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ARTICLE

Territorial and foraging behaviour of juvenile Mediterranean trout under changing conditions of food and competitors

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Abstract: Territoriality is probably the most important ecological mechanism regulating densities in stream-living salmonids. Body size is typically regarded as the best predictor of territory size, but food abundance and competitor density may be key driving factors. However, a global analysis of literature data showed no clear patterns on the relative causal role of those factors on determining territory size in juvenile salmonids. Thus, in a factorial experiment, we estimated to what extent simultaneous variations of fish size, competitor density, and food abundance affected the size of foraging and defended areas of Mediterranean brown trout (*Salmo trutta*). In contrast with former studies, we found that foraging areas were larger than defended territories. Foraging and territorial behaviour changed significantly under varying density and feeding regimes. Foraging areas decreased with increasing competitor density and food availability, and there was a strong interaction between these two factors. Defended territories decreased with increasing density, irrespective of food abundance. Although our findings showed a significant allometric relationship between fish length and territory size, the data contained much unexplained variability. Our findings suggest that defended areas are relatively fixed for a given trout length. However, at extremely high population densities, defended areas decreased. Thus, under extreme competition, such as during critical periods right after emergence, trout may subdivide available habitat and thereby moderate density declines.

Résumé : La territorialité est probablement le mécanisme écologique le plus important dans la régulation de la densité chez les salmonidés vivant dans les cours d'eau. Si la taille du corps est typiquement considérée comme étant la meilleure variable prédictive de la taille du territoire, l'abondance de la nourriture et la densité des concurrents pourraient jouer un rôle important. Une analyse globale des données publiées n'a toutefois révélé aucun motif clair quant aux rôles causaux relatifs de ces facteurs dans la détermination de la taille du territoire de salmonidés juvéniles. Nous avons donc estimé, dans le cadre d'une expérience factorielle, la mesure dans laquelle des variations simultanées de la taille des poissons, de la densité des concurrents et de l'abondance de la nourriture influaient sur la taille des aires d'approvisionnement et des aires défendues pour des truites de mer (*Salmo trutta*) méditerranéennes. Contrairement à des études antérieures, nous avons constaté que les zones d'approvisionnement étaient plus grandes que les territoires défendus. Les comportements d'approvisionnement et territoriaux changeaient significativement en fonction des régimes de densité et d'alimentation. Les aires d'approvisionnement diminuaient quand la densité des concurrents et la disponibilité de nourriture augmentaient, et il y avait une forte interaction entre ces deux facteurs. L'aire des territoires défendus diminuait quand augmentait la densité, quelle que soit l'abondance de la nourriture. Si nos résultats montrent une relation allométrique significative entre la longueur des poissons et la taille du territoire, les données renferment beaucoup de variabilité non expliquée. Nos constatations donnent à penser que l'aire défendue ne varie pas beaucoup pour une longueur de truite donnée. Cependant, pour des densités de population extrêmes, les aires défendues diminuaient. Aussi, dans des situations de concurrence extrême, comme les périodes critiques juste après l'émergence, les truites pourraient subdiviser les habitats disponibles et ainsi atténuer les baisses de densité. [Traduit par la Rédaction]

Introduction

Juvenile stream-dwelling salmonids defend feeding territories under both experimental and field conditions (Elliott 1990; Keeley 2000; Imre et al. 2004). They begin defending feeding territories shortly after emergence; obtaining a territory appears to be essential for survival. At this early stage, mortality is usually density-dependent and population size is regulated primarily via territorial behaviour (Elliott 2001). Territoriality might be also responsible for the effects of density dependence on individual growth (Ward et al. 2007; Parra et al. 2011). Further, territoriality plays a relevant role in setting carrying capacity for salmonids in rivers (Grant and Kramer 1990), because maximum population numbers are not only determined by the abundance and distribution of limited resources but also by how individuals compete for their use. Determining the maximum number of individuals a system can support is a primary goal of fisheries management and is important in assessing the effects of human actions on threatened populations (Ayllón et al. 2012*a*). Carrying capacity models for salmonids should account for both resource dynamics and territorial behaviour, though this second aspect is frequently neglected in population dynamics modeling. To fill this gap, Ayllón et al. (2012*b*) developed a model in which the maximum population abundance is limited by fluctuating habitat conditions and regulated through the behavioural adjustment of the size of feeding territories as a function of fish

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body size. Body size is the strongest predictor of territory size in salmonids, but any ecological factor affecting the body–territory size relationship could lead to changes in the maximum population abundance.

Classical models of optimal territory size (Hixon 1980; Schoener 1983) predict that feeding territories for energy-maximizing animals (i.e., those whose potential reproductive success is positively correlated with their net energetic intake) vary inversely with food availability and competitor density. Competitor and resource abundances may change over time, so animals must be flexible in their territorial behaviour. Salmonid fish are known to defend feeding territories and adjust their aggressive behaviour to changing environmental conditions. Both field and laboratory work provides support for this prediction in territorial salmonids (Elliott 1990; Keeley 2000; Toobaie and Grant 2013). In addition to the energetic benefits or costs of defense, space requirements for young salmonids are also directly related to body size through metabolic demands (Grant and Kramer 1990; Keeley 2000). Previous observational studies that measured territory size in young salmonids found an allometric relationship with body size (Elliott 1990, brown trout (*Salmo trutta*); Keeley and Grant 1995, Atlantic salmon (*Salmo salar*); Keeley 2000, rainbow trout (*Oncorhynchus mykiss*)), which was also predicted by in silico simulation experiments (Ayllón et al. 2010, for brown trout). However, other studies did not find this relationship, for example, Steingrímsson and Grant (2008) for Atlantic salmon.

A global analysis of previous observational and experimental studies on territorial juvenile salmonids shows no clear patterns and even reveals somehow contradictory results, on the influence of food abundance or competitor density on either territory size or how individuals scaled territories with body size. To date, only Keeley (2000) has evaluated how juvenile salmonid territory size changes in response to simultaneous changes in food abundance and competitor density (but see Keeley and Grant 1995 and Keeley and McPhail 1998 in field studies), despite the fact that under natural conditions these factors act simultaneously, and their interaction could have strong consequences on the adjustment of territory size. An experimental manipulation of the major determinants of territory size can determine the direction of causation and the interactions between factors and help incorporate them into population dynamics modeling.

Most of the information concerning the territorial behaviour of juvenile salmonids comes from northern latitudes (Sundström et al. 2003; Steingrímsson and Grant 2008; Toobaie and Grant 2013). The question of whether stream-dwelling salmonids show a similar territorial behaviour throughout their distribution range has been long neglected. In particular, factors controlling brown trout territory size in Mediterranean areas are unknown, despite the relevance that this may have for population management, especially when global warming is increasingly threatening their persistence (Almodóvar et al. 2012; Ayllón et al. 2013). The few existing experimental studies of brown trout territorial behaviour come from northern populations (Deverill et al. 1999; Johnsson et al. 2000; Sundström et al. 2003). Only Elliott (1990) developed a predictive model for territory size of 0+ Atlantic brown trout, which provides a baseline from which the maximum area of a territory can be calculated based on fish length.

In this study, we investigated the effects of simultaneous variations of fish size, competitor density, and food abundance on the territory size of Mediterranean brown trout. We predicted that territory size would be inversely proportional to food abundance and density of surrounding competitors and positively correlated with fish size. We also predicted that those factors would interact when trout are establishing territories. We tested these predictions in a factorial experiment using a distinct Mediterranean lineage of brown trout. The model developed by Elliott (1990) was additionally used to test whether brown trout territorial behaviour differs between Mediterranean and Atlantic lineages.

Materials and methods

Experimental setup

In April 2010, about 2 weeks after emergence, 0+ brown trout were stocked into experimental channels at the Uña Hatchery (40°13′N, 1°58′W) near Cuenca, Spain. Fish were allowed to acclimate for 6 weeks before experiments started in June 2010. Fish were the offspring of wild breeders caught at the Mundo River (Segura River basin) as part of a supportive breeding program that stocks recreational fisheries. Brown trout from the Segura River basin belong to a Mediterranean lineage (Machordom et al. 2000).

Experiments were carried out between June and September 2010. To analyze the effects of food abundance and competitor density on the territorial behaviour of young brown trout, the experiment had a factorial design, consisting of two factors (food and density) and three levels per factor (low, intermediate, and high). We used six parallel artificial channels without a substrate in the indoor part of the hatchery (to avoid predation), each measuring 3.3 m × 0.5 m (1.65 m^2). Each channel was divided into three 1.0 m × 0.5 m (0.5 m^2) sections (experimental units) to allow for simultaneous replicates. Therefore, 18 experimental units were available for the experiments. Mesh screens were placed at both ends of each of the experimental units to prevent the escape of any fish. Water was supplied directly from the Rincón stream (Júcar River basin). The water entering the channels was filtered through fine-mesh nylon screening to remove any invertebrates that might have entered from the river. Light and temperature were ambient, with water temperature ranging from 10 to 12 °C across the experimental period. We assigned treatment levels to experimental units to eliminate any potential upstream–downstream effects. We randomly assigned treatments such that each level of experimental factors appeared once in the upper, middle, and lower channel positions.

Fish were fed live zooplankton (water flea (*Daphnia pulex*)) and chironomid and simulid larvae. Prior to the experiments, we estimated a mean satiation ration for the low-density treatment (i.e., the maximum quantity of food a trout consumed when under low competition). We randomly varied the feeding times for several days, then calculated a mean satiation ration (number of items consumed by individual fish). The low food ration (LFR, 500 individuals·m^{-2}) was equal to the satiation ration, and the intermediate (IFR) and high (HFR) food rations were the double and the quadruple of the satiation ration, 1000 and 2000 individuals·m^{-2}, respectively. Similar proportions of each prey type were used in each treatment. Food levels were within the upper range typically found in productive streams in Spain (Almodóvar et al. 2006; Nicola et al. 2010); therefore, it represented the largest amount of food encountered by juvenile salmonids in the wild. Similar food rations have been used by others (Keeley 2000; Imre et al. 2004; Toobaie and Grant 2013).

To test our predictions, it was essential to elicit aggressive defensive behaviour among the experimental trout. Once this behaviour was guaranteed, we could assess the size of territories under various conditions of food and competitors. Experimental competitor density was calculated using mean body size and percent habitat saturation (PHS) as described by Grant and Kramer (1990). PHS measures the total percentage of the streambed occupied by territories of all salmonids in a stream and has been used by some authors to assess the level of competition (Parra et al. 2011, 2012). We experimentally induced competition by increasing the density levels to double or quadruple the 100% habitat saturation (i.e., all the available space occupied by brown trout territories). According to the logistic model of Grant and Kramer (1990), the probability of observing a density-dependent response in the PHS levels tested in our experiments (100%, 200%, and 400%) was between 0.90 and 1.00. The review by Grant and Kramer (1990) showed that 19 of 31 studies of various salmonid species had mean PHS values over 100% (range 105%–775%). Hence, our experimental range (100%–400%) could reflect juvenile densities observed elsewhere in natural salmonid populations shortly after emergence. Thus, the low (LCD), intermediate (ICD), and high (HCD) competitor densities were 100% saturation (46 individuals·m^{-2}), 200% saturation (92 individuals·m^{-2}), and 400% saturation (184 individuals·m^{-2}), respectively. Each experimental unit received 23, 46, or 92 trout, which corresponded to LCD, ICD, and HCD treatments, respectively. There were two replicated experimental units for each density level and food ration level combination; altogether, we used 966 trout that averaged 32.82 ± 3.71 mm in length and 0.51 ± 0.16 g in mass. Trout occasionally died during the experiments (less than 5% of total used trout); the number of deaths was similar across treatments. We replaced dead trout with new trout of similar size to maintain the experimental densities. Replacement trout were reared in channels containing the same competitor densities as the treatment channels. Replacement trout might have found it harder than resident fish to establish new territories (see Johnsson and Forser 2002); however, they induce aggressive behaviour in the resident fish.

Behavioural measurements

Brown trout behaviour was recorded using a digital video camera on a tripod. Each experimental unit was recorded for 30 min once every week from June to September. The times of recording were randomized to ensure that each experimental unit was observed at different times of day (0900–1200, 1200–1500, or 1500–1800) during the experiment. In all, 288 recordings were obtained (18 experimental units × 16 weeks). We decided to analyze data only from recordings performed every 2 weeks to include a higher variability in fish body length; therefore, 144 recordings were analyzed. At the start of each recording, food was distributed throughout the section to simulate invertebrate drift. The first 5 min of each recording were not used for data collection because fish were somewhat disturbed by the camera setup and needed a few minutes to return to their original feeding positions.

Recordings were played with VLC Media Player software (VideoLAN, France) for data collection. From each 30 min recording, the position of each trout within the experimental section was examined first. Only trout with a clear centrally located holding position (i.e., those fish that typically initiated aggressive acts and foraging attempts from a single central place maintained during the entire 30 min recording) were considered for data collection. Multiple foraging stations were never observed. For each focal fish, all foraging movements and aggressive interactions with surrounding individuals were registered and measured. The foraging radius was defined as the distance travelled by a fish from its holding position to the point where it captured a food item (see Keeley 2000); each foraging attempt involved an attack on a single prey and return to the same central place. Similarly, the aggressive radius was the distance travelled by a fish from its holding position to the point where an intruder fish provoked an aggressive response; each aggressive act involved an aggressive response (mainly chases and nips) until the intruder was chased away, then a return to the same central place.

To measure the distances, each experimental unit acted as an X, Y coordinate system, with the 0, 0 (X, Y) position in the lower left corner of the unit, as seen on screen. The software PMeter (Pegtop, Germany) was used to place a ruler on the display screen to measure the distances and the length of each focal fish. Actual distances and fish lengths were calculated from a system of grid lines spaced 20 cm apart that were drawn on the bottom of each channel for scale. The foraging and defended areas of each focal trout were defined as the mean foraging and aggressive radii, respectively, assuming that the territory is a circle (Keeley and Grant 1995; Keeley 2000). To examine the allometry of territory size, we used the local competitor density instead of the treatment density. To calculate the local density, we ranked all measured aggressive radii for each recording and selected the longest one for each recording (maximum aggressive radius; MAR). For each aggressive and foraging movement within a treatment, we counted the number of trout within the circle defined by the treatment-specific MAR. The local density (individuals·m^{-2}) was then calculated as the number of trout within the circle divided by its area.

Statistical analyses

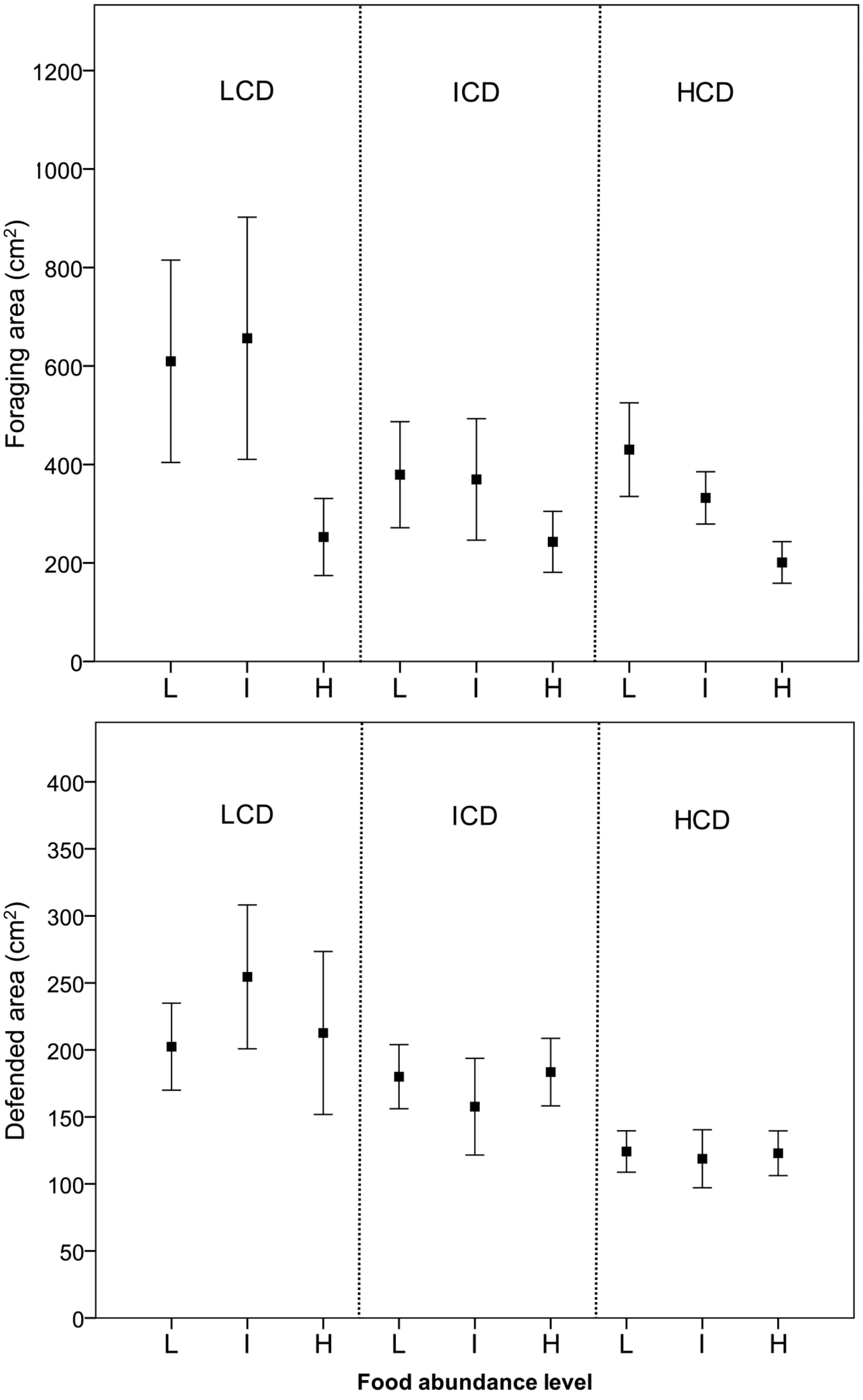
Prior to analysis, all continuous variables were subjected to Shapiro–Wilk tests for normality. When necessary, variables were log-transformed before analyses to meet the assumptions of parametric tests. General linear models (GLMs) were used to assess the effects of food abundance and competitor density on the foraging and defended areas. First, an analysis of covariance (ANCOVA; density and food treatments as covariates) was used to test for differences in size between foraging and defended areas. Second, to test the prediction that territory size decreases with increasing food abundance and competitor density, two-way analyses of variance (ANOVA) and subsequent Tukey's tests were used to determine whether there was a main effect of competitor density, food abundance, or their interaction on foraging and defended areas among experimental fish. Third, we used least squares regressions to examine the effects of local density and fish length on defended areas. Finally, the models given by Elliott (1990) were employed to estimate the expected defended area of each experimental trout. According to this model, the maximum area defended is linearly proportional to fish size on a log–log scale, but the relationship is significantly different for trout greater and less than 40 mm in length. The length of each experimental trout was used to calculate their expected defended areas using the power functions from Elliott (1990). The range of fish lengths used in Elliott's experiment (~22–60 mm) was comparable to the range used in the present study (21–67 mm). Observed defended areas (ODA; data from this study) and predicted defended areas (PDA; Elliott 1990) were then compared by ANCOVA tests (fish length as covariate). Before using ANOVA and ANCOVA, the assumption of homogeneity of variances was verified through Levene's test. All statistical analyses were performed using SPSS version 19 statistical software (SPSS Inc., Chicago, Illinois). The critical significance level for all statistical tests was set at $\alpha = 0.05$.

Results

Juvenile brown trout foraged and defended space around a primary holding station, but the relative use of space was different. In all treatment levels, foraging areas (mean = 394.6 cm^2; min.–max. = 1.2–3676.4 cm^2; N = 544) were significantly larger than defended areas (mean = 168.9 cm^2; min.–max. = 3.6–1 566.0 cm^2; N = 822; ANCOVA, $F_{[3,1333]} = 50.54$, $P < 0.001$). Foraging and aggressive behaviours of juvenile brown trout were directed mainly towards lateral and upstream directions from a central located foraging station; fish tended to move laterally most often.

Mean foraging areas were dependent on food abundance (two-way ANOVA, $F_{[2,506]} = 4.40$, $P = 0.013$) and competitor density ($F_{[2,506]} = 8.36$, $P < 0.001$). The interaction between food abundance and competitor density was also significant ($F_{[4,506]} = 6.36$, $P < 0.001$). Thus, foraging areas significantly decreased with increasing density of competitors and the amount of available food (Fig. 1). Regarding the effect of food abundance, post hoc tests showed that mean foraging areas of LFR and IFR treatments were similar, with means of 401.5 and 423.5 cm^2, respectively; however, the mean foraging area in the HFR treatment was significantly smaller (285.1 cm^2) than that in the LFR and IFR treatments (Tukey tests, $P = 0.012$ and $P = 0.017$, respectively). It is worth noting that the mean foraging area in the HFR treatment was similar in all density treatments (Fig. 1). Concerning the density effect, mean foraging areas were similar between ICD and HCD treatments, with means of 327.1 and 310.8 cm^2, respectively; however, the mean foraging area in the LCD treatment was significantly larger (468.8 cm^2) than that in the ICD and HCD treatments (Tukey tests, $P = 0.010$ and $P = 0.004$, respectively). The foraging area decreased with increasing food availability within each density treatment (Fig. 1).

Fig. 1. Mean ± SE of foraging and defended areas (cm²) of 0+ brown trout under nine experimental treatment combinations of competitor density (low, LCD: percent habitat saturation (PHS) = 100%; intermediate, ICD: 200% PHS; high, HCD: 400% PHS) and food abundance (L: low; I: intermediate; H: high). See Materials and methods for details.



Conversely, mean defended areas were dependent on competitor density (two-way ANOVA, $F_{[2,826]} = 21.06$, $P < 0.001$) but not on food abundance ($F_{[2,826]} = 0.761$, $P = 0.468$). There was no significant interaction between food abundance and competitor density ($F_{[4,826]} = 2.185$, $P = 0.069$). Thus, mean defended areas were similar among low (LFR, 167.6 cm²), intermediate (IFR, 170.4 cm²), and high food rations (HFR, 166.3 cm²). However, defended areas gradually decreased with increasing competitor density (LCD: mean = 212.4 cm²; ICD: mean = 179.5 cm²; HCD: mean = 120.1 cm²; Tukey tests, LCD–ICD, $P = 0.034$; LCD–HCD, $P < 0.001$; ICD–HCD, $P < 0.001$). Further, within each density treatment, mean defended areas were similar among food abundance levels, which evidenced the lack of interaction among factors (Fig. 1). Consequently, we did not control for food abundance to estimate the allometry of defended areas.

Since neither food abundance nor its interaction with competitor density significantly influenced defended areas, we pooled the data to compare observed (ODA) against expected (PDA) defended areas by density treatment. There was a clear effect of competitor density on the size of the defended areas, so comparisons were carried out separately for the different density treatments. Observed and predicted size of defended areas were similar in LCD (mean ODA = 216.3 cm², mean PDA = 252.7 cm²; ANCOVA, $F_{[1,427]} = 3.08$, $P = 0.080$) and ICD treatments (mean ODA = 176.7 cm², mean PDA = 185.3 cm; $F_{[1,671]} = 0.83$, $P = 0.362$). However, the mean observed defended area in the HCD treatment was significantly smaller than that predicted by Elliott's (1990) model (mean ODA = 122.3 cm², mean PDA = 385.1 cm²; $F_{[1,547]} = 434.5$, $P < 0.001$; Fig. 2).

After controlling for the effect of local density of competitors on the size of defended areas ($\log_{10}$ defended area (cm²) = 2.688 − 0.326 $\log_{10}$ local density (individuals·m⁻²); $F_{[1,816]} = 111.69$, $P < 0.001$, $r^2 = 0.35$), size of defended area (i.e., residuals of local density versus defended area) increased significantly with fish size; however, the explanatory power of the model was not high (residuals = −0.789 + 0.529 $\log_{10}$ length (cm); $F_{[1,816]} = 19.21$, $P < 0.001$, $r^2 = 0.15$). There was a significant relationship between the size of defended areas and fish length, but high unexplained variance was also noted.

Discussion

Juvenile brown trout showed territorial behaviour according to the central-place territorial model, which assumes that sit-and-wait individuals forage and attack intruders from, and return to, a single foraging station (Elliott 1990; Grant and Kramer 1990). Our findings showed that trout actively defended a territory that decreased in size as competitor density increased, irrespective of food abundance. From its central position, trout moved away from that territory to feed, to a distance according to food availability and density of competitors.

Our results support the hypothesis that increasing competitor density decreases the territory size (both foraging and defended areas) in brown trout. However, the size of the defended areas in our study did not change inversely with food abundance. Our findings do not agree exactly with the traditional optimality models (Hixon 1980; Schoener 1983), which assign the same importance to food abundance as to competitor density. Few studies exist on changes in territory size of juvenile salmonids in response to simultaneous changes in food abundance and competitor density. Actually, only Keeley (2000) tested this with rainbow trout and confirmed the predictions of the optimality models, but without a significant interaction between food abundance and competitor density. Table 1 summarizes 10 published studies (field and laboratory) on the effects of food abundance and density of competitors on the size of defended areas in juvenile salmonids. In all laboratory studies, there was a significant effect of competitor density on the size of the defended area, while only 60% of field studies showed this effect. Consistent with our study, the experiment of Imre et al. (2004) found that the size of the areas defended by juvenile *O. mykiss* decreased with increasing local population and did not change with variable food abundance. However, studies in the natural environment have contradictory results. Gunnarsson and Steingrímsson (2011) found that invertebrate drift abundance had no effect on the size of defended areas of juvenile brown trout, but areas unexpectedly increased with competitor density. The same authors reported the opposite results for Arctic char (*Salvelinus alpinus*) in the same study. Keeley and Grant (1995) observed a significant effect of drift abundance on the size of defended areas of juvenile Atlantic salmon, but no effect of intruders' pressure and competitor density (intruder pressure meaning the number of aggressive interactions between a focal fish and intruders per hour). Keeley and McPhail (1998) found that the size of the areas defended by juvenile *O. mykiss* was inversely related to the abundance of drifting invertebrates and local competitor density, but no effect of intruders' pressure. Finally, Dill et al. (1981) found that the size of defended areas of juvenile *O. mykiss* was inversely related to benthos abundance in the juvenile coho salmon (*Oncorhynchus kisutch*), this effect being more clear when intruders' density increased. However, these authors found no effect of variable drift abundance on territory size.

Fig. 2. Frequency (%) distribution of observed (ODA) and predicted (PDA) defended areas (cm²) of 0+ brown trout under low (LCD: 100% PHS), intermediate (ICD: 200% PHS) and high (HCD: 400% PHS) competitor density. PDA was calculated using the power functions from Elliott (1990) and length of each experimental trout. See Materials and methods for details.

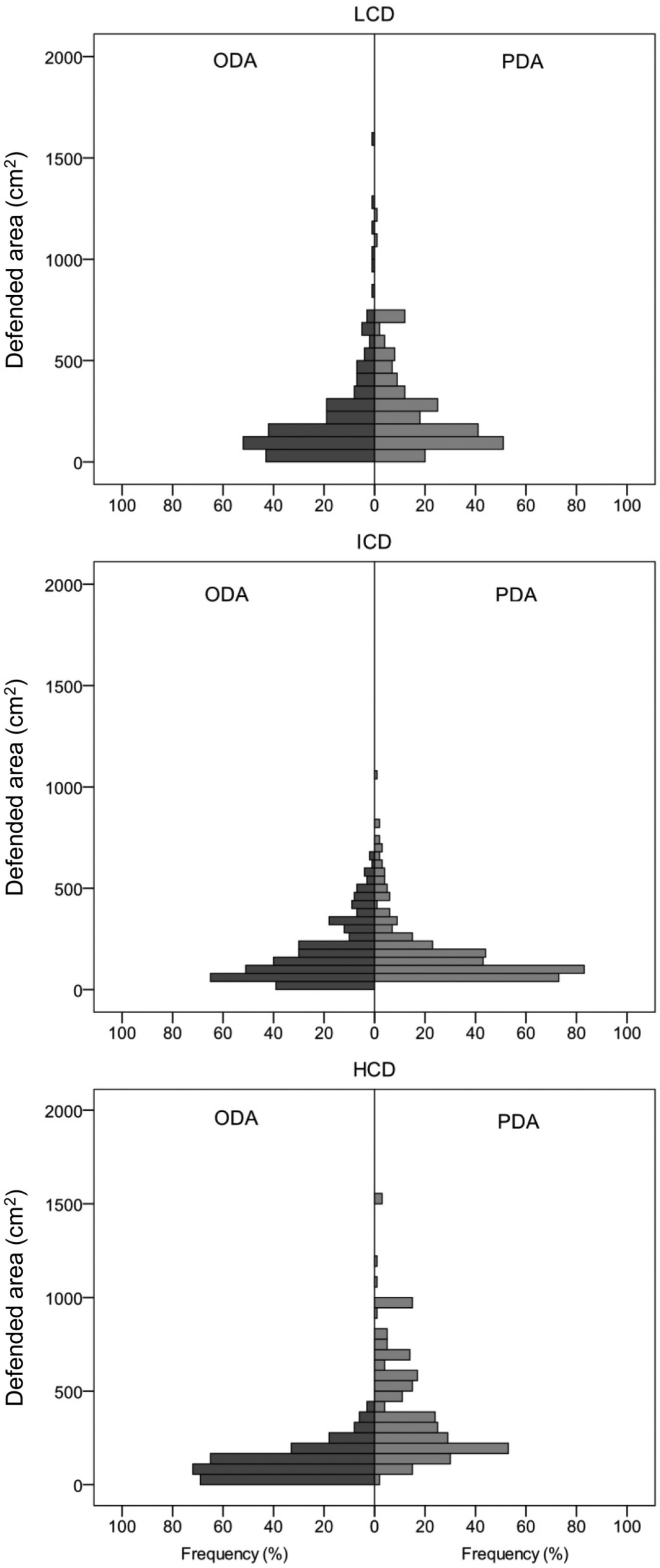


Table 1. Effects of food abundance and competitors on territory size of juvenile salmonids in present and published studies.

Reference	Species	Type*	Factors†	Competitors†	Food	Effects†,‡
Keeley and McPhail 1998	*O. mykiss*	F, O	D, IP, FA	D = 1–7 individuals·m^{-2} IP = 4–27 individuals·h^{-1}	Drift, 18.0–993.1 mg dry mass·m^{-2}·h^{-1}	D, sig. T↓ when ↑D IP, NS FA, sig. T↓ when ↑FA
Keeley 2000	*O. mykiss*	L, E	D, FA, D × FA	D = 32–127 individuals·m^{-2}	Pellet, 1.44–5.76 g·day^{-1}	D, sig. T↓ when ↑D FA, sig. T↓ when ↑FA D × FA, NS
Imre et al. 2002	*O. mykiss*	L, E	D	D = 30–65 individuals·m^{-2}	Pellet, 1.44 g·day^{-1}	D, sig. T↓ when ↑D
Imre et al. 2004	*O. mykiss*	L, E	FA	D = 24.8 individuals·m^{-2}	Pellet, 0.09–2.88 g·day^{-1}	D, sig. T↓ when ↑D FA, NS
Wood et al. 2012	*O. mykiss*	L, E	D	D = 4–12 individuals·m^{-2}	Pellet, 5% fish biomass	D, sig. T↓ when ↑D
Toobaie and Grant 2013	*O. mykiss*	L, E	FA	D = 8 individuals·m^{-2}	Pellet, 0.62%–20% fish wet body mass	FA, sig. T↓ when ↑FA
Dill et al. 1981	*O. kisutch*	F, O	D, FA	D = 5–125 individuals·m^{-2}·min^{-1}	Benthos, 2–60 mg·100 cm^{-2} Drift, 0.5–15 mg·m^{-2}·min^{-1}	FA (drift), NS FA (benthos), sig. T↓ when ↑FA
Keeley and Grant 1995	*S. salar*	F, O	D, IP, FA	D = 1–6 individuals·m^{-2} IP = 1–21 individuals·h^{-1}	Drift, 10.5–518.7 mg dry mass·cm^{-2}·h^{-1}	D, NS IP, NS FA, sig. T↓ when ↑FA
Lindeman et al. 2015	*S. salar*	F, E	D	D = 0.25–8 individuals·m^{-2}	Natural food supply (not measured)	D, sig. T↓ when ↑D
Gunnarsson and Steingrímsson 2011	*S. alpinus*	F, O	D, FA	D = 0.3–12 individuals·m^{-1} radius	Drift, 0.1–443.6 individuals·min^{-1}·net^{-1}	D, NS FA, sig. T↓ when ↑FA
Gunnarsson and Steingrímsson 2011	*S. trutta*	F, O	D, FA	D = 0–6.7 individuals·m^{-1} radius	Drift, 1.5–179.6 individuals·min^{-1}·net^{-1}	D, sig. T↑ when ↑D FA, NS
This study	*S. trutta*	L, E	D, FA, D × FA	D = 46–184 individuals·m^{-2}	Invertebrates, 500–2000 individuals·m^{-2}	D, sig. T↓ when ↑D FA, NS D × FA, NS

Note: Review only includes studies where territory size, competitors' pressure (either density or intruder pressure), and food abundance were directly measured.

*Laboratory, L; field, F; experimental, E; observational, O.

†D, density; IP, intruder pressure; FA, food abundance.

‡T, territory size; sig. = $P < 0.05$; NS = $P \geq 0.05$.

Table 2. Allometric relationships between fish length and territory size in juvenile salmonids in present and published studies.

Reference	Species	a	b	r^2	N	L (mm)	Unit (L, T)
Grant and Kramer 1990	Interspecific	−2.83	2.61	0.87^{***}	23	25–150	cm, m^2
Keeley and McPhail 1998	*O. mykiss*	−2.26	2.47	0.71^{***}	50	30–50	cm, m^2
Keeley 2000	*O. mykiss*	−1.77	3.05	0.55^{***}	68	30–60	cm, res
Keeley and Grant 1995	*S. salar* < 51 mm	−3.23	3.91	0.88^{***}	48	29–51	cm, m^2
Keeley and Grant 1995	*S. salar* > 51 mm	−0.63	1.12	0.86^{***}	46	56–130	cm, m^2
Steingrímsson and Grant 2008	*S. salar*	−0.37	0.53	0.01NS	50	30–55	cm, m^2
Grant et al. 1989	*S. fontinalis*	0.95	2.48	0.70^{***}	23	25–85	cm, cm^2
Gunnarsson and Steingrímsson 2011	*S. alpinus*	−2.40	3.02	0.11NS	31	34–54	cm, m^2
Elliott 1990	*S. trutta* < 40 mm	−2.84	3.45	0.97^{***}	501	22–40	mm, cm^2
Elliott 1990	*S. trutta* > 40 mm	−0.90	2.24	0.96^{***}	182	40–60	mm, cm^2
Gunnarsson and Steingrímsson 2011	*S. trutta*	−3.89	4.75	0.15^{*}	30	33–46	cm, m^2
This study	*S. trutta*	−0.79	0.53	0.15^{***}	816	21–67	cm, res

Note: intercept = a, slope = b, coefficient of determination = r^2, sample size = N, fish length = L, and territory size = T. Regression equations were $\log_{10} T = a + b \log_{10} L$ (units of variables are indicated), except in Keeley (2000) and this study where T were the residuals (res) from the linear regression between density and territory size. ***, $P < 0.001$; *, $P < 0.05$; NS, not significant ($P \geq 0.05$).

On the other hand, in our experiments the amount of available food determined the size of the foraging areas. When competitor density increased, both defended and foraging areas were significantly reduced, but the latter decreased even more when food abundance increased. To our knowledge, there are no previous estimates of foraging areas in brown trout. The estimates for other salmonids only indicate that aggression distances are larger than foraging ones (Grant et al. 1989; Keeley and Grant 1995; Keeley 2000; Imre et al. 2002; Steingrímsson and Grant 2008), which is the opposite of our experiments. Keeley (2000), in a very similar experiment, found that maximum sizes of foraging and defended areas were the same. In agreement with our results, Keeley (2000) and Imre et al. (2004) found an inverse relationship between foraging areas of rainbow trout and both food abundance and stocking density.

While some previous studies on juvenile salmonids have indicated a negative relationship between food abundance and defended areas (Slaney and Northcote 1974; Dill et al. 1981; Keeley 2000), others only found a weak negative relationship (Keeley and Grant 1995; Keeley and McPhail 1998; Wood et al. 2012; Toobaie and Grant 2013) or no relationship (Imre et al. 2004; Gunnarsson and Steingrímsson 2011) (Table 1). In general, previous studies suggest that the size of the defended area changes very little with increasing food abundance and that only very large increases in food abundance would decrease defended areas in natural streams. However, our experimental brown trout did not seem to adjust defended areas even at very high levels of food abundance. Our study is the first laboratory experiment where live invertebrates have been used instead of pellets (Keeley 2000; Imre et al. 2004; Wood et al. 2012), simulating the available food in wild conditions. Food abundance was manipulated to remain within the upper range found in Spanish productive streams (Almodóvar et al. 2006; Nicola et al. 2010). Therefore, it seems that food abundance needs to be even higher to be a limiting factor when defending a territory. As Imre et al. (2004) pointed out, the intense competitive pressure exerted by neighbors under conditions of extremely high density and impossibility of emigration (as in our study) could prevent territory holders from expanding their territories when food abundance is low. In this regard, our results agree with those found in previous experimental studies of salmonids and other animals (reviewed by Adams 2001). Alternatively, defense of a given area may have other implications for trout beyond feeding. They may simply maintain a minimum necessary physical space for growth when energy requirements are already fulfilled; previous studies have shown that juvenile trout grow larger in larger spaces (Greenberg and Giller 2001). Under this hypothesis, trout should be flexible in changing their foraging behaviour (increasing foraging area as food abundance decreases) to meet their metabolic requirements but defend only a minimum necessary physical space.

Irrespective of food abundance, brown trout showed an innate behaviour to defend an area against intruders. The size of the area was reduced when competitor density increased. To our knowledge, this is the first study showing experimentally how defended areas of juvenile brown trout change with variable competitor density. A similar study was carried out under wild conditions in Icelandic rivers, and the authors did not find a negative effect of competitor density on territory size (Gunnarsson and Steingrímsson 2011). However, fish densities in that study were much lower (mean = 1.46 individuals·m^{-2}) than those used in the present study (46, 92, and 184 individuals·m^{-2}). The same pattern has been observed in experimental and field studies of other salmonids where competitor density was low (Keeley and Grant 1995, *S. salar*, mean = 3.2 individuals·m^{-2}; Keeley and McPhail 1998, *O. mykiss*, mean = 2.9 individuals·m^{-2}). In contrast, a negative significant relationship between competitor density and territory size has been reported at higher density conditions (Keeley 2000, *O. mykiss*, 74 individuals·m^{-2}; Imre et al. 2002, *O. mykiss*, 46 individuals·m^{-2}; Imre et al. 2004, *O. mykiss*, 25 individuals·m^{-2}; Wood et al. 2012, *O. mykiss*, 1.9–14.8 individuals·m^{-2}; Lindeman et al. 2015, *S. salar*, 0.25–8 individuals·m^{-2}). At low densities, territoriality may play a smaller role, as individuals have foraging areas large enough to survive and grow (note however that dominance plays a very important role since the most dominant individuals would occupy the positions providing the best conditions to grow; Newman 1993). As a result, density-dependent mortality is typically observed in salmonids only at high densities, while density-dependent effects on growth are stronger at relatively low densities (Imre et al. 2005; Einum et al. 2006).

Although our findings showed a significant trend where the size of defended territories increased with fish length, data still contained a high amount of unexplained variability. A similar outcome was obtained by Gunnarsson and Steingrímsson (2011) for Icelandic brown trout in wild conditions. In general, there are disparate results reported in the salmonid literature. Steingrímsson and Grant (2008) and Gunnarsson and Steingrímsson (2011) did not find a significant allometric relationship between territory and fish size in other salmonids (Table 2). This contrasts with Elliott's (1990) study on brown trout that found a close relationship between fish length and the area of the defended territory. Likewise, other authors have found a negative relationship in other salmonids (see review in Table 2). The scaling of territory size with body size was lower in our study than in other studies of salmonids (Table 2). During the experiments, we observed that fish were often distributed throughout the water column rather than confined to the bottom of the channel. Gunnarsson and Steingrímsson (2011) suggested that under high PHS values, juvenile salmonids might defend three-dimensional territories, and Ayllón et al. (2010) showed that the allometry of territory volume would be a better predictor of brown trout spatial requirements than territory area. Thus, under keen competition, the spatial territory geometry may change. This could explain the low explanatory power of our allometric model and may be considered in future research. Alternatively, it is possible that the strongly competitive conditions imposed in our experiment prevented trout from acquiring the area required to fulfill their theoretical metabolic demands. The slope (*b*) of the defended area versus fish length regression in juvenile salmonids reported in the present (Table 2) and previously published (fish length 21–85 mm) studies ranged from 2.24 to 4.75 (mean 3.12), which extends the range published by Grant and Kramer (1990). The rate at which salmonids scale territories to body size is highly species-specific.

The role that territorial behaviour plays in the regulation of population size depends on how territory size responds to population density. Our findings show that on the one hand, territory size (both foraging and defended areas) decreases with increasing fish density. On the other hand, the size of the defended area is relatively fixed for a given length of fish; our results were comparable to those predicted by allometric regressions for similar sized trout in an Atlantic population (Elliott 1990). Therefore, it can be concluded that at densities at which all available habitat is saturated, the defended area would be set by fish length, being just qualified around narrow ranges by local density. Only when competitor density was markedly extreme (four times the 100% PHS) did territory size fall drastically below the expected values. This suggests that under extreme competition, such as during the critical period right after emergence, trout subdivide available habitat and therefore moderate the magnitude of density decline due to density-dependent mortality. After some extreme point, trout may even cease to be territorial because it is not profitable in terms of energy gain to defend a territory anymore (Elliott 1994). Therefore, it can be concluded that trout maintain territories determined mainly by fish size regardless of available food, and only under exceptionally high competition do they substantially decrease territory size. Brown trout is flexible in its territorial behaviour under variable competitor pressure, as are other vertebrate species (Maher and Lott 2000), but under natural conditions an extremely high density of competitors is needed to significantly change their territory size. The model developed by Elliott (1990) did not control for the density factor, and his experimental trout remained at lower densities than used in our experiments. However, it seems to have a great predictive power except in conditions of extreme competition.

To summarize, territory size of juvenile brown trout is flexible under severe intraspecific competition, thus lending support to optimal territory size models. The scarce estimates of PHS in Iberian brown trout populations close to carrying capacity (Ayllón et al. 2010; Parra et al. 2011) indicate a mean PHS around 52% (range 34%–76%) in summer, which corresponds to a probability of a density-dependent response of less than 0.80, according to the logistic model of Grant and Kramer (1990). Our findings indicate that under this scenario, the defended areas would be set by fish length and would only slightly adjust depending on the local competitor density. Thus, territories will set a maximum density for a particular habitat, lending support to our previous work estimating the carrying capacity of brown trout in Mediterranean populations (Ayllón et al. 2012*a*, 2012*b*, 2013). It should be noted that studies based on observations of territorial individuals provide information regarding the space and food requirements of the dominant individuals, but studies accounting for the diverse behavioural strategies displayed (dominants versus subordinates, territorial versus nonterritorial) are still needed. This new approach could reveal the average spatial requirements of all fish in the population, which may be relevant for predictive modeling in populations or conditions with a high proportion of nonterritorial fish. In addition, a review by Grant and Kramer (1990) showed that 19 of 31 studies of different salmonid species reported mean PHS values over 100% (range 105%–775%). Therefore, there are natural conditions of severe competition where defended areas would be determined less by fish length and much more by competition, as we observed here.

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