Agonistic Behaviors of The Anemonefish *Amphiprion ocellaris* Living with Their Host Anemones

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Abstract. Agonistic behaviours, defined as an individual's aggressive behavior towards a conspecific, facilitate a social ranking throughout the animal kingdom, particularly within anemonefish group. In this study, we investigated the agonistic behaviors of the specialist anemonefish *Amphiprion ocellaris* living with different host anemones. Juvenile fish were exposed to their natural and unnatural host anemones in laboratory, and their agonistic behaviors were assessed through the occurrence of bites, the occurrence of chases, and the time spent in chilling behavior. The fish exhibited a higher frequency of bites and spent more time in chilling behavior ($p<0.01$) when residing within their natural anemone host, *Stichodactyla gigantea*. In contrast, when living within *S. haddoni,* where survival was less assured, fish exhibited more chases ($p<0.05$), which were less likely to injure conspecifics. The fish also engaged more in biting behavior ($p<0.001$) once establishing symbiosis within the natural host *S. gigantea*. These results suggest that biting is important to the establishment of the social hierarchy, while the chasing behavior is crucial for maintaining the hierarchy across time, which is important for reproduction potential. These findings imply that by adjusting their agonistic behavior, coral reef fish could make a trade-off between survival and reproduction in unfavorable environmental conditions.

1. Introduction

Agonistic behavior can be defined as an individual's aggressive behavior towards a conspecific. This behavior can manifest in various ways depending on the species and occurs when conspecifics compete for the same resources, which is common in social groups. Reef fishes across the Pacific and Atlantic Oceans exhibit recurring patterns of agonistic behaviors. These local conflicts typically occur between species that are closely related and have similar functions [1]. Social rank plays a crucial role in modulating agonistic behavior for individuals living in a hierarchical dominance system. For instance, aggression between different social ranks helps maintain the hierarchy in the fairy basslet, *Gramma loreto* (Grammatidae), ensuring that the highest-ranked fish have privileged feeding positions [2]. Furthermore, the environment can influence dominance by restricting access to resources

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such as food, space, and mates. Therefore, it is vital for these individuals to carefully select their habitat before establishing themselves.

Anemonefish-anemone symbiosis is a classic example of symbiotic interaction in tropical coral reefs [3]. Twenty-eight species of anemonefish belong to *Amphiprion* and *Premnas* genus, living within the stinging tentacles of ten species of anemonefish-hosting anemones. In this mutualistic relationship, both species benefit from each other. It has been proven that the number of anemonefish engaged in the interaction is positively correlated with the increase in the host's surface area. The presence of anemonefish leads to more frequent asexual reproduction and enhanced anemone survivorship. On the other hand, association with anemones is a highly advantageous strategy for resident anemonefish. Anemonefish benefit from protection against potential predators and food from the remains of the anemone's prey. By maintaining this association, anemonefish can have a higher lifespan, which is twice as long as other pomacentrid species and approximately six times longer than other marine species of comparable size [4].

Anemonefish live in groups with strict size-based hierarchies, in which the largest individual is the dominant one and the only female. If the female dies, the second largest individual will become a female and will in turn dominate the group [5]. To maintain her social rank, the female frequently shows agonistic behaviors toward other members of the group, while the subordinate individuals receive charges and show submissive responses [6,7]. Within each group, numerous aggressive interactions appear in order to uphold size discrepancies among individuals. These interactions are important to etablish social hierarchy and sexual differentiation [6,7]. Both male and female members exhibit more aggressive behavior compared to ambisexual individuals. Their behaviors are primarily aimed at intruders of the same sexual orientation rather than those of the opposite sex. Notably, female residents demonstrate notably aggressive conduct towards female intruders, while male residents tend to engage in side-by-side swimming more frequently with male intruders rather than with female or ambisexual intruders [8]. Many studies have shown the crucial aspect of calls in maintaining hierarchy in anemonefish [6,9]. In fact, when the dominant expresses agonistic behaviors such as chasing or biting, they also make dominant vocalization, whereas the subordinates make submissive vocalization at the same time [6,9]. Both species of anemonefish, *A. perideraion* and *A. percula*, showed that behavioral patterns depend on rank-specific dynamics, with higher-ranked individuals exhibiting both aggression and helping behaviors more often, while lower-ranked individuals only indicated help. [10]. Yllan [11] also provide evidence that behavior between social fish ranks of anemonefish *A. clarkii* are plastic and highly influenced by social context, which seems to be a primary factor influencing cooperation and intra-group aggressive encounters within this species. During the process of migrating among host anemones, juvenile *A. clarkii* individuals exhibiting shy-submissive behavior are more likely to be accepted by larger individuals, This behavior helps to avoid the risk of being attacked and bitten, thereby enhancing the individual's chances of survival. In contrast, bold-aggressive individuals tend to be rejected and forced to relocate to another host anemone due to their reluctance to accept a subordinate status [12].

In the field, we observed the associations between anemonefish with certain host anemones, for example, the anemonefish *A. ocellaris* is recognized as "a specialist", which is mainly found in or near three species of anemones (native or natural host species): *Heteractis magnifica*, *Stichodactyla gigantea*, and *Stichodactyla mertensii*. Under unfarvorite condition, this species can acclimatize to living with anemones they do not associate in the field (unnatural host); however, it would offer less fitness in terms of growth than those with the natural host [13]. Unfortunately, little is known about agonistic behaviors of anemonefish when they live with different host anemones, and whether these agonistic behaviors can help to explain the less comfort of unatural host anemone toward the anemonefish residents. Our study will therefore compare the aggressive behaviors, including chasing, biting, and chilling behaviors of anemonefish as a function of their host changing over time. Specifically, the variables recorded in this study were based on our expectation to understand the potential influence of the host anemone species on the agonistic behaviors of *A. ocellaris*. These findings will help to achive a better understanding of the strategies that anemonefish use to establish and maintain social hiarachies under unfavorable environmental conditions, in which they might be forced to switch to unnatural hosts.

2. Materials and methods

2.1 Anemonefish and sea anemone rearing

2.1.1 Anemonefish rearing

For this study, the false anemonefish *A. ocellaris* was collected at Nha Trang Bay, Khanh Hoa, following local and national guidelines. A seawater recirculation system was developed at the wetlab of Nha Trang University, Vietnam, which allowed the rearing of breeding pairs of *A. ocellaris* in separate 70 L glass tanks. Water was constantly recycled and filtered using ceramic filter. A terracotta pot was put in breeding tanks so the fish could lay eggs on a solid and cleanable substrate. No anemones were present in these breeding tanks [13]. Environmental parameters were monitored to ensure that the rearing conditions were as close as possible to the natural environment. Breeding pairs were fed with a frozen mixture of shrimp, oysters, liver, and commercial fish pellets, to which vitamin supplements were added. After 6 months in these conditions, brood pairs started to breed. The egg incubation lasted for 6-8 days, depending on the temperature of the tank water, and was taken care of by their parents. On expected day of hatching, eggs were relocated to the nursery tank prepared two hours prior to sunset. Larvae were fed by rotifers *Brachionus* sp. from 4 days post hatching (dph), and *Artemia* sp. *nauplii* was gradually introduced until larvae were only fed with *Artemia* (5 *nauplii* per mL) by 10 dph. At 30 dph, juvenile fish were transferred to a 160-L tank without anemones, where they were fed with *Artemia* twice a day. These individuals were the post-settlement naive juveniles used in the behavior experiment.

2.1.2 Anemone rearing

Host species for the experiment were chosen based on the host choice specifications of anemonefish *A. ocellaris,* the availability of the hosts in Nha Trang, and their potential for maintenining in an aquarium. Six anemone species were provided by local tropical fish shops, including *Stichodactyla gigantea* as a natural host for *A. ocellaris*, and five non-natural hosts: *Stichodactyla haddoni*, *Entacmaea quadricolor*, *Macrodactyla doreensis*, *Heteratis crispa,* and *Heteractis malu* [14]. Anemones were reared in 200 L glass aquaria fitted with a recycling system, in which the environmental parameters were strictly monitored. Natural rocks were placed in the aquaria for the anemones to attach to. The anemones were fed with small pieces of shrimp once a week. Three months prior to any experimental work, anemones of the same color and size was placed with their natural rocks in the same position in each experimental tank. In this way, any influence of spatial cues and color variations were avoided [13].

2.2 Experimental design

Post-settlement naive juveniles of 60 dph were introduced into experimental tanks. The experimental design consisted of 3 x 200 L experimental tanks containing the six host anemone species. The experiment was therefore performed in triplicate. The environmental conditions were kept the same in the rearing tanks. The frequency of feeding was slowed down to once a day to minimize the deterioration of the water quality for the anemones. In the field, *A. ocellaris* live in a group consisting of monogamous breeding pair and up to eight non-breeding subordinates [15]. Therefore, a selection of individuals was made to form groups of 8 individuals composed of two large fish, two small fish and four medium-sized fish. This selection allowed an initial hierarchy to be established once the experiment began. The experiment was divided into three intervals in which the availability of host anemones was different. During the initial period (60–69 days post-hatching), no alterations were made to the conditions. Subsequently, at the onset of the second phase (69–78 days post-hatching), the natural host species (*S. gigantea*) was removed from the experimental tanks. As the third stage commenced (78–92 days post-hatching), the most popular of the five unnatural host species (*S. haddoni*) was removed from the experimental tank. In positive control tanks, no anemones were removed during the whole time of the experiment. Negative control tanks contained anemonefish that living with rubber anemones [13].

2.3 Data collection

To determine if the behavior of the post-settlement juvenile *A. ocellaris* changes when the fish live with different host anemones, the behavior of the fish was recorded in the experimental group. Fish established symbiosis with anemones once they were introduced to anemones; however, our behavior recording began three days after the establishment of symbiosis to ensure regular behavior for each interval. A GoPro Hero 5 Black (www.gopro.com) was positioned above experimental tanks. Individuals were then filmed every two days at four different times of the day, including morning (8:00-9:00), noon (11:00-15:00), afternoon (16:00-17:00) and night (21:00-22:00) until the end of the interval. Finally, there were three days of recording per interval. Only one video per time of day was considered for the analysis due to time constraints. Depending on the availability of recordings, 3 minutes of each video were taken into account. Unfortunately, data analysis could not be completed on all videos. During the second interval of the first replicate, fish chose *H. crispa* over *S. haddoni*, which was therefore removed from our analysis. During the third interval, no fish was associated with any host anemone, despite the presence of the four unnatural anemones: *E. quadricolor*, *M. doreensis*, *H. crispa*, and *H. malu*. In addition, at certain time of the day, technical problems occur that constrain the data analysis, such as the reflection of light on the water surface, the absence of some fish in the camera frame, or the fact that the fish sometimes remain hidden under the host anemone. As the result, our data table contains not available values (NA). It is also possible that some individuals died or disappeared before the end of the experiment. Some of them were taken for an additional study on the protein composition of the skin mucus. For negative control group, where fish were placed with artificial rubber anemones, individuals exhibited an initial attraction to the color of these anemones. However, their stay within the rubber anemones was brief, as they subsequently preferred to position themselves near outlet-water pipes or seek refuge behind rocks. In the PC groups, fish rapidly established a connection with their natural host, *S. gigantea,* and did not transition to another host anemone for the entirety of the experiment [13]. Consequently, we did not record any agonistic behaviors exhibited by fish in these groups. In total, we used data from 29 recording videos across 3 different experimental tanks. Each variable had 195 data points available.

2.4 Variables Measured

Agonistic behavior is any social behavior related to fighting. The term has broader meaning than aggressive behavior because it includes threats, displays, retreats, placation, and conciliation. Chen & Hsieh, 2017 considered aggressive interactions including bites and chase. Therefore, in this study we measured the number of bites, chases between fish as the variables of agrresive behavours. A bite was considered to be a contact between the fish's mouth and the body of a conspecific, causing the conspecific to move away. Chasing behavior consisted of accelerating a distance of at least one body length towards a conspecific [8]. A bite might be accompanied by chase behavior, but this is not always the case. A new variable, which was a time spent in the chilling behavior of the fish toward their host anemone, was determined in this study to measure the acclimation levels of individuals within the host anemone. Chilling behavior was taken into account when fish did not actively swim in contact with the tentacles of the host anemone. Instead, the fish was completely surrounded or only rubbing its belly against the tentacles. This variable describes how close the anemonefish are to their host anemone, reflecting fish refuge quality. The behavioral variables were analyzed using Behavioral Observation Research Interactive Software (BORIS), which allows the recording of a wide range of behavioral data from several subjects observed during the same observation period [16].

2.5 Data analysis

All analyses and simulations were performed with the program R, version 4.1.2 (R Development Core Team 2020). The raw data obtained from the experiments were tested for normality using the Shapiro-Wilk test prior to data analysis. Since the data were obtained by counting behaviors, a generalized mixed-effects model with poisson distribution that applied for non-parameter variables was performed to test the effect of anemone host species (interval) on the occurrence of bites and chaseses and chilling behaviors on fish, taking into account the effects of time of day, and time of interval. In this model, treatment tank (replicate) as a random factor and host species time of interval, and time of day was used as fixed factor. To fit the mixed-effects model, the package lme4 and the function *lme()* were used [17], which is appropriate for analyzing generalized linear mixed-effects models with non-normal distributions (such as Poisson) for counting data. Multiple comparisons by multcomp (*glht*) was applied to perform post hoc if an overall significant differrence was detected. We used generalized mixed-effects model to test for differences the influence of the host species time interval and time of the day on the agnostic behavior. Replicates were used as a random factor; the host anemone species, time of interval, and time of day were used as fixed factors.

2.6 Ethics statements

This study followed the National Regulations for Ethical Guidelines for the Use of Animals in Research in Vietnam, anemonefish is not listed in two groups: IB (endangered and critically endangered) and IIB (threatened and rare species) (Decree32/, 2006/ND-CP, 2006). Therefore, this study does not require any permit or ethical approval. The authors also have Federation of European Laboratory Animal Science Associations (FELASA) Category C accreditation to implement the best practice of using animals in research.

3.Results and Discussion

3.1 Influence of host anemone species on the agonistic behaviors of the false anemonefish *Amphiprion ocellaris*

The naïve post-settlement *A. ocellaris* behaved differently when they lived with two anemone host species. The number of bites was significantly higher when fish lived within the natural host *S. gigantea* (Fig. 1a and GLMM for poisson data: $p<0.01$; File S1.1), while the number of chases increased significantly when fish lived within the unnatural host *S. haddoni* (Fig. 1b, GLMM for poisson data: $p<0.05$; File S1.2). For the chilling behavior, individuals who lived within *S. gigantea* anemone showed a significantly higher mean time spent in this behavior than individuals who lived within *S. haddoni* anemone (Fig. 1c;

p<0.001; File S1.3). These results indicate that fish showed different agonistic behaviors depending on the host anemone species with which they were associated.

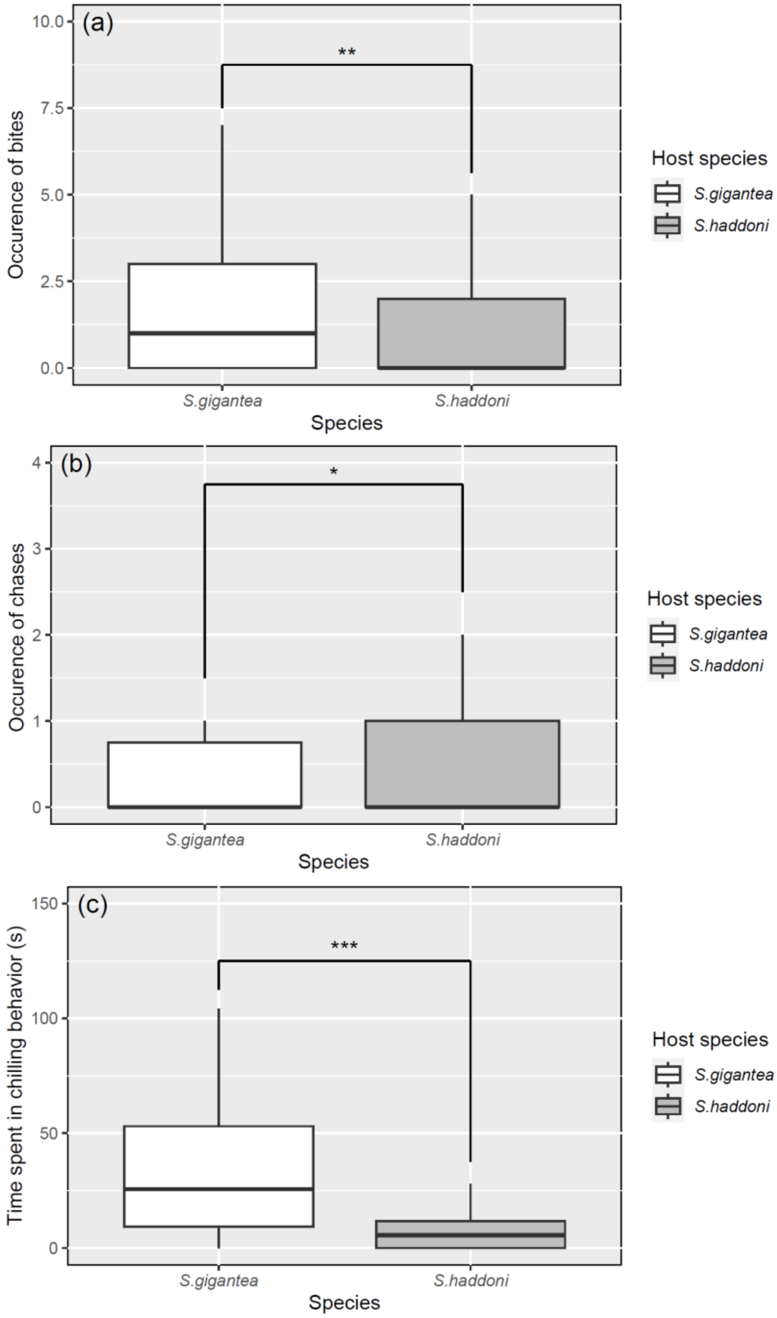

Fig.1. Comparisons of agonistic behaviors of post settlement *Amphiprion ocellaris* living across the different host anemones species available. (a) Occurrence of bites, (b) occurrence of chase and (c) Time spent in chilling behavior.

Host species seem to have an influence on the agonistic behavior of the post - settlement *A. ocellaris*. Indeed, the number of bites was higher when fish lived within the natural host

S. gigantea. In contrast, the number of chases was higher when fish lived within the unnatural host anemone *S. haddoni*. Such different behaviors of fish living with the two species of host anemones could be explained by the anatomy of the host species, which would allow for more or less good visibility of the fish. *S. gigantea* is an anemone with long tentacles, making visibility between the fish more difficult than with *S. haddoni*, which has shorter tentacles. At the end of the day and during the night, *S. haddoni* folded up by itself and formed folds, representing the only possible hiding place for the anemonefish (*A. Lempereu*r pers. obs). However, during the day, *S. haddoni* was wide open, and the visibility between the fish was therefore much greater than with *S. gigantea*. Thus, when the fish lived with *S. gigantea*, the chances of encountering conspecifics were at a much shorter distance than with *S. haddoni* (*A. Lempereur* pers. obs). This difference in distance during meetings could explain why individuals express more bites when they live with *S. gigantea* and more chases when they live with *S. haddoni*.

The time spent in chilling behavior was much greater when fish lived with *S. gigantea* - the natural host anemone, than those lived with *S. haddoni* - the unnatural host anemone (Fig.1c). It was therefore assumed that the anemonefish *A. ocellaris* was more comfortable in contact with the tentacles of the anemone *S. gigantea* than with those of *S. haddoni*. This assumption is consistent with a previous host choice study in which *A. ocellaris* anemonefish chose their natural host *S. gigantea* over *S. haddoni,* as that the latter was more toxic than the natural host. This study also indicated that *S. gigantea* offered better fitness in terms of growth than *S. haddoni* [13].

It's a known fact that a trade off between survival and reproduction shapes an individual's life. Individuals have to breed to ensure the survival of the species, but this is only possible if the individuals themselves survive until the breeding events. Thus, anemonefish *A. ocellaris* living in an anemone that provides better fitness would be more likely to cause injuries to their conspecifics to gain faster access to reproduction because survival is already more or less guaranteed. In contrast, individuals living in an anemone that does not provide such fitness would be less likely to attack their conspecifics and more likely to ensure their own survival. Among the two agonistic behaviors observed, biting is much more likely to injure a conspecific than chasing. The latter would have more of an intimidating role, it may be followed by a bite, but the chase itself does not cause physical damage to conspecifics. It has indeed been observed that conspecifics that have been bitten move away from the aggressor more often than when they are chased. Moreover, when an individual was bitten, the latter would sometimes riposte and bite the aggressor in turn (*A. Lempereur* pers. obs). Thus, it was assumed that a bite would be more effective in judging the strength of the conspecific and play a crucial role in the establishment of the hierarchy by ensuring dominance. On the other hand, chase would also be useful in maintaining this hierarchy, even in conditions where survival takes priority over reproduction.

3.2 Influence of time interval and time of day on the agonistic behaviors of the false anemonefish *Amphiprion ocellaris*

3.2.1 Biting

For the occurrence of bites, there was not a significant interaction effect between host species and times of day ($p=0.14$, File S1.4), but a significant effect of time of day was found (Multifactorial GLM for poisson distribution: $p<0.001$, File S1.4). A post-hoc comparison using the T test with Bonferroni correction indicated that the occurrence of bites was significantly different between noon and afternoon and between night and noon (Fig. 2a). However, the number of bites did not differ significantly between the morning and afternoon. In contrast, there was a significant interaction between host species and time of interval on the occurrence of bites, indicating differential effects of host species depending on the time of interval (M GLM for poisson distribution: $p<0.05$; File S1.5). Post-hoc comparison using the T test with Bonferroni correction indicated that the difference between host species was significant on day 1 of the interval (Fig. 2b, $p<0.001$; File S1.6). However, the occurrence of bites didn't differ between individuals living with *S. gigantea* and *S. haddoni* during days 3 and 5 of the interval.

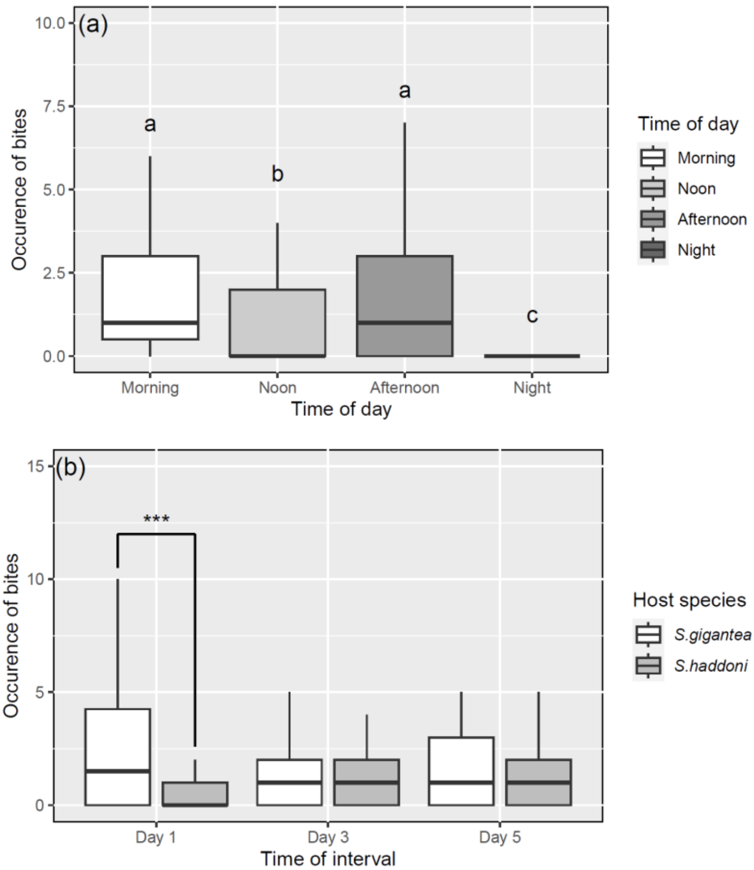

Fig. 2. Comparisons of occurrence of bites of post settlement *Amphiprion ocellaris* living with the different host anemones (a) across different times of a day, (b) between the host anemone species across different time intervals.

A significantly higher occurrence of bites during the day than during the night likely linked to the typical behavior of diurnal reef fish. The trade-off between food consumption and the risk of predation compels diurnal reef fish to engage in feeding activities during daylight while seeking shelter at night to avoid potential predators [18]. Moreover, the occurrence of bites was significantly weaker during noon than in the morning or afternoon. This result is consistent with other coral reef fish behaviors, which assume that these fish actively feed during the middle of the day [18]. Thus, the biting behavior might be present in the trade-off between survival and reproduction. When individuals spend time to feed and favor their survival, they spend less time to bite and thus put aside access to reproduction.

The number of bites was higher when the fish lived within *S. gigantea* than they did within *S. haddoni*. However, it appears that this difference between the two host species was significant only during day 1 of the experimental interval. Our recording began three days after the encounter of fish with anemones, waiting for the establishment of symbiosis before the measurements. Therefore, the host species seems to influence the establishment of symbiosis and thus indirectly influence the establishment of hierarchy made through biting behaviors.

3.2.2 Chasing

For the occurrence of chases, fish performed fewer chases at noon or night than those in morning or afternoon (Fig3.a). There was a significant effect of the time of the day on the occurrence of chases (GLMM for poisson distribution: $p<0.05$, File S1.7). Post-hoc comparison using the T test with Bonferroni correction indicated that there were fewer chases at noon or night than in the morning or afternoon. However, the number of chases did not significantly differ between noon and night. We also didn't find a significant interaction effect between host species neither (Fig.3.b) with time of interval (GLMM for poisson distribution: $p=0.14$, File S1.8) nor with time of day ($p=0.94$).

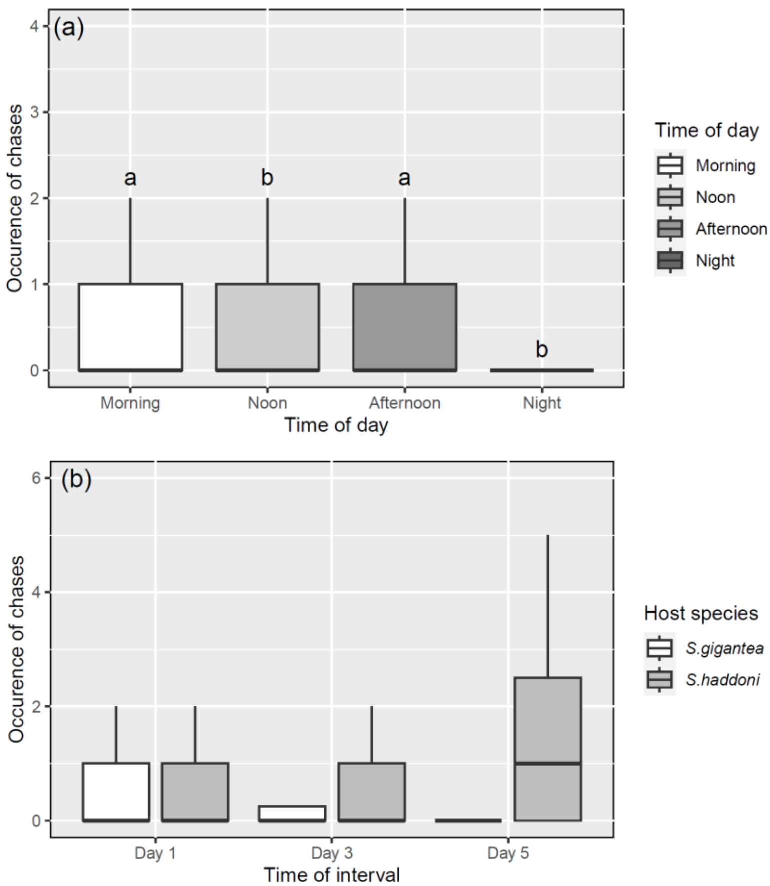

Fig.3. Comparison of occurrences of chases of post settlement *Amphiprion ocellaris* living with the different host anemones (a) across the different times of day and (b) between host species across the different time of interval.

Like the occurrence of bites, the time of the day influences the occurrence of chases. We observed the same pattern with the occurrence of bites during the day, where agonistic behavior was less important when fish were actively feeding. However, the occurrence of chases was observed to not differ between noon and night, while the occurrence of bites was significantly smaller during the night than at any other time of the day. Therefore, the risk of being chased is likely more frequent than the risk of being bitten in group of *A. ocellaris*.

The establishment of hierarchy was not permanent and must be maintained throughout time [8]. When we compare agonistic behaviors between host species across different time intervals, we didn't observe differences, which implies that the chasing and biting behaviors observed between the two host anemones depend more on the anatomy of the anemone than the time spent within it. To resume, the fact that the occurrence of chases was more frequent in the group of *A. ocellaris* than the occurrence of bites and that she seems to depend on the anemone's anatomy could support the assumption made before that the chase wasn't useful to establish the hierarchy but to maintain it across time.

3.2.3 Chilling

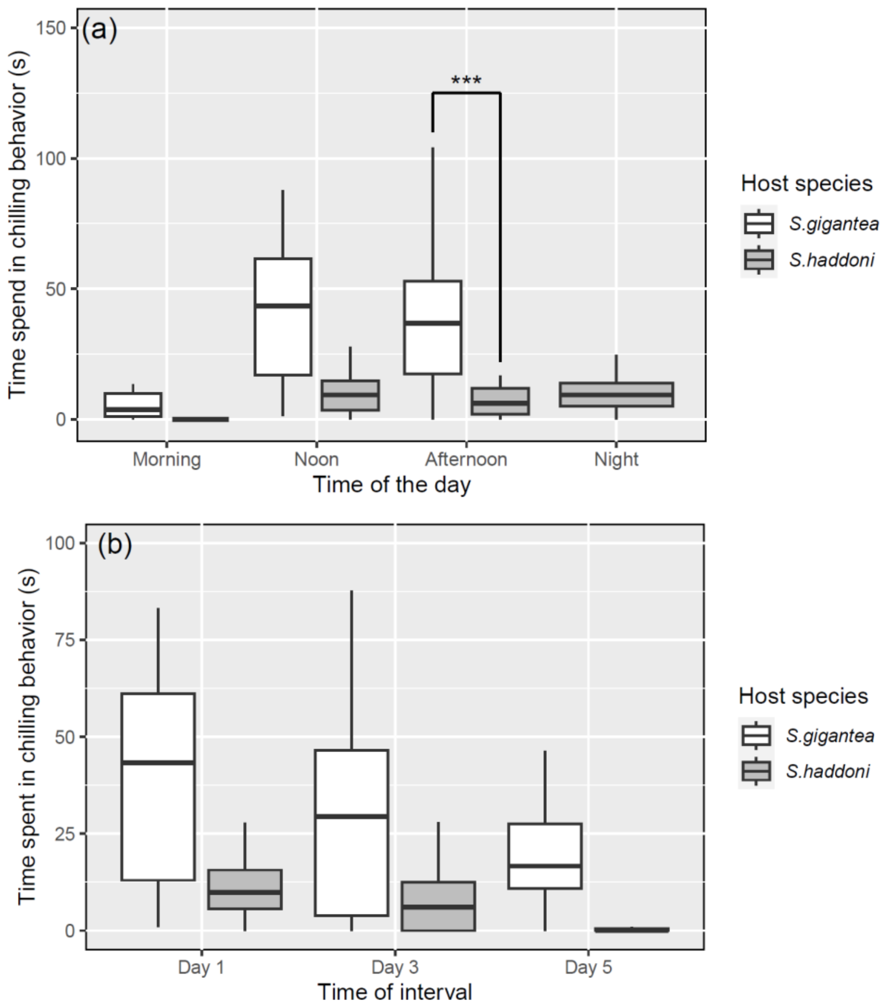

Fig.4. Comparison of the mean time spent in chilling behavior by individuals between the host anemone species across the different time of day. Medians are given by the solid line and boxes indicate 25th and 75th percentiles.

There was not a significant interaction between the host species and time of interval on the mean time spent in chilling behavior (Multifactorial LMM: *p=0.94;* File S1.9). The simple effect of the time of interval was also not significant (*p=0.46,* File S1.9). However, there was a significant interaction effect between host species and time of day, indicating differential effects of host species depending on the time of day (Multifactorial LMM: *p<0.001*, File S1.10). Post-hoc comparison using the T test with Bonferroni correction indicated that the time spent in chilling behavior significantly differed across the two host species during afternoon (Fig.4, *p<0.001*, File S1.11). We noticed that the comparison of chilling behavior across host anemone species could not be performed for the night because there were no values available for these chilling behaviors when individuals lived with *S. gigantea* during this time of day.

Time spent in chilling behavior was clearly higher when individuals lived within *S. gigantea*. This difference in chilling behavior between host species depends on the time of day. In fact, individuals spent more time in chilling behavior when they lived within *S. gigantea* and during the afternoon. It was at this time of the day (in the morning) that anemonefishes were the most engaged in agonistic behaviors. Being less toxic than *S. haddoni*, *S. gigantea* should allow more extended contact with their tentacles. It should represent a more comfortable situation for fishes and allow the establishment of a higher number of agonistic behaviors and therefore, a more efficient global social judgment. We also observed a non-significant effect of host species depending on the time of intervals. This result is consistent with a previous study proving that quantity and quality of anemones' toxins were still highly conserved even under uncomfortable conditions [19]. It should be a reason why the time spent within anemones did not influence the time spent in chilling behavior by individuals.

To sum up, biting behavior was more intensively expressed by individuals who lived within *S. gigantea* than within *S. haddoni* following the establishment of symbiosis, supporting a faster establishment of fish social hierarchy within the natural host anemone species. In fact, if symbiose is easier to establish with *S. gigantea*, individuals could repoduce more quickly (through the establishmen t of a social hierarchy) due to guaranteed survival. It also explains the differences in the occurrence of bites between host species during the begining of the experimental intervals. Once established, hierarchy appeared to be maintained over time, by chasing behaviors. Individuals didn't need to prove their strength but were reminded of the hierarchy established without injuries. Individuals who lived in a less comfortable environment, such as *S. haddoni*, seemed to produce fewer behaviors likely to injure conspecifics and thus should have had a slower establishment of hierarchy. It would therefore seem that the efficiency of establishing a hierarchy through aggressive behavior differs according to the host anemone species with which the anemonefishes interact.

4. Conclusion

Our study has shown that adjusting levels of agonistic behaviors is the strategy of juvenile *A. ocellaris* used to establish and maintain social hiarachies under unfavorable environmental conditions. A context that allows better fitness likely leads to a higher occurrence of bites, more engagement in the chilling behavior, while the occurrence of chases increases when fish live with unfarvorable host species. The occurrence of chases seems more important in the context of individuals being threatened. The host anemone species appears to shape the agonistic behavior of *A. ocellaris* with which they interact, regardless to fitness, anatomy, or physiology of the host. These findings on agonistic behaviors warrant further investigation using broader comparative approaches across a wider range of coral reef fish species that utilize sociality research in the context of climate change, which could threaten the preferred host species and leave for only unfavorable ones.

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Antoine Lempereur selected the recordings, generated and analysed the data, and drafted the manuscript. H-T. T.N. performed the experiment, videotapings, helped to analyze the data and edited the manuscript.

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