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Human activity selectively affects a dynamic defensive mutualism

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Human presence and urbanization alter many species' vulnerability and perceived risk, but little research has investigated how anthropogenic impacts affect behaviour in dynamic defensive mutualisms. As human activities continue to expand in marine communities, it is important to understand how they may affect risk assessment in behaviourally dependent symbionts. Shrimpgobies (*Ctenogobiops* spp.) and snapping shrimp (*Alpheus* spp.) in Mo'orea, French Polynesia participate in an obligate, symbiotic relationship in areas where humans recreate. We quantified hiding time, flight initiation distance and time allocated to different behaviours to first describe this defensive mutualism, then determined whether human activity directly impacted it. We found that goby behaviour significantly explained variation in shrimp behaviour. Specifically, shrimp varied in how long they remained in their burrow, how long they remained in their burrow after their goby partner(s) emerged, the rate at which they excavated their burrows and the time spent outside their burrows as a function of goby behaviour. Our findings suggest this dynamic mutualism was selectively affected by humans. Human activity, measured by both presence and abundance, explained some variation in multiple goby behaviours that directly influence variation in shrimp behaviour.

Symbiotic mutualistic relationships are reciprocally beneficial interactions that may involve two or more species (Leigh, 2010). Mutualism has evolved many times because it enhances the inclusive fitness of all members of the partnership (Leigh, 2010). One type of mutualism is defensive, in which one organism protects the other from threats (Belt, 1874; Clay, 1988). Most commonly studied in ants and plants, where ants provide protection from herbivory while the plant provides nest space and nutrients for the ant colony (Boucher, 1985); however, defensive mutualisms are not restricted solely to plant–animal interactions. In terrestrial systems, ants protect aphids (Hemiptera) from predation in exchange for honeydew (Nelson & Mooney, 2022; Way, 1963). In aquatic systems, anemonefish (Amphiprioninae spp.) provide nutrients (Porat & Chadwick-Furman, 2004) and protection to sea anemones (Actiniaria spp.) from predatory butterflyfish (Chaetodontidae spp.), while sea anemones provide anemonefish protection from predation and a place to reproduce (Fautin et al., 1989). Additional research on this marine system has previously shown that group size and behaviour of commensal damselfish (*Dascyllus* spp.) impacts hiding time of their magnificent sea anemone (*Heteractis* spp.) partners (Lim et al., 2016).

In some mutualisms, protection from predation is one-sided. Two textbook examples include ant–aphid mutualisms (Depa et al., 2020) and the mutualism observed between Gobiidae and Alpheidae (Karplus et al., 1972; Karplus & Tuvia, 1979; Longley & Hildebrand, 1941; Yanagisawa, 1984). In this obligate relationship, shrimp dig burrows (Yanagisawa, 1984) in which gobies need to safely reside and reproduce (Magnus, 1967). In exchange, shrimp receive nutrients via goby excrement (Kohda et al., 2016) and ectoparasites (Jaafar et al., 2014) and receive predator warning cues via goby tail flicks (Burns et al., 2019; Karplus, 1979; Preston, 1978). Because shrimp behaviour is closely associated with the behaviour of its goby partner (Burns et al., 2019), this relationship can be viewed as 'dynamic mutualism', in which the behaviour of one partner is influenced directly by the other. While this system has been the focus of many studies involving their unique coevolution (Lyons, 2012; Thacker et al., 2011; Thompson et al., 2005) and communication methods (Preston, 1978), factors that influence their linked behavioural decisions are understudied.

To understand the dynamics of this mutualism we must first understand goby antipredator behaviour. All prey must assess predation risk; underestimating predation risk can lead to death

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and the loss of future potential fitness, while overestimation may reduce the time allocated to activities such as foraging or mating (Ydenberg & Dill, 1986). For refuging species, there are two common ways to quantify risk assessment: flight initiation distance (FID), defined as the distance between the predator and the prey the moment the prey decides to flee, and hiding time, the length of time an individual takes to re-emerge from cover (Cooper & Blumstein, 2015). FID represents the point at which the subject's perceived risk of being caught is equal to the cost of fleeing (Ydenberg & Dill, 1986), functioning as a good indicator of how dangerous the subject perceives the risk. While FID is broadly applicable, some prey seek refuge, and for these species, hiding time is a relevant metric to understand the point at which the cost of re-emergence is low relative to the benefit of hiding. An individual's hiding time, the time at which an individual perceives the risk of being depredated upon re-emergence to be lower than the cost of forfeiting foraging opportunities, may be shorter than when an individual perceives re-emergence to result in a greater loss in overall fitness (Blumstein & Pelletier, 2005; Martìn & Lopez, 2015).

Humans often influence antipredator behaviour (Spiga et al., 2017). For instance, the presence of ecotourists are often associated with increased tolerance in animals (Sanzogni et al., 2015) and decreased fearfulness (Geffroy et al., 2015); however, the effect of anthropogenic presence on dynamic, interdependent behavioural decisions of each partner in a dynamic mutualism has yet to be studied. Previous work has shown that both goby FID and the latency to re-emerge can be reduced in areas frequented by SCUBA divers (Valerio et al., 2018). Although anthropogenic effects on goby antipredator behaviour have been studied, and goby/shrimp behaviours have been found to be linked (Burns et al., 2019), no prior work has asked whether and how humans influence the dynamic mutualism.

We studied the behavioural dynamics of shrimp–goby partnerships to examine whether anthropogenic presence impacts antipredator behaviours in this defensive mutualism. We first examined the influence of the number of shrimp–goby partnerships and of goby patterns of vigilance on FID and hiding time among shrimpgobies and snapping shrimp in the presence of a simulated predator. This was done via FID and by quantifying several key shrimp and goby behaviours. Given the importance of coordination in this coevolved system, it is important to understand whether and how humans affect it. Thus, we then examined the influence of two proxies of human disturbance (distance to shore and study site).

METHODS

Study Population and Site

We studied fierce shrimpgobies, *Ctenogobiops feroculus*, and their symbiotic Djeddah snapping shrimp, *Alpheus djeddensis*, which have been previously studied in this region (Burns et al., 2019). Marbled snapping shrimp, *Alpheus rapax*, have also reported in this area and are virtually identical to *A. djeddensis* (DecaNet eds., 2024; Randall, 2005). Previous studies have demonstrated that cryptic speciation is common in *Alpheus* shrimp (Mathews, 2006) and that commonly identified *A. djeddensis* shrimp are likely multiple species (Karplus & Thompson, 2012; Thompson et al., 2005). Thus, it is likely that our results and those of others may be conflated from these two otherwise cryptic species.

We worked at two sites, selected due to the presence of large sand flats and coral rubble, which host large populations of gobies and shrimp, in Mo'orea French Polynesia (Fig. 1). Tema'e Beach (17°29′50.9″S, 149°45′26.3″W), a popular public beach within the Nuarei marine protected area. We also worked at a nonmarine protected area back reef along the north shore (17°29′03.3″S, 149°50′24.0″W), with comparatively few human visitors (hereafter referred to as 'Hilton').

Field Data Collection

From 25 January to 9 February 2024, between 0700 and 1030 hours, we measured flight initiation distance (FID), censused human activity and collected the video footage used to quantify behavioural metrics. Field data collection included FID, goby number, shrimp number, burrow depth, time of FID, distance from shore (Tema'e site only) and human presence (Tema'e site only). We began trials by setting a video camera (Vemont Action Camera) ca. 5–20 cm from a burrow entrance to record goby and shrimp activity. We recorded the time of camera placement and referenced this as the beginning of the 10 min waiting period (Fig. 2). This initial approach drove both the goby and shrimp into their burrow, marking hide start time. We noted the number of gobies and shrimp observed at the burrow, confirmed during video scoring. We then left the burrow to repeat this process at additional burrows spaced at least 3 m apart from each other. Of the burrows that could be confirmed from our video recordings, 183 burrows had one shrimp present, 22 burrows had two shrimp present, 179 burrows had one goby present and 26 burrows had two gobies present. A singular burrow with three gobies was recorded, but we omitted this obvious outlier from analysis.

Approximately 10 min following camera placement, we returned to each burrow to collect FID measurements (Chan et al., 2019). If a goby had not re-emerged after 10 min, we left and returned following a second 10 min period to collect FID. FID measurements were conducted by advancing a 3 m pole capped with a 6.6 cm funnel towards the guarding goby to simulate a predator's approach. Depending on burrow depth, FID was conducted either standing or swimming against the current to maintain a steady position in the water column. The pole was pushed towards the goby at a steady speed of 0.5 m/s at 45° until the goby entered the burrow, at which point we noted distance, as 'Stop 1', using the marked increments (in cm) on the pole. After marking Stop 1, we continued to slide the pole until the end reached the burrow's entrance, and to quantify starting distance, noted the amount of the pole that had been extended at this second stop, 'Stop 2' (Fig. 3). If the goby did not re-emerge after an additional 10 min, we collected the camera without performing our FID protocol. Following FID, the depth (cm) of the burrow entrance was recorded, using the marked pole, and the distance from shore was measured by an observer on the beach using a rangefinder (Bushnell Sport 850, Overland Park, KS, U.S.A.) at the Tem'ae site. The observer also censused humans that passed them in the water, recording the time and their distance from shore.

Quantifying Behaviour

We analysed video recordings using methods developed by Burns et al. (2019), recording and quantifying the time that gobies spent engaged in each of the following behaviours: 'hide' (staying inside the burrow), 'guard' (standing guard at the burrow entrance) and 'out' (leaving the burrow completely, out of frame of the camera). Similarly, we quantified the time that shrimp spent engaged in each of the following behaviours: 'inside' (within the burrow) and 'outside' (outside the burrow within the frame of the camera). We infer that when gobies and shrimp were outside the burrow they perceived it to be relatively safe.

We used these behaviours to calculate a variety of metrics. We defined goby hiding time as the latency for the goby to enter the

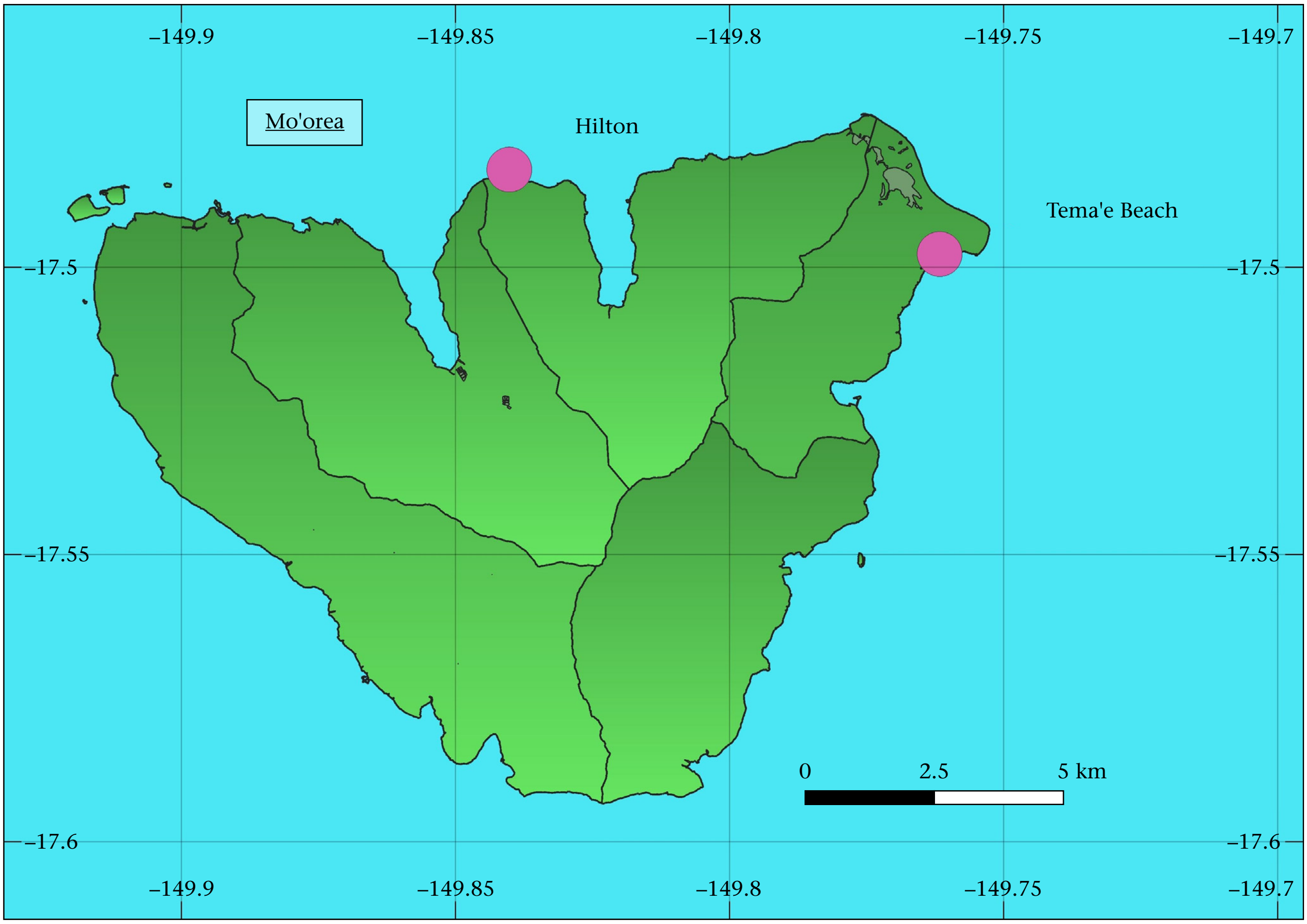

Figure 1. Map of the island Mo'orea, French Polynesia. Study sites are labelled in pink.

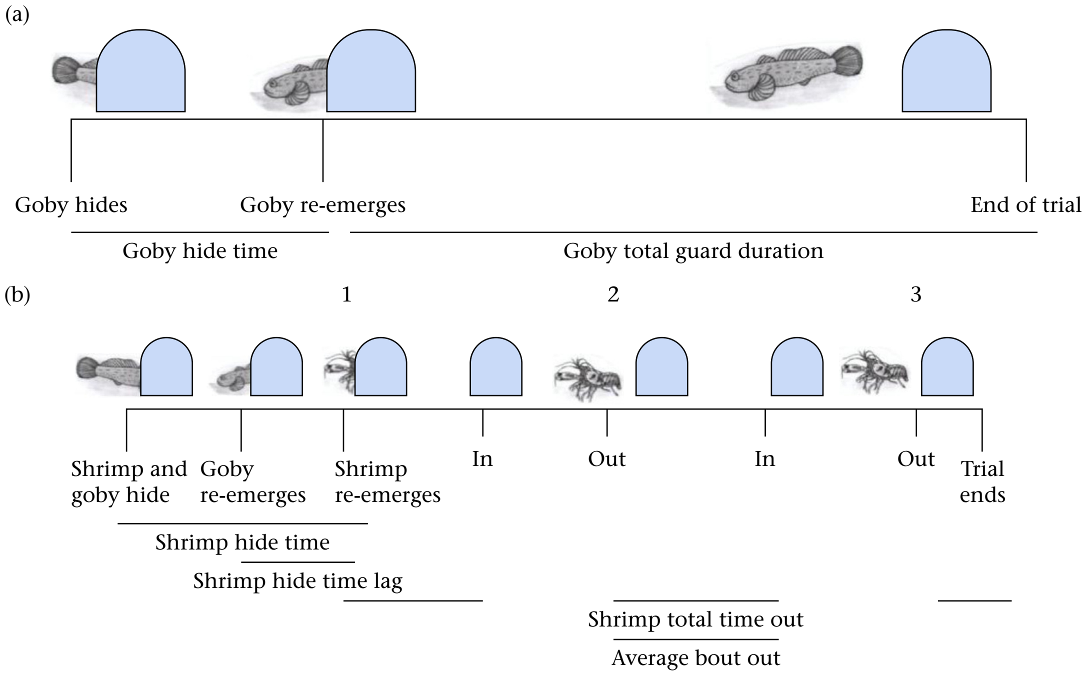

Figure 2. Behavioural measures and quantifiable data measured for (a) goby and (b) shrimp. Goby behaviours included hide time, time until initial re-emergence and total guard duration (total time guarding the burrow). Shrimp behaviours included hide time, time until initial re-emergence, hide time lag, the difference in time between the goby's and the shrimp's initial re-emergence, total time out, total time spent outside the burrow and average bout out (average time the shrimp was out of the burrow during each out event).

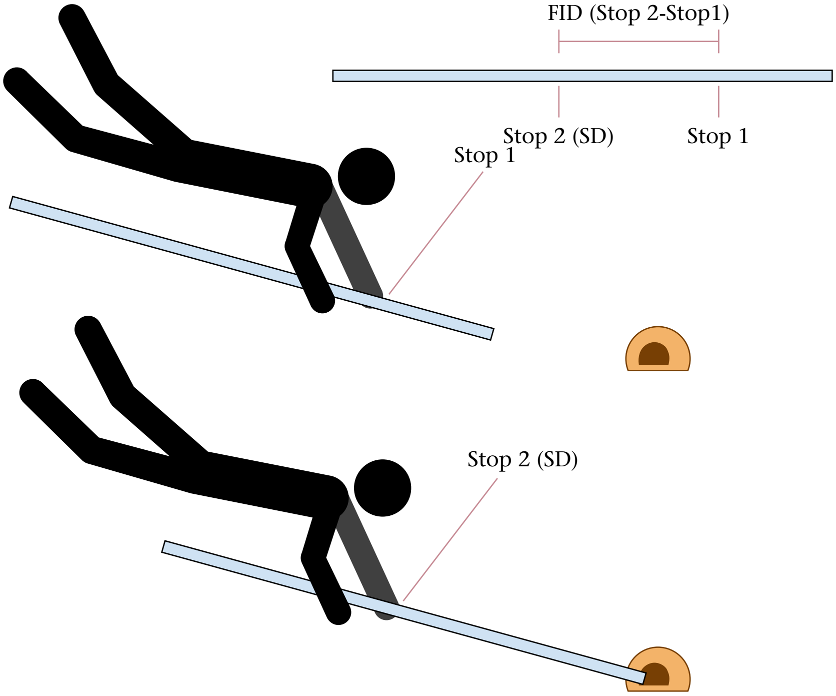

Figure 3. Illustration of researcher collecting data on flight initiation distance (FID). The researcher remained still while pushing the pole towards the burrow. When the goby initiated hiding in the burrow, the researcher recorded ‘Stop 1’. Once Stop 1 was measured, the researcher remained in place and continued moving the pole towards the burrow. Once the end of the pole reached the end of the burrow, ‘Stop 2’ starting distance (SD) was measured. FID was calculated by subtracting Stop 1 from Stop 2.

guard state after hiding when the camera was initially placed. We calculated total goby guard time as the total amount of time at least one goby was in the guard state, using functions that determined overlapping guard time, then subtracted these intervals from the summed goby guarding durations. We calculated FID, as defined above, as the difference between the starting distance and Stop 1, which was marked when the goby fled into the burrow. We defined shrimp hiding time as the latency to re-emerge, calculated by subtracting the time the shrimp re-emerged in the video from the initial starting time when the camera was placed. We defined shrimp hiding time lag as the time the shrimp took to re-emerge after the goby had re-emerged, calculated by finding the time difference between the hiding time of the shrimp and the hiding time of the goby. We calculated shrimp rate out by the number of times the shrimp left the burrow, divided by the total time of the video. We defined shrimp average bout out as the average amount of time spent outside the burrow. We defined shrimp total time out as the total time spent out of the burrow, summed across all bouts.

Statistical Analyses

First, we wanted to describe the dynamics of the mutualism by identifying which shrimp behaviours were influenced by their goby partner(s). To do this, we fitted models explaining each of our five shrimp behavioural metrics as a function of all three goby behavioural metrics as well as goby number (see Results). We also included shrimp number to determine whether shrimp presence affected shrimp behaviour. We used a negative binomial distribution to model shrimp hiding time (Venables & Ripley, 2002), and we fitted a two-component hurdle model to study shrimp total time out (Cameron & Trivedi, 2005, 2013; Mullahy, 1986; Zeileis et al., 2008) because the data did not meet the distributional assumptions of linear models through transformation. The hurdle model included a zero mass component, which predicted the probability of the shrimp emerging from the burrow, and a positive observations component, which employs a truncated count distribution (Heilbron, 1994; Mullahy, 1986). This approach was used because our data for shrimp total time out contained many structural zeros, due to trials where a goby and/or shrimp never re-emerged during the experiment. We fitted linear models to the shrimp hiding time lag, shrimp rate out and shrimp average bout out variables, using the ‘lm()’ function in base R (R Core Team, 2024). Because our data for shrimp hiding time lag and shrimp average bout out were right-skewed, we ln-transformed them before analysis. We verified model assumptions using the ‘check_model()’ function from the package ‘performance’ (Lüdecke et al., 2021).

Then, we examined how the variables that affected shrimp behaviour might be influenced by human activity to assess the influence of anthropogenic presence on the behaviour of one symbiont through its dependence on the other. To do this, we formally quantified human activity by testing the distribution of human activity as a function of distance from the shore at Tema'e. Using an Anderson–Darling test in the ‘DescTools'' package (Anderson & Darling, 1952, 1954; Marsaglia & Marsaglia, 2004), we found that human activity was not uniform ($P < 0.001$) and declined as a function of distance from the shore. We considered Hilton and Tema'e to have minimal and substantial overall human presence, respectively. We included water depth as a predictor because we expected gobies to be less affected by human disturbance at greater depths than in the shallows.

After confirming that shore distance was an accurate proxy for human presence, we fitted models to explain each of our three goby behavioural metrics, as well as goby and shrimp number, as a function of site and depth or shore distance (see Results). We also fitted models to explain shrimp number and goby number as a function of our anthropogenic proxies because we found them to be explained by goby behaviours. We found that shore distance and depth were highly correlated ($r = 0.89$), preventing us from including them simultaneously as predictors. We continued to include goby number and shrimp number as predictors in these models to study how they affected goby behaviours. When we fitted models using shore distance, we restricted the data set to observations collected only at Tema'e because shore distance was a metric there of human activity. We used a negative binomial distribution to model goby hiding time (Venables & Ripley, 2002), as justified above. We fitted linear models to total goby guard time and FID. The time-guarding model violated distributional assumptions, and after exploring a variety of transformations, we created a permutation test ($N = 1000$ permutations) to calculate P values. Together, these models helped us draw conclusions about how human presence impacted shrimp–goby behavioural dynamics.

Ethical Note

Permission to work in Mo'orea, French Polynesia was granted by Convention d'accueil number 130005820 approved on 24 November 2023. Experiments were approved by the Institutional Animal Care and Use Committee of the University of California Los Angeles (protocol number 2000-147, approved on 28 November 2023). By design, animals were not captured or otherwise touched during camera placement or the FID trials, which were brief. Researchers observed that most animals resumed their normal activity quickly. Experiments were limited to the morning and subjects were not retested.

RESULTS

Our final data set contained 240 experimental camera deployments, although not every variable could be recorded for every deployment, and technical issues prevented video recording in some cases. Gobies that did not re-emerge within 20 min were not able to be scored for hiding time or FID. Additionally, shore distance was only measured as a proxy for human activity at Tema'e beach. Models were therefore fitted with refined data sets containing only the deployments with complete data for all of the model's factors. The sample size of each model is given in Supplementary Tables S1–S13.

Do Gobies Influence Shrimp Behaviour?

A number of goby behaviours were significantly associated with shrimp behaviours (Tables 1–2). When gobies spent more time guarding the burrow, shrimp re-emerged sooner after their partner fish, re-emerged sooner after being flushed by camera placement, emerged from the burrow more frequently, spent more time outside the burrow (count hurdle) and were more likely to emerge from the burrow (zero hurdle). When gobies hid for longer, shrimp hid for longer as well, but re-emerged sooner following the goby's re-emergence. Goby and shrimp numbers also had significant effects on shrimp behaviour. When two gobies were present, shrimp took longer to re-emerge after the gobies re-emerged. When there were two shrimp, the shrimp to less time to re-emerge after the goby re-emerged, re-emerged sooner after camera placement, spent more time outside the burrow (count hurdle) and were more likely to re-emerge from the burrow (zero hurdle). Goby FID explained no significant variation in shrimp behaviour. Detailed results are outlined in Fig. 4 and Supplementary Tables S1–S5.

Do Humans Influence Goby Behaviour?

We found that our proxies of human disturbance explained some select goby behaviours (Table 2). Gobies guarded less at Tema'e than at Hilton, and with increasing distance from shore at Tema'e. When gobies had two shrimp partners, the gobies tended to re-emerge sooner and guard for longer. Interestingly, no goby behavioural variation was explained by goby number. Shrimp numbers decreased farther from shore at Tema'e. Goby number was not explained by anthropogenic or environmental variables. Gobies guarded less at greater depths. Detailed results are outlined in Supplementary Tables S6–S13 and Fig. S1.

Table 1
Summary model results examining the influence of goby behaviour on variation in shrimp behaviour

	Shrimp HT	Shrimp HT lag	Shrimp TT out		Shrimp rate out	Shrimp average bout out
			Count model	Zero hurdle		
Goby number		+				
Shrimp number	−	−	+			+
Total goby guard duration	−	−	+	+	+	
Goby HT	+	−				
FID						

HT: hiding time; TT: total time. Significant positive (+) and negative (-) model coefficients are indicated. Full model details and the sample size for each model are given in Supplementary Tables S1–S5. ‘Shrimp TT out’ was fitted as a hurdle model, which included both a count model to explain variation in shrimp that emerged and a zero hurdle model examining the probability that shrimp would emerge.

Table 2
Summary model results examining the influence of anthropogenic and environmental proxies on variation in goby behaviours and shrimp/goby numbers

	Behaviour metric	Anthropogenic		Environmental		
		Shore distance	Site (Tema'e)	Shrimp number	Goby number	Depth
Site	Goby HT	NA		−		
	Goby total guard	NA	−	+		−
	Goby number	NA			NA	
	Shrimp number	NA		NA		
Shore distance	Goby HT		NA	−		NA
	Goby total guard	−	NA			NA
	Goby number		NA		NA	NA
	Shrimp number	−	NA	NA		NA

HT: hiding time. Anthropogenic and environmental proxies were run as mixed effect model predictors of each respective behavioural metric. Significant positive (+) and negative (-) model coefficients are indicated. ‘NA’ denotes untested correlations. Full model details and results are given in Supplementary Tables S6–S13.

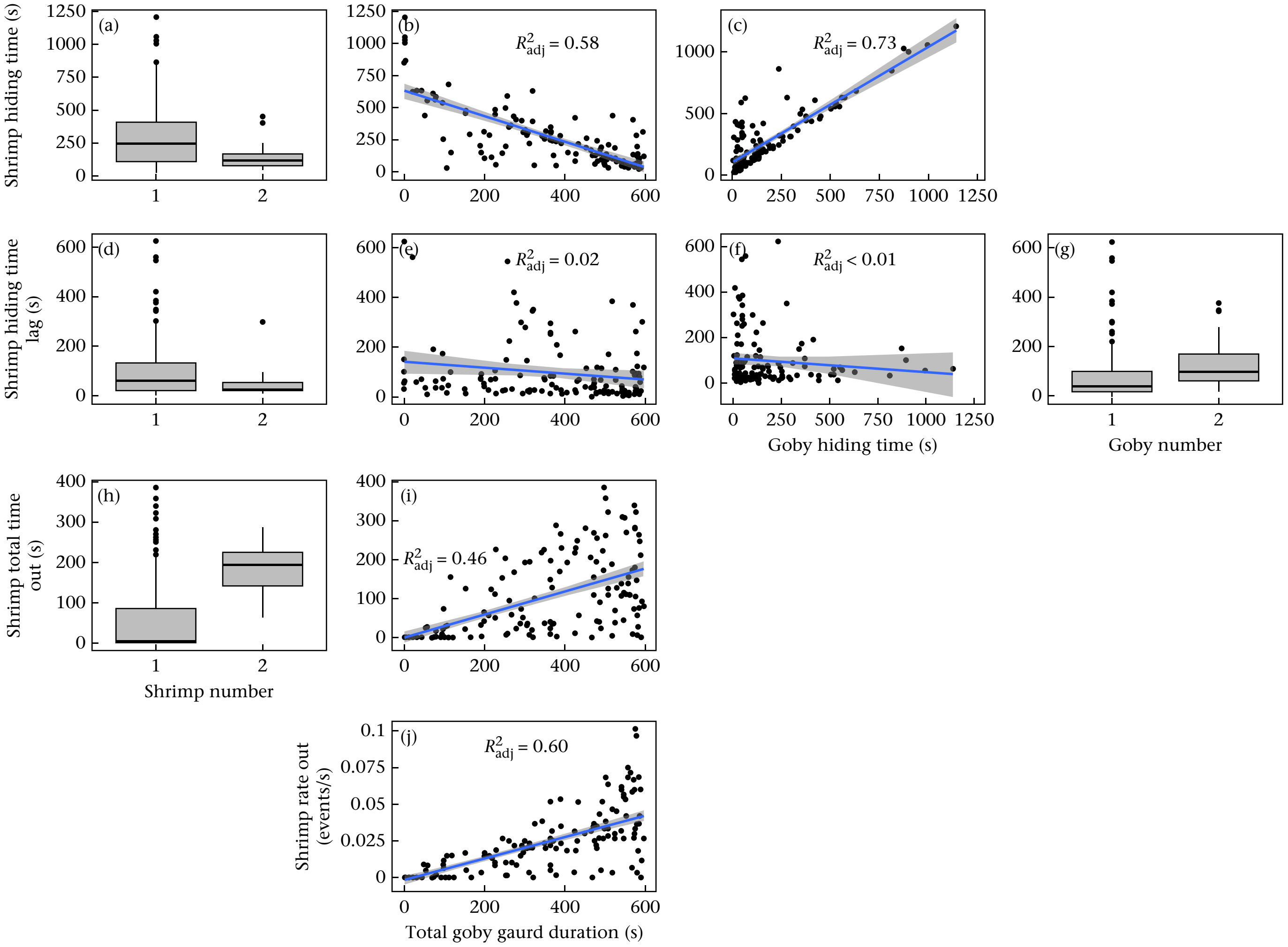

Figure 4. Relation between shrimp behaviours, goby behaviours and environmental factors: (a) shrimp hiding time as a function of the number of shrimp; (b) shrimp hiding time as a function of total goby guard duration; (c) shrimp hiding time as a function of goby hiding time; (d) shrimp hiding time lag as a function of shrimp number; (e) shrimp hiding time lag as a function of total goby guard duration; (f) shrimp hiding time lag as a function of goby hiding time; (g) shrimp hiding time lag as a function of goby number; (h) shrimp total time out as a function of shrimp number; (i) shrimp total time out as a function of total goby guard duration; (j) shrimp rate out as a function of total goby guard duration.

DISCUSSION

Overall, our results show how shrimp behaviour depends on goby behaviour in this dynamic defensive mutualism. When gobies guarded more, shrimp engaged in more risky behaviours, such as spending more time outside of their burrow and re-emerging sooner and more frequently, which may attract predator attention because of their movement and increased visibility (Bednarski et al., 2012; Wachowitz & Ewert, 1996). To clarify our connection between shrimp rate out and risk, we acknowledge that while the cleaning tasks performed by the shrimp do require movement in and out of the burrow, we do not consider each retreat back a flight response. Instead, we hypothesize that a shrimp may be more inclined to emerge more frequently while performing its usual cleaning activities when its goby partner is guarding because it can sense a lower risk of ambush by a predator and feels safe enough to be out in the open. Burns et al. (2019) noted that guarding further increased the risk of predation because it made the burrows more obvious to predators. These associations suggest that the shrimp's safety depends on their goby partner's vigilance.

Interestingly, goby hiding time was only significantly associated with two shrimp behaviours, shrimp hiding time and latency from the goby's re-emergence to the shrimp's re-emergence (shrimp hiding time lag). Unsurprisingly, the longer the shrimps took to re-emerge, the longer the gobies took to re-emerge, since shrimp never re-emerged before their goby partner. However, these shrimp had a lower hiding time lag, meaning they followed their goby partners out of the burrow more quickly. From an ultimate perspective, this may reflect an attempt to mitigate the increased fitness costs of remaining inside their burrows, since hiding time can vary with changing lost opportunity cost (Dill & Fraser, 1997). Goby hiding time was not associated with shrimp behaviours that occurred after the shrimp's initial re-emergence, suggesting that hiding time may influence one, but not all, perceptions of risk.

In addition to goby behaviour, we found that the number of shrimp and the number of gobies also explained variation in shrimp behaviour. When there were two shrimp, the shrimp re-emerged sooner after the camera was placed, re-emerged sooner after their goby partners, spent more total time outside their burrow, had longer bouts outside their burrow and were more likely to re-emerge. We hypothesize that shrimp experienced risk dilution, as the chances of an individual being depredated decreases as group size increases (Foster & Treherne, 1981). Indeed, the addition of the second shrimp reduced shrimp hiding time by 5%. We calculated this assuming there were two gobies present and by setting total duration, goby hiding time and FID to their mean values (which, for our scaled continuous variables, was 0). Counterintuitively, we found that when there were two gobies, shrimp waited longer to re-emerge after their goby partner. One possible explanation for this increased caution is that the gobies were engaged in other social activities that precluded antipredator vigilance. Indeed, we saw gobies engage in reproductive signalling; they had blackened eyes (Blom et al., 2016; Olsson et al., 2017, 2022) and darkened anal fins (Blom et al., 2022; Forsgren, 1997), both of which are associated with aggression and reproduction in sand gobies.

While we were initially surprised that variation in goby FID had no measurable effect on shrimp, upon further reflection, perhaps this was not surprising. Considering that snapping shrimp are blind, our results may be explained by the fact that shrimp cannot assess goby FID, but instead respond only to those goby behaviours they can physically monitor. However, in other systems, FID is correlated with latencies to return to relaxed behaviour (Møller et al., 2016; Ortiz-Jimenez et al., 2022; Sih, 1992), so FID could have been part of a behavioural syndrome of goby behaviours. Future studies on individually marked animals are required to properly evaluate this.

We have shown that this dynamic mutualism can be influenced by human activity. Variation in a key goby behaviour that was associated with shrimp behaviour was also associated with both proxies of human presence. The total time gobies guarded was lower at the highly visited Tema'e, as well as when gobies were studied farther from shore. The fact that gobies guarded less at the popular Tema'e beach than at Hilton was likely because they were disturbed more. Somewhat paradoxically, gobies also guarded less when observed farther from shore, where presumably there were fewer people. This might reflect a potential confounding effect of depth because, overall at both sites, gobies observed in deeper water guarded less. While gobies likely guarded less at the more popular site (Tema'e) because they were hiding more, they may guard less in deeper water for the opposite reason: because they were disturbed less often (by humans or predators) and felt safe enough to spend more time out of the burrow, engaging in low-vigilance activities. This explanation would align with the fact that we did not find a change in goby hiding time at greater depths. Further research is warranted.

These findings are consistent with many studies documenting negative impacts of human disturbances on reef fish (Albuquerque et al., 2014; Bergseth et al., 2016; Dearden et al., 2009). However, our findings do not align with a previous goby study, which found that gobies had shorter hiding times and shorter FIDs at high-frequency dive sites (Valerio et al., 2018), a finding that is consistent with an habituation-like process (Čapkun-Huot et al., 2024).

That gobies guarded less at the site where humans were present suggests that anthropogenic presence disrupts this mutualistic relationship. Titus et al. (2015) highlighted the fact that not all species in a community respond similarly to increased human activity and we should not expect all species to increase tolerance to anthropogenic activities. Our findings suggest that while marine-protected areas protect and support marine species and ecosystems, the increased human presence they attract may have detrimental effects on at least one critical behaviour in a dynamic defensive mutualism.

Together our findings show that the goby–shrimp dynamic defensive mutualism is selectively affected by human presence, which will likely become a greater issue as the global population increases (Gerland et al., 2022) and natural area tourism increases (Calandra et al., 2022; Madi-Moussa et al., 2019). Because we found that both gobies and shrimp dynamically varied their behaviour, we can assume some degree of plasticity. Such behavioural plasticity may increase survival in rapidly changing environments (Snell-Rood, 2013), which provides some hope that the goby–shrimp mutualism can survive increased human activity. Future research specifically studying plasticity at the individual level will be revealing.

Author Contributions

Bailey Franco: Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Cooper Kinne:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Savannah Licciardello:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Hali Muir:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Holland J. Smith:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Sean O'Fallon:** Writing – review & editing, Supervision, Data curation. **Daniel T. Blumstein:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Data curation, Conceptualization.

Data Availability

Data and code are posted at OSF - https://osf.io/8hpf2/?view_only=0d0673bd33644235b4170e50d3ca72f5.

Declaration of Interest

None.

Acknowledgments

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2024.10.014.

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