Nest orientation patterns in river blennies *Salaria fluviatilis*

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Running head: Nest orientation in river blennies

The entrances of nests established under small stones by male river blennies (*Salaria fluviatilis*) in two rivers of the Ebro basin in eastern Spain were randomly oriented in slow-flowing sites. However, in fast-flowing stretches or under large stones, nest entrances tended to open at an angle of *c*. 30° relative to current flow direction, i.e. near a southeast direction. As current velocity increased, males positioned their nest entrance closer and closer to the direction of flow. Selective nest entrance orientation reduced significantly the speed of current reaching the nest entrance such that current velocity was similar (5-7 cm s^{-1}) for all nests, regardless of stone size, prevailing current speed, or study site. However, male mating success, measured as egg clutch area, was not related to current speed at the nest entrance but instead, it increased with nest stone size and decreased with deviations from a southeast direction. The reasons for female river blenny preference for this specific nest orientation are unknown but may be related to patterns of water flow, and hence oxygenation of the eggs, in the nest.

Key words: Blenniidae; mating success*;* nesting behaviour

INTRODUCTION

Nearly half of all teleost fish families show parental care of offspring, and within these families, solitary paternal care is by far the most common care pattern (Gross & Shine, 1981). Paternal care in fish is usually associated with the presence of a nest within which eggs are laid. Fish nests are located on a variety of open substrates (e.g. rock, sand, vegetation, etc.), or are sometimes located within shelters (e.g. mollusc shells) or crevices offering limited access.

Relatively little is known about the characteristics of good nest sites in fish. A large surface area is the nest feature most commonly related to higher male mating success (Bisazza *et al*., 1989; Côté & Hunte, 1989; Lindstrøm, 1988; Hastings, 1992; Nellbring, 1993; DeWitt, 1993). Size-assortative nest site choice is common (e.g. Lugli *et al*., 1992), and experiments with artificial nests have suggested that competition among males is not necessary to produce such patterns (Kvarnemo, 1995). Males may therefore be balancing the benefits of having a large surface area, which can accommodate large clutches, with the costs of maintaining and defending large nests from predators and/or competitors when choosing a nest site. Other nest features which are occasionally important for male reproductive success include few or small, tight-fitting entrances (Crabtree & Middaught, 1982; Koppel, 1988; Kortschal, 1988; Lavery, 1991), a low degree of internal fouling (Hastings, 1988 *a, b*), high nest ornamentation (Barber et al., 2001), position away from egg-predators (Östlund-Nilsson, 2000) and concealment (Sargent & Gebler, 1980).

Nest orientation could also be important. The hole-nesting convict cichlid *Cichlasoma nigrofasciatum* (Günther, 1867), for example, prefers to spawn in cavities facing dark areas, since this makes the brood less conspicuous to visual predators (Lavery, 1991). For freshwater fishes living in fast-flowing waters, preference for specific nest orientations could allow males to improve nest conditions in a difficult environment and aid in parental care tasks such as egg fanning and nest cleaning. There is evidence that paternal males in riverine species try to avoid the full force of strong current, which can damage the eggs or the nest structure itself. Nest distribution within fast-flowing water courses is often non-random, being biased towards the river edges, where current is slower (e.g. Piller & Burr, 1999; Moore *et al*., 1999). In addition, fish species that use fragile materials like vegetation for nest building (e.g. *Gasterosteus aculeatus* (Linnaeus 1758)) often choose to spawn in slow-flowing habitats or in sheltered sites where the current is absent (Mori, 1994). Careful positioning of the nest entrance, for example in a downstream direction, could reduce egg damage from strong current and the risk of nest plugging from materials floating downstream, while still allowing some water circulation which could prevent egg silting and decrease fanning effort.

The aim of this study was to examine nest preference in river blennies (*Salaria fluviatilis* Asso, 1801), a species with paternal care living in moderately- to fast-flowing rivers which should benefit from selective nest orientation. River blennies are widely distributed in freshwater rivers around the Mediterranean, but usually in small, very localised populations of conservation concern (Bianco, 1995; Changeux & Pont, 1995; Elvira, 1995). During the breeding season, which extends from the end of May to the end of July (Vinyoles, 1993), males excavate a nest cavity under a stone by sweeping the substratum with their caudal fin and carrying small stones out of the nest with their mouth. Access to the nest is usually through a single entrance hole. Females attach clutches of adhesive eggs in a monolayer under the nest stone (Wickler, 1957; DV, personal observations), and after fertilisation, females leave the nest. Males provide sole care of the eggs for 10-14 days until they hatch. Parental care consists of brood defence, nest cleaning (including carrying faeces away from the nest) and egg fanning. Breeding males spawn preferentially under larger stones (Freeman *et al*., 1990) and large stones usually harbour larger clutches (Côté *et al*., 1999). In this study, we specifically asked whether nest entrance orientation was random relative to stream flow direction in two rivers of the Ebro basin in eastern

Spain. We examined the role of upstream current speed and nest stone size on entrance orientation. Finally, we measured the consequences of specific entrance orientations for male mating success in one of the two rivers.

MATERIALS AND METHODS

STUDY SITES

We examined nest-site orientation in two populations of river blennies in separate rivers within the River Ebro drainage, in Catalonia, eastern Spain. The first was located in the River Matarraña, a small chalk stream tributary of the lower River Ebro, into which it flows via the reservoir of Ribarroja. The Matarraña flows mainly northward but meanders to such an extent in its last 20 km that its direction is at times practically reversed. This river has a pluvial regime characteristic of Mediterranean lowland rivers. The study site was located near Fayón, 10 km from the Ebro and some 80 km west of Tarragona. At this location, the direction of flow varied from 340^o to 160^o. Although river dimensions are highly variable, at the time of data collection (June 1988), the river was 8-9 m wide and 30-40 cm deep. Seventy nests were found in three adjacent nesting areas in a 150-m stretch of river.

The second population was located in the River Noguera Pallaresa, an affluent of the River Segre, which drains Pyrennean rivers into the river Ebro. The Noguera Pallaresa flows approximately southwards and is under pluvio-niveal regime typical of Pyrenean streams. River blennies were found in a small channel, parallel to the main bed of the river, near Tremp (180 km north-west of Barcelona). The channel was separated from the main river by small islets of shrubs. As in the River Matarraña, the direction of flow varied from 340^o to nearly due south. In

June 1997, thirty-two nests were found in a 37-m long stretch of the river, which was 5-6 m wide. Water depth averaged 20 cm on the study site. The two study sites are approximately 150 km apart by waterway.

FIELD MEASUREMENTS

Nests were located by searching stretches of rivers with riffles, examining the underside of stones for blenny eggs. For each nest encountered, we measured the size of the nest stone (maximum long and short axes to the nearest cm) and replaced the nest stone in it original position. Males typically returned to their nest stone within minutes of this procedure. After assessing manually the position of the nest entrance, current speed immediately in front of the nest stone at substrate level (heretofore referred to as upstream current) and current speed at the nest entrance were obtained with an electronic velocity metre (March-McBirney current metre, model 201). The orientation of the nest entrance relative to surface current direction (with 0^o representing current origin) was recorded with a protractor placed over the nest stone. For nests in the River Noguera Pallaresa, the long and short axes of all clutches were measured to the nearest mm and multiplied to estimate clutch area as in Côté et al. (1999).

In both rivers there were no accumulations of gravel or sand on either the upstream or downstream edges of the nest stones which might interfere with the activity of the male. It was thus assumed that the entire perimeter of the nest stones was available to the male at the time of excavating the nest entrance.

DATA ANALYSIS

Only nests with a single entrance (i.e. 100% of nests (*N* = 70) in the River Matarraña and

81.3% of nests (*N* = 26) in the River Noguera Pallaresa) were considered. Circular statistics were used to analyse nest orientation patterns (Batschelet, 1981). Nest orientations were compared for two categories of upstream current speeds: low (≤ 15 cm/s) and high (> 15 cm/s) current velocities. Long and short axis measurements for each stone were multiplied to obtain nest stone area, which is an accurate measure of stone size (Côté *et al*., 1999). The River Matarraña had a wider range of stone sizes than the Noguera Pallaresa due to gravel extraction activity in the latter (Côté *et al*., 1999). Matarraña nests were therefore divided into two categories: small nest stones of less than 700 cm^2, which was the maximum nest stone size in the River Noguera Pallaresa, and large nest stones (> 700 cm^2), and nest orientations were then compared for both categories of upstream current speeds. Nest entrance orientation was expressed relative to the direction of current (with current origin = 0^o).

Non-parametric statistics were used for habitat variables which showed heterogeneous variances between rivers. When multiple tests were performed, significance levels were corrected using the sequential Bonferroni method (Rice, 1989). Real probability values are reported throughout. When performing one-way analyses of variance, group means were compared *a posteriori* using Scheffé's tests.

RESULTS

There were significant differences in habitat characteristics measured at nest sites between the two rivers. The River Noguera Pallaresa had smaller nest stones than the River Matarraña (mean stone size $\underline{+}$ 1 SD, Noguera Pallaresa: 318.3 $\underline{+}$ 144.1 cm^2, $N = 26$; Matarraña: 591.2 $\underline{+}$ 549.4 cm^2, $N = 70$; Mann-Whitney U test: $z = 2.3$, $P = 0.02$). Water depth was shallower and upstream current speed was also significantly slower in the River Noguera Pallaresa (mean water depth ± 1 SD: 23.3 ± 4.7 cm; mean upstream current speed ± 1 SD: 8.3 ± 5.7 cm s^{-1}, *N* = 26) than in the River Matarraña (mean water depth ± 1 SD: 34.8 ± 7.1 cm; mean upstream current speed ± 1 SD: 24.9 ± 17.0 cm s^{-1}, *N* = 70; Mann-Whitney U tests, *P* < 0.0001 for the two pairwise comparisons).

ORIENTATION OF NEST ENTRANCES

In the River Noguera Pallaresa, nest entrances were randomly distributed around the nest stones at slow upstream current velocities (≤15 cm/s) (Rayleigh's test: *P* = 0.1; Fig. 1). However, at higher upstream current velocities (>15 cm/s), the entrances excavated by males showed a significant bias towards the lee of the nest stones, sheltered from the current (Rayleigh's test: *P* = 0.03; mean angle relative to current = 145.9° ± 48.2°; Fig. 1). The mean entrance angle was to the right, or southeast, of the current direction but was not significantly different from it (i.e. the 95% confidence interval of the mean entrance, 95% CI = 98° - 194° encompassed 180°, the current direction). Note, however, that confidence limits for the mean entrance angle are large because of the small sample size.

Similar results were found in the River Matarraña for small nest stones (≤700 cm^2), i.e. nest stones than encompassed the range of sizes in the River Noguera Pallaresa. Thus, in the Matarraña, entrances under small nest stones in low upstream current velocities (≤15 cm/s) were uniformly distributed [Rayleigh's test: *P* = 0.09; Fig. 2(a)], whereas at higher upstream current velocities, a significantly non-random distribution of nest entrance orientations in the lee of the nest stones was found [Rayleigh's test: *P* < 0.00001; mean angle relative to current = 151.2° ± 9.4°; Fig. 2(a)]. The mean entrance orientation was significantly different from the main current direction (i.e. 95% CI = 142° - 161°), showing a preference for nest entrances to the right, or southeast, of the main current direction.

For the larger nest stones (>700 cm^2) in the River Matarraña, the entrance orientation was significantly non-random at both low and high upstream current velocities (low velocity: Rayleigh's test, $P = 0.0001$; high velocity: Rayleigh's test, $P < 0.0001$). At low current velocities, entrances faced almost directly downstream [mean angle relative to current = $172.3^o \pm 21.2^o$; Fig. 2(b)], whereas at high current velocities, entrances faced a near southeast direction [mean angle relative to current = $152.3^o \pm 19.9^o$; Figure 2(b)]. The deviation from main current direction was significant for nests in high current velocities (95% CI = 132^o - 172^o), but not for nests in low current velocities (95% CI = 151^o - 194^o).

The mean orientation of entrances in the River Noguera Pallaresa for nests at high current velocities (Fig. 1) was not significantly different from that found in the Matarraña for nests of similar characteristics [Fig. 2(a)] (Watson-Williams test: $F_{1,47} = 0.096$, $P = 0.76$). In the River Matarraña, the mean direction of all nests located in high velocity sites [Figures 2(a) and 2(b)] tended to be different from the mean direction of nests in low current velocities [Figure 2(b)] (Watson-Williams test: $F_{1,60} = 3.32$, $p = 0.073$).

CURRENT SPEED AT NEST ENTRANCE

In the River Noguera Pallaresa, current speed at the nest entrance was not significantly different for nests located in high and low upstream current speeds ($t_{24} = 1.44$, $P = 0.16$; Table 1). Similarly, in the River Matarraña, current speed at the nest entrance was not significantly different for both nests in high and low upstream currents and for large and small nest stones (ANOVA: $F_{3,66} = 1.54$, $P = 0.21$; Table 1). Finally, current speed at the nest entrance was not different between the two rivers (Noguera Pallaresa: mean ± 1 SD = 5.6 ± 4.2 cm s^{-1}; Matarraña: 7.7 ± 7.0 cm s^{-1}; $t_{94} = 1.42$, $P = 0.16$).

In both rivers, nests located in low current velocities showed no significant reduction in current speed at the nest entrance compared to current speed upstream of the nest stone (Table 1). These nests had entrances facing in any direction [for small nest stones, Fig. 1 & 2(a)] or nearly opposite to the current [for larger nest stones; Fig. 2(b)]. By contrast, nests located in higher current velocities experienced a significantly slower current at the nest entrance than that found in front of the nest stone (Table 1). This effect fell just short of significance for the River Noguera Pallaresa. The significant reduction in current speed at the entrance in the River Matarraña was achieved by building the nest entrance closer to the current direction (i.e. angle of 180^o) as current speed increased in front of nests ($r^2 = 0.11$, $F_{1,51}=6.6$, $P=0.013$; Fig. 3). The sample size of nests was too limited to examine this relationship for the River Noguera Pallaresa.

MALE MATING SUCCESS AND NEST ORIENTATION

Male mating success, as measured by clutch size, was significantly related to nest stone size for nests with single entrances in the River Noguera Pallaresa ($r^2 = 0.15$, $F_{1,24} = 4.22$, $P = 0.05$; clutch size (in mm^2) = 4.79 x stone size (in cm^2) + 1640.92). Mean residual clutch size (corrected for nest stone size using regression) was not significantly different for nests in low and high upstream current velocities (low velocity: mean ± 1 SD = -220.9 ± 1621.5 mm^2, N =21; high velocity: 927.6 ± 1567.3 mm^2, $N = 5$; $t_{24}= 1.43$, $P = 0.17$). However, residual clutch size for nests with entrances opening towards the southeast (i.e. $153^o \pm 25^o$ relative to main current direction) was significantly larger than for nests opening in other directions (near southeast: mean ± 1 SD = 1059.3 ± 1872.9 mm^2, $N = 9$; other orientations: -560.8 ± 1230.5 mm^2, $N = 17$; $t_{24} = 2.66$, p = 0.014). Neither upstream current speed nor current speed at the nest entrance was significantly different between nests facing southeast and those facing in other directions (upstream current speed: southeast: 8.6 ± 5.5 cm s^{-1}, other orientations: 8.1 ± 5.9 cm s^{-1}, t_{24} =

0.24, $P = 0.81$; current speed at nest entrance: southeast: 5.4 ± 4.7 cm s^{-1}, other orientations: 5.6 ± 4.0 cm s^{-1}, $t_{24} = 0.13$, $P = 0.9$).

Such results were not found when comparing nests with entrances facing what is assumed to be the most sheltered orientation (i.e. directly opposite the oncoming current or near 180 ± 25^{o}) and nests open at other orientations. Thus, residual clutch size for nests opening near 180^{o} was not significantly different than for nests opening at other orientations (near 180^{o}: mean ± 1 SD = -69.6 ± 2419.2 mm^2, $N = 6$; other orientations: 20.9 ± 1422.3 mm^2, $N = 20$; $t_{24} = 0.12$, $P = 0.91$).

DISCUSSION

Male river blennies orient their nests in a non-random direction in fast-flowing waters. In two rivers separated by more than 150 km, river blenny nest entrances were most frequently oriented towards, although not directly in, the lee of the nest stones when current speed exceeded 15 cm s^{-1}. This orientation resulted in a significant decrease in current velocity measured at the nest entrance compared to prevailing current speed. Non-random nest entrance orientation in fast current appears adaptive since males with nest entrances facing southeast had relatively larger clutches than males with nest entrances facing in other directions.

Both current speed and nest stone size affected the orientation of river blenny nest entrances. While nest entrances were generally at an angle of *c*. 30^{o} relative to current flow direction (i.e. facing approximately a southeast direction) at high current velocities, they were usually oriented randomly at slower current speeds. This pattern was observed in both rivers for nest stones of comparable sizes (≤ 700 cm^2). Moreover, as upstream current velocity increased in the River Matarraña, males positioned their nest entrance closer and closer to the direction of flow. The effect of nest stone size was visible only in the slower-flowing areas of the River

Matarraña. At these locations, entrances of nests under small stones were oriented randomly while those under larger stones faced predominantly downstream.

Through selective nest positioning, males appear to control the speed of current reaching the nest entrance. Indeed, while in slow-flowing sites where the orientation of small nests was random, current speed in front of the nest entrance did not differ from current speed upstream of the nest, in faster-flowing sites where most nests faced southeast, current speed in front of nests was significantly slower than upstream current. Selective nest orientation with respect to prevailing current speed thus resulted in a similar current velocity at the nest entrance for all nests, whether located in fast- or slower-flowing sites, under large or small stones, or whether in the Noguera Pallaresa or the Matarraña. This occurred despite a three-fold difference in mean upstream current velocity between the two rivers. The moderate (5-7 cm s^{-1}) current speed at the nest entrance achieved through selective nest positioning may generate suitable water circulation within the nest, which may be beneficial in terms of flushing out debris (Morris, 1955) and oxygenating the eggs. The latter may be particularly important to males since oxygen levels influence the cost of egg ventilation in many parental fish species (e.g. Jones & Reynolds, 1999).

Female river blennies appear to be sensitive to both nest size and nest orientation. They deposit their eggs preferentially in nests under large stones (Côté *et al*., 1999) and in nests facing in a southeast direction (this study). We found that a difference in nest stone size does not explain the larger clutches found in southeast facing nests. Moreover, current speeds upstream of the nest and at the nest entrance were similar for nests facing southeast and those facing in other directions. A southeast-facing entrance *per se* thus seems to be the specific nest feature preferred by females, rather than the effect of selective positioning on current at the nest entrance. The reasons for this preference are not clear. In terrestrial birds and mammals, nests are often oriented towards the south or southeast in the northern hemisphere because of the favourable temperature microclimate afforded by such sites (e.g. Ontiveros, 1999; Gainzarain *et al*., 2000; Wiebe, 2001). However, in relatively fast-flowing water, localised increases in temperatures which would be high enough to accelerate egg development (e.g. Gadomski & Caddell, 1996) are unlikely to be realised. It is possible that females are choosing nests with entrances opening at a specific angle from prevailing current, rather than a southeast direction. Unfortunately, both rivers in this study flowed in the same geographic direction at the study sites, precluding a direct test of this hypothesis. If so, the presence of a clear bias for one side of the prevailing current (i.e. the right-hand side when facing upstream) would remain to be explained.

If having a southeast orientation or a nest opening at an equivalent angle deviating from the main current yields higher mating success, why do all males not position their nest entrances in this direction? Although we assumed that males could choose any location around the periphery of the nest stone for the nest entrance, they may in fact have been restricted in their choice by the position of nests of neighbouring males such that the optimal southeast orientation was not available. Alternatively, male condition could influence nest orientation, such that males in poorer condition may choose alternative orientations, such as facing upstream, which could reduce the costs of parental care although the risks of egg damage may be higher. Adopting a southeast nest orientation could therefore be a reliable signal of male quality, and females should be sensitive to indicators of male condition since male river blennies in poor condition resort to cannibalism of eggs in their care (Vinyoles *et al*., 1999).

Nest orientation by male river blennies thus appears to vary with environmental conditions. A southeast-facing orientation results in a reduction in current speed at the nest entrance in fast-flowing water and males with entrances facing in this direction receive more eggs. Comparative studies in rivers flowing in different geographic directions should be undertaken to determine whether orientation relative to current or to true North is important to females. In addition, studies of hydrodynamics examining how water flow entering the nest varies in relation with entrance orientation, current speed and nest stone size are now required to elucidate the reasons for female preferences for specific nest orientations. We predict that selective nest orientation will result in optimal water flow inside the nest for egg hygiene and oxygenation.

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Figure captions

FIG. 1. Orientation of river blenny nest entrances in the River Noguera Pallaresa for slow current areas ($\leq$ 15 cm s^{-1}; open points) and areas of faster flow (> 15 cm s^{-1}; filled points). Each point represents a nest, and all nest stones in this river were small ($\leq$ 700 cm^2). The wavy arrow indicates the direction of prevailing current. The long thin arrow represents the mean orientation of nests in fast flow relative to prevailing current. Mean orientation of nests in slow flow is not shown since those nests were randomly orientated.

FIG. 2. Orientation of river blenny nest entrances in the River Matarraña for (a) small nest stones ($\leq$ 700 cm^2) in slow current areas ($\leq$ 15 cm s^{-1}; open points) and faster currents (>15 cm s^{-1}; filled points and solid arrow), and (b) large nest stones (> 700 cm^2) in slow (open points and dashed arrow) and faster flow (filled points and solid arrow). Each point represents a nest. The wavy arrow indicates the direction of prevailing current. The long thin arrows represent the mean orientation of nests relative to prevailing current when nests are significantly non-randomly orientated.

FIG. 3. Relationship between absolute deviation of nest entrance orientation from prevailing current direction (i.e. 180^o) and current speed upstream of nest stone in the River Matarraña.

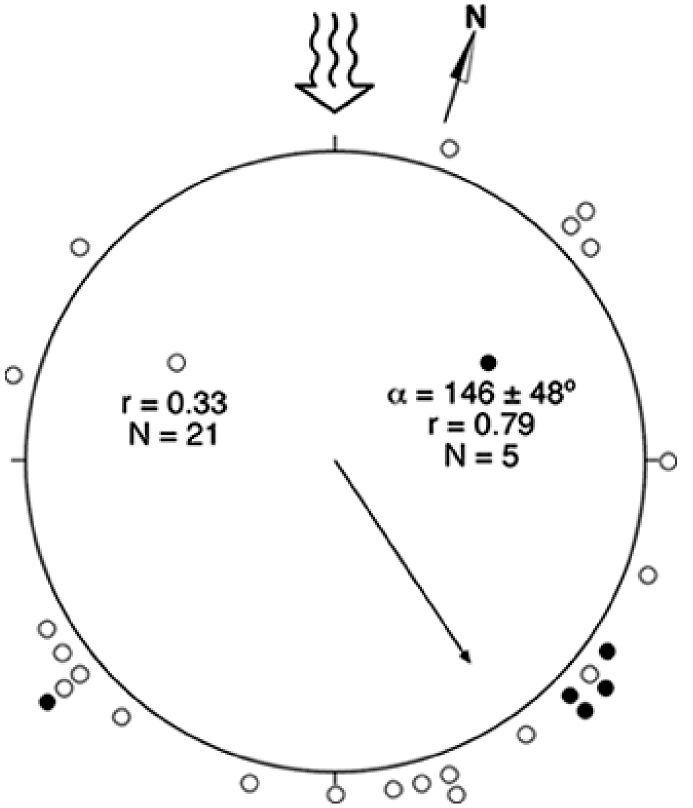

FIGURE ½

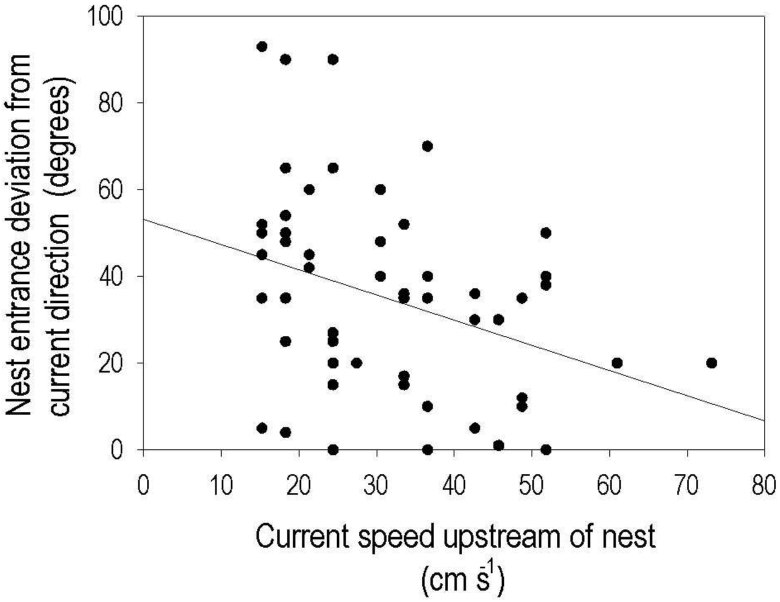
Nest entrance deviation from current direction (degrees)
100
80
60
40
20
0
0
10
20
30
40
50
60
70
80
Current speed upstream of nest (cm s-1)

FIGURE 3

TABLE I. Current speed upstream of nests and at nest entrance, for small (≤700 cm^2) and large (>700 cm^2) nest stones in slow (≤15cm s^{-1})and fast (>15cm s^{-1}) current. Asterisks indicate results that remained significant after Bonferroni correction.

Site	Nest stone size	Current speed		Paired *t*	df	*P*
	(mean area ± SD; cm^2)	Upstream of nest (cm s^{-1})	At nest entrance (cm s^{-1})			
Noguera Pallaresa	Small (341.5 ±147.2)	Slow (5.9 ± 2.9)	5.0 ± 3.9	1.08	20	0.29
	Small (220.9 ± 81.6)	Fast (18.0 ± 3.8)	7.9 ± 5.0	2.99	4	0.04
Matarraña	Small (308.7 ± 137.6)	Slow (7.2 ± 5.1)	5.7 ± 7.0	0.54	7	0.61
	Small (346.8 ± 165.7)	Fast (32.0 ± 14.4)	7.8 ± 6.8	10.84	43	<0.0001*

Large (1377.2 ± 594.1)	Slow (1.4 ± 2.2)	5.1 ± 7.0	1.79	8	0.11
Large (1250.4 ± 703.2)	Fast (29.5 ± 10.2)	11.5 ± 7.7	3.54	8	0.008*