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To cite this version:

Marius Dhamelincourt, Mathieu Buoro, Jacques Rives, Stellia Sebihi, Cédric Tentelier. Individual and group characteristics affecting nest building in sea lamprey (Petromyzon marinus L. 1758). Journal of Fish Biology, 2020, pp.1-9. 10.1111/jfb.14601 . hal-03036001

HAL Id: hal-03036001
https://hal.inrae.fr/hal-03036001

Submitted on 9 Mar 2022

Individual and group characteristics affecting nest building in sea lamprey (*Petromyzon marinus* L. 1758)

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Funding information

Funding information: functioning was financed by Pôle Gestion des Migrateurs Amphihalins dans leur Environnement. M.D. PhD is financed by Univ. Pau & Pays Adour and UPV/EHU.

Abstract

Nest-building relates to reproductive effort, sexual selection, intersexual conflict and cooperation, and may be linked to individual phenotype and interindividual interactions. In particular, larger individuals having more energy reserves are expected to build more, larger nests, without having to trade intrasexual competition for cooperative nest building. Capture-Mark-Recapture (CMR) and nest survey of sea lamprey (*Petromyzon marinus* L. 1758) were combined to assess the relationship between individuals and nesting activity on a spawning ground, throughout a breeding season, during which we observed 202 nests and captured 114 individuals. On average, males and females stayed 8.33 ± 1.02 and 3.57 ± 1.04 days on the spawning ground, visited 2.26 ± 1.72 and 1.67 ± 1.17 nests and encountered 2.33 ± 2.13 mates for males and

2.29 ± 1.32 mates for female, respectively, and the number of mates encountered increased with the number of nests visited. Body size had no effect on duration of presence on spawning ground, number of nests visited, number of individuals per nest, sex ratio on nest or nest volume. Bigger nests were found at the end of the season and were not necessarily built by more individuals. Our work brings insights on the mating system and cooperative nest building in sea lamprey and may inform managers who want to estimate sea lamprey populations via nest surveys.

Keywords: behavioural ecology, mating system, nest, *Petromyzon marinus*, population management, reproductive strategy

Introduction

Nest building relates to several dimensions of evolutionary and behavioural ecology, such as habitat choice, reproductive effort, sexual selection or offspring survival. Nests can also be used to assess species presence or estimate populations in case of low breeder's detectability (Iles et al., 2019). When each individual builds one nest, and when each nest is built by a single individual, population assessment is straightforward. However, in some species, each individual can build several nests in a breeding season (Gamboa, 1981; McPherson et al., 2003; Nores and Nores, 1994) and the number of nests built by each individual may depend on phenotypic characteristics such as body size (Cargnelli and Neff, 2006) or on environmental parameters such as habitat availability. Identifying the variables linked to the number of nests per individual is important to both understand the behavioural ecology of nesting and to make a realistic estimation of the breeder's population from nest census. Furthermore, a nest can be the result of monoparental building (Aas et al., 2011; Rushbrook et al., 2008) but sometimes two or more individuals are involved(Franks et al., 1992), including non-breeding helpers (Skutch, 1961). In such cases, the number of individuals contributing to nest construction is the outcome of interindividual conflict around competition and cooperation, and may affect the physical characteristics of the nest (Soler et al., 1998; Svensson and Kvarnemo, 2003). Here again, understanding the factors that determine the number of individuals involved in the construction of a nest and its consequences on nest characteristics would both shed light on costs and benefits of cooperative nest building and improve population estimates from nest counts.

Sea lamprey (*Petromyzon marinus* L. 1758) builds nests that are both indicators of population size and the result of interindividual interactions. Lampreys remove stones and cobbles with their mouth and release them downstream so that the resulting nest consists of a pit carpeted with sand or gravel, followed by a mound of cobbles and stones. From the perspective of population assessment, these structures are easily detectable (Taverny and Elie, 2010; Waldman John et al., 2008) and provide excellent indicators of the presence of sea lamprey (Johnson, 1987). The number of nests found on a spawning ground could also be used to infer the number of spawners, an important data in the context of both protected populations in Europe and Northern America (Beaulaton et al., 2008; Hansen et al., 2016; Rogado et al., 2005; Rondinini et al., 2013) and invasive populations in Laurentian Great Lakes (Applegate, 1950; Hansen, 1999). However, accurately inferring the number of individuals from nest counts requires a good knowledge of both the number of individuals per nest and the number of nests built per individual. These two variables are the result of individual behaviour, which may depend on individual and environmental factors. Sea lamprey is known to be mostly monogamous but more than two individuals can be observed on a nest (Applegate, 1950; Manion and Hanson, 1980; Migradour, 2010). If the number of individuals per nest is relatively well known, there is little information on the factors explaining it. Nevertheless, lower sex ratios (proportion of males) seems to be associated with high number of individuals per nest (Johnson, 1987), in particular towards the end of the spawning season, when females outnumber males (Applegate, 1950). Sea lamprey also tends to visit several nests (Gilmore, 2004) but the number of nests constructed by each individual is unknown as well as the individual variability of this number. The aim of this study is to investigate the relationship between individuals and nesting activity by combining mark-recapture and nest survey of a sea lamprey spawning ground throughout a breeding season. We expect larger individuals to spend a longer time in the spawning ground and visit more nests because they have more important energy reserves and more gametes to spend (Docker, 2019; Hardisty, 1964; Kieffer and Tufts, 1998; Mackereth et al., 1999; Salam and Davies, 1994; Smith and Marsden, 2007). We also predict that males should spend more time on the spawning site and visit more nests than females because sexual selection is expected to be stronger on males (Andersson, 1994). Regarding the number and phenotype of individuals per nest in the context of cooperative nest building and sexual selection, several predictions can be made. First, if cooperation is a way for smaller individuals to build nests efficiently despite lower energy reserves, we predict that the number of individuals on a nest should be inversely related to their body length and mass, as observed across different lamprey species (Brumo, 2006; Jang and Lucas, 2005; Stone, 2006; Takayama, 2002; Zydlewski et al., 2012). However, other factors such as the progress in spawning season may affect the number of individuals per nest. In particular, cooperative nest building may be more frequent, hence the number of individuals per nest be higher, by the end of the season, when individuals get time- or energy-limited (Applegate, 1950). Second, the proportion of females on a nest is expected to increase with the body size of the longest male, if large males are more attractive to females and more efficient at ousting other males from the nest during intrasexual competition (Docker, 2015; Manion and Hanson, 1980). Finally, if cooperation allows more efficient nest building, we predict that the size of a nest should increase with the number of individuals building it (Mundahl and Sagan, 2005) and with their body size (as observed across species; Johnson et al. (2015). Lampreys being poikilotherms, nest size may also increase with water temperature if individuals are more efficient in nest building at higher temperature (Beamish, 1974).

Material and methods

Study site and experimental period

The study took place in the 1 km long bypass reach of the Halsou hydroelectric power plant on the Nive river (Halsou dam, 43° 22’ 21.38” N, 1° 24’ 53.134” W), a 79 km long river situated in Northern Basque Country, France, and draining a basin of 1030 km^2. This reach is composed of riffles, runs and pools, and offers a variety of microhabitats potentially adapted to nest construction by sea lamprey, as attested by the 100 nests found in this reach on a previous survey (Migradour, 2010) . The study period corresponded to the sea lamprey spawning period in the Nive, from May 6 to June 24, 2019. The monitoring was intended to be continuous, but was skipped on 19 days (May 11, 12, 17, 18, 19, 20, 21, 22, 23, 26, 27 and June 5, 6, 7, 8, 16, 21, 22, 23) because of unfavourable conditions of observation (high flow or turbid water). It was finally stopped when no new individual had been observed for one week. Throughout the study period, water temperature was monitored using a probe (Solinst Llevelogger) placed at the downstream boundary of the study area.

Capture-Mark-Recapture

Each day of the study period, we waded through the zone in order to mark or recapture sea lamprey. For the first capture, each individual was marked using two T-bar tags (FD-94, Floy Tag, USA) inserted at the base of the anterior dorsal fin with a tagging gun. Each tag bore one or two colours among pink, green and blue, and could be placed either on the left or right side of the fin, yielding 364 permutations that allowed individual recognition from resight without actual recapture. Because each tag also had a unique number, individuals bearing ambiguous colour code could be recaptured to be identified. For each individual the date, nest ID (if captured on a nest), mass, length, and sex were noted at first capture, while date and nest ID were noted at subsequent resights. Mass was measured with a digital spring scale (± 10 gr) using a bag of known mass to place the individual. Length was measured with a rule (± 1 cm) stuck in a PVC gutter in order to immobilize the individual. Males have a thick dorsal bulge absent in the females allowing easy visual sex identification for mature individuals (Taverny and Elie, 2008). After tagging, the individual was maintained by hand for a few seconds on a rock on the nest or close to the capture site, until it attached to the rock with its mouth, a releasing method which limits the risk of downstream drift. The subsequent occasions corresponded to a visual identification of the coloured tags (resight). But if only one tag remained, the individual was recaptured to identify the tag numeric code. In that case, a tag with the same colour code than the missing one was added.

Ethical statement

The care and use of experimental animals complied with the French animal welfare laws, guidelines and policies as approved by the ethical committee for birds and fishes in the French region Nouvelle Aquitaine (authorization #20190314155511268).

Nest measures

When a nest occupied by a sea lamprey was found during the daily survey, it was marked with a unique number written on a stone and its GPS coordinates were recorded. We also noted the date, time and identity of individuals on it (lampreys were marked if necessary). Each nest was subsequently monitored daily until no more individual was observed on it, and its diameters and depth were then measured. Lateral (perpendicular to the current) and longitudinal (parallel to the current) diameters of the excavated area were measured using a measuring tape (± 1 cm). Water depth ± 1 cm) was measured at the deepest point of the excavated area and at the upstream verge of the nest, using a vernier gauge. The difference between these two measures corresponded to the depth of the nest excavated by sea lampreys. The volume of the nest pit was then estimated assuming a half-ellipsoid shape, with the following equation:

$$Volume = \frac{2}{3}\pi \times \frac{lateral\ diameter}{2} \times \frac{longitudinal\ diameter}{2} \times nest\ depth \tag{1}$$

1 Statistical analyses

Mark-recapture data were analysed using a dynamic multistate occupancy model with augmented population (Kery and Schaub, 2011) . The multistate approach allowed to separate explicitly the observation process – i.e. individual captures (seen or not) – from the dynamic process – i.e. life histories (alive or not, on site or not) – avoiding potential confusion between these parameters. The capture of an individual i at time t (noted $y_{i,t}$) is dependent of the state of the individual at time t (i.e. alive or not, on site or not) and the probabilities of capture $p_{i,t}$. The state of the individual at time t (noted $z_{i,t}$) is then dependent of the probabilities of survival $\phi_{i,t}$ and of being present on site $y_{i,t}$. $y_{i,t}$ and $z_{i,t}$ are sampled in categorical distributions with $y_{i,t}$ taking the values 1 (seen) or 2 (not seen) and $z_{i,t}$ taking the values 1 (not yet entered) or 2 (alive) (see Kery and Schaub (2011) for more information). Capture and survival probabilities have been considered constant over time. However, effects of individual length and sex were tested on both y_i and ϕ_i to account for their effects on residence time (inferred from survival probability) and capture probability (that may indicate a difference in activity) using a logit link function to ensure that probabilities lie on [0, 1]:

$$\ln\left(\frac{\Phi_i}{1-\Phi_i}\right) = \theta_1 + \theta_2 \times sex_i + \theta_3 \times length_i \tag{2}$$

$$\ln\left(\frac{p_i}{1-p_i}\right) = \beta_1 + \beta_2 \times sex_i + \beta_3 \times length_i \tag{3}$$

With θ_1 and β_1 being the intercepts, θ_2 and θ_3 the effects of sex and length on survival and β_2 and β_3 the effects of sex and length on capture probability. Length data was centred and sex data was coded in 0 (female) or 1 (male).

The entry probability $\gamma_{i,t}$ was estimated at each occasion t and was considered independent of individual phenotypes. We assumed a non-linear relationship with time:

$$\ln\left(\frac{\gamma_{i,t}}{1-\gamma_{i,t}}\right) = \alpha_1 + \alpha_2 \times (t-1) + \alpha_3 \times (t-1)^2 \tag{4}$$

Finally, the population size N_{super} was then inferred conditionally on the probabilities estimates using an augmentation data procedure (andrew Royle and Dorazio, 2012). The model was fitted using a bayesian approach allowing to assess estimates of parameters of interest and the uncertainties associated. We used non-informative prior information for all hyper-parameters (see supplementary material: Table 4). We ran 2 MCMC chains and retained 25000 iterations. Convergence and stationarity of chains were obtained after an initial burn-in of 15000 iterations. Brooks–Gelman–Rubin diagnostic was performed to verify Markov chains convergence sampling (Brooks and Gelman, 1998). We ensured that the MCMC convergence criteria (Rhat) was below 1.1 for all model parameters. Uncertainties in model parameters were reported using credible intervals at 95 % ($\mathrm{CI}_{95\%}$). We evaluated the statistical significance of parameters (i.e. regression coefficients by ensuring that the $\mathrm{CI}_{95\%}$ did not overlap with 0. Medians of effect sizes, $\mathrm{CI}_{95\%}$ (within brackets) and confidence that the parameter is significantly positive or negative (i.e. do not overlap with 0 and differ from the sign of the median; hereafter, P</ >0) are subsequently reported. We compared models (i.e., different combinations of effects) using DIC ("Deviance Information Criterion") and chose the most parsimonious one. Data and code to run analysis are available in the INRAE dataverse repository , under the name "Individual and group characteristics affecting nest building in sea lamprey".

The detection process combined the physical capture of fish (state known) and the resight information based on colored tags identification. The detection matrix $\gamma_{i,t}$ (see section above) is based on capture and resight information only. However, the recovery of fish during the survey informed about the states of these individuals (on site and alive respectively). Using the Bayesian approach we were able to use this information to partially fill up the unknown matrix $z_{i,t}$, allowing better estimation of parameter of interest (survival and detection probabilities), computation speed and convergence. For instance, if an individual i was observed alive few days after first capture, it indicated that the fish was alive before and then we fixed its survival history to 2 (i.e., $z_{i,t}$ = 2 at each occasion t since first capture). We assumed that individual didn't leave the site after entrance during the breeding season. In turn this approach facilitates the estimation of the detection and entry probabilities. For skipped observation days because of unfavourable conditions $\gamma_{i,t}$ was set to NA (see above for days detail). A first dummy occasion was added for $\gamma_{i,1}$ and $z_{i,1}$ corresponding to individuals not seen and not on site.

To test the effect of individual covariates on the number of visited nests per individual (i.e. number of different nests where an individual was observed at least once) a generalized linear model was used with sex, length, and mass as individual covariates. Date (expressed as the number of days since the beginning of the experiment) was tested as an environmental covariate. The number of individuals observed on a nest was also modelled with a generalized linear model, using average length and mass of individuals, as well as water temperature and date as independent variables. For both models, a Poisson distribution with a Log link function was used. In both cases the full model was then reduced using a stepwise selection procedure based on Akaike's criterion (*stepAIC* function in *MASS* package; Venables and Ripley (2002)).

Sex-ratio analysis was performed with a linear mixed model (*lmer* function in *lme4* package; Bates et al. (2015)) assuming a binomial distribution of the sex-ratio variable with a Logit link function. The identity of the biggest male on the nest was included as a random effect, and its length and mass as well as date and water temperature were included as fixed effects. The best model among all those nested in the full model was selected using the Akaike's criterion.

Variables explaining nest size were assessed using a linear model fitted to the log-transformed volume variable. Individual covariates were mean length and mass of all individuals observed on the nest, and the total number of individuals seen on the nest. Date and water temperature were used as environmental covariates. A stepwise selection procedure with Akaike's criterion was then performed. This model was applied on two datasets. One dataset corresponded to the totality of the nests where one or several individuals were found. The other was the same dataset without the nests where only one individual was found. In that case, the resulting nest could only be a construction attempt with a subsequent individual departure (Applegate, 1950; Hardisty and Potter, 1971; Manion and Hanson, 1980).

All statistical analyses were performed using R software version 3.5.1 (R Core Team, 2020). The Bayesian analyses were conducted using the *Rjags* package (4-10 version) as an interface to the JAGS software (Plummer, 2003).

Results

Over the course of the spawning season, 114 individuals (58 females and 56 males) were captured. Mean length and mass were 695 ± 41 cm/887 ± 179 g for females and 742 ± 48 cm/1019 ± 208 g for males. Seventy-four of the 202 nests observed were measured. The mean depth, lateral and longitudinal diameters were respectively 30 ± 17 cm, 119 ± 58 cm and 116 ± 50 cm corresponding to a mean volume of 640 000 ± 72 000 cm^3. Summary of posterior distributions of parameters of interest for the dynamic multistate occupancy model are given in Table 1. DIC values and Gelman and Rubin diagnosis are provided in supplementary material (Table 5 and Table 6). Estimates of the coefficients of regression for the probability of capture pi indicate no effect of sex (β_2: -0.26 [-1.03 ; 0.49]; P>0 = 25 %) nor of body length (β_3: -0.001 [-0.01 ; 0.00]; P>0 = 5 %). Thus, the probability of capture was estimated at 0.63 [0.53 ; 0.71] for female and 0.49 [0.38 ; 0.61] for male. Estimates for the survival probability ϕ_i indicate an effect of sex (θ_2 : 0.86 [0.20 ; 1.52]; P>0 = 99 %) but not of body length (θ_3 : 0.00 [-0.00 ; 0.01]; P>0 = 90 %) suggesting a higher survival probability for males compared to females (males: 0.88 [0.83; 0.91]; females: 0.72 [0.66 ; 0.77]). Considering these survival probabilities, residence time can be estimated to 8.33 ± 1.02 days for males and 3.57 ± 1.04 days for females. Using the more parsimonious model (i.e. no body length effects on survival and capture probability), the model estimated that 177 [154 ; 219] lampreys have spawned on the study site over the season.

The number of nests visited per individual was affected by sex, with males and females visiting on average 2.26 ± 1.72 and 1.67 ± 1.17 nests, respectively (Table 2, Figure 1). The number of nests visited did not depend on body length. The number of individuals found on nests varied between one (usually a male) and seven, and most of the nests with more than one individual were attended by a pair (Table 3). The number of individuals and the sex ratio per nest were linked to none of the tested variables (Table 2). Across the nests where they were observed, males and females encountered on average 2.33 ± 2.13 and 2.29 ± 1.32 mates. The number of mates encountered increased with the number of nests visited for both males (Spearman's ρ = 0.39; p = 0.005; Figure 2a) and females (Spearman's ρ = 0.55; p < 0.001; Figure 2b). Nest volume increased with time in the season (Table 2, Figure 3) and with the number of individuals on it when all nests were included in the model, but not when nests with a single individual were excluded (Table 2; Figure 3). Nest volume was affected by neither individual size nor temperature.

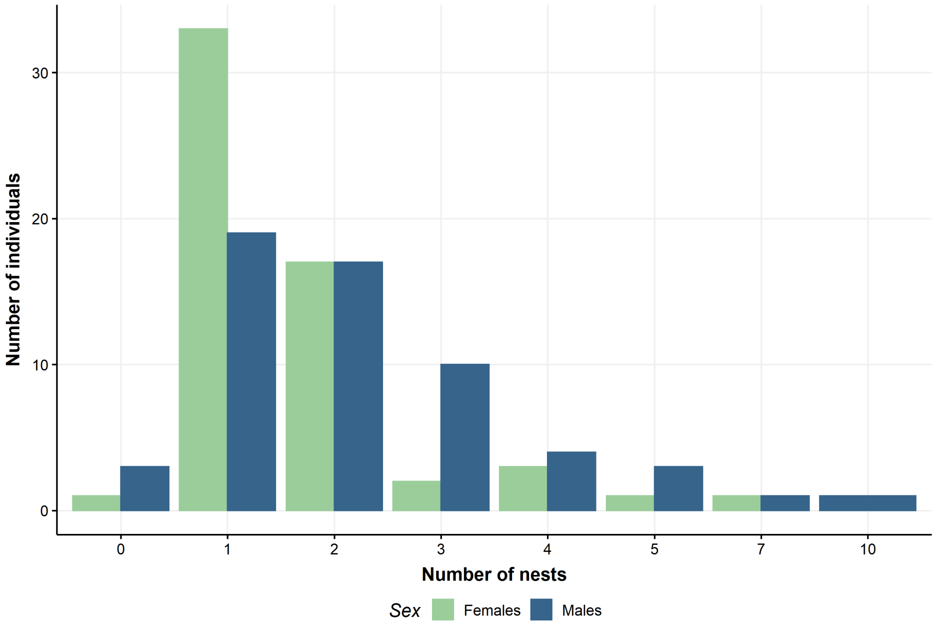

Figure 1: Number of nests visited per individual as a function of sex. A null number of nests corresponds to individuals found outside of nests.

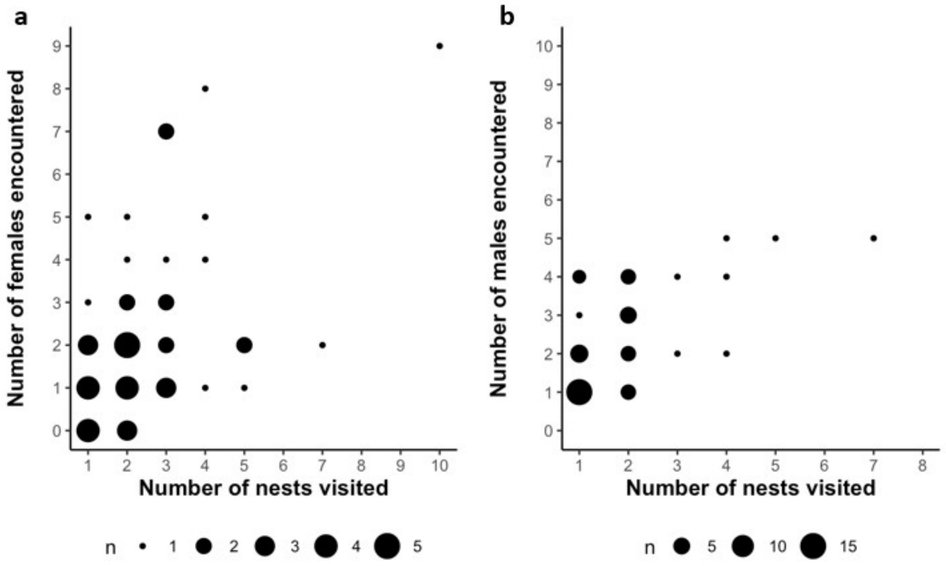

Figure 2: Number of nests visited and number of mates encountered for male (a) and female (b) sea lamprey. The size of the point relates to the number of individuals.

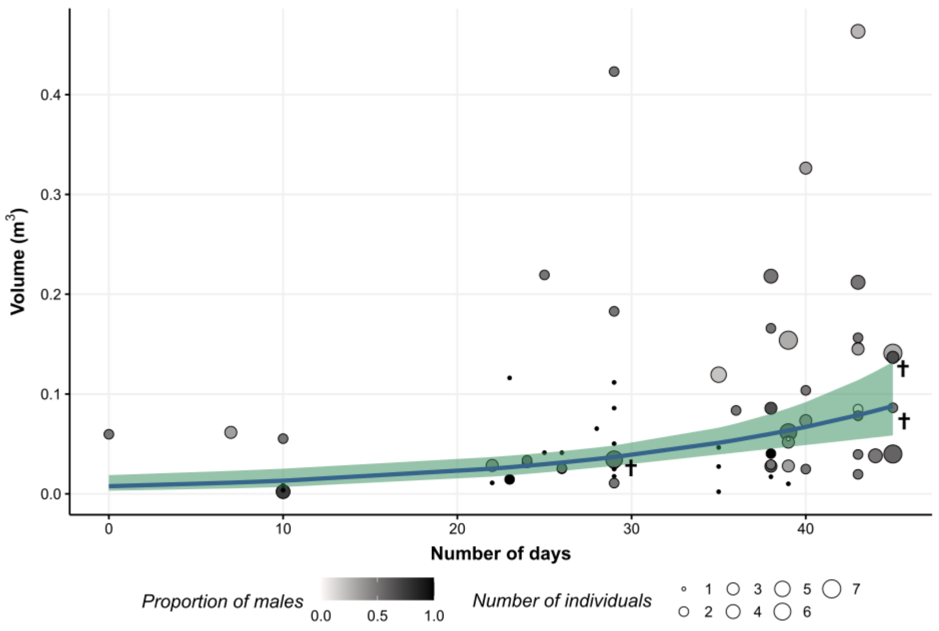

Figure 3: Data (points) and model predictions (line) of nest volume for all nests as a function of time for the linear model fitted to the log-transformed volume variable. Relationship between male proportion and volume such as relationship between number of individuals and volume are also indicated. † indicates reused nests.

Table 1: Parameters of Capture-Mark-Recapture model with a posteriori distribution for each parameter. 95 % credible intervals are indicated in brackets. Models were fitted in a Bayesian framework. Medians and 95 % credible intervals are reported. P</ > provides the proportion of negative or positive posterior values, that is, confidence that the effect is negative or positive, respectively. Effects were considered significant when $p < 0.05$.

Parameter	Calculated probability	Definition	Posterior distribution		
			Median	95 % credible interval	P>0
α_1	γ_t	-	-4.69	[-5.59 ; -3.92]	0
α_2	γ_t	-	-0.04	[-0.11 ; 0.05]	0.17
α_3	γ_t	-	0.00	[0.00 ; 0.01]	1
θ_1	ϕ_i	*Intercept for the probability of survival* ϕ_i *(logit scale), i.e. survival probability for an average individual*	1.05	[0.59 ; 1.54]	1
θ_2	ϕ_i	*Effect of sex on the survival probability* ϕ_i *(logit scale)*	0.86	[0.20 ; 1.52]	0.99
θ_3	ϕ_i	*Effect of length on the survival probability* ϕ_i *(logit scale)*	0.00	[-0.00 ; 0.01]	0.90
β_1	p_i	*Intercept for the probability of capture* p_i *(logit scale), i.e. capture probability for an average individual*	0.39	[-0.18 ; 1.00]	0.91
β_2	p_i	*Effect of sex on the capture probability* p_i *(logit scale)*	-0.27	[-1.03 ; 0.49]	0.25
β_3	p_i	*Effect of length on the capture probability* p_i *(logit scale)*	-0.01	[-0.01 ; 0.00]	0.05
Nsuper	-	*Population size*	177	[154 ; 219]	1

Table 2: Summary of generalized linear models fitted to the different variables describing the relationship between nests and individuals. Mixed model was used for the sex-ratio per nest, with identity of the biggest male as the random effect. Regression coefficients and their standard errors are given only for variables retained on the model with the lowest AIC among the global model with all effects and all possible submodels. Values in italics indicate coefficients significantly different from zero (z-test for Poisson and binomial distribution, t-test for Lognormal distribution) with $^{*}P \leq 0.05$, $^{**}P \leq 0.01$ $^{***}P \leq 0.001$.

		Independent variables				
Dependant variable	Distribution	Sex (male)	Mean length	Time	Number of individuals	R-Squared
Number of nests per individual	Poisson	0.30 (0.10)*	-	-	-	0.07
Number of individuals per nest	Poisson	-	-0.00 (0.00)	0.01 (0.01)	-	0.11
Sex-ratio per nest	Binomial (random = biggest male identity)	-	-	-0.03 (0.01)	-	0.02
Nest volume ($\geq$ 1 individual)	Lognormal	-	0.00 (0.00)	0.04 (0.01)**	0.19 (0.09)*	0.36
Nest volume (> 1 individual)	Lognormal	-	-	0.04 (0.01)**	-	0.27

Table 3: Number of nests per combination of males and females count. Data is indicated only for nests were individuals were observed (N = 69).

	0 male	1 male	2 males	3 males	4 males
0 female	-	21	2	0	0
1 female	1	21	3	1	0
2 females	1	9	3	0	0
3 females	0	0	0	2	1
4 females	0	1	0	0	0
5 females	0	1	2	0	0

Discussion

In this study we assessed the relationship between sea lamprey individuals and nesting activity by combining Capture-Mark-Recapture and nest survey of spawning ground throughout a breeding season. Our results showed significant differences between sex on survival and duration on the spawning ground, confirming our initial hypothesis that males spend more time on the site and visit more nests than females. However, our results disprove our second hypothesis that larger individuals spend a longer time in the spawning ground and visit more nests. Furthermore, the number of individuals and sex ratio per nest were affected by neither individual size nor the timing in the season. Finally, larger nests were dug by more individuals but not by larger ones, and occurred more frequently at the end of the spawning season. Altogether, our results contribute to improve our understanding of sea lamprey ecology and should favour better estimation of populations by nest counts. While most nests contained a single pair or a few individuals, most males and females were observed on more than one nest and with more than one mate, indicating that the sea lamprey mating system may be more polygynandrous than the monogamous/polygynous system suggested from mere observation of individuals per nest. Accordingly, Scribner and Jones (2002) used genetic parentage analysis on 62 adults and 475 larvae to show that 61 % of adults from each sex had more than one mate. In our data, the number of nests for males and females (average of 2.26 ± 1.72 and 1.67 ± 1.17 nests respectively) is probably underestimated because 114 over 177 probable lampreys on site were observed while only 69 of the 202 observed nests were occupied by one or more lamprey when we detected them. The number of mates increased with the number of nests visited by lamprey of both sexes, which should benefit from higher mating success either through a higher probability of gamete fertilization or through more genetically diverse offspring (Rodríguez-Muñoz and Tregenza, 2009). Regarding the effect of sex on individual longevity and mobility, with males lasting longer on the spawning ground and visiting more nests, our results are consistent with previous work on lamprey (Hagelin and Steffner, 1958; Jang and Lucas, 2005) and for other species (Hutchings and Gerber, 2002; Williams and Rabenold, 2005), male-biased mobility being observed preferentially within polygynous species (Greenwood, 1980). This sex difference could be the result of stronger sexual selection acting on males (Andersson, 1994), which would increase their mating success by extending their individual breeding season (Apollonio et al., 1989; Friedl and Klump, 2005). Beside direct male-male contests or female choice, sexual selection on the duration of male spawning season may have thereby favoured larger males, which bear more energetic reserves (Soulsbury, 2019). However, body size had no effect whatsoever. Size had none of the expected effects on individual duration of presence on spawning ground, number of nests visited, number of individuals per nest, sex ratio on nest or nest volume. This absence of effect contrasts with both theoretical predictions based on sexual selection or cooperation and some correlations observed within or across species of lampreys or other nest digging fishes, especially between body size and number of individuals per nest or nest size (van den Berghe and Gross, 1984). An explanation for this lack of effect could be the low variability in body size among the individuals we sampled. The coefficient of variation was only 6.5 % for males and 5.8 % for females. It usually does not exceed 10% in sea lamprey (Hansen et al., 2016; Steir and Kynard, 1986). This low variability is likely to make it more difficult to detect an effect with our sample size. Furthermore, power analysis made on body size reveals that the power was 33 % for the effect of length on the number of individuals per nest and 14 % for the effect of length on nest volume if we consider a R^2 of 0.02 which corresponds to a small effect according to (Cohen, 1988). Time had an effect only on nest size, with bigger nests at the end of the spawning season. This effect was due neither to the enlargement of already existing nests by late spawners, which occurred on only three occasions in our data, nor to a warmer temperature, which was not retained in the model. Given the short reproductive lifespan of individuals compared to the duration of the spawning season, the prediction that nearly exhausted individuals should be more likely to build nests cooperatively would be more efficiently tested by closely monitoring all the nests built by each individual through its reproductive lifespan. Although not linked to individual body size, nest volume was positively affected by the number of individuals visiting them. This result is in accordance with the trend found for the American Brook lamprey (Mundahl and Sagan, 2005). However, the absence of effect when the analysis was performed without nests attended by only one individual indicates that this positive effect could be due to the qualitative difference between actual nests and digging attempts by a single individual, reported by previous studies (Applegate, 1950; Manion and Hanson, 1980). It seems therefore that the benefit of collaborative building does not lie in bigger nests, which are supposed to provide better protection to embryos (Gauthey et al., 2017; Steen and Quinn, 1999). An alternative benefit could be a faster construction of the nest when more individuals are involved. Indeed, nests can take up to three days to be completed (Applegate, 1950), which represents a substantial part of the individual reproductive lifespan. Observing the whole process of nest building, for example with video recording, would allow to test whether digging duration depends on the number of individuals. Such observations would also give access to the relative investment of each individual and interindividual interactions (aggression, mating), unveiling some aspects of the resolution of conflict around cooperation in a reproductive context (Buston and Zink, 2009). Beyond the insights it gives and the questions it opens on the mating system and cooperative nest building in sea lamprey, our work may also inform managers who want to estimate population size via nest surveys. Nest counts can provide a relative estimate of population abundance (Kynard and Horgan, 2019) and, based on the average number of individuals per nest between 2 and 2.5 (Applegate, 1950; Manion and Hanson, 1980), some authors proposed to multiply the number of nests on a river by this factor to estimate the number of spawners (Gracia et al., 2016; Migradour, 2010). Our results suggest that such a method would overestimate the number of spawners because the majority of them actually visit several nests (considering 202 nests and the factor of 2.46 used by Migradour in 2010, the population estimated in our case would be 497 individuals instead of 177 estimated with our model). Moreover, the absence of relationship between nest size and number of individuals (>1) indicates that nest volume is not usable to correct the number of individuals per nest when estimating sea lamprey population via nest survey.

Author contribution

M.D.: ideas, data generation, data analysis, manuscript preparation; M.B.: data analysis, manuscript preparation; J.R.: data generation; S.S: data generation; C.T.: ideas, funding, data analysis, manuscript preparation.

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Supplementary material

Table 4: Non-informative prior information used for all hyper-parameters included in the model. 95 % confidence intervals of a priori means are indicated in brackets.

	Parameter	*a priori* distribution	
	Distribution	Mean	Standard deviation
α_1	Normal	$0_{-1960,1960}$	1000
α_2	Normal	$0_{-1960,1960}$	1000
α_3	Normal	$0_{-1960,1960}$	1000
θ_1	Normal	$0_{-1960,1960}$	1000
θ_2	Normal	$0_{-1960,1960}$	1000
θ_3	Normal	$0_{-1960,1960}$	1000
β_1	Normal	$0_{-1960,1960}$	1000
β_2	Normal	$0_{-1960,1960}$	1000
β_3	Normal	$0_{-1960,1960}$	1000

Table 5: Mixed model results for analyzes of differences between zones for nest characteristics, density and diversity of macroinvertebrates and α diversity indices, with nest identity as a random effect. With $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

Model	DIC
γ (t), ϕ(sex + length), p(sex + length)	1561
γ (t), ϕ(sex + length), p(sex + length + sex*length)	1562
γ (t), ϕ(sex), p(sex)	1565
γ (t), ϕ(sex + length + sex*length), p(sex + length + sex*length)	1566
γ (t), ϕ(sex + length), p(.)	1567
γ (t), ϕ(sex + length + sex*length), p(sex + length)	1567
γ (t), ϕ(sex), p(.)	1568
γ (t), ϕ(sex + length + sex*length), p(.)	1569
γ (t), ϕ(length), p(.)	1583
γ (t), ϕ(length), p(length)	1585
γ (t), ϕ(.), p(sex + length + sex*length)	1594
γ (t), ϕ(.), p(length)	1595
γ (t), ϕ(.), p(.)	1597
γ (t), ϕ(.), p(sex + length)	1598
γ (t), ϕ(.), p(sex)	1600
γ (.), ϕ(.), p(.)	1786

Table 6: Gelman and Rubin Convergence diagnosis for parameters of the model. “Upper C.I.” corresponds to the upper limit of the Potential Scale Reduction Factor (PSRF) indicating convergence of the Markov chains when near to 1.

Parameter	Upper C.I.
α_1	1.00
α_2	1.00
α_3	1.00
θ_1	1.02
θ_2	1.01
θ_3	1.00
β_1	1.06
β_2	1.06
β_3	1.02
$Nsuper$	2.53