

Sex-dependent use of information on conspecific feeding activities in an amphibian urodelian

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Summary

1. Animals can make decisions by observing the behaviour of others. Their decisions vary depending on whether the benefits of using such information exceed the costs. Thus, it is worthwhile to explore the potential costs associated with different sources of information to understand the consequences of sociality. Previous studies focused mainly on the costs inherent to information gathering, whereas sex differences with regard to the costs arising from information use have received less attention.

2. To explore this further I performed two complementary experiments. The first experiment aimed to examine individual responses to different combinations of information types that are likely to appear in nature, to test whether there is a sex-dependent response in the Bosca's newt, *Lissotriton boscai*. I tested the time needed for individuals to eat food items by trial-and-error tactics (personal information), and when a conspecific, which was eating or not, was added to the food cue. The second experiment aimed to evoke social interactions that are likely to arise after the choice of using information on conspecific feeding activities is made. I examined the potential costs associated with direct competition between same-sex pairs in food-limited conditions.

3. Results of experiment 1 revealed that in both sexes the latency to eat food items was shorter in the presence of non-feeding conspecifics, but only females took advantage when information related to feeding activities were added to the food cue. Results of experiment 2 showed that when faced with a limited resource of food, females were more prone to engage in costly interactions.

4. This study suggests that the balance between costs and benefits associated with the short-term use of information on conspecific feeding behaviour in combination with food cues may differ between sexes. Differential information uses by sexes might have profound consequences in intraspecific relationships and in the evolution of vertebrates' social systems.

Key-words: social information, personal information, foraging, Bosca's newt, *Lissotriton boscai*, Urodela

Introduction

Spatiotemporal variation in the environment generates uncertainties regarding physiological or behavioural decisions that will affect the fitness of organisms. Information about environmental parameters may reduce this uncertainty, allowing receivers to adjust their responses. When environmental variation is so high that the information cannot be transferred genetically or prenatally, other mechanisms such as information gathering should evolve. This possibility encompasses three sources of information: personal information obtained by direct interaction with the environment using trial-error tactics (Valone 1991), the presence of conspecifics, which may indicate habitat suitability (Stamps 1988), and socially acquired

information obtained by observing the behaviour of others (Giraldeau *et al.* 2002). It is known that the use of these types of information may impart different types of benefits as well as costs (Dall *et al.* 2005; Kendal *et al.* 2005). Therefore, it is worth exploring the potential costs and benefits associated with the use of these sources of information for understanding the causes and consequences of social influences on behavioural decisions. Different species, sexes or phenotypes might be subjected to different cost : benefit ratios depending on key factors such as the costs of information sampling, the costs of competition for the target resource and the success of resource detection (Danchin *et al.* 2001; Giraldeau *et al.* 2002; Nocera *et al.* 2006; Pasinelli *et al.* 2007). Relying on the behaviour of conspecifics which are exploiting the target resource should impart higher success in detection and lower searching time than relying on trial-error tactics or on

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the conspecific presence regardless of their activity. On the other hand, making use of social information from conspecific behaviour may also increase the competition level when individuals are simultaneously exploiting the same resource. Thus, it is expected that animals should use one or more of these information types only when the benefits exceed the costs (Dall *et al.* 2005; Kendal *et al.* 2005). Theoretical and empirical studies have focused mainly on the costs inherent to the gathering of social information, such as incompatibility with personal information (Giraldeau *et al.* 2002), or increased predation risk (Coolen *et al.* 2003). However, the costs arising after the choice, such as costly interactions with conspecifics when simultaneously exploiting the target resource, have been rarely considered (Danchin *et al.* 2001; Seppan en *et al.* 2007).

Behavioural differences between sexes arising from cost : benefit ratio differences has been reported across taxa, such as antipredatory behaviour (Bernal *et al.* 2007; Cooper & Wilson 2007), foraging (Magurran & Maci as-Garcia 2000; Beck *et al.* 2007) or aggressiveness (Rosvall 2008). Specifically, competition is often higher within sexes than between sexes, and the intensity of intrasexual competition is often sex-biased (Magurran & Maci as-Garcia 2000; Clutton-Brock 2007). Thus, it is expected that when there are inter- and intrasexual differences in the competition level, males and females might use the information types differently depending on the balance between costs and benefits. However, given sex differences across taxa in many life-history traits besides behaviour (Van Damme *et al.* 2008) there is surprisingly little evidence of sex-dependent influence on the use of social information (Doligez *et al.* 1999; Arag on *et al.* 2006a; Nocera *et al.* 2006), and it is lacking in a foraging context. We can use theory to predict that while intra-male competition involves the access to mates, females compete with each other for resources that allow them to increase their reproductive output, such as breeding sites, parental care, social rank or food (Summers 1989; Holekamp *et al.* 1996; Magurran & Maci as-Garcia 2000; Rosvall 2008). Depending on the cost : benefit ratio of intrasexual competition for mates or other resources, selective forces would favour aggressiveness in the sex that gains important benefits from costly interactions (Clutton-Brock 2007; Rosvall 2008).

Many studies on socially acquired information have focused on conspecific foraging activities as a source of information about when, where, what, and how to eat. This has been showed to occur for a variety of bird (Valone & Templeton 2002), mammal (Galef & Giraldeau 2001) and fish species (Coolen *et al.* 2003). In amphibians, social foraging has recently been documented (Sontag *et al.* 2006). The goals of this study are: (i) to examine whether the response of Bosca's newt, *Lissotriton boscai*, to different combinations of information types in a foraging context is sex-dependent, and (ii) to resemble the conditions inherently associated with the choice of using information on feeding conspecifics, and test whether the level of competition for the limited source of food is sex-dependent. In the first experiment, I tested the time elapsed to eat food items when an individual was confronted with personal information in the presence of food, with the

combination of a conspecific presence and food, and with the combination of a conspecific actually eating and food. I performed a second experiment to examine the potential costs associated with direct competition for limited food in clumped conditions, measuring the time that individuals spent in close proximity and the degree of agonistic interactions. It is expected that eating in close proximity would promote social interactions.

I selected *L. boscai* as a model of an amphibian because: (i) it is found in high densities in most of its geographic distribution (Montori & Herrero 2004) and social interactions between individuals in the aquatic phase are frequent (e.g. Mouta-Faria 1995), (ii) individuals inhabit shallow and slow-running clear water where visual communication is favoured, but abundant aquatic vegetation may hinder prey detection (Montori & Herrero 2004), (iii) the success of food intake (the location of which is unpredictable) may be crucial in this species since individuals have to survive first the summer when they enter dormancy, and then the winter when prey abundance decreases, and (iv) the feeding behaviour of this species is visually conspicuous.

Materials and methods

STUDY SPECIES

Lissotriton boscai is a small newt endemic to the Iberian Peninsula. It inhabits shallow streams of slow-running clear water with aquatic vegetation, and is one of the most aquatic newts (Montori & Herrero 2004). Active adults can be observed in the water all year except for mid-summer when they become terrestrial for estivation, and the breeding period encompasses all the aquatic phase (Caetano 1982). Sexual dimorphism in this species is less evident than in other newt species, which appears to be a consequence of divergent selective pressures as females are larger than males (Montori & Herrero 2004; Fig. 1). The diet of adults consists of a variety of invertebrate taxa, such as oligochaeta, mollusca, insecta and arachnida (Montori & Herrero 2004). After detecting food, individuals typically approach slowly and position their snout close to the prey, assessing palatability by chemical exploration while showing a static posture. They then conspicuously shake their entire body to aspire and gulp the prey. In spring 2007 and 2008, I collected 82 adult newts (41 males and 41 females) from a stream located in Navia (Asturias province, northern Spain). Individuals were weighed (males: mean \pm SE = 1.11 ± 0.02 g; females: mean \pm SE = 1.49 ± 0.03 g) and their length measured (males: mean \pm SE = 68.5 ± 0.56 mm; females: mean \pm SE = 76.2 ± 0.56 mm). Newts were individually housed 2.5 km from the capture site in aquaria (20 \times 30 cm) containing water and aquatic vegetation from the stream of origin. To standardize the motivation to eat during trials, the day of capture all newts were fed with only one food item, and then they were acclimated to their aquaria during 2 days with no food before the experiments.

EXPERIMENT 1: RESPONSES TO COMBINATIONS OF INFORMATION TYPES

The aim of this experiment was to measure the time focal individuals needed to obtain food when personal information, the presence of a conspecific in a food patch, or information on conspecific feeding

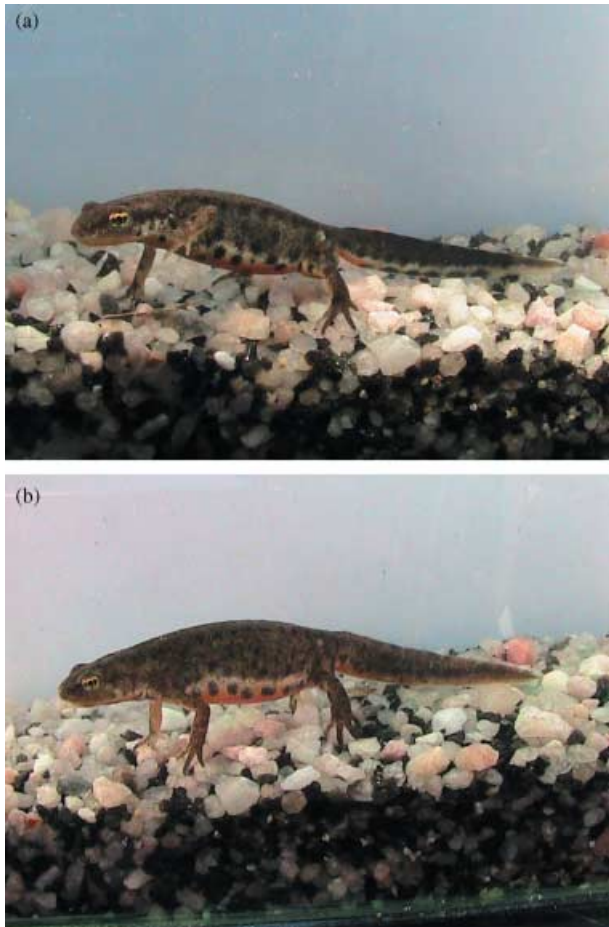


Fig. 1. Adult (a) male and (b) female Bosca's newts, *Lissotriton boscai*.

behaviour was available. This experiment was designed to resemble natural situations in which individuals responded to three possible combinations of the three above-mentioned types of information. Thus, each type of information was additively presented through three different treatments (i.e. food as a cue, food + presence of a conspecific, or food + presence of a conspecific + the conspecific feeding behaviour). Since the visual perception of the conspecific behaviour and his mere presence are unavoidably concomitant, the visual effects of these two types of information can only be manipulated additively.

The existence of behavioural syndromes in urodelyans has been documented (Sih *et al.* 2004), and this can influence information use as demonstrated in other ectothermic vertebrates (Aragón *et al.* 2006b). This might bias the test if behavioural syndromes are not randomly distributed through the treatments. To reduce error variance, each individual responded to the three treatments in a repeated measures design (Quinn & Keough 2002), in a randomized and balanced order of presentation. This protocol effectively prevented an effect of individual prior experience (van Bergen *et al.* 2004), as the order of treatment presentation did not affect the latency to eat the food item (one-way ANOVA: $F_{2,48} = 0.85$, $P = 0.43$). For each trial, the focal individual (hereafter observer) was confined to an opaque cylinder (8 cm in diameter) at one side of the experimental aquaria (20×30 cm) during 5 min for habituation, and to standardize their location before the beginning of trials. On the opposite side, a transparent cylindrical receptacle (closed at the bottom) of the same size was placed with or without a conspecific depending on the treatment.

The side where cylinders were located was randomized and counter-balanced. In all treatments two food items were present at the beginning of trials.

In the personal information treatment (hereafter PI) there was no conspecific in the transparent cylindrical receptacle whereas food was the only cue. In the presence of conspecific treatment (hereafter PI+PC), and in the treatment of information on conspecific feeding behaviour (hereafter PI+PC+CFB), there was a conspecific inside (hereafter demonstrator), in addition to the presence of food in the aquarium. Conspecific chemical cues may influence site selection in this species (Aragón *et al.* 2000). Therefore, their feeding movements in the aquatic environment might provoke an increase in the flow of conspecific chemical cues, which would be an augmentation of the social cues involved in the presence of conspecifics, rather than specifically informing that the conspecifics are eating. The use of transparent cylindrical receptacles prevented the flow of demonstrator chemical cues, and held constant the location of the demonstrator. Each of the two food items was threaded to the end of two threads and fixed to the same point on the exterior side of the transparent receptacle so that the items remained together at the ground level, allowing newts to eat on this food patch after the 5 min of habituation. In the PI+PC+CFB treatment, the two food items were threaded exactly in the same way as explained above except one of the items, which was fixed to the interior side of the cylindrical receptacle, both items at the same point and at ground level. This ensured feeding behaviour by the demonstrator. Food items were pieces of *lumbricus*, all of the same size (1 cm) and found in the same stream of origin. This procedure ensured an equal number of food items at the beginning of trials and across treatments. However, as in a natural situation, the number of food items present in the PI+PC+CFB treatment was reduced once the demonstrator ate one. Still, both males and females were faced with the same conditions, and the patterns of responses found in both experiments cannot be explained by a reduction of items during trials (see results). Since the two items were fixed at the same point in the experimental conditions it was assumed that they were perceived by newts as a single cue in a single food patch. Nevertheless, it is always worthy to experimentally rule out other possibilities even when the results are conservative. Thus, after the second experiment in 2008, I performed an additional control experiment using 20 males and 20 females with the same conditions as in the PI treatment, except that half of individuals were presented with two food items and the other half with one item. As expected, the latency to eat the food did not differ between sexes (two-way ANOVA: $F_{1,35} = 0.33$, $P = 0.56$) or food conditions ($F_{1,35} = 0.60$, $P = 0.44$) as main effects, and the interaction was not significant ($F_{1,35} = 0.09$, $P = 0.76$).

To avoid dominance asymmetries, observers and demonstrators were size matched so that they were within 2 mm of the same size. To begin a trial, the opaque cylinder of the observer was gently removed, allowing the observer to move freely through the aquarium. I performed 60 trials ((10 observer males + 10 observer females) \times 3 treatments) in the morning when individuals were fully active. Observers and demonstrators were of the same sex to avoid courtship behaviours that might override the test. Maximum duration of trials was 30 min. No newt was tested more than once per 4 days. Data were analysed using repeated measures ANOVAs with treatments as the within-subject factor, sex as the between-subject factor, and the latency to eat an item as the response variable. The interaction between factors was included in the analyses to test whether the response to different combinations of information was dependent on sex. I then planned comparisons (Quinn & Keough 2002) for males and females separately and depending on the type of question. First,

to verify that there are no baseline differences in the activity rate or exploration capacity, I compared using one-way ANOVA the latency to eat a food item by their own personal information between males and females. Then, I performed comparisons between two treatments where the only difference was an additional type of information. To test whether the addition of a conspecific to the food cue may modify the newts' response, I compared using repeated measures ANOVAs the latency to eat food in absence of a conspecific with that in presence of a non-feeding conspecific (i.e. PI vs. PI+PC). To examine the response when the information on conspecific foraging behaviour was added to the other two types of information, the same analysis was performed comparing between the latency in the presence of a non-feeding conspecific and the latency when the demonstrator was eating (i.e. PI+PC vs. PI+PC+CFB). It has been argued that not only the behaviour but also the mere presence of conspecifics can be a source of social information as it may give information on patch quality and/or indicate the location of resources (Valone & Templeton 2002; Danchin *et al.* 2004). Thus, in case of no significant differences between PI+PC and PI+PC+CFB, a further comparison between PI and PI+PC+CFB was made. The latency in seconds was log-transformed to meet the assumptions underlying linear models (Quinn & Keough 2002).

EXPERIMENT 2: SOCIAL INTERACTIONS IN A FORAGING CONTEXT

This experiment aimed to test: (i) whether there are sex differences in the paired newts' behaviour under competitive and non-competitive conditions, and (ii) whether the level of social interactions changes after the first feeding event. Focal newts responded to two different treatments (with or without competition for a limited source of food) in a random order of presentation. For each treatment focal newts were paired with different individuals of the same sex and recorded with a camcorder aligned perpendicularly to the experimental aquarium. On the competition treatment, the behaviour of individuals was recorded in the presence of two food items in a 6-cm diameter petri dish located in the centre of the aquarium. Thus, this treatment provided a limited clumped source of food. In the control treatment, the same conditions were maintained except the dish was empty. For each trial, two size matched newts were located on each side at an equal distance to the dish. Newts were confined to two opaque cylinders during 5 min before each trial began. I performed 40 trials (10 pairs for each sex \times 2 treatments). All trials were performed in the morning and lasted 10 min.

To verify whether the experimental design reliably induced competitive conditions when food was present, I compared the level of total agonistic interactions per pair, which are inherently costly (Huntingford & Turner 1987), between the competition and control treatments. Each agonistic interaction consisted of a single quick bite performed by one of the two individuals. Since each focal newt responded to two treatments, these data were analysed using repeated measures ANOVAs with the treatment as the within-subject factor and the sex as the between-subjects factor. When the interaction term was significant, I used Tukey's HSD test to perform *post hoc* comparisons (Quinn & Keough 2002).

To compare the behavioural responses between the absence and the potential presence of information on conspecific feeding behaviour under competitive conditions (in the competition treatment), data were split into two periods: before and after the first time that one individual performed feeding activities. To test whether the appearance of feeding activities is congruent with an increase of social interactions I scored the proportion of time that pairs of newts

spent in close proximity (< 1 cm apart), either before and after the first feeding activity. I also compared the number of agonistic interactions per pair before and after the first feeding activity. Data were analysed using a repeated measures ANOVA with periods as the within-subject factor and sex as the between-subject factor.

Finally, I compared between the potential observer and the demonstrator (the one that began to show feeding activities) the number of bites performed by each newt after the first feeding event. As in this case the statistical unit is the pair, these data were analysed using a repeated measures ANOVA with the pair as the within-subject factor and sex as the between subject-factor. Additionally, I conducted Pearson's correlations between the number of agonistic interactions under competition performed by the demonstrator newt and the corresponding potential observer newt. Thus, a positive association would suggest that agonistic interactions can be costly not only to one of the partners but to both. The same procedure was conducted for the control condition except that in this case newts cannot be assigned as potential observers and demonstrators. Agonistic interactions never came to the point of injuries or persistent attacks and did not lead to sustained attempts to escape. Data on agonistic interactions and proportion of time that newts spent in close proximity were analysed using the square root and the angular transformations respectively to meet the assumptions underlying the application of linear models (Quinn & Keough 2002).

Morphometric traits of size, weight and corpulence were included in the initial models of both experiments to verify that size matching of pairs effectively ruled out asymmetries in competitive ability. Corpulence is defined as a size-specific measure of weight which was estimated by taking the residual score of the linear regression of body weight on length. Additionally, I used one-way ANOVAs to verify that morphometry of demonstrators/partners were similar between treatments in both experiments. For all analyses significance was set at an α -level of 0.05. No pairing of individuals was repeated in any of the experiments. Both experiments were performed with water at 14.5 °C, which was within the temperature range measured in their stream (13.5–15.5 °C), and within the range during the entire aquatic phase of this species (Mouta-Faria 1995). After the experiments, newts were fed and returned healthy to their capture point.

Results

EXPERIMENT 1: RESPONSES TO COMBINATIONS OF INFORMATION TYPES

There were no significant differences between treatments in demonstrator's length (one-way ANOVA, males: $F_{1,20} = 0.01$, $P = 0.92$; females: $F_{1,18} = 0.02$, $P = 0.89$), or weight (males: $F_{1,20} = 0.21$, $P = 0.65$; females: $F_{1,18} = 0.48$, $P = 0.82$). Similarly, demonstrator's corpulence did not differ significantly between treatments (males: $F_{1,20} = 0.31$, $P = 0.58$; females: $F_{1,18} = 0.11$, $P = 0.73$). Furthermore, the size-matching between observers and demonstrators effectively ruled out dominance asymmetries since these traits were not significantly associated with the responses of focal individuals ($0.52 < \text{all } P < 0.99$).

All newts were active during trials in both experiments. In experiment 1, demonstrators inside the cylinder showed similar behavioural patterns, such as resting, walking and ascending to breathe, except that in the PI+PC+CFB treatment they also showed feeding behaviour. Of the 60 trials,

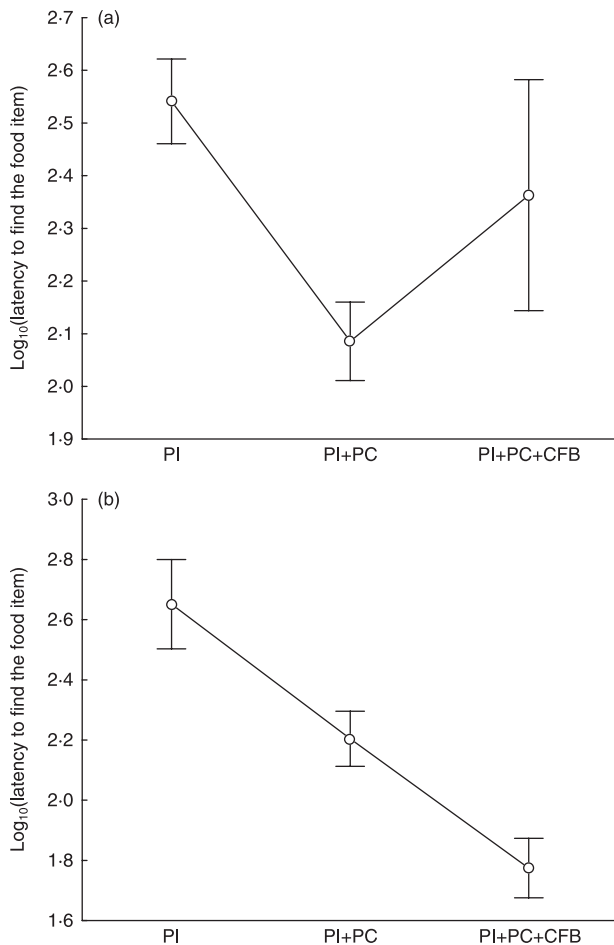


Fig. 2. Latency (s) (mean \pm 1SE) of Bosca's newts to eat a food item when faced with only their personal information from the food itself (PI), the presence of a conspecific and food (PI+PC), and information on conspecific feeding behaviour and food (PI+PC+CFB), in (a) males and (b) females.

there were two males in the PI+PC+CFB treatment, and one female in the PI treatment that did not eat the food item after 30 min. There were no significant differences between the latency of males and females to eat food by their own personal information (PI treatment: $F_{1,15} = 0.39$, $P = 0.53$; Fig. 2). There were no significant differences between sexes in the latency to eat the food item as a main effect (between-subject factor: $F_{1,15} = 1.09$, $P = 0.31$). However, there was a significant effect of the treatment (within-subject factor: $F_{2,30} = 11.02$, $P = 0.0002$), and the interaction between sex and treatment was also significant ($F_{2,30} = 5.59$, $P = 0.008$; Fig. 2).

In the case of females, this latency was longer when using only their personal information than when the presence of a conspecific was added to the food cue (PI vs. PI+PC comparison: $F_{1,8} = 6.22$, $P = 0.037$; Fig. 2), and longer in the presence of the non-feeding conspecific than when the conspecific was eating (PI+PC vs. PI+PC+CFB: $F_{1,8} = 16.22$, $P = 0.003$). In the case of males their latency was also longer when using only their personal information than when the presence of the non-feeding conspecific was added to the food cue (PI vs. PI+PC: $F_{1,7} = 60.44$, $P = 0.0001$). Regarding the comparison

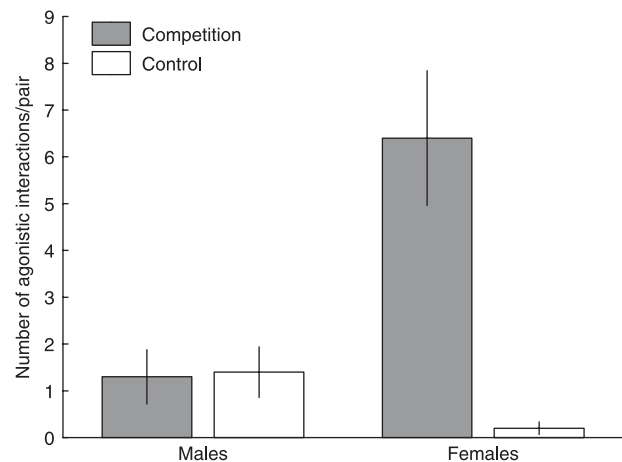


Fig. 3. Number of agonistic interactions (mean \pm 1SE) performed within same-sex pairs of Bosca's newts during staged encounters in the competition treatment (with food items) and in the control treatment (without food items).

between feeding and non-feeding conspecifics, males showed a different response to that of females, although it was not statistically significant (PI+PC vs. PI+PC+CFB: $F_{1,7} = 2.16$, $P = 0.18$). Additionally, there were no significant differences in the latency of males to eat food between the treatments of personal information and information on feeding conspecifics (PI vs. PI+PC+CFB: $F_{1,7} = 0.55$, $P = 0.48$).

EXPERIMENT 2: SOCIAL INTERACTIONS IN A FORAGING CONTEXT

There were no significant differences between treatments in partner's length (one-way ANOVA, males: $F_{1,18} = 0.03$, $P = 0.87$, females: $F_{1,18} = 0.66$, $P = 0.42$), weight (males: $F_{1,18} = 0.49$, $P = 0.48$, females: $F_{1,18} < 0.01$, $P > 0.99$), or corpulence ($F_{1,18} = 0.67$, $P = 0.42$, females: $F_{1,18} = 0.20$, $P = 0.65$). These traits were not significantly associated with the responses of focal individuals ($0.16 < \text{all } P < 0.93$).

There were feeding events in all trials under competition except for one. The comparison of agonistic interactions per pair revealed no significant effect of sex as a main effect (between-subject factor: $F_{1,18} = 1.25$, $P = 0.27$), whereas the total number of agonistic interactions was significantly higher under competition than in the control treatment (within-subject factor: $F_{1,18} = 24.24$, $P < 0.001$), and the interaction between sex and treatment was also significant ($F_{1,18} = 33.52$, $P < 0.0001$; Fig. 3). Thus, the degree of agonistic interactions per pair was significantly higher in the case of females under competition than in the other cases (Tukey's test: all $P < 0.03$), whereas there were no significant differences among the other cases (all $P > 0.45$).

Once the competition treatment data were split into two periods, and the case with no feeding event was removed, the results revealed that nearly all agonistic interactions occurred after one of the two newts began feeding activities. There was only one agonistic interaction performed before the first feeding event. Regarding the proportion of time that newts

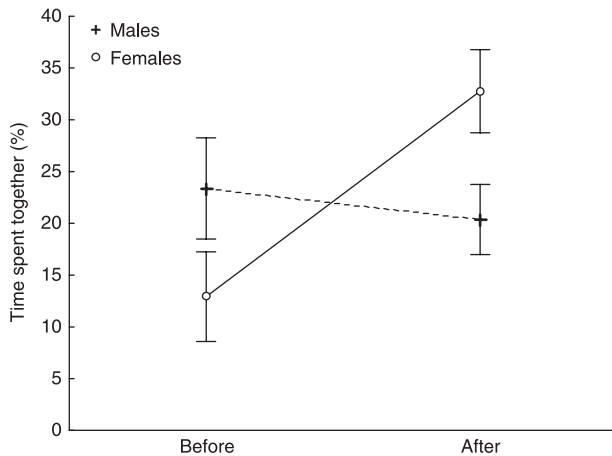


Fig. 4. Time (mean \pm 1 SE) that same-sex pairs of Bosca's newts spent together before and after the first feeding event during staged encounters in the competition treatment.

spent in close proximity, there was no significant effect of sex (between-subject factor: $F_{1,17} = 0.32$, $P = 0.85$) or the period (within-subject factor: $F_{1,17} = 3.71$, $P = 0.07$) as main effects. However, the interaction between sex and periods was significant ($F_{1,17} = 14.15$, $P < 0.01$; Fig. 4). *Post hoc* comparisons showed that the time that female pairs spent in proximity was significantly higher after the first feeding event (Tukey's test: $P < 0.01$), whereas there were no significant differences among the other cases (all $P > 0.18$).

When considering separately the agonistic interactions performed by the potential observers of the feeding event and by the demonstrators of this information in the competition treatment, the results showed that the level of agonistic interactions was higher in females than in males regardless of being observer or demonstrator (between-subject factor: $F_{1,17} = 11.33$, $P < 0.01$). Interestingly, the number of agonistic interactions performed by the potential observers was higher than that performed by the demonstrators, regardless of sex (within-subject factor: $F_{1,17} = 6.82$, $P = 0.018$; Fig. 5). For this analysis the interaction term was not significant ($F_{1,17} = 1.22$, $P = 0.28$). Finally, there was a positive association between the number of agonistic interactions performed by the potential observer and the demonstrator in the competition treatment ($r = 0.46$, $F_{1,17} = 4.67$, $P = 0.04$), whereas the correlation was not significant in the control treatment ($r = 0.05$, $F_{1,18} = 0.05$, $P = 0.81$).

Discussion

Experiment 1 was designed to resemble a natural situation in which individuals had access to different combinations of different types of information to better capture the biological meaning of the responses. Thus, since treatments were presented in an additive way, it is not possible to know whether the differential response observed was due to a given type of information working alone or in combination with other types of information. However, each type of information were

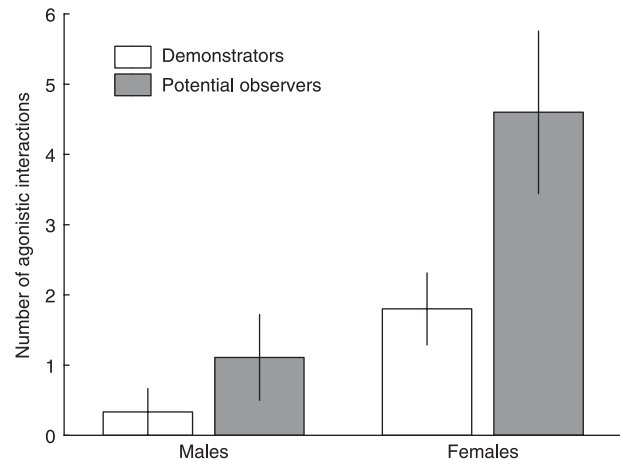


Fig. 5. Number of agonistic interactions (mean \pm 1 SE) performed by demonstrators and by potential observers of information on conspecific feeding behaviour during staged encounters in the competition treatment.

added in a randomized stepwise manner, which allowed comparisons between two treatments that only differed in one type of information. Therefore, the differential response to the treatments should be interpreted as the contribution of the additional type of information to the combination, which does not necessarily imply the same pattern if they had been perceived alone.

PERSONAL INFORMATION AND PRESENCE OF CONSPECIFICS

The latency to eat in experiment 1 was longer when individuals had access to food only by trial-and-error, and this pattern was similar for both sexes. Thus, individuals took advantage to exploit a discretely distributed food source when a non-feeding conspecific was presented in combination with the food cue. The presence of conspecifics as a source of information is not restricted to adults in amphibians. A recent study showed that the presence of food in combination with the initial presence of tadpoles of the toad *Bufo americanus* enhanced aggregation, compared to an identical food patch without tadpoles (Sontag *et al.* 2006). More generally, the use of information from the presence of conspecifics has been described in a variety of taxa (Stamps 1988; Serrano *et al.* 2004; Michelena *et al.* 2005), which is not surprising because it can integrate various commodities simultaneously (access to food or mates, protection from predators, temperature maintenance, etc.). Thus, the use of individuals as cues regardless of their activities does not necessarily imply access to the same resource simultaneously and in close proximity. In fact, even in territorial species individuals may take advantage from the conspecific presence (e.g. Stamps 1988; Muller *et al.* 1997). However, in a scenario in which the value of the information is auto-correlated in time and space, the short-term use of social information in a given activity (independently or in combination with other information types) should be favoured when the costs of competition do not exceed the benefits (Seppan en *et al.* 2007).

PRESENCE OF CONSPECIFICS AND INFORMATION ON FEEDING BEHAVIOUR

The results of experiment 1 showed that males and females responded differently when information provided by the feeding activities of conspecifics was added to the food cue. The latency of females to eat was shorter when information from feeding activities was provided, whereas males did not take advantage of this combination of information. In addition, two male individuals did not eat the food item when faced with a conspecific eating. These findings are not a by-product of differences in exploration capacity or activity rate between males and females, as there were no differences in the 'personal information' treatment. Besides, the results on the randomized order of presentation and those of the control experiment demonstrated that the results of experiment 1 cannot be explained by other possibilities. Accordingly, other studies showed that various phenotypes may use social information in different ways. For example, individuals may respond differently to social information depending on their physical condition (Aragón *et al.* 2006a), age (Dugatkin & Godin 1993; Doligez *et al.* 2004; Parejo *et al.* 2007), or dispersal status (Aragón *et al.* 2006b). Specifically, the response to social information has been previously shown to be dependent on sex in birds (Doligez *et al.* 1999; Nocera *et al.* 2006) and reptiles (Aragón *et al.* 2006a). Despite the fact that other forms of social information have already been described in ectothermic vertebrates (McGregor 2005; Aragón *et al.* 2006a; Swanson *et al.* 2007), social information in foraging activities has been previously shown only in fishes (Coolen *et al.* 2003). Thus, the results presented here support accumulating evidence that the use information for feeding activities (here in combination with other information types) is not restricted to cognitively sophisticated vertebrates.

When males were faced with information regarding feeding activities, there were no significant differences in the latency to eat either with the presence of a non-feeding conspecific together with food or with personal information alone. Taken together, results of experiment 1 suggest that in the case of males, the net benefit of using information from individuals as cues was higher than the use of information on conspecific feeding behaviour.

THE MECHANISM

While experiment 2 was not designed to test the response to different combinations of information, it resembled the circumstances that individuals would face after the choice of using information on feeding conspecifics. Experiment 2 revealed that all agonistic interactions, except for one, occurred after the appearance of feeding behaviour by one of the individuals. Furthermore, the level of agonistic interactions performed by the potential observers in experiment 2 was higher than that performed by demonstrators (those that began to show feeding activities), independently of the sex. Thus, in this species, foraging at the same site, where food is limited, implies direct competition with conspecifics of the

same sex. Although, experiment 2 cannot reveal what sources of information individuals are using, the facts that potential observers were more aggressive and that agonistic responses within pairs were not unidirectional are compatible with the results of experiment 1. The short-term use of information that will unavoidably involve exploiting a limiting food resource in proximity of conspecifics, will be costly in terms of competition. An additional potential associated cost is the incompatibility of the use of social information with the other types of information (Giraldeau *et al.* 2002). Thus, engaging in agonistic interactions can be costly, not only because of the risk of injury or energetic expenditures but also because it is time consuming (Huntingford & Turner 1987), which might reduce the integration of two types of information. Because access to food is beneficial but agonistic interactions are costly, it follows that individuals can be subject to a trade-off, and therefore the use of information on conspecific feeding behaviour should be favoured by a net benefit.

In agreement with the first experiment, experiment 2 also revealed differences between sexes. The appearance of feeding activities is concomitant with a substantial decrease in the distance between females but not between males. Moreover, only females increased their aggressive response in relation to the control treatment. Both results go in the same direction indicating that females are more prone to engage in costly interactions to access food. Therefore, the higher motivation of females to compete in a foraging context should be due to a higher net benefit. Taking the results of both experiments together, the sex differences in the use of conspecific information (at least in combination with other information types) can be explained by differences in the balance between the benefits of food intake and the costs inherent to agonistic interactions.

Whereas there are many studies focusing on the intensity of intrasexual competition and the evolution of traits that increase competitive ability in males, this is less understood for females. The cost : benefit ratio may change as a function of the value of the disputed resource. Thus, although both sexes compete to ultimately increase their fitness, males of many species compete to increase their mating opportunities whereas females often compete for resources that increase their reproductive output (Clutton-Brock 2007). Previous studies that have found intense female competition for breeding sites in fish (Buston 2003), parental care in amphibians (Summers 1989) or social rank in mammals (Holekamp *et al.* 1996), are also coincident with females being larger than males. Further, it has been demonstrated that the prevalence of female aggressive behaviour is beneficial for access to a critical resource (Rosvall 2008). Thus, intense competition combined with greater development of traits conferring competitive ability in one sex, should reflect greater benefits of acquiring critical resources (Clutton-Brock *et al.* 2006). *Lissotriton boscai* females are also larger than males (Montori & Herrero 2004), and the present results showed that competition for food is higher among females. Interestingly, agonistic interactions among *L. boscai* males are frequent during courtship interferences (Mouta-Faria 1995), suggesting

that the cost : benefit ratio may change depending on the value of the disputed resource for each sex. In *L. boscai* there is a continuous reproductive effort for females, which may last for a period of 8 months (Montori & Herrero 2004). To continuously afford this energetic expenditure it would be valuable to increase their foraging success, even if the foraging strategy entails an increase of the associated costs. Similarly, in another context of the costs and benefits of foraging, it has been shown that female guppies (*Poecilia reticulata*) may take greater predation risks than males by eating at dangerous food patches because the energetic gains outweigh the possibility of capture (Abrahams & Dill 1989). In mammals, it is known that food availability is a crucial factor affecting females' reproductive performance. For instance, fertility among high-ranking females of spotted hyaena (*Crocuta crocuta*) is less vulnerable to fluctuations in the food supply than among low-ranking females (Holekamp *et al.* 1996).

To conclude, this study showed that when faced with the addition of information on conspecific feeding behaviour only females increased their foraging success over other combinations of information. Also, the level of costly interactions between females was higher when eating on the same patch. Such interactions are likely to arise when using short-term information on conspecific feeding activities. Therefore, the sex-dependent response to different combinations of information types can be explained by differences in the cost : benefit ratio that changes as a function of the value of that resource for each sex. This study supports previous studies arguing that not all sources of information are always advantageous (Giraldeau *et al.* 2002; Valone & Templeton 2002; Coolen *et al.* 2003; Dall *et al.* 2005; Seppanén *et al.* 2007). There is empirical evidence supporting the idea that under specific circumstances fish, birds, and mammals may rely more on some sources of information while ignoring others (Kendal *et al.* 2005). The present findings expand this phenomenon to amphibians at least with regard to combinations of information types, which warrant future research on the relative contributions of the independent, additive or synergistic effects of information types.

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