

Sticklebacks show consistent prey share hierarchies within but not between patchy and sequential prey distributions

D. E. F. Taylor, D. Cownden & M. M. Webster

School of Biology, University of St Andrews, St Andrews, UK

Keywords

competition; predation; scramble competition; social foraging; prey distribution.

Correspondence

Mike M. Webster, School of Biology, Harold Mitchell Building, University of St Andrews, St Andrews, Fife KY11 8RX, UK. Tel: +44 (0) 1344 461690

Email: mike.m.webster@gmail.com

Editor: Jean-Nicolas Volff

Received 13 January 2016; revised 7 March 2016; accepted 14 March 2016

doi:10.1111/jzo.12350

Introduction

Competition is a largely inevitable consequence of living in groups (Krause & Ruxton, 2002; Ward & Webster, 2016). When social animals compete amongst themselves for resources or dominance, hierarchies can emerge. The structure of hierarchies may be influenced both by individual differences in ability to compete effectively, or through self-organizing processes, such as through winner and loser effects (Chase *et al.*, 2002; Franz *et al.*, 2015). Hierarchies form in markedly different contexts, from leadership and travel initiation (Sueur, 2011; Nagy *et al.*, 2013), to access to mating opportunities (Chen, Beekman & Ward, 2011), to competition over food resources (David *et al.*, 2007). The mechanisms which determine an individual's place within the hierarchy may well differ between these different contexts. Ability to compete for mating opportunities may be to a lesser or greater extent under hormonal control for example (e.g. Beehner *et al.*, 2006; Oliveira, Silva & Canário, 2009), while the ability to lead groupmates may depend more upon experience, assertiveness or sociability (Burns *et al.*, 2012; Flack *et al.*, 2012; Ioannou, Singh & Couzin, 2015). Given this, we might reasonably predict that hierarchy structure should be context-specific. Indeed, this was found to be the case in pigeons *Columba livia*, where hierarchies based upon leadership whilst in flight, and aggression during foraging were seen to be completely independent of one another (Nagy *et al.*, 2013).

Travelling and foraging are clearly separate domains, but even within broad, functional contexts we might expect to see a

Abstract

When animals compete, hierarchies can emerge. If the outcome of competition under different conditions is dependent upon different sets of attributes, then we may expect to see hierarchies that are domain-specific, rather than domain general. We tested this idea by comparing prey share hierarchies within shoals of sticklebacks *Gasterosteus aculeatus* as they foraged for patchily distributed or for drifting prey. We found that prey share was correlated across pairs of patch- and pairs of drift-foraging trials, but not between the two conditions, suggesting that separate repeatable but independent prey share hierarchies arise for each type of prey distribution. We discuss possible underlying mechanisms and ecological implications of this finding.

degree of condition-dependency of hierarchy structure, if performance under different conditions depends upon different attributes. We explored this idea by comparing the prey share hierarchies seen within shoals of stickleback fish *Gasterosteus aculeatus* as they competed for sequentially arriving, drifting food, and for food arranged in static patches. Previous work has shown that stable prey share hierarchies characterized by a minority of fish consuming most of the prey can form and persist for several weeks in this species (Webster & Hart, 2006, 2007). Prey intake under the scramble-competition conditions associated with drifting food (Ward, Webster & Hart, 2006) is known to positively correlate with individual activity and boldness (Webster, Ward & Hart, 2007, 2009). Effectively competing for patchily distributed food may also entail elements of scramble competition, however, aggression may also play more of a role too; in an earlier study, aggressive contest competition and kleptoparasitism rates declined over time in groups held under drift-foraging conditions, but remained constant when groups are presented with patchily distributed prey, suggesting that these play a more important role in determining prey share under such conditions (Webster & Hart, 2006). In this study, we tested groups of fish multiple times in patch- and drift-foraging trials, predicting that prey share hierarchies would be stable within patch- and drift-foraging trials, but not between them.

Materials and methods

Sticklebacks were collected from the Kinnessburn stream, St Andrews, UK using mesh traps in October 2014. In the labora-

tory they were initially housed in groups of 40 in 90L aquaria for 1 month. They were maintained at 8°C on a 12 h light:12 h darkness cycle and fed daily with bloodworms. The aquaria contained a layer of gravel, artificial plants, and were equipped with external filters. Following this, unsexed, non-reproductive fish were divided into 16 groups of five fish each and each group was moved to its own visually isolated 45L aquarium, furnished as described above. Fish within each group were familiar to one another, and were size matched to within 5 mm length (range across groups 35–45 mm). Each fish was fitted with a non-invasive, uniquely coloured 5 mm diameter plastic disc tag on its left pelvic spine (Webster & Laland, 2009). Fish were given 1 week to acclimate, before being tested the following week.

Each group was tested in four foraging trials, two in which the prey were presented simultaneously in a single patch, and two in which the prey were presented sequentially, simulating drifting food. The order of these foraging trials was randomized for each group. Both patch- and drift-foraging trials were conducted in an aquarium measuring 45 × 30 × 30 cm (Fig. 1). The aquarium contained a 1 cm deep layer of sand and was filled with water to a depth of 25 cm. The two short sides and one long side of the aquarium were screened with black plastic sheets to minimize external disturbance. A 4 cm wide strip of black plastic was placed above the tank down the long side with four 5 mm holes placed 8 cm apart to allow prey to be delivered (in the drift-foraging trials only). A removable 10 cm diameter, 30 cm tall perforated colourless plastic cylinder was placed against one of the short side of the tank, equidistant from either longer side. This was used to hold the group of five fish prior to the start of the trial. A black plastic hide was placed in front of the unscreened side of the tank. Within this we placed a Logitech C600 (Logitech International S.A., Lausanne, Switzerland) web-camera connected to a laptop computer.

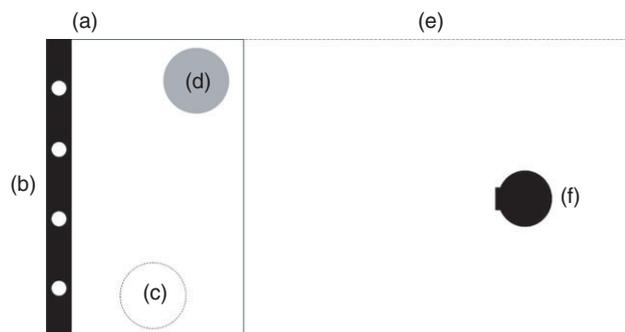


Figure 1 Test arena, consisting of a glass tank (a) screened on three sides with black plastic sheeting and measuring 45 × 30 cm, water depth 20 cm. A black plastic strip (b), 4 cm wide was present in both drift- and patch-foraging trials. This contained four holes, at equal intervals, used to deliver prey in the drift foraging trials. A removable 10 cm perforated plastic holding unit (c) was used to house the fish during the settling period at the start of the trial. In the patch-foraging trials only, prey were provided within a 10 cm diameter patch, located at (d). The uncovered front of the tank was abutted by a black plastic shelter (e), containing a webcam (f), used to record the trials.

In both types of foraging trial 15 dead bloodworms were used as prey. In the patch-foraging trials these were arranged within a 10 cm diameter patch next to the short wall of the tank opposite the starting position of the test subjects. The prey were added to the tank one minute before the fish were added. The group of five fish were carefully netted from their housing tank placed into the holding cylinder and allowed to settle for 10 min. Following this, the holder was gently removed from the tank, beginning the trial. The trial ran for a further 10 min, after which the fish were removed and return to their holding tank. In the drift-foraging trials, prey were introduced through the four holes in the plastic strip attached to the top of the tank (described above). As in the patch-foraging trials, the group of five fish was first held within the holding cylinder for 10 min. Following their release, we began to add the prey items. Each prey item was delivered in 1 cm³ of tank water using a pipette. One prey item was dropped every 30 s through one of the holes and a randomly predetermined order. The fish typically consumed the prey as it sank to the bottom of the tank. After the final prey item had been delivered the trial continued for a further 150 s, allowing the fish to find any uneaten prey, giving a total trial time of 10 min. Each group was tested once a day over a 4 day period. Immediately after being tested, fish groups were returned to their holding tanks. All were given access to food after testing, to standardize hunger levels between trials.

Statistical analysis

From the trial videos we recorded the number of prey items eaten by each fish. We compared the amount of food eaten per group in each of the four trials using a Friedman test. We investigated whether prey share within groups varied between the four trials by calculating the coefficient of variation of prey share for each group and trial, and comparing these, also using a Friedman test.

With respect to stability in individual prey share, we first performed exploratory analyses by calculating the Pearson product moment correlation coefficient for individual prey share within groups between the two patch-foraging trials, between the two drift-foraging trials and between the mean patch- and mean drift-foraging prey shares for each group, enabling us to estimate the degree to which performance was repeatable across these trials. These were meta-analysed using Stouffer's weighted Z method, to obtain a single test statistic for each comparison (Whitlock, 2005).

We then used maximum likelihood estimation to fit six statistical models describing variation and consistency in individual foraging ability to the data on individual prey share across groups, using corrected Akaike's information criterion (AICc) to select the models which best described the observed patterns of prey share (Burnham & Anderson, 2002).

Model 1 described our prediction that prey share hierarchies would be stable within patch- and drift-foraging trials, but not between them. Models 2–5 describe alternatives to this prediction. Model 2, with individual differences in prey capture ability that acted identically across both foraging modes, corresponded to the alternative hypothesis that prey share

hierarchies would be stable both within and between foraging modes. The previous work of Webster & Hart (2006) largely ruled out two other alternative predictions, namely that there would be no individual differences in prey capture ability in the foraging tasks (the scenario described by our Model 3), and that there would be individual differences in prey capture ability, but that these differences would not be stable over time (our Model 4). Our Models 5 & 6 were a mixture of Models 1 and 3, in that fish were modelled as having individual differences in prey capture ability in one of the foraging modes, patch or drift, but not in the other.

We chose to model these various hypotheses as mixtures of multinomial distributions. Although more complicated models may have provide better fits to the data, testing our hypotheses required fitting individual level parameters, and as there were relatively few observations per individual, we decided to use a simple family of models. The number of prey capture observations was 960, 16 groups with 4 trials per group and 15 prey items per group, and the number of individual fish was 80, 16 groups with 5 fish per group, for a total of 12 observations per individual.

Model 3 sat at one extreme where each trial by each group was modelled as coming from the same multinomial distribution, and Model 4 sat at the other extreme where a different multinomial distribution was posited and fitted for each trial by each group. Model 1 posited and fitted two multinomial distributions for each group, one for their patch trials and one for their drift trials. Model 2 posited a single multinomial distribution for each group which applied to both patch and drift trials. Models 5 and 6 were a blend of Models 1 and 3, positing a single multinomial distribution for all groups on patch (Model 5) or drift (Model 6) trials, respectively, while positing a different multinomial distribution for each group on the alternative trial type (drift or patch).

Results

Total prey intake per group did not vary across the four trials (Friedman test: $n = 16$, $X^2 = 2.64$, $df = 3$, $P = 0.450$). Prey share within groups was unequal but did not vary across the four trials (Friedman test of coefficient of variation in individual prey intake, $n = 16$, $X^2 = 4.90$, $df = 3$, $P = 0.179$, Fig. 2a, b). Prey share within groups was positively correlated within the pairs of patch and drift trials (Stouffer's Z trend, $P = <0.001$ and 0.027 respectively). Between patch and drift trials, however, we saw no evidence of any correlation ($P = 0.751$, Fig. 3).

Of the six models that we fitted to the data, Model 1 was the best supported (Table 1), minimizing information loss when approximating the true prey share distribution. This allows us to infer with confidence that there are persistent individual differences in prey capture ability, and that these individual differences in ability are distinct across food distribution types.

Discussion

In line with our prediction, we found prey share hierarchies to be specific to prey distribution; individual prey shares were largely positively correlated within the two patch- and the two

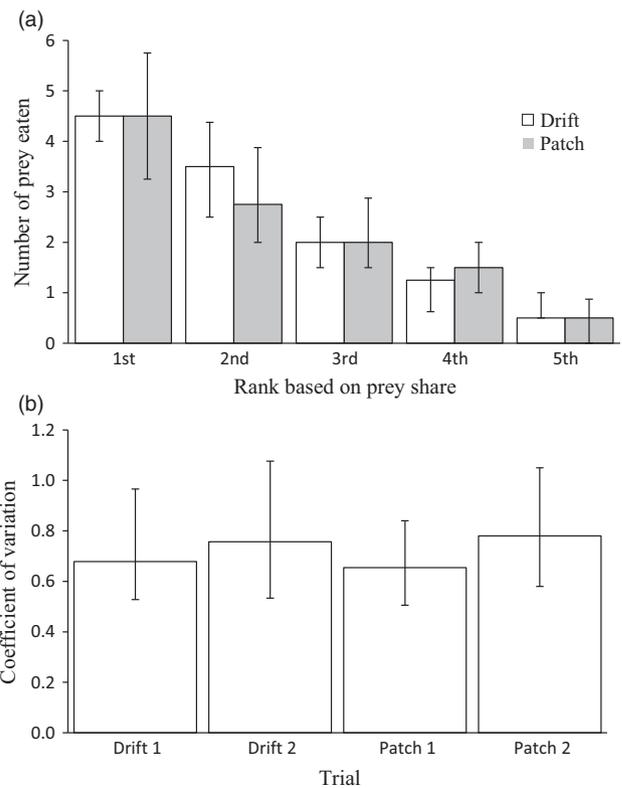


Figure 2 (a) Median (\pm quartiles) prey intake by rank (mean of both trials within each prey delivery treatment). (b) Coefficient of variation in individual prey intake across the four trials (median \pm quartiles).

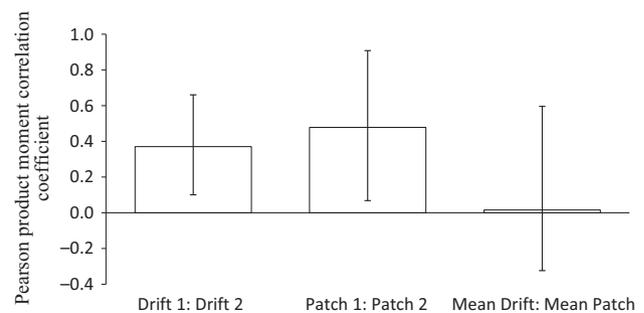


Figure 3 Pearson correlation coefficients of individual prey share within groups (median \pm quartiles). To obtain median scores, individual correlation coefficients were converted to Fisher's z scores. These were ranked and the 9th highest value was taken as the median, with the 5th and 13th highest values were used as the quartiles. These were then converted back from Fisher's z scores to correlation coefficients and used to produce the figure.

drift-foraging trials, however, there was little support for any relationship in prey share hierarchy between the two prey provision treatment types. Given that individual prey intake varied between prey distribution treatments, it seems unlikely that individual differences in metabolic rate or energy requirements alone can account for our findings. One plausible explanation

Table 1 Support (AICc) for the six models fitted to our data. Model 1, in which feeding performance was consistent within feeding modes but independent between them, was the best supported

Model	Parameters (Estimated)	Negative Log Likelihood	AIC _c	Δ (AIC _c -AIC _c)
1. Individual, unrelated differences across modes	192 (160)	429.38	1243.00	0
2. Individual differences, consistent across modes	96 (80)	575.00	1324.69	81.68
3. No individual differences	2 (1)	686.74	1375.48	132.48
4. Individual differences never consistent	384 (320)	291.52	1543.05	300.05
5. Individual differences in Patch, but not Drift	98 (81)	553.50	1284.09	41.09
6. Individual differences in Drift, but not Patch	98 (81)	565.10	1307.27	64.27

for this finding is that performance under different foraging conditions is determined by different combinations of behavioural attributes or behavioural syndromes (Sih, Bell & Johnson, 2004). Such a link has already been demonstrated in sticklebacks, where more active and bolder individuals also tend to be superior competitors under drift feeding conditions, possibly because such individuals are simply more likely to encounter drifting food sooner than their less active group mates or because they are more willing move into the open to reach food once they have detected it (Webster *et al.*, 2007, 2009). Boldness and activity may be less important in shaping performance when competing for patchily distributed prey, though it is interesting to note that boldness was positively correlated with prey intake in sticklebacks that were tested alone (Jolles, Manica & Boogert, 2016). Here, then there is scope for further research that builds in this study by identifying the behavioural correlates of social foraging performance under these different conditions.

It is conceivable that resource defence may play a role in determining foraging success for patchily distributed resources. Defence of food patches has been widely observed in a range of species (Garber, 1988; Bryant & Grant, 1995; Vahl *et al.*, 2005). It is not clear whether any form of resource defence was employed by the fish in our study. We saw no differences in total prey intake, nor any differences in disparity in prey share, (measured as the coefficient of variation in prey intake within each group) between patch and drift prey delivery treatments, as might be expected if patchy prey were defended. Moreover, we saw very little evidence of contest competition or overt aggression, though we note that agonistic behaviours such as these may be poor indicators of the kinds of social interference effects that might limit food intake at patches (Vahl *et al.*, 2005). For species where defence of food resources by dominant individuals does occur (Grant & Guha, 1993; Grand & Grant, 1994), prey distribution, the degree to which it is clumped in space and time, is likely to have significant implications for the effectiveness of resource defence strategies. Further research into the use of defence tactics across a continuously varied range of prey distributions in such species would be valuable, since it would allow researchers to test predictions about the effectiveness of such strategies and the flexibility with which they are deployed and abandoned.

The findings of our study imply that for groups of generalist species that forage for different food types, we may not be able to build an accurate picture of individual relative foraging performance based upon foraging performance observed only under a narrow set of conditions. Instead, it may be necessary

to gather data on performance across a range of different foraging types, and to take into account the competitive abilities of all group members across these, given that social foraging interactions are known to depend strongly upon the combinations of behavioural phenotypes present within the group (Giraldeau & Caraco, 2000). A number of studies have recently addressed the question of how expression of individual personality traits influences and is influenced by that of the group (reviewed by Webster & Ward, 2011; Magnhagen, 2012) and it would be useful to extend this work further by exploring the expression of traits affecting food competition across different food distributions. Taking such an approach may enable researchers to explain a greater proportion of the variation seen in competitive interactions among social animals.

Skew theory, largely applied to competition over opportunities to reproduce, has also been suggested to apply to foraging interactions; dominant individuals may expel effective competitors for food resources, whereas poorer competitors may quit groups to seek better access to food (Hamilton, 2000). High rates of fission and fusion, coupled with low group fidelity have been described for some animal groups, including some shoaling fishes (Hoare *et al.*, 2000), and it would be interesting to determine the extent to which this reflects poor competitors moving between areas containing differently prey distributions or groups containing individuals with different competitive abilities. Conceivably, the rules governing patch quitting likelihoods invoked by classic foraging models (Charnov, 1976) may also apply to group membership, with individuals being more likely to switch groups if their prey intake drops below some threshold level.

Finally, it would be useful to determine how broadly these findings apply to other modes of foraging, and more generally still, when groups of animals are faced with different tasks or problems within other broad behavioural contexts, such as navigation through different types of environment.

Acknowledgements

This work was supported by the School of Biology's Experimental Research Project (BL4201) program, (module BL4201: Experimental Research Project) at the University of St Andrews, UK.

References

- Beehner, J.C., Bergman, T.J., Cheney, D.L., Seyfarth, R.M. & Whitten, P.L. (2006). Testosterone predicts future dominance

- rank and mating activity among male chacma baboons. *Behav. Ecol. Sociobiol.* **59**, 469–479.
- Bryant, M.J. & Grant, J.W. (1995). Resource defence, monopolization and variation of fitness in groups of female Japanese medaka depend on the synchrony of food arrival. *Ani. Behav.* **49**, 1469–1479.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer Science & Business Media.
- Burns, A.L., Herbert-Read, J.E., Morrell, L.J. & Ward, A.J.W. (2012). Consistency of leadership in shoals of mosquitofish (*Gambusia holbrooki*) in novel and in familiar environments. *PLoS ONE* **7**, e36567.
- Charnov, E.L. (1976). Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136.
- Chase, I.D., Tovey, C., Spangler-Martin, D. & Manfredonia, M. (2002). Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proc. Natl. Acad. Sci.* **99**, 5744–5749.
- Chen, T., Beekman, M. & Ward, A.J.W. (2011). The role of female dominance hierarchies in the mating behaviour of mosquitofish. *Biol. Lett.* **7**, 343–345.
- David, B.O., Closs, G.P., Crow, S.K. & Hansen, E.A. (2007). Is diel activity determined by social rank in a drift-feeding stream fish dominance hierarchy? *Ani. Behav.* **74**, 259–263.
- Flack, A., Pettit, B., Freeman, R., Guilford, T. & Biro, D. (2012). What are leaders made of? The role of individual experience in determining leader–follower relations in homing pigeons. *Ani. Behav.* **83**, 703–709.
- Franz, M., McLean, E., Tung, J., Altmann, J. & Alberts, S.C. (2015). Self-organizing dominance hierarchies in a wild primate population. *Proc. R. Soc. Lond. B Biol. Sci.* **282**, 20151512.
- Garber, P.A. (1988). Diet, foraging patterns, and resource defense in a mixed species troop of *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. *Behaviour* **105**, 18–34.
- Giraldeau, L.A. & Caraco, T. (2000). *Social foraging theory*. New Jersey: Princeton University Press.
- Grand, T.C. & Grant, J.W. (1994). Spatial predictability of food influences its monopolization and defence by juvenile convict cichlids. *Ani. Behav.* **47**, 91–100.
- Grant, J.W. & Guha, R.T. (1993). Spatial clumping of food increases its monopolization and defense by convict cichlids, *Cichlasoma nigrofasciatum*. *Behav. Ecol.* **4**, 293–296.
- Hamilton, I.M. (2000). Recruiters and joiners: using optimal skew theory to predict group size and the division of resources within groups of social foragers. *Am. Nat.* **155**, 684–695.
- Hoare, D.J., Ruxton, G.D., Godin, J.-G.J. & Krause, J. (2000). The social organization of free-ranging fish shoals. *Oikos* **89**, 546–554.
- Ioannou, C.C., Singh, M. & Couzin, I.D. (2015). Potential leaders trade off goal-oriented and socially oriented behavior in mobile animal groups. *Am. Nat.* **186**, 284–293.
- Jolles, J.W., Manica, A. & Boogert, N.J. (2016). Food intake rates of inactive fish are positively linked to boldness in three-spined sticklebacks. *J. Fish Biol.* (Online DOI: 10.1111/jfb.12934).
- Krause, J. & Ruxton, G.D. (2002). *Living in groups*. Oxford: Oxford University Press.
- Magnhagen, C. (2012). Personalities in a crowd: what shapes the behaviour of Eurasian perch and other shoaling fishes? *Curr. Zool.* **58**, 35–44.
- Nagy, M., Vásárhelyi, G., Pettit, B., Roberts-Mariani, I., Vicsek, T. & Biro, D. (2013). Context-dependent hierarchies in pigeons. *Proc. Natl. Acad. Sci.* **110**, 13049–13054.
- Oliveira, R.F., Silva, A. & Canário, A.V. (2009). Why do winners keep winning? Androgen mediation of winner but not loser effects in cichlid fish. *Proc. R. Soc. Lond. B Biol. Sci.* **276**, 2249–2256.
- Sih, A., Bell, A. & Johnson, J.C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* **19**, 372–378.
- Sueur, C. (2011). Group decision-making in chacma baboons: leadership, order and communication during movement. *BMC Ecol.* **11**, 26.
- Vahl, W.K., Lok, T., Van der Meer, J., Piersma, T. & Weissing, F.J. (2005). Spatial clumping of food and social dominance affect interference competition among ruddy turnstones. *Behav. Ecol.* **16**, 834–844.
- Ward, A.J.W. & Webster, M.M. (2016). *Sociality: the behaviour of group-living animals*. Berlin: Springer International Publishing.
- Ward, A.J.W., Webster, M.M. & Hart, P.J.B. (2006). Intraspecific food competition in fishes. *Fish Fish.* **7**, 231–261.
- Webster, M.M. & Hart, P.J.B. (2006). Kleptoparasitic prey competition in shoaling fish: effects of familiarity and prey distribution. *Behav. Ecol.* **17**, 959–964.
- Webster, M.M. & Hart, P.J.B. (2007). Prior association reduces kleptoparasitic prey competition in shoals of three-spined sticklebacks. *Ani. Behav.* **74**, 253–258.
- Webster, M.M. & Laland, K.N. (2009). Evaluation of a non-invasive tagging system for laboratory studies using three-spined sticklebacks *Gasterosteus aculeatus*. *J. Fish Biol.* **75**, 1868–1873.
- Webster, M.M. & Ward, A.J.W. (2011). Personality and social context. *Biol. Rev.* **86**, 759–773.
- Webster, M.M., Ward, A.J.W. & Hart, P.J.B. (2007). Boldness is influenced by social context in threespine sticklebacks (*Gasterosteus aculeatus*). *Behaviour* **144**, 351–371.
- Webster, M.M., Ward, A.J.W. & Hart, P.J.B. (2009). Individual boldness affects interspecific interactions in sticklebacks. *Behav. Ecol. Sociobiol.* **63**, 511–520.
- Whitlock, M.C. (2005). Combining probability from independent tests: the weighted Z-method is superior to Fisher's approach. *J. Evol. Biol.* **18**, 1368–1373.