick, O. & Kullberg, C. 1995. Escalated fighting behaviour incurs increased predation risk. *Animal Behaviour*, **49**, 235–239.

Klimley, A. P. & Holloway, C. F. 1999. School fidelity and homing synchronicity of yellowfin tuna, *Thunnus albacares*. *Marine Biology*, **133**, 307–317.

Krause, J. & Ruxton, G. D. 2002. *Living in Groups*. Oxford: Oxford University Press.

Krause, J., Godin, J. J. & Brown, G. 1996. Phenotypic variability within and between fish shoals. *Ecology*, **77**, 1586–1591.

Lachlan, R. F., Crooks, L. & Laland, K. 1998. Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour*, **56**, 181–190.

Laland, K. N. & Williams, K. 1997. Shoaling generates social learning of foraging information in guppies. *Animal Behaviour*, **53**, 1161–1169.

Langley, R. 1979. *Practical Statistics Simply Explained*. New York: Pan Books.

Lusseau, D. 2003. The emergent properties of a dolphin social network. *Proceedings of the Royal Society of London, Series B*, **270**, 186–188.

Lusseau, D. & Newman, M. E. J. 2004. Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of London, Series B*, **271**, 477–481.

Magurran, A. E. & Queiroz, H. L. 2003. Partner choice in piranha shoals. *Behaviour*, **140**, 289–299.

Metcalfe, N. B. & Thomson, B. C. 1995. Fish recognize and prefer to shoal with poor competitors. *Proceedings of the Royal Society of London, Series B*, **259**, 207–210.

Muller, A. E. & Thalmann, U. 2000. Origin and evolution of primate social organisation: a reconstruction. *Biological Reviews of the Cambridge Philosophical Society*, **75**, 405–435.

Seppa, T., Laurila, A., Peuhkuri, N., Piironen, J. & Lower, N. 2001. Early familiarity has fitness consequences for Arctic char (*Salvelinus alpinus*) juveniles. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 1380–1385.

Slotow, R. & Paxinos, E. 1997. Intraspecific competition influences food return–predation risk trade-off by white-crowned sparrows. *Condor*, **93**, 642–650.

Swaney, W., Kendal, J., Capon, H., Brown, C. & Laland, K. N. 2001. Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, **62**, 591–598.

Utne-Palm, A. C. & Hart, P. J. B. 2000. The effects of familiarity on competitive interactions between threespined sticklebacks. *Oikos*, **91**, 225–232.

Vonhof, M. J., Whitehead, H. & Fenton, M. B. 2004. Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveals a novel social structure among bats. *Animal Behaviour*, **68**, 507–521.

Ward, A. J. W. & Hart, P. J. B. 2003. The effects of kin and familiarity on interactions between fish. *Fish and Fisheries*, **4**, 348–358.

Ward, A. J. W. & Hart, P. J. B. 2005. Foraging benefits of shoaling with familiars may be exploited by outsiders. *Animal Behaviour*, **69**, 329–335.

Ward, A. J. W., Botham, M. S., Hoare, D., James, R., Broom, M., Godin, J. G. J. & Krause, J. 2002. Association patterns and shoal fidelity in the three-spined stickleback. *Proceedings of the Royal Society of London, Series B*, **269**, 2451–2455.

Ward, A. J. W., Thomas, P., Hart, P. J. B. & Krause, J. 2004a. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, **55**, 561–568.

Ward, A. J. W., Hart, P. J. B. & Krause, J. 2004b. The effects of habitat- and diet-based cues on association preferences in three-spined sticklebacks. *Behavioral Ecology*, **15**, 925–929.

Ward, A. J. W., Holbrook, R. I., Krause, J. & Hart, P. J. B. 2005. Social recognition in sticklebacks: the role of direct experience and habitat cues. *Behavioral Ecology and Sociobiology*, **57**, 575–583.

Webster, M. M. & Hart, P. J. B. 2006. Kleptoparasitic prey competition in shoaling fish: effects of familiarity and prey distribution. *Behavioral Ecology*, **17**, 959–964.