Lay summary

Previous social experiences can reinforce and impair future leadership, but only for the bold. By pairing three-spined sticklebacks with different subsequent partners, we show that the personality of previous partners can carry over to later interactions and affect leadership but not following behaviour. Only bold individuals were influenced by such previous experiences; shy fish were mostly responsive to their current partners actions. These findings help understand the emergence and maintenance of social roles within groups.

The role of previous social experience on risk-taking and leadership in three-spined sticklebacks

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Short title: Previous social experience affects leadership behavior

Abstract

The emergence of leaders and followers is a key factor in facilitating group cohesion in animals. Individual group members have been shown to respond strongly to each other's behavior and thereby affect the emergence and maintenance of these social roles. However, it is not known to what extent previous social experience might still affect individual's leading and following tendencies in later social interactions. Here, by pairing three-spined sticklebacks (*Gasterosteus aculeatus*) with two different consecutive partners, we show a carry-over effect of a previous partner's personality on the behavior of focal individuals when paired with a new partner. This carry-over effect depended on the relative boldness of the focal individual. Relatively bold but not shy fish spent less time out of cover and led

their current partner less if they had previously been paired with a bolder partner. By contrast, following behavior was mainly influenced by the personality of the current partner. Overall, the behavior of relatively bold fish was more consistent across the stages while shy fish changed their behavior more strongly depending on the current context. These findings emphasize how the history of previous social interactions can play a role in the emergence and maintenance of social roles within groups, providing an additional route for individual differences to affect collective behavior.

Key words: boldness, collective decision-making, leadership, personality, responsiveness, shoaling

1. INTRODUCTION

The emergence of leaders and followers plays a major role in promoting group coordination and cohesion, with important consequences for the social lives of humans as well as many non-human animals (Krause and Ruxton 2002; Conradt and Roper 2009; Dyer et al. 2009; King, Johnson, and Van Vugt 2009). There is a growing body of evidence that individuals differ in their social roles, with some individuals having a strong influence on group behavior while others mostly follow (e.g. Reebs 2000; Harcourt et al. 2009; Nagy et al. 2010; Flack et al. 2012; Nakayama et al. 2013). A key focus has been to determine what factors predict which group members will become leaders (Conradt and Roper 2003; Couzin et al. 2005; King, Johnson, and Van Vugt 2009). Many such factors have been identified in a large range of species: body size (Krause, Reeves, and Hoare 1998; Reebs 2001), hunger level (Krause, Reeves, and Hoare 1998; McClure, Ralph, and Despland 2011; Nakayama, Johnstone, and Manica 2012), dominance (Peterson and Jacobs 2002; King et al. 2008; Jolles et al. 2013), social affiliations (King et al. 2008; Jacobs et al. 2011), sex (Peterson and

Jacobs 2002; Barelli et al. 2008), age (Réale and Festa-Bianchet 2003; Sueur and Petit 2008), boldness (Beauchamp 2000; Ward et al. 2004; Harcourt et al. 2009; Kurvers et al. 2009), sociability (Brown and Irving 2014), and knowledge or experience (Reebs 2000; Couzin et al. 2005; Dyer et al. 2009; Flack et al. 2012).

In recent years a few studies have started to go beyond the search for such predictive factors and have shown that the actual dynamics of interactions amongst individuals play an important role in leading and following behavior (Harcourt et al. 2009; Nakayama et al. 2012; Nakayama et al. 2013; Pettit et al. 2013; Ward et al. 2013). For example, although bold individuals typically lead and shy individuals mainly follow (Beauchamp 2000; Harcourt et al. 2009; Kurvers et al. 2009; Nakayama et al. 2013), these differences in leading and following are strongly enhanced by social feedback (Harcourt et al. 2009; Nakayama et al. 2012). Furthermore, although bolder individuals are generally less responsive to their partner's behavior, both bolder and shyer individuals readily adjust to their partner when in the following role (Nakayama et al. 2012; Nakayama, Johnstone, and Manica 2012). These findings not only highlight the important modifying role of social feedback, they also suggest the exciting possibility that interactions with previous partners may play a role in later leading and following behavior. As also highlighted in the human leadership literature (Amit et al. 2009; Emery 2010; DuBrin 2013), addressing this key outstanding issue may contribute to our understanding of the emergence and maintenance of leadership and ultimately of collective behavior and group decision-making.

Most gregarious animals live in highly dynamic groups in which they interact with multiple conspecifics (Krause and Ruxton 2002), and a strong influence of previous social experience has already been shown for neophobic and aggressive behavior (Hsu and Wolf 1999; Frost et al. 2007). In a previous study on leadership, fish were shown to change their behavior based on a partner's ability to successfully locate food during joint trips, with

experience overriding personality differences in the tendency to follow but not to lead (Nakayama et al. 2013). Here by pairing three-spined sticklebacks (*Gasterosteus aculeatus*) with two different consecutive partners, we investigated how previous social experience with other individuals affected the propensity of fish to leave cover, to lead, and to follow their current partner during joint trips. If individuals fine-tune their behavior based on previous experiences, this potentially represents a mechanism through which social roles can be reinforced. Since bold individuals are known to be less responsive than shy individuals during social interactions (Pike et al. 2008; Nakayama et al. 2012; Nakayama, Johnstone, and Manica 2012), we hypothesized that bolder fish would be more consistent in their behavior across different social and non-social environments and shyer fish to be more responsive to the present context. We therefore predicted that the behavior of bolder fish would be mainly explained by their own personality and to a lesser extent by that of their current and previous partners, while for shyer fish the personality of their current partner would be the main determinant of their behavior. This approach provides a unique opportunity to describe important new aspects of social feedback and personality that have thus far been neglected in studies on group movements and leadership.

2. MATERIALS AND METHODS

(a) Subjects and housing

We collected three-spined sticklebacks using a sweep net during the summers of 2010 to 2012, from a small branch of the river Cam (Cambridge, UK). Large groups of fish (~ 200 individuals) were housed in a temperature-controlled laboratory (T = 14°C ± 1°C) with a constant light regime (lights on from 09:00 to 19:00 h) and kept in large glass holding aquaria (120 x 60 x 60 cm) that contained artificial plants, aeration and under-gravel filtration. Fish were fed frozen bloodworm (*Chironomidae*) larvae *ad libitum* once a day

before the start of the experiment. During the experimental period, feeding was rationed to one bloodworm a day to standardize hunger levels. All fish used for the experiment were of similar length (50 mm ± 7 mm from tip of snout to caudal peduncle) and were taken from a single population to minimize population-specific genetic effects that may influence personality (Bell 2005). Although the exact age of the fish could not be determined, all caught individuals were juveniles and are expected to only vary in age by a few weeks. Sex of the fish was not identified as the temperature and photoperiod regime in the lab prevented the fish from becoming sexually mature (Borg, Bornestaf, and Hellqvist 2004).

(b) Experimental set-up

During the experimental period, we housed fish individually in custom holding tanks (60 x 30 x 40 cm) lined with gravel and divided lengthwise into six compartments by transparent perspex partitions. Five compartments were used to house a fish each and contained an artificial plant at one end and a white perspex plate (2 x 2 cm) at the other end where food was delivered. The remaining compartment contained the under-gravel filter and was not used to house any fish. Partner fish were never housed in adjacent compartments. Fish were allowed to acclimatize in their individual compartments for three days before the start of testing.

To investigate fish's propensity to explore a risky area and lead and follow conspecifics, we used a tank set-up previously used in our lab for similar experiments (Harcourt et al. 2009; Nakayama et al. 2012; Nakayama, Johnstone, and Manica 2012). In short, experiments took place in four identical experimental tanks (70 x 30 x 30 cm), each divided lengthwise with either an opaque white perspex partition or a transparent perspex partition to create two long lanes (see Figure S1.). Each lane was lined with gravel in a slope ranging from a deep (15 x 15 cm; 14 cm depth) 'safe area' that contained an artificial plant

to an increasingly shallow 'exposed' area (4 cm depth at the other side). Only when fish had fully emerged from this safe area we defined them to be 'out of cover'. No food was provided during the trials and fish were thus not rewarded for leaving cover. This set-up reflects the ecologically relevant problem where fish can either rest in a safe place or explore a risky area in search of food (analogous to the exposed area where food is delivered in their holding compartments). Fish prefer to spend time under cover but, even in the absence of food in the experimental tank, keep making regular trips out of cover to explore the exposed area. Since fish have different preferences for the number and length of trips out of cover they make yet prefer to synchronize their activities and shoal together, there is a conflict on the timing of leaving and returning to cover. We have used this ecologically relevant setup to look at the emergence of leaders and followers in a number of previous papers (e.g. Harcourt et al. 2009; Harcourt et al. 2010). The walls of the tank were covered by white perspex to minimize any disturbances from outside the tank. When not running experiments, the water of the experimental tanks was oxygenated with an air stone. HD video cameras (Camileo X100, Toshiba Corporation, Japan) were used to record fish movements from a fixed position above each tank.

(c) Experimental procedure

We tested four batches of fish (N = 136 in total), each over a 7-day cycle (Nov-Dec 2011 and Nov-Dec 2012) and randomly selected 44 fish as focals, 44 as partner for the 'first pairing', and 44 as partner for the 'second pairing'. Fish were tested across three stages. We started by testing fish in the experimental tank in isolation to quantify their boldness ('isolation stage'). On day one and two, each fish was put in one of two lanes of the experimental tank that were separated by an opaque partition so that fish could not interact with eachother. The behavior of each fish was recorded for an hour each day. After a rest

day, we randomly paired each focal fish with a partner ('previous pairing stage'), and put the two fish in the same experimental tank, but this time with a transparent partition so that they could interact. Behavior was recorded for an hour on each of two consecutive days. Finally, we paired each focal with a new socially naïve partner and observed their behavior for another two one-hour sessions over two consecutive days ('current pairing stage'). On each testing day, fish were transferred to the deep end of the tank using a dip net and allowed to acclimatize to the tanks for seven minutes before we tracked their movements. After each trial, fish were moved back to their housing compartment. For each experimental cycle, we randomized the daily testing order as well as the assignment to tank and to the left and right lanes of a tank. Fish were housed in their individual compartments for a week before their first pairing to minimize any social experiences from being housed with conspecifics in social housing tanks.

(d) Data analysis

We tracked the exact movements of the fish at 10 frames/s using automated motion tracking software (AnTracks, version 0.99). For tracking we used a background subtraction acquisition method that determined what pixels differed between the video and a background image that was created from a random five-minute period in each one-hour recording. As processing parameters we used gauss subtraction, gauss blur, dilate and final thresholding for which we adjusted the levels according to the specific light levels in each video to ensure fish movements were tracked correctly. After tracking was complete we checked all trajectories for each video. Any possible noise tracked by the software was eliminated and discontinuous trips where the software had lost track of the fish for a few frames were joined.

Data were analyzed in R 3.0.2 (R Development Core Team). Based on the positional coordinates of both members in a pair we calculated the relative time fish spent out of cover and their number of trips out of cover. On average, fish spent 12.89% of the time out of over (range 0 - 62.3%) and were consistent in this proportion of time out of cover across the two days of the isolation stage ($r_s = 0.55$, $N = 136$, $P < 0.001$). Therefore we used the average proportion of time individuals were out of cover across both days as the boldness score for each fish, an approach commonly adopted for examining the boldness personality trait (e.g. Harcourt et al. 2009; Magnhagen and Bunnefeld 2009; King et al. 2013). Ten fish that did not come out of cover during the isolation stage were excluded.

The behavior of pairs of fish in a similar setup but without previous experience has been described in detailed in previous work (Harcourt et al. 2009; Nakayama et al. 2012; Nakayama, Johnstone, and Manica 2012; Nakayama et al. 2013). In this paper, we focus on the effect of previous experience (the first pairing) on later interactions (the second paring). We focused on the proportion of time spent out of cover by the focal fish, and on the number of trips it made out of cover on its own, as a leader, and as a follower. Leading was defined as a fish going out of cover and being joined by its partner; following as a fish going out of cover to join its partner that is already out. We considered the effects on leading and following behaviour separately as previous work has shown that different factors (e.g. success of a partner in finding food) may affect the tendencies to lead and follow in different ways (e.g. Nakayama et al. 2013). For each of the four variables (time out of cover, and the three types of trips), we used linear models with the focal fish own boldness, the boldness of the previous partner and that of the current partner as predictors. We started with full models with all the predictors, and obtained a minimal model by backwards stepwise elimination (i.e. sequentially dropping terms until all terms retained in the model were significant). Statistics for non-significant terms were obtained by fitting the minimal model with each

non-significant term added individually. As previous work has shown that the relative personality between partners is a key predictor of collective movements and leadership (Harcourt et al. 2009; Nakayama et al. 2013), we ran separate models for focals bolder than their second partner (bold focals) and focals relatively shyer than their second partner (shy focals). Results based on the absolute boldness scores were qualitatively similar and are documented in the supplementary material. As our dataset consists of batches in two subsequent years we additionally ran all models with year as an extra fixed factor and found it had no significant effect in any of the models. The residuals for all models were visually inspected to ensure homogeneity of variance, normality of error and linearity. Finally, paired t-tests were used to investigate how the risk-taking behavior of bold and shy focals changed across the isolation and two pairing stages. Repeatability across the six days of the experiment was estimated following the method by Lessells & Boag (1987). All results with $0.10 > P > 0.05$ are reported as trends and $P \leq 0.05$ as significant. Means are quoted ± SE throughout.

3. RESULTS

We focus on the data collected during the second pairing and investigate how the personalities of the previous and current partner affect the behavior of focal fish bolder than their current partner (bold focals) and focal fish shyer than their current partner (shy focals). The relative boldness of focal fish ranged from -0.62 for shy focals to +0.50 for bold focals (mean ± SE = -0.09 ± 0.03).

(a) Time spent out of cover

Bold focals spent more time out of cover the bolder they were themselves (Fig. 1A) but also the shyer their previous partner had been ($F_{2,7} = 18.77$, $P = 0.002$; Table 1), together

explaining more than 80% of the variance ($R^2 = 0.84$). The personality of their current partner had no effect on the time bold focals were out of cover ($F_{1,7} = 0.04$, $P = 0.84$). By contrast, shy focals tended to spend more time out of cover the bolder their current partner ($F_{1,22} = 4.11$, $P = 0.055$; $R^2 = 0.16$), while their own personality ($F_{1,22} = 0.33$, $P = 0.571$; Fig. 1B) and that of their previous partner ($F_{1,22} = 0.04$, $P = 0.845$) had no significant effect.

(b) Number of trips

The number of solo trips, when focal fish went out and returned to cover without being followed by their partner, was relatively higher in bold compared to shy focals ($t = 2.56$, $P = 0.028$; 13.8 ± 4.24 and 2.65 ± 1.02 trips respectively). Bold focals went on more solo trips the bolder they were themselves ($F_{1,8} = 6.60$, $P = 0.033$; $R^2 = 0.45$) while the personality of the current partner and the previous partner had no effect on this behavior ($F_{1,7} = 0.09$, $P = 0.777$; $F_{1,7} = 1.67$, $P = 0.237$ respectively; Table 1). The number of solo trips made by shy focals was not explained by either their own personality ($F_{1,22} = 0.17$, $P = 0.687$), that of their current partner ($F_{1,22} = 0.25$, $P = 0.624$) or that of their previous partner ($F_{1,22} = 0.11$, $P = 0.743$).

There was no significant difference in the number of joint trips led by bold and shy focal fish during the second pairing ($t = 1.31$, $P = 0.211$; 7.15 ± 2.14 and 3.96 ± 1.19 trips respectively). Bold focals led more trips the relatively bolder the focal individual (Fig. 2A) but also the shyer their previous partner ($F_{2,7} = 12.98$, $P = 0.004$; Fig. 2B; Table 1), together explaining 79% of the variance. The personality of the current partner did not affect the number of leadership trips for bold focals ($F_{1,6} = 1.53$, $P = 0.262$). By contrast, shy focals led more trips the bolder their current partner ($F_{1,22} = 5.75$ $P = 0.025$; $R^2 = 0.21$), while their own personality ($F_{2,21} = 0.28$, $P = 0.600$) and that of their previous partner ($F_{2,21} = 0.13$, $P = 0.719$) had no effect.

There was no difference in the number of trips bold and shy focals followed their current partner out of cover (t = 1.91, P = 0.083; 7.15 ± 2.14 and 2.91 ± 2.45 trips respectively). Bold focals followed their partner more the bolder it was (Fig. 3) and the shyer their previous partner had been ($F_{2,7}$ = 41.74, P < 0.001; Table 1), together explaining 92% of the variance. Bold focal's own personality did not play a role ($F_{1,6}$ = 2,28, P = 0.182). Shy focals followed more the bolder their current partner was ($F_{1,21}$ = 7.78, P = 0.011; Fig. 3; R^2 = 0.26), with no effect of their own personality ($F_{1,21}$ = 0.60, P = 0.448) and that of their previous partner ($F_{1,21}$ = 0.39, P = 0.537).

c) Behavioral consistency across the stages

Bold focals were highly repeatable in the time they spent out of cover on the six days across the three stages (ICC = 0.76, 95% CI: 0.55 - 0.92), while shy focals were not (ICC = 0.17, 95% CI: 0.05 - 0.35). On average, bold focals spent similar amounts of time out of cover during the isolation stage and the first pairing (t_9 = 1.81, P = 0.104) but tended to spend less time out of cover during the second pairing compared to the isolation stage (t_9 = 2.18, P = 0.058). By contrast, shy focals spent more time out of cover when they could see their partner compared to when in isolation (first pairing: t_{31} = -2.29, P = 0.029; second pairing: t_{31} = -2.62, P = 0.013). Additionally, looking at focals based on their absolute boldness category (with bold fish spending more time out and shy fish less time out than the average focal fish) we found bold fish (ICC = 0.65, 95 % CI: 0.47 - 0.82) were more consistent than shy fish (ICC = 0.17, 95 % CI: 0.04 - 0.39), as reflected by their non-overlapping confidence intervals.

4. DISCUSSION

In this study, we show for the first time that the effect of the personality of a previous social partner can carry over to later social interactions, modulating the willingness of individuals to go out of cover and lead their partner. By contrast, the tendency to follow was mainly affected by the personality of an individual's current partner. Although bolder fish were more consistent than shyer fish in the time they spent out of cover across the contexts, it was only bold fish that were susceptible to social reinforcement by their previous social interactions. Shyer fish behaved much more flexibly and responded most strongly to their current partner.

Previously, some studies have shown that previous social experience may affect neophobia and aggression (Hsu and Wolf 1999; Frost et al. 2007) and that experience within the same pair may override personality differences in leadership tendencies (Nakayama et al. 2013). Here we show for the first time how social experiences with previous partners may affect later leadership behavior: the bolder their previous partner, the relatively less time bold focals spent out of cover, making them less successful in taking the lead. These findings help answer the important question in the leadership literature of what makes an initiator successful in triggering collective movement (Petit and Bon 2010). Although bolder individuals are less sensitive to failure in recruiting a partner, they are responsive to their partner's behavior when it has taken on the role of leader. This may be especially the case when bold focals are paired with a relatively bold partner. In such a situation, bold focals partner is relatively more likely to take the lead compared to a shyer partner. Consequently, the focal individual may be less likely to be followed, resulting in a reduction of positive feedback in leadership and reduced performance in the pair (Nakayama et al. 2013). Such experience may then subsequently modulate focal fish' willingness to go out of cover and lead their partner. Not only does this finding highlight that bolder individuals may be more susceptible to social reinforcement than shy individuals, it indicates that for leadership social

experience is important. To be an effective leader, an individual may need experience with good followers, providing positive social feedback and leading experience, and ultimately more successful leadership. These findings may have potential for our understanding of human leadership as a lack of knowledge of the social dynamics underlying leadership has been highlighted in the social sciences (Amit et al. 2009; Emery 2010; DuBrin 2013). Future studies could look in more detail at the extent of the difference in personality scores between the partners and determine the effect it may have on collective behavior.

The finding that bold but not shy focals were affected by a previous partner might be explained by the fact that shyer individuals are in general more sociable (Ward et al. 2004; Pike et al. 2008) and behaviorally less consistent (Nakayama, Johnstone, and Manica 2012), than bold individuals. Indeed, we found that the current partner's personality explains much more of shy focals' behavior than that of bold focals, which is in line with previous studies reporting that shy individuals are more responsive to the actions of their (current) group members (Pike et al. 2008; Nakayama et al. 2012; Nakayama, Johnstone, and Manica 2012). This may also explain the more general finding that shy but not bold focals spent considerably more time out of cover when there was a conspecific present compared to when they were in isolation. Interestingly, in contrast to the time spent out of cover and leading behavior, following behavior of both bold and shy focals was primarily explained by the boldness of their current partner. This result is in line with a number of recent studies that have shown that both bold and shy individuals are responsive when in the following position (Nakayama et al. 2012; Nakayama, Johnstone, and Manica 2012) and that experience may override personality differences in the tendency to follow but not in the tendency to lead (Nakayama et al. 2013). Together, these findings thus suggest that regardless of an individual's own personality, its tendency to follow mainly depends on the behavior of its current partner(s). Leadership, in contrast, is particularly dependent on a

bolder personality type, with a modifying effect of social feedback from previous experiences.

Overall, our findings demonstrate a general difference in responsiveness between shy and bold individuals. Although both bold and shy individuals adjusted their behavior, bold individuals were more consistent in their behavior than shy individuals but adjusted their behavior based on their previous partner, suggestive of social reinforcement. In contrast, shy individuals mostly adjusted their behavior based on their current partner. These results support two recent theoretical models that showed how a co-evultionary process between responsiveness and consistency may eventually result in populations that consist of highly responsive individuals that follow and behaviorally consistent individuals that mainly lead (Johnstone and Manica 2011; Wolf, Van Doorn, and Weissing 2011). Furthermore, these findings are highly relevant in the light of the idea that individual differences can be seen as behavioral specializations (Dall et al. 2012). If individuals differ in the extent that they change their behavior based on previous and current experiences, this represents a potential mechanism through which social roles can be generated and reinforced to create even longer lasting differences between individuals. In other words, personality differences may be maintained in populations because of their role in social coordination (see also King, Johnson, and Van Vugt 2009).

Whilst the study of collective behavior, from pairs of individuals to groups of thousands of individuals, was initially mostly focused on homogeneous interaction rules (Couzin and Krause 2003; Petit and Bon 2010; Vicsek and Zafeiris 2012), individual differences are increasingly taken into account when examining group behavior (Conradt and List 2009; Herbert-Read et al. 2012; Jolles, Ostojić, and Clayton 2013). Here we go one step further by showing that social dynamics *across* time and social contexts may have a considerable effect on individual and thereby group behavior. Our study is the first to

demonstrate that leadership roles are affected by social experiences from previous partners and that this depends on an individual's personality, with bold but not shy fish being affected by the personality of a previous partner. These findings help understand how leading and following behavior emerge and are maintained and highlight the important influence current as well as previous social experiences can have on individual and collective behavior.

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TABLES

Table 1.

LMs of proportion of time out, number of solo trips, number of led trips, and number of trips followed by bold and shy focal fish

	Bold focals				Shy focals			
	Estimate	SE	*F*	*P*	Estimate	SE	*F*	*P*
Proportion of time out								
Constant	0.10	0.10		0.391	0.05	0.10		0.662
Personality focal	**0.80**	**0.16**	**23.80**	**0.002**	0.03	0.37	0.01	0.939
Personality current partner	0.07	0.32	0.04	0.844	0.45	0.22	4.11	0.055
Personality previous partner	**-0.46**	**0.19**	**6.01**	**0.044**	-0.03	0.15	0.04	0.847
Nr of solo trips								
Constant	-0.05	1.33		0.974	1.16	0.24		< 0.001
Personality focal	**6.61**	**2.57**	**6.60**	**0.033**	-1.01	2.47	0.17	0.687
Personality current partner	-1.48	5.04	0.08	0.777	0.78	1.57	0.25	0.624
Personality previous partner	-3.72	2.88	1.67	0.237	0.35	1.05	0.11	0.743
Nr of led trips								
Constant	1.18	0.78		0.174	-0.09	0.72		0.899
Personality focal	**4.28**	**1.23**	**12.13**	**0.010**	-1.37	2.56	0.28	0.600
Personality current partner	2.62	2.12	1.53	0.262	**3.71**	**1.55**	**5.75**	**0.025**
Personality previous partner	**-3.88**	**1.39**	**7.79**	**0.027**	0.38	1.05	0.13	0.719
Nr of followed trips								
Constant	1.05	0.47		0.062	-0.08	0.72		0.917
Personality focal	1.63	1.08	1.51	0.182	-1.96	2.53	0.60	0.447
Personality current partner	**11.73**	**1.41**	**68.84**	**< 0.001**	**4.30**	**1.54**	**7.78**	**0.010**
Personality previous partner	**-2.93**	**1.06**	**7.51**	**0.029**	0.65	1.04	0.39	0.537

These analyses looked at focals that were bolder than their final partner ($N = 10$) and focals that were shyer than their final partner ($N = 24$). Statistics for significant terms, shown in

bold, were derived from the minimal model containing only significant terms while statistics for non-significant terms were obtained by running the minimal model with the term added individually. Coefficient estimates represent the change in the dependent variable relative to the baseline category and can therefore be interpreted as measures of effect size. All personality scores and response variables were square-root transformed.

FIGURE CAPTIONS

Figure 1.

The proportion of time focal fish spent out of cover during the current pairing was (A) positively correlated with the boldness scores of bold focals ($N = 10$), but (B) not significantly correlated with the boldness scores of shy focals ($N = 24$). Boldness scores were square-root transformed.

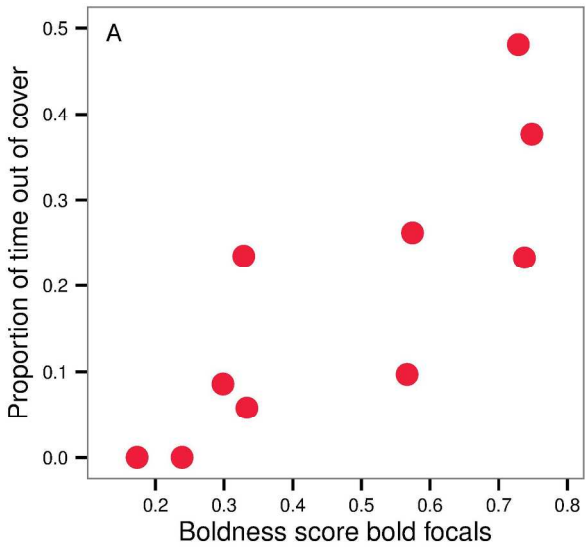
Figure 2.

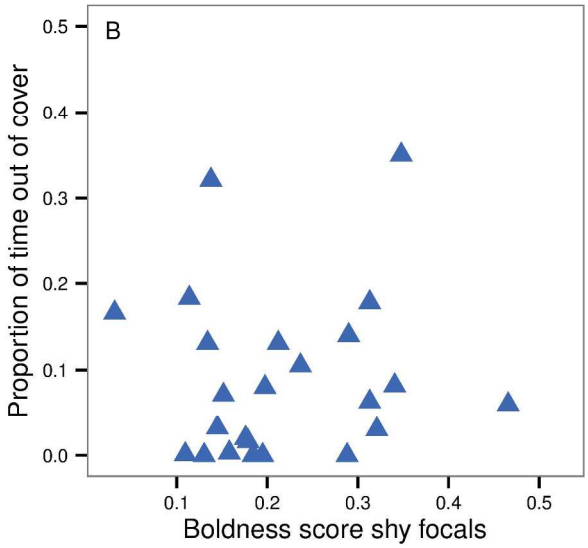
The number of trips bold focals ($N = 10$) initiated and were joined by their partner during the current pairing was (A) positively related to their own boldness score and (B) negatively related to the boldness score of their previous partner. The y-axis of plot b shows residuals of the model on leading trips with focal boldness score as the only factor. Scores above 0 indicate individuals were joined more than may be expected based on their own boldness score and scores below 0 individuals were joined less than may be expected based on their boldness score. Boldness scores and number of leading trips were square-root transformed.

Figure 3.

The number of trips focals went out of cover and joined their partner (following) during the current pairing is positively related to the boldness score of the current partner, both for bold

focals (N = 10, circles) and shy focals (N = 24, triangles). Boldness scores and the number of following trips were square-root transformed. Two data points of the bold focals overlap at the origin because they both never followed and had a partner with a boldness score of 0.





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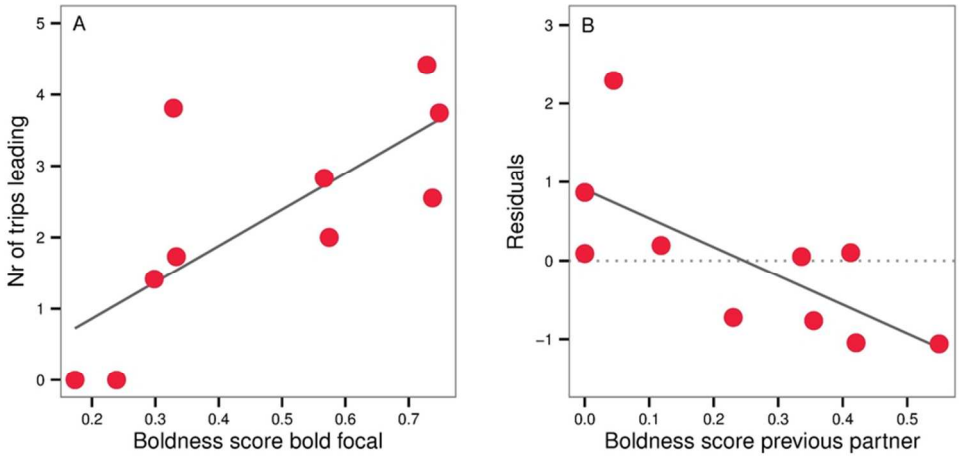

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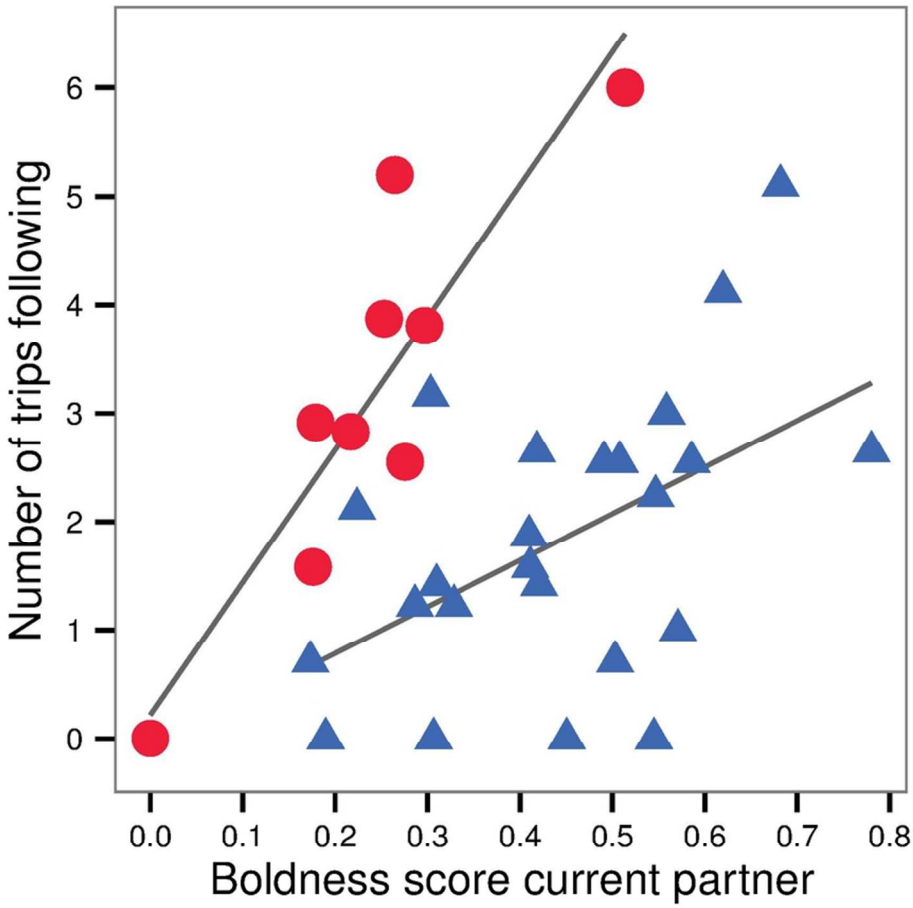

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