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RESEARCH ARTICLE

Fighting over burrows: the emergence of dominance hierarchies in the Norway lobster (*Nephrops norvegicus*)

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ABSTRACT

Animals fight over resources such as mating partners, territory, food or shelter and repeated contests lead to stable social hierarchies in different phyla. The group dynamics of hierarchy formation are not characterized in the Norway lobster (*Nephrops norvegicus*). Lobsters spend most of the day in burrows and forage outside of them according to a diel (i.e. 24 h-based) activity rhythm. Here, we use a linear and generalized mixed model approach to analyse, in seven groups of four male lobsters, the formation of dominance hierarchies and rank-related changes in burrowing behaviour. We show that hierarchies emerge within 1–3 days and increase in steepness over a period of 5 days, while rank changes and number of fights gradually decrease over a 5-day period. The rank position determined by open area fights predicts the outcome of fights over burrows, the time spent in burrows, and the locomotor activity levels. Dominant lobsters are more likely to evict subordinate lobsters from their burrows and are more successful in defending their own burrows. They spend more time in burrows and display lower levels of locomotor activity outside the burrow. Lobsters do not change their diel activity rhythms as a result of a change in rank, and all tested individuals showed higher activity at night and dusk compared with dawn and daytime. We discuss how behavioural changes in burrowing behaviour could lead to rank-related benefits such as reduced exposure to predators and energy savings.

KEY WORDS: Contest behaviour, Fitness, Locomotor activity, Steepness, Biological rhythms, Temporal niche

INTRODUCTION

Contest behaviours are common among animal taxa and result from conflicts over fitness-related resources (Wilson, 1975; Huntingford and Turner, 1987; Hardy and Briffa, 2013). Animals fight for access to mates, territory, food or shelter (Huntingford and Turner, 1987). In social groups, dominance hierarchies emerge from repeated interactions between pairs of individuals and a consistent outcome in favour of the same dyad member (Drews, 1993). Many dominance hierarchies are linear and can be characterized by their steepness (De Vries et al., 2006). Steepness is defined as the size of the absolute differences between adjacently ranked individuals in

the overall success in winning dominance encounters (i.e. dominance success; De Vries et al., 2006). The formation and maintenance of linear dominance hierarchies is characterized by a gradual polarization (increased steepness) of dominance ranks over time, leading to a reduction in the frequency and duration of agonistic interactions (Chase, 1982; Hemelrijk, 1999; Issa et al., 1999; Goessmann et al., 2000; Kravitz and Huber, 2003; Herberholz et al., 2007). The social rank in a hierarchy depends on physical superiority (size, strength) or on specific previous experiences of the group members such as wins in previous encounters, prior residency, or knowledge of resource value (Ranta and Lindström, 1992, 1993; Rutherford et al., 1995; Barki et al., 1997; Goessmann et al., 2000).

Animals invest considerable energy into winning contests and suffer injuries in escalated fights (Briffa and Sneddon, 2007; Briffa, 2013). This raises questions regarding the adaptive benefits of being dominant. Evidence from numerous studies on mammals shows a positive relationship between dominance rank and reproductive success (Ellis, 1995). Similarly, in the female mate choice of fish (Paull et al., 2010) and crustaceans (Atema and Steinbach, 2007), dominant males profit by being preferred over subordinates. In most crustaceans, however, females are receptive for only a short period of the year (Jormalainen, 1998) but male contests take place throughout the year. This highlights the importance of other non-reproductive resources such as food and shelter as drivers for the formation of dominance hierarchies (Stocker and Huber, 2001; Herberholz et al., 2007; Fero and Moore, 2008).

In decapod crustaceans, the social rank usually correlates with access to shelter (e.g. Gherardi and Daniels, 2004). Shelters or burrows constitute important ecological resources to avoid predation (e.g. Blanchard and Blanchard, 1989; Jennions et al., 2003) or secure mating success (e.g. Simmons, 1986; Backwell and Passmore, 1996; Atema and Steinbach, 2007). In the American lobster, *Homarus americanus*, dominant males sequentially attract and mate with multiple females as a result of securing suitable mating shelters (Atema and Steinbach, 2007). Dominant crayfish, *Orconectes propinquus*, are more successful in shelter evictions than lower ranked crayfish, a behaviour that is correlated with control over space and shelter and hence important for predator avoidance and access to food (Fero and Moore, 2008).

The social rank can also be linked to the biological rhythm of animals (Bovet, 1972; Hansen and Closs, 2005). The diel (i.e. 24 h-based) partitioning of time in the use of ecological resources, such as shelters, can provide fitness advantages (Kronfeld-Schor and Dayan, 2003). Circadian clocks help organisms to anticipate and stay synchronized with periodical diel fluctuations of environmental variables, and have been documented in all phyla. The most important environmental synchronizers are diel cycles of light and temperature (Dunlap et al., 2004). These temporal cues determine a diel temporal niche (partitioning on a 24 h temporal scale; Castillo-Ruiz et al., 2012; Hut et al., 2012). However, such partitioning is not

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rigid and can be by-passed and modified by other abiotic and biotic cues with a mechanism that is defined by switching or shifting (Castillo-Ruiz et al., 2012; Hut et al., 2012) that may be also associated with energy balance (Schmidt-Nielsen, 1972; Hut et al., 2012). Information on how dominance hierarchies affect biological rhythms of animals is scarce, and unknown for invertebrates. Bovet (1972) demonstrated that when a group of four long-tailed field mice (*Apodemus sylvaticus*) were co-housed for a long period of time, the dominant individual had a different diel activity pattern compared with the other three subordinates. Similarly, individual giant kokopu fish (*Galaxias argenteus*) were shown to partition their diel activity according to their rank (Hansen and Closs, 2005) when food was limited. Unfortunately, in previous studies the hierarchy was not described quantitatively (e.g. steepness or linearity), limiting the conclusions from these studies.

The Norway lobster *Nephrops norvegicus* (Linnaeus 1758) (hereafter referred to as *Nephrops*) is a burrowing decapod inhabiting muddy bottoms of continental shelves and slopes of the Mediterranean Sea and European Atlantic Ocean (Farmer, 1975; Sardà, 1995; Bell et al., 2006). Chapman and Rice (1971) were the first to mention fighting behaviour of *Nephrops* over burrows in the wild; the observed ritualized dyadic fight was then described in the laboratory by Katoh et al. (2008), demonstrating that lasting dyadic dominance relationships are based on the assessment of chemical signals released with urine. The locomotor activity of *Nephrops* outside the burrows is under the control of the circadian clock and a light-driven burrow emergence behavioural rhythm has been characterized in the laboratory in the presence of artificial burrows (Aguzzi and Sardà, 2008; Katoh et al., 2013; Sbragaglia et al., 2013a). *Nephrops* burrow emergence is nocturnal in shallow water, while becoming diurnal in deep water. Such switching is driven by light intensity as demonstrated by Chiesa et al. (2010). This behavioural shift is probably coupled to the daily vertical migration of predators and prey (Aguzzi et al., 2015) and to the fact that the burrow represents a perfect strategy to escape predators as suggested by stomach contents data of many predators (Serrano et al., 2003).

Here, we characterized the behavioural changes occurring during the formation and maintenance of a dominance hierarchy in a group of four size-matched *Nephrops*. We provided four burrows to allow each lobster to display its specific daily burrowing behavioural rhythm. The rationale of this experimental design comes from the classic field observations by Chapman and Rice (1971) and new laboratory findings by Aguzzi et al. (2011) demonstrating a strong burrow-centred territoriality in the Norway lobster; fighting behaviour over burrows occurred even if these were not a limited resource (Aguzzi et al., 2011). Social interactions may influence circadian activity and lead to temporal niche partitioning (Castillo-Ruiz et al., 2012). So, in order to study the effect of a dominance hierarchy on the daily burrowing activity rhythm of *Nephrops* each individual needed access to a burrow.

We hypothesized that there will be rank-related changes in competition over burrows as the hierarchy develops. High dominance ranks are expected to confer significant benefits by: (i) winning more fights over burrows; (ii) increasing the time spent in burrows; and (iii) concentrating their diel activity rhythms to night hours and inducing a temporal shift in subordinates.

MATERIALS AND METHODS
Compliance with ethical standards
The species used in this study is not an endangered or protected species. Sampling and laboratory experiments followed the Spanish legislation and internal institutional (ICM-CSIC) regulations

regarding animal welfare. Animal sampling was conducted with the permission of the local authority (Generalitat de Catalunya). We used the lobsters obtained in one single event of capture/sampling for several experimental activities in order to maximize the cost/benefit ratio and comply with the 3Rs principles (Russell and Burch, 1959).

Animal sampling and acclimation
Animals were collected at night-time by a commercial trawler on the shelf area (100 m depth) off the Ebro delta (Tarragona, Spain). All sorting operations on the deck and the transportation of individuals to the laboratory followed the methodology described in Aguzzi et al. (2008). In the laboratory, specimens were transferred to an acclimation facility, hosted within a light-proof isolated chamber under the following conditions: (i) constant temperature of 13±1°C, as reported for the western Mediterranean continental slope throughout the year (Hopkins, 1985); (ii) random feeding time, in order to prevent entrainment through food-entraining oscillators, as shown for crustaceans (Fernández De Miguel and Aréchiga, 1994); and (iii) a light–darkness (LD) cycle, matching the duration of photoperiod at the latitude of Barcelona (41°23′0″N). LD transitions were gradually achieved within 30 min, in order to avoid lobster photoreceptor degeneration (i.e. rhabdom deterioration and visual pigments photolysis), as occurs when animals are subjected to sudden bright light exposure (Gaten et al., 1990). The acclimation facility hosted individual cells (25×20×30 cm) made with plastic nets of different sizes, allowing full oxygenation and recirculation of water, but not contact among animals in order to avoid injuries due to fighting.

Experimental set-up
The experimental tank used in this study was previously developed by Aguzzi et al. (2011). Briefly, the tank (150×70×30 cm) was endowed with four burrows of 25 cm length with an inclination of 20 deg to the entrance (see Fig. S1). Burrows were built by assembling PVC pipes, considering the information we have from field studies (Rice and Chapman, 1971). As burrow size is correlated to animal size, we built the artificial burrows according to an average lobster size of 45.00 mm (cephalothorax length). Sand was glued to the bottom of the tank and on the internal walls of the burrows to reproduce the habitat and facilitate locomotion of lobsters. The rest of the tank was painted in black to facilitate video-image analysis (see below). The tank was equipped with two different sources of LED illumination (monochromatic blue: 472 nm; infrared: 850 nm). Monochromatic blue lighting was installed to simulate LD conditions, while infrared (IR) light allowed video-recording during darkness. A strip of LED photodiodes (blue LEDs, *N*=84; IR LEDs, *N*=108) was inserted into a transparent methyl methacrylate tube (140 cm long and 16 mm in diameter) and placed along the sides of the tank to get a uniform illumination (see also Sbragaglia et al., 2013a). LD cycle was controlled using the Arduino board 'Arduino Uno' (http://www.arduino.cc), which is an open source electronics platform based on easy-to-use hardware and software.

Animals and experimental design
The intermoult adult male lobsters used in this study had a cephalothorax length (CL; mean±s.d.) of 43.92±2.08 mm (*N*=28). The right claw was 68.41±7.92 mm in length and the left claw was 68.66±8.58 mm. Individuals were randomly distributed among seven independent groups and the differences in CL and claw length were used as proxy for matching resource holding potential (RPH; Maynard Smith and Parker, 1976; see also Table S1). The day

before each experimental trial, a group of four lobsters was randomly selected from the acclimation tanks and different tags (Fig. S1) were fixed on the cephalothorax with fast-acting glue, which was removable at the end of the experiment without damage to the cuticle. Animals were then left in isolation (physical and chemical) for 24 h to ensure recovery from stress induced by handling and by previous chemical-mediated dominance relationships that could have been established in the acclimation facility (Katoh et al., 2008). Isolation took place in individual aquaria (25×20×30 cm) hosted in the same light-proof isolated chamber of the acclimation facility. Each isolation tank had an independent open water system with the same conditions (i.e. water temperature and photoperiod) of the experimental tanks. The experimental trials started between 11:00 and 14:00 h when lobsters were transferred from isolation to the experimental tank (Fig. S1). Each trial lasted 5 days during which lobsters were exposed to a 12 h:12 h blue LD cycle (lights on and off at 08:00 and 20:00 h, respectively). LD transitions were gradually achieved within 30 min (see above).

The behaviour of lobsters was recorded using a digital camera (UI-1545LE-M, IDS, Obersulm, Germany), with a 1280×1024 pixel resolution and a wide-angular objective of 6.0 mm, F1.4 screw C 1/2 lens (IDS), and a polarized filter. The camera was placed on a tripod 1.5 m directly above the tank. Image acquisition was controlled by the ISPY open source camera security software (http://www.ispyconnect.com) creating a 5-day time-lapse video at a frequency of acquisition of 1 s. All experimental trials were run between June 2013 and July 2014 at an environmental temperature of 13±0.5°C. The tank was provided with a continuous open flow (4 l min^{-1}) of filtered seawater at 13±1°C.

Behavioural analysis
The 5-day time-lapse videos were manually analysed by a trained operator (V.S.) on days 1, 3 and 5, by annotating (i) the winner and loser of each agonistic interaction (Atema and Voigt, 1995) during which both members were out of the burrow, (ii) the number of evictions (times that a lobster evicts or is evicted from a burrow), and (iii) the time spent inside burrows by each lobster. In particular, an agonistic interaction was considered when two lobsters approached frontally within a distance of less than one body length and one of them showed a clear losing behaviour (walking backwards, walking away and accelerating, or tailflipping; for more details, see Atema and Voigt, 1995; Katoh et al., 2008). We considered two consecutive agonistic interactions when the time gap between them was at least 15 s, as previously reported for this species (Katoh et al., 2008). A successful eviction was scored when a lobster (intruder) approached a burrow in which there was another lobster (resident) and the resident left the burrow suddenly or after they had fought for it. Fights to get possession of burrow were usually longer than fighting in open space and characterized by short breaks (e.g. durations between 10 s and 1 min), so we considered two consecutive evictions as two distinct events when the time gap between them was at least 2 min. The core output of this behavioural analysis was a 4×4 matrix for each representative day (1, 3, 5) reporting the number of wins for all possible dyads.

Automated behavioural tracking
In order to evaluate the correlation between hierarchy and locomotor activity rhythms, automated tracking was used to calculate the distance covered by lobsters out of the burrows (García Del Arco et al., 2016; see also Fig. S2). The time-lapse videos were analysed using an automated behavioural tracking routine developed in

'Python' (Python Language Reference, version 2.7; available at www.python.org using OpenCV library). The customized script is available upon request from the corresponding author. The final output of the behavioural tracking was a time series of movement (cm) for each lobster binned at 10 min intervals.

Interaction matrix treatment and statistics
Dominance hierarchies can be characterized by two properties: linearity and steepness (De Vries, 1995; De Vries et al., 2006). Here, we only analysed the steepness of the hierarchy as the group size was too small to apply linearity statistics. Ranks were analysed for days 1, 3 and 5 by taking into account each animal's wins and losses in all interactions, generating an interaction matrix (Wilson, 1975; Huntingford and Turner, 1987; Hardy and Briffa, 2013). We used both ordinal ranks ('1, 2, 3, 4 ranking' and 'α, β, γ, δ ranking' with 1 or α being the most dominant lobster) and cardinal ranks (David's score, with 3 being the highest value of dominant rank) to characterize relative position in the hierarchy. The David's score identifies the overall success of an individual that is determined by weighting each dyadic success measure by the unweighted estimate of the interactant's overall success, so that relative strengths of the other individuals are taken into account. Then the values are normalized to the highest potential David's score that can be obtained by an individual in a group of size N. Thus, defeating a high-ranking animal is weighted heavier than defeating a low-ranking one (De Vries et al., 2006). We then used the values of steepness to characterize the formation of the dominance hierarchy. Steepness values are between 0 (egalitarian hierarchy) and 1 (despotic hierarchy). Moreover, we considered it as a proxy of dominance hierarchy stability, when after a randomization test with 10,000 runs the steepness had a P value <0.05. The P value is used to test whether the observed steepness differs significantly from zero. If it does, the hierarchy is considered to be established. All matrix analysis was performed using the R packages 'steepness' and 'DyaDA' (Leiva et al., 2010; https://cran.r-project.org/web/packages/steepness/index.html).

Statistical approach
We modelled the data using mixed models (Zuur et al., 2009). We focused on the following response variables: (i) steepness values (the value of steepness was eliminated from two groups at day 5 because of the presence of observational zeros in the matrix, when one lobster remained for the whole 24 h in the burrow); (ii) frequency of agonistic interactions (this justified the low absolute values reported in the results); (iii) number of times a lobster succeeded in evicting other lobsters; (iv) number of times a lobster was evicted; (v) the amount of time each lobster spent in burrows; and (vi) locomotor activity out of the burrow. Then we used the following fixed effects: day number (as continuous variable); time (with four levels: day, from 1 h after light dimmed on to 1 h before light dimmed off; dusk, from 1 h before to 1 h after light dimmed off; night, from 1 h after light dimmed off to 1 h before light dimmed on; dawn, from 1 h before to 1 h after light dimmed on); rank of lobsters (normalized David's score or ordinal rank position); and cephalothorax length. Finally, we used day number, groups and individuals as random effects. We implemented one model for each response variable cited above (see Table 1). We modelled steepness, agonistic interactions and burrow occupancy time using linear mixed models (LMM), whereas number of evictions and distance covered out of the burrow were modelled by means of generalized linear mixed models (GLMM) using a Poisson family distribution. Locomotor activity and time spent in burrows were log transformed

Table 1. Summary table with the structure of the full models

Response variable	Fixed effects	Random effects
(i) Steepness	Day number	Day number; groups
(ii) Agonistic interactions	Day number	Day number; groups
(iii) Number of evictions won	CL; day number; rank	Day number; groups; individuals
(iv) Number of evictions suffered	CL; day number; rank	Day number; groups; individuals
(v) Time in burrows (log)	Day number; time; rank	Day number; groups; individuals
(vi) Locomotor activity (log)	Day number; time; rank; rank×time	Day number; groups; individuals

Response variables used in models (i) and (ii) were obtained for each group, whereas models (iii), (iv), (v) and (vi) included response variables calculated for each lobster. CL, cephalothorax length.

as necessary to meet modelling assumptions (normal distribution and heteroscedasticity).

The specific structure of each full model is reported in Table 1. A top-down approach was then used to select the best model (Zuur et al., 2009). The fitting of the models has been evaluated following information criteria statistics based on deviance (Bolker et al., 2009). Additionally, R^2 (marginal and conditional) measures have been used for quantifying the proportion of explained variance by the fixed and random effects in each model (Nakagawa and Schielzeth, 2013). We chose the model that met these criteria in

decreasing order of priority: (1) a higher marginal R^2, as it reflects the explained variance by means of the fixed effects included in the model; (2) a higher conditional R^2, as it reflects the explained variance of the fixed and random effects included in the model; and (3) a lower information criteria statistical value, as it represents a better fit of the model.

This resulted in the following models for the different response variables investigated (Table 2): (i) the simplest model that better described the temporal changes of steepness did not include random effects; (ii) the selected model for describing temporal changes in the frequency of agonistic interactions corresponded to a random intercept model with groups as random effect; (iii) the simplest model selected to describe the number of evictions won was a random-effects (intercepts and slopes) model; (iv) the simplest model describing the number of times lobsters suffered evictions was the same as for eviction success but with a significant effect of size (CL); (v) the simplest model that described the changes of burrow occupancy did not include random-effect parts; (vi) the simplest model that described the changes in locomotor activity was a random intercept model without interaction between rank and time. Wald chi-squared tests were carried out for making decisions concerning fixed effects, while multicomparisons within different marginal means for each level of the same fixed term were calculated with Tukey's *post hoc* test (95% confidence intervals). Finally, the Pearson correlation coefficient between the frequency of agonistic interactions and the locomotor activity out of the burrow was estimated using daily (1, 3 and 5) pooled data according to time

Table 2. Summary table of the selected models

Models	Goodness of fit	Fixed effect	Estimate
(i) Steepness RV~1+Day	AIC: −4.91 BIC: −2.41 R^2: 0.30	Intercept Day number	0.55 (0.049)*** 0.056 (0.020)*
(ii) Agonistic interactions RV~1+day+time+1|groups	AIC: −384.12 BIC: −353.32 $R^2_{GLMM(m)}$: 0.15 $R^2_{GLMM(c)}$: 0.34	Intercept Day number Time (dusk) Time (night) Time (dawn) Time (day)	0.018 (0.0048)*** −0.0019 (0.0008)* [a] 0.031 (0.004) [a] 0.030 (0.004) [b] 0.018 (0.004) [b] 0.014 (0.004)
(iii) Number of evictions won RV~rank+1|groups/individuals	AIC: 272.65 BIC: 292.10 $R^2_{GLMM(m)}$: 0.22 $R^2_{GLMM(c)}$: 0.61	Intercept Rank (ordinal)	1.36 (0.46)** −0.80 (0.16)***
(iv) Number of evictions suffered RV~rank+CL+1|groups/individuals	AIC: 327.35 BIC: 349.23 $R^2_{GLMM(m)}$: 0.43 $R^2_{GLMM(c)}$: 0.73	Intercept Rank (ordinal) CL	15.09 (6.12)* 0.74 (0.17)*** −0.39 (0.14)**
(v) Time in burrows (log) RV~1+day+rank	AIC: 260.42 BIC: 288.04 $R^2_{adjusted}$: 0.10	Intercept Day number Rank (ordinal)	8.74 (0.22)*** 0.09 (0.029)* −0.26 (0.063)***
(vi) Locomotor activity (log) RV~1+day+rank+time+1|groups	AIC: 990.15 BIC: 1043.17 $R^2_{GLMM(m)}$: 0.12 $R^2_{GLMM(c)}$: 0.37	Intercept Day number Rank (cardinal) Time (dusk) Time (night) Time (dawn) Time (day)	4.93 (0.34)*** −0.15 (0.029)*** −0.27 (0.042)*** [a] 5.97 (0.32) [a] 6.07 (0.32) [b] 5.15 (0.32) [b] 5.01 (0.32)

The simplest selected models are reported together with their goodness of fit and fixed effects estimation with errors between parentheses. (i) Selected model for steepness did not include random effects. *R*-squared index was used for the final model. (ii) Selected model for agonistic interactions corresponded to a random intercept model including heterogeneity due to groups. (iii) Selected model for number of evictions won corresponded to a random-effects (intercepts and slopes) model. (iv) Selected model for number of evictions suffered corresponded to a random-effects (intercepts and slopes) model. (v) Selected model for time spent in burrows (log) did not include a random-effect part. Heterogeneity due to groups was included, and adjusted *R*-squared index was used for this final model. (vi) Selected model for locomotor activity (log) corresponded to a random intercept model including heterogeneity due to groups. *P*<0.05; **P*<0.01; ***P*<0.001. Letters (a,b) in brackets indicate the output of Tukey's *post hoc* test (a>b). AIC, Akaike's information criterion; BIC, Bayesian information criterion; $R^2_{GLMM(m)}$ and $R^2_{GLMM(c)}$, marginal and conditional R^2, respectively.

Table 3. The emergence of the dominance hierarchy in each of the seven groups

Group	Day no.	Rank				Normalized David's score				Steepness	P-value
1	1	α	β	γ	δ	2.16	1.76	1.53	0.54	0.51	0.238
	3	β	γ	α	δ	1.87	0.75	2.85	0.52	0.81***	<0.001
	5	β	γ	α	δ	1.76	0.66	2.93	0.64	0.80**	0.002
2	1	α	β	γ	δ	2.05	1.68	1.56	0.71	0.41	0.456
	3	γ	β	α	δ	1.14	1.88	2.17	0.80	0.48*	0.011
	5	γ	β	α	δ	1.37	1.50	2.23	0.90	–	0.003
3	1	α	β	γ	δ	2.78	1.45	1.26	0.51	0.70*	0.021
	3	γ	δ	β	α	1.67	0.61	1.69	2.01	0.42*	0.039
	5	α	δ	β	γ	2.95	0.46	1.57	1.01	0.80**	0.003
4	1	α	β	γ	δ	2.75	1.37	1.34	0.53	0.67*	0.035
	3	α	δ	β	γ	2.90	0.32	2.02	0.75	0.90***	<0.001
	5	α	δ	β	γ	2.20	0.78	1.51	1.50	–	<0.001
5	1	α	β	γ	δ	2.05	1.63	1.38	0.93	0.36	0.575
	3	β	γ	α	δ	1.98	1.17	2.71	0.13	0.86***	<0.001
	5	β	γ	α	δ	2.11	0.88	2.75	0.27	0.86***	<0.001
6	1	α	β	γ	δ	2.21	1.85	1.50	0.45	0.56	0.153
	3	β	α	γ	δ	1.27	2.96	1.08	0.69	0.70*	0.023
	5	γ	α	δ	β	1.14	2.93	0.57	1.35	0.73**	0.013
7	1	α	β	γ	δ	2.28	1.83	1.23	0.65	0.55	0.144
	3	γ	α	β	δ	1.54	2.14	2.00	0.32	0.59*	0.017
	5	β	α	γ	δ	1.96	2.19	1.51	0.33	0.60**	0.007

The position of the lobsters in the hierarchy at days 1, 3 and 5 is expressed with ordinal ranks (rank) and also with cardinal rank (normalized David's score). The steepness of the hierarchy is then reported for each day together with the P value (*P<0.05; **P<0.01; ***P<0.001). The P value is used to test whether the observed steepness differs significantly from the steepness to be expected under the null hypothesis of random win chances for all pairs of individuals.

of the day (day, dusk, night, dawn). All analyses were run using the last version of R (https://www.R-project.org/) with additional packages 'lsmeans' (Lenth, 2016), 'car' (https://CRAN.R-project.org/package=car), 'nlme' (https://CRAN.R-project.org/package=nlme) and 'lme4' (https://CRAN.R-project.org/package=lme4).

RESULTS

The social hierarchies of seven groups of Norway lobsters developed gradually, becoming more stable over the course of 5 days. At the end of day 1, only two groups had an established hierarchy indicated by a steepness (S) significantly different from 0 (group 3, S=0.7, P=0.021; group 4, S=0.67, P=0.035; Table 3, Fig. 1). On days 3 and 5, all groups had fully developed hierarchies (Table 3). Changes in rank (expressed as normalized David's score, Ndv) were less frequent from day 3 to day 5 (seven rank changes) than from day 1 to day 3 (20 rank changes; permutation test with 9.999 replications; P<0.001; Fig. 1). Moreover, hierarchies become

steeper over the experiment. In fact, day number had a significant ($\chi^2_{1,17}$=7.22, P<0.01) effect on steepness. Hierarchy steepness increased linearly (estimated value±s.e., 0.056±0.020) over time (model i in Table 2; Fig. 2A).

Concurrent with the stabilization of the hierarchy, day number had a significant ($\chi^2_{1,84}$=5.23, P<0.05) effect on the frequency of agonistic interactions. Contest frequency decreased linearly (−0.0019±0.0008) throughout the experiment (model ii in Table 2; Fig. 2B). Time of day had a significant effect ($\chi^2_{3,84}$=28.73, P<0.001) on overall agonistic interactions (model ii in Table 2; Fig. 2C); fighting was more frequent at dusk (0.031±0.004) and night (0.030±0.004) than at dawn (0.018±0.004) or during daytime (0.014±0.004) with more marked differences on days 3 and 5 (Fig. 2C).

Rank significantly ($\chi^2_{1,84}$=25.31, P<0.001) affected the chance of winning a fight over a burrow (model iii in Table 2; Fig. 3A). The decrease of one ordinal rank position was associated with a 55% ($e^{-0.80}$) decrease in the number of evictions won. Body size, in
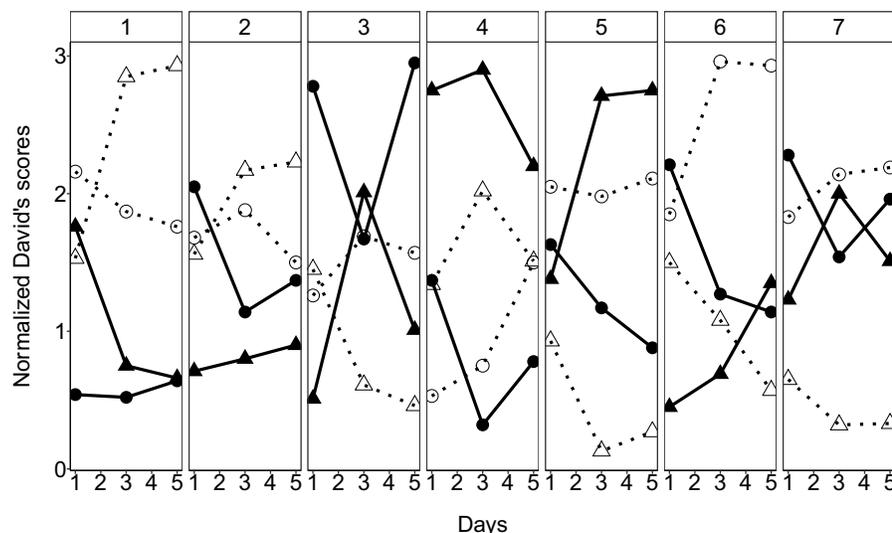

Fig. 1. Temporal changes of the dominance index in the Norway lobster, Nephrops norvegicus. Dominance is expressed with the normalized David's scores for days 1, 3 and 5 for each of the groups analysed (1–7) in this study. In each plot, the four symbols indicate the four tags used to distinguish lobsters. Crossing of the lines indicates a rank reversal between days.
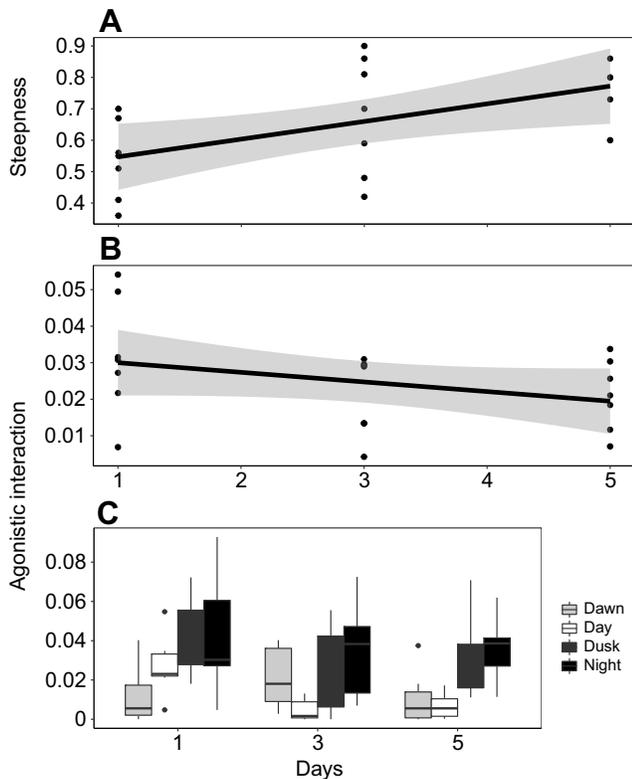
Fig. 2. Emergence of dominance hierarchy and temporal modulation of agonistic interactions. The values of steepness (A) and frequency of agonistic interactions (B) were measured over the 5 days of the experiment (N=7). The black line indicates the linear modelling fit together with the standard error (grey area). (C) Box plots of the distribution of agonistic interactions among the four times of observation (dawn, day, dusk and night) during the 5 days of the experiment (N=7).

Fig. 3. Fighting over burrows. (A,B) Number of evictions won according to the rank of the lobsters (A; 1=α; 2=β; 3=γ; 4=δ) and to the size [B; expressed as cephalothorax length (CL)]. (C,D) Number of evictions suffered according to the rank of the lobsters (C) and to the size (D). The data refer to all the observations (days 1, 3 and 5) for the four lobsters in each group (N=7) for a total of N=84. Size data are presented with a linear modelling fit function (black line) and 95% confidence interval (grey area).

contrast, did not predict the number of evictions won (Fig. 3B). Rank also significantly ($\chi^2_{1,84}$=19.95, P<0.001) affected the chance of getting evicted from a burrow (model iv in Table 2; Fig. 3C). The decrease of one ordinal rank was associated with a 109% ($e^{0.74}$) increase in the number of evictions suffered. In contrast to its lacking influence on evictions won, size of the lobsters significantly ($\chi^2_{1,84}$=7.54, P<0.01) affected the chance of getting evicted (model iv in Table 2; Fig. 3D); larger lobsters suffered fewer evictions.

Day number significantly ($\chi^2_{1,82}$=3.99, P<0.05) affected the time spent in burrows. Burrow occupation increased linearly (0.09±0.029) throughout the experiment (model v in Table 2; Fig. 4A). Rank of the lobsters significantly ($\chi^2_{1,82}$=12.74, P<0.001) affected the occupancy of burrows; a decrease in the ordinal rank of lobsters was accompanied by a decrease of time spent in burrows (Table 2; Fig. 4B).

Day number significantly ($\chi^2_{1,332}$=27.50, P<0.001) affected locomotor activity. Activity decreased linearly (−0.15±0.029) over time (model vi in Table 2; Fig. 5A). Locomotor activity was affected by cardinal ranks (normalized David's score Ndv; $\chi^2_{1,332}$=13.23, P<0.001). It decreased linearly (−0.27±0.042) from low to high ranks (Ndv) (Table 2; Fig. 5B). Time of day also significantly ($\chi^2_{3,332}$=100.12, P<0.001; model vi in Table 2; Fig. 5C) affected locomotor activity. Lobsters were overall more active outside the burrows at night (6.07±0.32) and dusk (5.97±0.32) than at dawn (5.15±0.32) or during daytime (5.01±0.32). There was no difference between ranks in the locomotor activity across the different time periods of the day. The simplest selected models for locomotor
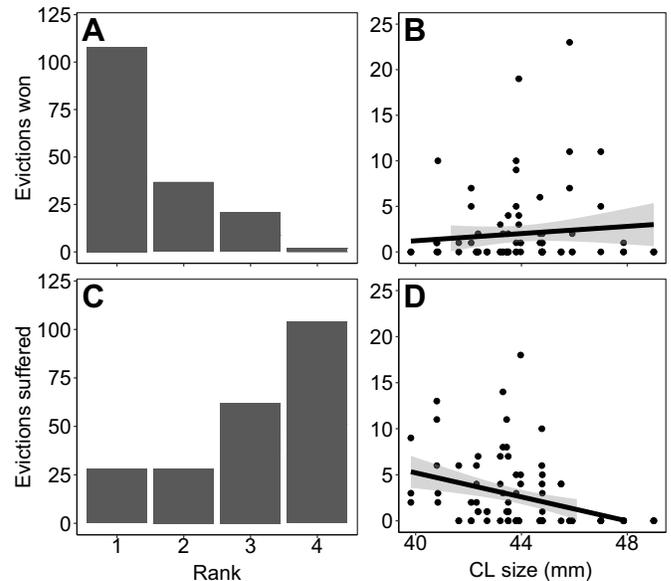
activity did not find a significant interaction effect between time of day and rank (model vi in Table 2). This suggests that a change in dominance rank does not result in a shift in diel activity pattern.
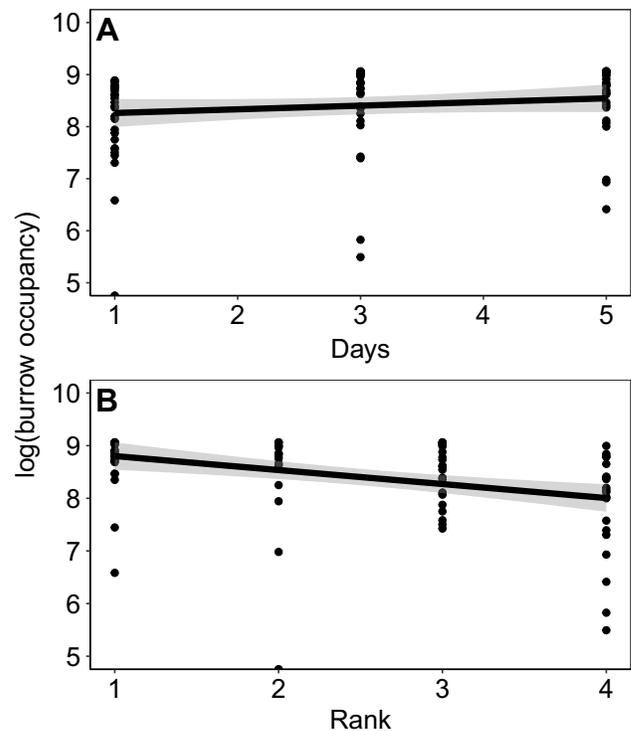

Fig. 4. Emergence of dominance hierarchy and burrow occupancy. Time spent in burrows according to the days of experiment (A) and rank (1=α; 2=β; 3=γ; 4=δ) of the lobsters (B). Data are presented with a linear modelling fit function (black line) and 95% confidence interval (grey area). The data refer to all the observations (days 1, 3 and 5) for the four lobsters in each group (N=84).
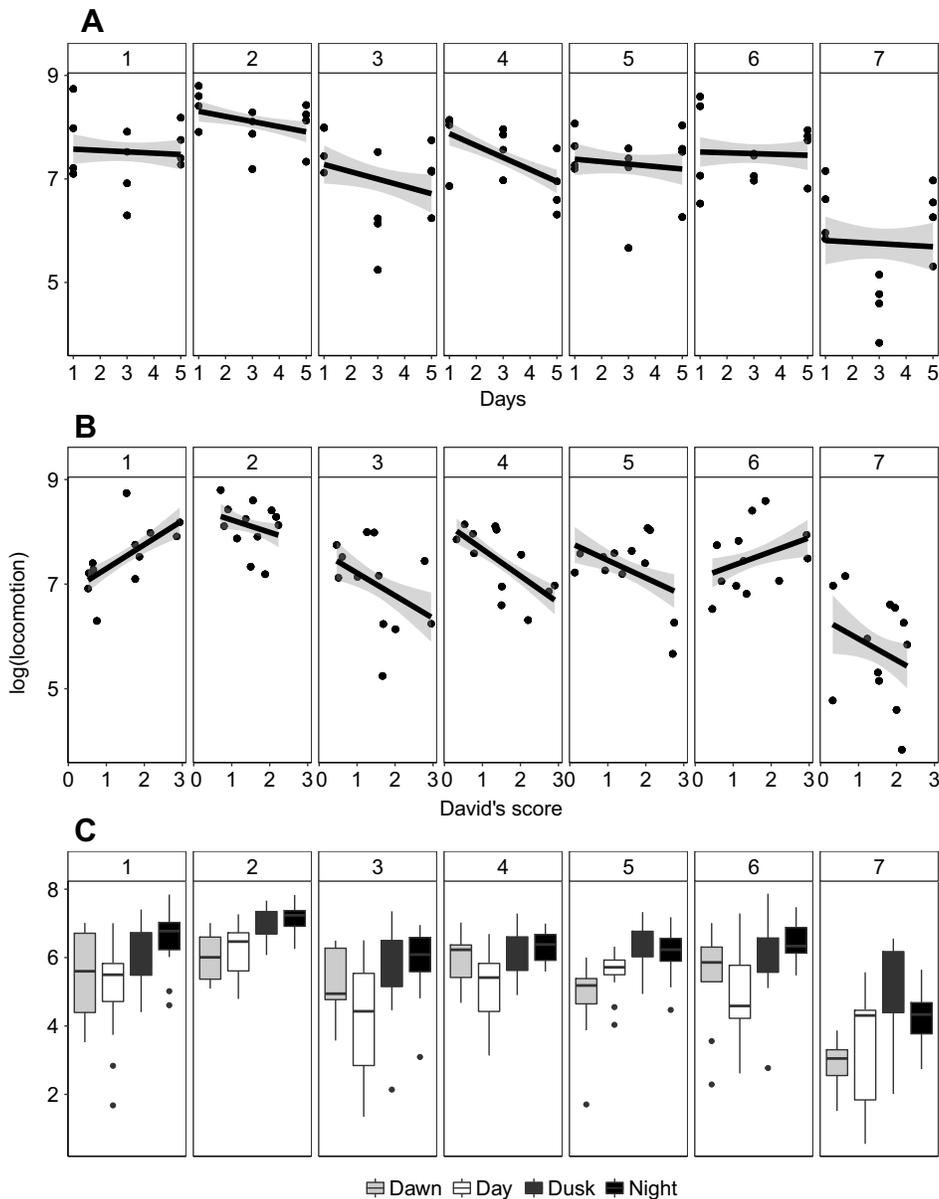
Fig. 5. Emergence of dominance hierarchy, locomotor activity and its temporal modulation. Locomotor activity recorded in the seven different groups of the experiment over the 5 days of the experiment (A) and according to the rank (normalized David's score: a value between 0 and 3 in our study) of the lobster (B). Data are presented with a linear modelling fit function (black line) and 95% confidence interval (grey area). (C) Box plots of the distribution of locomotor activity among the four times of observation (dawn, day, dusk and night) for the seven groups studied.

Finally, we found a significantly positive correlation (r=0.81; N=84; P<0.001) between frequency of agonistic interactions and locomotor activity outside the burrow (see also Fig. S3).

DISCUSSION

Our study characterized for the first time the group dynamic of dominance hierarchy formation in *Nephrops*. Concurrent with a gradual reduction in agonistic interactions, hierarchies markedly increased in steepness over a 5-day period. The emergence of a dominance hierarchy has rank-related consequences for members of the group. Higher ranked animals were more successful in evicting other lobsters and were evicted less frequently than lower ranked animals. Dominant lobsters spent a longer time inside the burrow and covered shorter distances during their movement outside the burrow compared with lower ranked lobsters. In the following sections the hierarchy formation in the Norway lobster is compared with that of other decapod crustaceans, and results are discussed to explain what could be the benefits that higher rank lobsters gain with the use of an important resource, the burrow.

Over the 5-day period the hierarchy steepness increased with a linear trajectory, indicating the tendency of the system to reach stability through polarization of dominance ranks. This is mirrored by a linear decrease in frequency of agonistic interactions, indicating that the more stable the system is, the fewer fights and rank reversals occur. Most studies of decapod crustacean agonistic behaviour use the degree of linearity to characterize stability of the dominance hierarchy (Allee and Douglas, 1945; Hazlett, 1968; Cobb and Tamm, 1975; Sastry and Ehinger, 1980; Vannini and Gherardi, 1981; Goessmann et al., 2000), although in small groups (less than six members) the probability of obtaining significant results just by chance is very high. Currently, there are no available statistical procedures to adjust P-values. Steepness is an appropriate index to characterize the hierarchy formation in small groups of animals (De Vries et al., 2006) and the available R package 'steepness' makes it easy to calculate (https://cran.r-project.org/web/packages/steepness/index.html). In this study, the steepness followed a linear trajectory, but an extension of the number of observations could lead to a more stable point of the hierarchy (i.e. higher values of

steepness). This would allow modelling of the dynamics of hierarchy systems with different trajectories (potential or plateau curves). Finally, we observed some rank reversals that did not prevent the hierarchy from reaching stability. Rank reversals have also been documented in studies on the cichlid fish *Oreochromis mossambicus* (Oliveira and Almada, 1996) and juvenile crayfish *Astacus astacus* (Goessmann et al., 2000), and in both cases, as we observed here, they did not influence the stability of the hierarchy.

There could be important benefits conveyed by a high rank status for *Nephrops* in shelter competition as well as in the dynamics of hierarchy emergence. Shelter is an important resource in decapod crustaceans. Crayfish (*Orconectes rusticus* and *O. virilis*) fights are longer and more intense in the presence of shelters than fights over food resources (Bergman and Moore, 2003). Shelter use also correlates with dominance hierarchy in *O. rusticus* (Fero et al., 2007). Seeking shelter in burrows during the daytime could be an effective strategy for *Nephrops* to avoid diurnal predation at continental margin depths where sunlight is reduced but still a major driver of benthopelagic coupling (Aguzzi et al., 2015). Although megabenthic crustaceans are the major prey of demersal predatory fish, *Nephrops* was found very rarely in the stomachs of these predators (Serrano et al., 2003). The main predator of *Nephrops* throughout much of its range is the Atlantic cod, *Gadus morhua* (Chapman, 1980; Johnson et al., 2013). Cod are active at day, dusk and dawn and show an activity pattern that allows them to consume both diurnal and nocturnal prey (Righton et al., 2001; Reubens et al., 2014). However, even cod consumption represents a relatively low mortality rate in *Nephrops* compared with the effects of commercial fishing (Johnson et al., 2013). This is probably due to the protection that burrows provide against most predators, so higher dominance ranks could confer benefits to lobsters by allowing an increased use of burrows. It must be considered that we provided one burrow per animal and lobsters preferentially occupied only one burrow independently of their ranks (see Fig. S4). Evictions without a consequent occupation of evicted lobsters' burrows may be related to a strategy of dominant lobsters to reduce aggressive interactions with conspecifics by forcing subordinates to emigrate (Hemelrijk, 2000; Fero and Moore, 2008) or by reducing competition for females. For example, in the American lobster (*Homarus americanus*) dominant males occupy shelters large enough to allow cohabitation with a female but regularly patrol the nearby shelters to evict other resident lobsters (Atema and Steinbach, 2007).

Reduced locomotor activity outside the burrow might further reduce susceptibility to predation, providing benefits to higher ranked *Nephrops* over lower ranks. Locomotor activity creates strong visual and mechanosensory stimuli that are perceivable by predatory fish. Moreover, in the presence of water currents, *Nephrops* activity out of the burrow is inhibited and in their quick excursions lobsters are preferentially oriented downstream, a strategy that could increase detection of predatory fish that preferentially move upstream in water flow (Sbragaglia et al., 2015). Finally, decreased activity confers an additional advantage by saving metabolic energy (Kramer and Mclaughlin, 2001). American lobsters subjected to extended exercise on an underwater treadmill showed an immediate and strong increase in heart and ventilation rate, revealing high energy costs of locomotion (Rose et al., 1998). A similar situation occurs also in *Nephrops* where diel locomotor activity rhythms are coupled with cardiac activity and oxygen consumption (Aguzzi and Sardà, 2008).

Agonistic behaviour and locomotor activity were positively correlated, and they both increased at night and dusk compared with day and dawn (see also Fig. S3). The parallel development of both agonistic and non-agonistic behaviours with a clear predictive value of the dominance rank supports the idea of common neural mechanisms for these behaviours (Herberholz et al., 2003). Interestingly, we did not detect clear peaks of activity at dawn, confirming previous results gained from individually tracked *N. norvegicus* (Sbragaglia et al., 2013b). Farca Luna et al. (2009) demonstrated that agonistic behaviour in the marbled crayfish is under the control of the circadian clock; the same could also be true for *N. norvegicus* but we cannot demonstrate it with our experimental design. Furthermore, the interaction between rank and time of the experiment did not have a significant impact on locomotor activity. It means that the rank of lobsters did not induce switches in diel locomotor activity; in fact, all lobsters increase their locomotor activity at night and dusk independent of their ranks. Different reasons may account for this. First, the period of observation could have been too short and extending it could lead to a higher stability of the system and maybe to a switch of daily activity, but in a related (unpublished) study we did not observe any changes in daily activity rhythms even after 10 days. Secondly, we cannot exclude that a more naturalistic setting including food and predator cues (e.g. odour) would have triggered more competition among lobsters and maybe a switch in the daily activity related to rank position. Our results suggest that in *Nephrops*, despite the presence of a temporal niche switching of burrowing activity rhythms driven by light intensity (Chiesa et al., 2010; Hut et al., 2012), agonistic interactions have no effect on such behavioural rhythms.

The benefits for higher ranks related to spending more time inside burrows and covering less distance outside of it in natural populations of Norway lobsters may be less significant today as predation mortalities are declining relative to those caused by commercial fishing (Johnson et al., 2013). However, the understanding of how dominance hierarchy influences burrow-related behaviour of *Nephrops* could be important for fishery management. One of the most popular assessment techniques of *Nephrops* abundances is underwater television surveying, where the presence of intact burrow complexes is used to assess the abundance of Norway lobsters on the basis of the postulated equivalence one burrow/one animal (reviewed by Sardà and Aguzzi, 2012). In this context, the present results are of relevance, indicating that in high-density areas dominant lobsters may evict subordinates and control several burrows at once. However, the results presented here must be interpreted with caution as the dynamic of burrow occupancy in a closed tank could be different from the open situation in the wild. Very little is known about *Nephrops* spatial ecology in the field in relation to size and sex. It is evident that lobsters in the wild are free to change burrows or even build new ones, rendering the field situation less competitive. For example, in the American lobster (*H. americanus*) the frequency and level of agonistic interactions observed in the field are much lower than those found in semi-natural laboratory settings (Stein et al., 1975; Atema et al., 1979; Karnofsky et al., 1989; Karnofsky and Price, 1989; Atema and Voigt, 1995; Atema and Steinbach, 2007). Aggressive interactions form an important part of burrow-related behaviour in Norway lobsters. Dominance hierarchies regulate access to burrows and could confer energetic and survival benefits primarily to the dominant animals. Burrow occupation may bring about additional benefits to high-ranked *Nephrops* males such as increased reproductive success (see study on American lobsters by Atema and Voigt, 1995). In contrast to *H. americanus*, female *Nephrops* do not appear to recognize the social status of males (T.B., unpublished

observation; and Katoh, 2011). Moreover, we do not know how important dominance and burrow occupancy are for female mate choice. Further investigations in semi-natural conditions or direct observations in the wild are necessary to get a better understanding of the behaviour of this ecologically and commercially important species.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: V.S., J.G., J.A., T.B.; Methodology: V.S., D.L., J.G., J.A., T.B.; Software: V.S., J.G.; Validation: V.S., D.L., J.G., T.B.; Formal analysis: V.S., D.L., J.G.; Investigation: V.S., A.A., J.G.; Resources: V.S.; Data curation: V.S., A.A., J.G.; Writing - original draft: V.S., D.L., J.A., T.B.; Writing - review & editing: V.S., D.L., J.A., T.B.; Visualization: V.S.; Supervision: J.A., T.B.; Project administration: J.A.; Funding acquisition: J.A.

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