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Human Presence at a Site Explains More Variation than Site MPA Status in Dusky Damselfish (*Stegastes nigricans*) Antipredator Responses to Humans

Megan Ashabranner [†], Sydni Bednarek [†], Travis Crane [†], Cordelia Kuiper Rauch [†], Catherine Tran [†], Taylor N. Bastian and Daniel T. Blumstein [*]

Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, USA; mkash@g.ucla.edu (M.A.); sydnibednarek@g.ucla.edu (S.B.); tcrane3314@g.ucla.edu (T.C.); ckuiperr@g.ucla.edu (C.K.R.); trancatherine04@g.ucla.edu (C.T.); taylor.n.bastian@gmail.com (T.N.B.)

* Correspondence: marmots@ucla.edu

† These authors contributed equally to this work and are listed alphabetically.

Abstract

The growing popularity of ecotourism is increasing human–wildlife interactions in coral reef ecosystems. Although often considered benign, interactions with humans can alter essential antipredator responses. Reef fish exposed to humans often modify their antipredator behavior. Prior work has shown that fish respond differently in marine protected vs. non-protected areas (MPAs), but it remains unclear whether these differences stem from protection status or differences in human presence. We studied dusky damselfish (*Stegastes nigrican)* antipredator behavior across three sites separated by MPA status and human activity. We also investigated how different durations of short-term exposure to snorkeler presence influenced risk assessment across these sites. We quantified antipredator responses using: (1) the proportion of time fish were displaced from their territory during different durations of snorkeler exposure, (2) post-treatment flight initiation distance (FID), and (3) latency to return after fleeing. Human presence explained more variation than MPA status in all metrics. Fish from reefs with high human presence remained in their territories longer during treatments, had shorter FIDs, and returned faster after fleeing. Our findings suggest that snorkeling induces immediate behavioral changes and alters risk assessment following exposure in damselfish, potentially compromising fitness-promoting behaviors and predation avoidance.

Keywords: ecotourism; antipredator responses; risk assessment; flight initiation distance; human disturbance; damselfish; coral reefs; marine protected areas; snorkeler disturbance

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1. Introduction

Human presence in coral reef ecosystems is increasing globally due to a growing interest in marine recreation and ecotourism [1–4], exposing more animals to human presence and activities. While some of these activities directly damage or alter coral reef ecosystems [5–7], ecotourism generally assumes that recreational activities are non-extractive and ecologically sustainable [8]. However, the mere presence of a human can affect animal behavior through various mechanisms [1,9,10]. For example, human disturbances are known to threaten animals and trigger antipredator responses [11], suggesting that

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humans elicit behavioral and physiological effects [1,10]. Snorkeling and diving in particular may alter the behavior of aquatic prey animals [12–14]. By engaging in antipredator behavior, animals redirect time and energy spent on vigilance and flight from other fitness-enhancing behaviors, such as territorial defense and social interactions [11,15,16]. Species of reef fish, particularly damselfish, may be especially vulnerable to this fitness trade-off, as they are territorial and allocate considerable time to vigilance [17–20].

In the face of growing anthropogenic pressure on marine ecosystems, the establishment of Marine Protected Areas (MPAs) seeks to restrict harmful human activity, such as fishing and boating, in ecologically important regions [21]. Paradoxically, these restrictions designed to protect marine life give rise to the pristine nature of MPAs, which is highly attractive to ecotourism and increases human exposure to animals in these areas [1,3,22–24]. This poses a dilemma for MPA management in striking a balance between restrictions on damaging human activities vs. harmful levels of human presence. When a no-take MPA in Mexico experienced a significant reduction in ecotourist visitation, fish abundance increased, suggesting that tourist presence inhibited fish behavior; when visitor levels returned to initial levels, fish density dropped again [14]. While MPAs are inherently attractive to tourists, there can be popular recreational areas within non-MPA sites as well.

Repeated exposure to benign human disturbance can reshape antipredator behavior across taxa. In terrestrial environments, persistent human presence has been linked to reduced antipredator responses to natural predators [9,25] and increased boldness while foraging [9,26], reflecting patterns in systems that frequently experience non-lethal human interactions [27]. In areas with high levels of ecotourism, animals that experienced repeated exposure to human presence exhibited shorter flight initiation distances (FIDs) in response to threat approaches [9,27–29]. Similarly, in marine environments, fish that are exposed to brief, infrequent risk events often exhibit stronger antipredator responses than those exposed to more common, prolonged events, even when the latter pose real threats [30]. In particular, reef fish can develop behavioral tolerance to humans [31] and anthropogenic noises [32], leading to reduced responses to these stimuli. Divers and snorkelers may also suppress territorial fish behaviors [12]. Moreover, fish in MPAs permit closer human approaches than those in non-protected areas [10,33]. Altogether, studies suggest that diverse human activities may drive variation in fish antipredator behavior.

In this study, we investigated the consequences of short-term human interactions on dusky damselfish (*Stegastes nigricans*) from three sites with varying protection status and levels of human presence. We quantified the immediate and residual behavioral responses of the fish to increasingly long durations of snorkeler interactions by studying their responses during the interaction, as well as shortly after. We used three metrics of risk assessment: (1) the proportion of time spent in hiding or away (displaced) from the core territory during the time a snorkeler is present; (2) the flight initiation distance (FID), defined as the distance at which prey flee from an approaching predator [16,34], measured following the snorkeling treatment by exposing the fish to a standardized non-human threat–in our case, an approaching pole; and (3) the subject's latency to return to its original territory following an experimental flush. We further compared responses based on whether individuals were located in an area with MPA status or an area with a high or low level of human presence.

Despite research showing that fish respond within and outside MPAs differently [10,33], it remains unclear whether protection status or human presence drives these differences. In terrestrial systems, the level of human presence of an area, rather than its reserve status, has been documented to have a significant influence on bird habituation [27], but much research remains to be conduct on marine systems to determine whether it is the type or magnitude of human behavior that is responsible for these differences. Despite growing evidence that long-term exposure to tourism or other chronic anthropogenic disturbances induces behavioral changes and reduced antipredator behavior across taxa [9,27–29,31], far less is known about how varying magnitudes of short-term, benign interactions with humans influence immediate and residual antipredator responses. Understanding these short-term dynamics might help predict how ecotourism influences reef fish behavior and further guide policies to minimize negative impacts [35].

We predicted that damselfish exposed to human presence would initially respond to a human observer by spending less time in their core territory, but that this response would diminish as the treatment time increases. We also predicted that longer treatment times would cause fish to tolerate closer experimental approaches and have reduced latencies to return to their territory following their flight. Additionally, we predicted that damselfish from areas with higher human presence would be more tolerant to threat approaches than those based solely on MPA status, because greater overall human presence would affect fish behavior more than fishing pressure.

2. Materials and Methods

2.1. Study Site and Species

We measured the latency to resume foraging and FID in dusky damselfish at three fringing-reef sites in Mo’orea, French Polynesia. One of our sites was located within a marine protected area (MPA), while the remaining two were non-MPA sites that differed in levels of regular snorkeler and swimmer presence. The selected non-MPA sites included Ta’ahiamanu Public Beach and a commercial jet ski launch site, which we referred to as “Jet Ski”. For our MPA site, we conducted research at Temae Public Beach. The Ta‘ahiamanu and Temae sites are public beaches characterized by high levels of swimmer and snorkeler visitation during our observation periods, whereas the Jet Ski site is characterized by minimal swimmer and snorkeler activity. Although Jet Ski is exposed to some motorized recreational activity, it still had a much lower level of human visitation overall (Table 1).

Table 1. Selected study sites (Ta’ahiamanu Public Beach, Commercial jet ski launch site, Temae Public Beach) with their coordinates, protection status (protected or unprotected), and level of overall human presence (high or low) based on field observations.

Site	**Coordinates**	**MPA Status**	**Human Presence**
Ta’ahiamanu Public Beach	17°29′ S 149°51′ W	Unprotected	High
Commercial jet ski launch site	17°48′ S 149°78′ W	Unprotected	Low
Temae Public Beach	17°50′ S 149°76′ W	Protected	High

We conducted experiments every other day from 18 January through 6 February 2026, between 730 h and 1600 h, on damselfish no deeper than 2.05 m below the surface. Given that dusky damselfish are highly territorial and defend patches of algae against other herbivorous fish or grazers [17–20], and that they are abundant and easy to observe in Mo’orea [36], we were able to move to different patches of the reef each day and be confident that we avoided resampling the same individuals and hence pseudoreplication.

2.2. Experimental Treatments

Snorkeling is a widespread, increasingly popular recreational activity that involves observing the underwater environment from the surface using a mask and snorkel [37]. Many species respond fearfully to direct gazing, as it often signals predatory intent [38–40]. Indian rock lizards (*Psammophilus dorsalis*) exhibited longer FIDs when approached with a direct gaze [41], and black iguanas (*Ctenosaurus similis*) associated the human face with increased predation risk [42]. Altogether, these studies suggest that eye orientation

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and direct observation can strongly influence an animal's perception of risk. With a wide variety of potential ecotourism and recreational activities, people behave differently in coral reefs depending on their individual interests. Divers with cameras spend up to 10 times longer interacting with animals during dives than divers without cameras, revealing that wildlife can experience variable durations of human presence during recreational activities [43]. By manipulating the duration of a snorkeler's direct gaze on a subject, we simulated how various snorkeling behaviors affect damselfish, ranging from quick passersby to prolonged observations by those with a keen interest in the fish.

We tested four different floating treatments, which are summarized in Table 2. Treatments were cycled in order (no float, 10 s float, 60 s float, and 180 s float) to balance the number of trials across treatments. Additionally, fewer trials were conducted on one day to ensure even numbers of trials.

Table 2. Snorkeling float treatments applied to damselfish, including description of the treatment duration (0 s, 10 s, 60 s, 180 s) and what type of interaction with an ecotourist the treatment serves to represent.

Treatment	Description	Ecotourism Simulation
No float	No snorkeler present above fish	No ecotourist exposure
10 s float	Snorkeler observes fish for 10 s	Brief passerby or momentary interest
60 s float	Snorkeler observes for 60 s	Moderate observation or brief engagement before moving on
180 s float	Snorkeler observes for 180 s	Extended observation from either highly engaged snorkeler or photographer

2.3. Measuring Antipredator Responses

On each experimental day, our team of five data collectors split into two groups: one of three and one of two. Team 1 was made up of Cordelia as the flusher and Sydni as the observer. On every other experimental day, Megan would join team 1 as a habitat data collector. Team 2 was made up of Travis as the flusher, and Catherine and Megan alternated between acting as the observer for team 2, with Megan acting as the observer when she was not working for team 1. When a team was made up of only two members, the two would work together to collect habitat data. For each trial, the team snorkeled through the reef until they located an appropriate subject to flush. One person was assigned the role of "flusher," and the other was assigned the role of "observer," which was the researcher who floated above the fish. Both the flusher and observer moved to a distance of 2–3 m from the subject and remained still for approximately 1 min to acclimate the fish to their presence [44]. During this time, the flusher estimated the subject's length from tip to tail (in centimeters) (see Minimizing error and observer differences section below), and both observers counted the number of conspecifics within a 1 m radius around the focal individual [45]. After the acclimation period to ensure that the subject was relaxed (defined as foraging, swimming, or non-observer-directed vigilance), we started the treatment. Given their territorial nature and limited movement away from their home sites, we established that the area they occupied during acclimation was their core territory.

At this point, the flusher signaled for the observer to begin one of the predetermined treatments, and the observer proceeded to float on the surface above the fish for 10 s, 60 s, or 180 s. For each trial, three behavioral response variables were measured: proportion of time displaced, FID, and post-flush latency to return (Table 3).

During the treatment, the flusher remained close behind the observer and repositioned them when necessary due to waves or currents, ensuring that the adjustments did not influence the focal fish's behavior. No floating observer was present during the control treatment. During the float treatments, the observer used a stopwatch to record the total time that the fish spent displaced from its initial position in its territory. The flusher tracked the observer's float time for each trial using a stopwatch and would signal the observer when to start and stop their float. Following the treatment, the observer returned to their original location (2–3 m away from the fish) and waited for the fish to resume typical, non-vigilant behavior (defined as when the fish stopped looking at the observer and/or flusher) before collecting FID data. For the control treatment, the observer watched the fish from a distance of 2–3 m for 60 s and recorded the total time the fish spent in hiding or away from its territory using a stopwatch.

We measured FID following the methods outlined in Overs et al. [44]. Once the focal fish resumed typical, non-vigilant behavior, the flusher pushed a 3 m pole with a 6 cm-diameter dark gray funnel at its end towards the fish at a constant speed of 0.5 m/s. The flusher stopped the pole in place once the fish fled from its original position and recorded this as the fish's flush distance. The observer also started their stopwatch when the fish fled. The flusher then measured the distance to the fish's original location and relayed this as the starting distance, the initial distance between the pole and the fish. FID was calculated by subtracting the flush distance from the starting distance. The pole was then quickly retracted by the flusher, and the observer noted its latency to return. The flusher then swam to the fish's location to measure and record the depth of the fish from the surface using the 1 cm markings on the FID pole. For the control treatment, the flush occurred after the 1 min observation period had concluded, and all else proceeded as described above.

We also recorded sea conditions using the Beaufort scale, whether it was raining, and the percentage of hard substrate at the trial location. To measure the hard substrate, we placed a 1 × 1 m^2 gridded quadrant (with 81 intersecting points) centered on the fish's location at the start of the observation [46]. We recorded the benthic habitat category at each intercept as either sand, rubble, hard substratum, live coral, or macroalgae [46] (Table 4). The number of intercepts of live coral cover and hard substratum was then summed and divided by the total of 81 intercepts to obtain the total hard substrate percent.

Table 3. Behavioral response variables (Proportion of Time Displaced, Flight Initiation Distance (FID), Post-flush Latency to Return) collected throughout each trial with the definition used in this study.

Behavioral Response Variable	**Definition**
Proportion of Time Displaced	The proportion of the treatment time that the subject spent hidden (50% of its body hidden) or away from its initial position in its core territory.
Flight Initiation Distance (FID)	Distance at which the fish flees from an approaching pole.
Post-flush Latency to Return	Time for the fish to return to its original location after fleeing from a flush exposure.

Table 4. Benthic habitat components used for determining the total hard substrate percent, and the definition of their characteristics. Components include sand, rubble, hard substratum, live coral, and macroalgae.

Benthic Component	**Sand**	**Rubble**	**Hard Substratum**	**Live Coral**	**Macroalgae**
Definition	Particles of sand.	Fragments of rock or coral that were greater in size than particles of sand [47].	Intact dead coral structure that did not have macroalgal coverage [48].	Living coral structure.	Whole, attached algae anchored by a holdfast [49] and larger than turf [46].

2.4. Observer Training

All observers were trained to visually identify subject size ranges by estimating the size of waterproof paper cutouts of the damselfish's typical length range (6 cm to 16 cm from tip to tail) underwater from 1.5 m away [45] until their estimates reached 95% accuracy. Similarly, to standardize the velocity of the flush, all flushers practiced pushing the pole at a specified rate of 0.5 m/s until they could consistently move the pole at this velocity underwater.

2.5. Statistical Analysis

All statistical analyses were performed in R version 4.5.2 [47]. We used the Jamovi version 2.6.45.0 interface for all models [50], with one exception: the analysis of the proportion of time displaced was coded in RStudio 23.12.1 [51]. Before performing our analysis, we plotted the distributions of our depths, starting distances, and Beaufort scale values. We excluded trials that had a starting distance below 2 m or above 3 m to standardize our methods. The majority of our measurements were conducted under Beaufort 0 or 1; to standardize experimental conditions, we eliminated six trials conducted at Beaufort 2 or 3. We also excluded trials with disruptive wave action during the trial, which occurred once. Despite conducting experiments to depths of 205 cm, we chose to limit our depth range to 50–150 cm, as we felt this 1 m range captured a biologically relevant range of risk perception and excluded values where the observer was either too close or too far from the fish. We included only trials in which there were no conspecifics between the fish of interest and the FID pole (this occurred once). Finally, we excluded all trials that had incomplete habitat data.

We first fitted models with key covariates and factors for each of our three response variables: the proportion of time displaced from the territory during treatment, FID, and latency to return after the flush. In all of our basic models, we included the main effect of treatment, as well as multiple covariates that we a priori expected might explain variation in the dependent variables. These covariates included fish length, because it has been shown to affect fish FID in prior studies [44,46,52]; depth, both because fish depth reflects the proximity of the float treatment to the fish and thus the intensity of the treatment, and because previous research has found that reef fish FID varies with water depth [53]; the number of conspecifics present, because group size may influence fish risk assessment [54,55]; and percent hard substrate because it has been shown to be associated with damselfish risk assessment [44,46,56]. In the FID models, we included starting distance, which often explains considerable variation in FID across species [57,58], including in damselfish [45,56].

Because there were only three sites–one MPA with high human presence, one non-MPA with high human presence, and one non-MPA with low human presence–human presence and MPA status were highly collinear. Therefore, we fitted separate models for each dependent variable: one for the effect of human presence and a second that included MPA status. Initial models included all two-way interactions among the listed a priori variables. For the FID model, we initially included all relevant three-way interactions among site, treatment, and starting distance and removed all nonsignificant interactions.

Afterwards, we checked the models' assumptions. The model for hiding time during float did not meet the assumptions for a general linear model, a generalized linear model with a beta regression, or a hurdle model; thus, we used lmPerm 2.14 in R to run a permutation test [59], which only assumed that the variables were independent.

The FID and post-hiding time data were ln-transformed, and subsequently met the assumptions for a general linear model using GAMLj version 3 [60]. These models showed no significant heteroscedasticity based on Breusch-Pagan tests; the residuals were normally distributed based on Kolmogorov–Smirnov and Shapiro–Wilk tests; there was no collinearity based on VIF values < 2; and the residual Q-Q plots were straight, indicating normality. We then checked for other potentially significant covariates and factors, including observer and wind speed on the Beaufort scale, and retained them only if they were significant. For each response variable, we compared models that included either human presence or MPA status using adjusted R^2 values and selected the model with the higher adjusted R^2 value as the better-fitting model. We report the results of the better-fitting model in the main text and include those of the secondary model in the Supplementary Material. For pairwise comparisons, we report Tukey-adjusted p-values for the GLM analysis and Bonferroni-adjusted p-values for the permutation analysis.

3. Results

3.1. Human Presence Explained More Variation than MPA Status

For each variable; proportion of time displaced, FID, latency-to-return; the model that included human presence (High or Low) as a covariate had higher adj. R^2 values, signifying that they explained more variation than the model that included MPA status (Y or N) as a covariate (Supplementary Tables S1–S9) (Table 5).

Table 5. Adjusted R^2 values for each of the two models made for each behavioral measure (proportion of time displaced, flight initiation distance, and post-flush latency to return). One model contains human presence (High or Low) as a covariate, and the other contains MPA Status (Y or N).

Behavioral Measure	**Human Presence Model Adj. R^2**	**MPA Model Adj. R^2**
Proportion of Time Displaced	0.523	0.489
Flight initiation distance (FID)	0.192	0.188
Post-flush Latency-to-Return	0.103	0.061

3.2. Treatment Explained Significant Variation in the Proportion of Time Displaced from Core Territory

Our final dataset for the proportion of time spent displaced during the float included 246 trials, which we analyzed using a permutation test. Studied fish were at an average depth of 104 ± 23.5 cm, had an average 1.68 ± 1.28 number of conspecifics around them, were located over an average hard substrate cover of 78.6 ± 18.9%, and were an average of 11.5 ± 2.6 cm long.

After controlling for the significant effects of observer, number of conspecifics, and hard substrate percent, as well as the non-significant effects of size and depth, we found significant main effects of treatment and human presence on the proportion of time displaced during each treatment (Tables 6 and 7). Pairwise comparisons for treatment revealed that fish were displaced significantly longer following any treatment compared to the control, and that fish were displaced more after the 10 s treatment than the 180 s treatment (Figure 1). Since there was a main effect of observer, we conducted post hoc pairwise comparisons and found that fish were displaced significantly longer when the tallest observer, Sydni (height = 179.7 cm), looked at them compared to the shortest person, Catherine (height = 157.5 cm), or the intermediate length person, Megan (height = 160.0 cm). There were no significant differences in displacement elicited between Catherine and Megan (Figure 2).

Table 6. Omnibus results from a permutation-based linear model examining human presence as a factor explaining variation in the proportion of time dusky damselfish were displaced from their territories during snorkeler exposure treatments. The model also includes treatment duration, observer identity, depth, fish size, number of conspecifics, percentage of hard substrate, and depth (model $p < 0.001$, adj. $R^2 = 0.523$) ($\eta^2 p$ = partial eta squared).

	p	**$\eta^2 p$**
Treatment (s)	<0.001	0.480
Observer	<0.001	0.045
Depth (cm)	0.098	0.002

Size (cm)	0.529	0.002
Number of Cons.	<0.001	0.016
Hard Sub. %	<0.001	0.010
Human Presence	<0.001	0.129

Table 7. Parameter estimates from a permutation-based linear model that includes human presence (reference "Low") as a variable to explain variation in the proportion of time fish were displaced from their territories during snorkeler exposure treatments. The model also includes treatment duration (reference 0 s control), observer identity (reference Catherine), depth, fish size, number of conspecifics, and percentage of hard substrate (model $p < 0.001$, adj. $R^2 = 0.523$).

Coefficients	**Estimate**	**SE**	***p***
Intercept	0.706	0.018	<0.001
Treatment 10 s	−0.397	0.027	<0.001
Treatment 60 s	0.194	0.027	<0.001
Treatment 180 s	0.132	0.027	<0.001
Observer Meg	−0.064	0.026	<0.001
Observer Syd	−0.018	0.024	0.007
Depth (cm)	0.0001	0.001	0.804
Size (cm)	0.005	0.007	0.529
Number of Cons.	−0.025	0.013	<0.001
Hard Sub. %	0.001	0.001	<0.001
Human Presence	0.110	0.018	<0.001

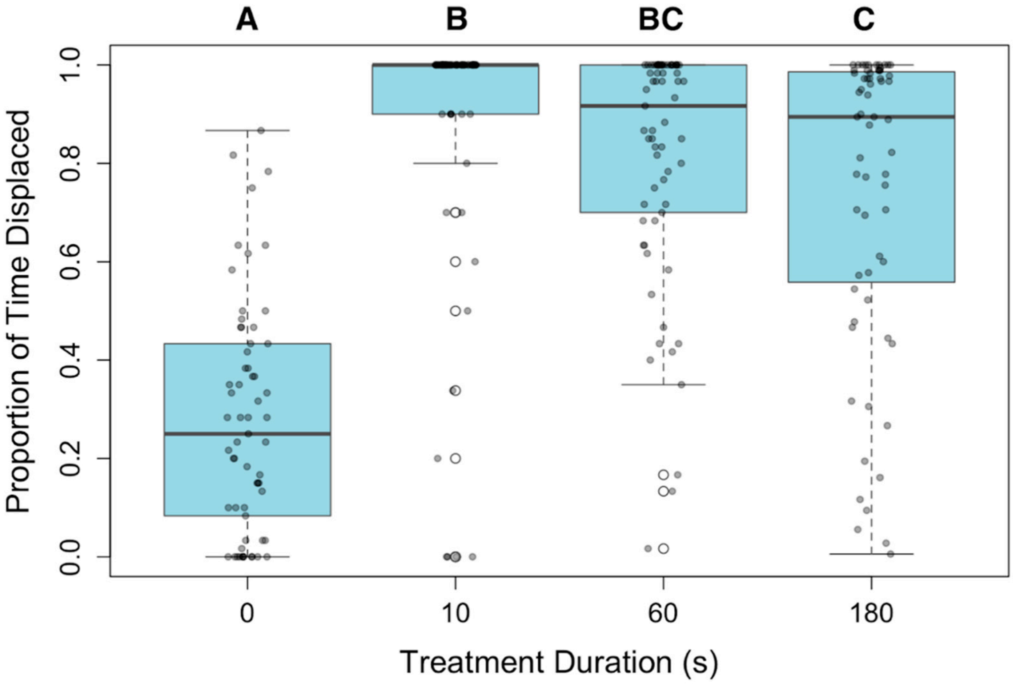

Figure 1. Marginal means (±95% confidence intervals) of the proportion of time displaced from territory across treatments for dusky damselfish. Different letters indicate significantly different responses, as determined by Bonferroni contrasts.

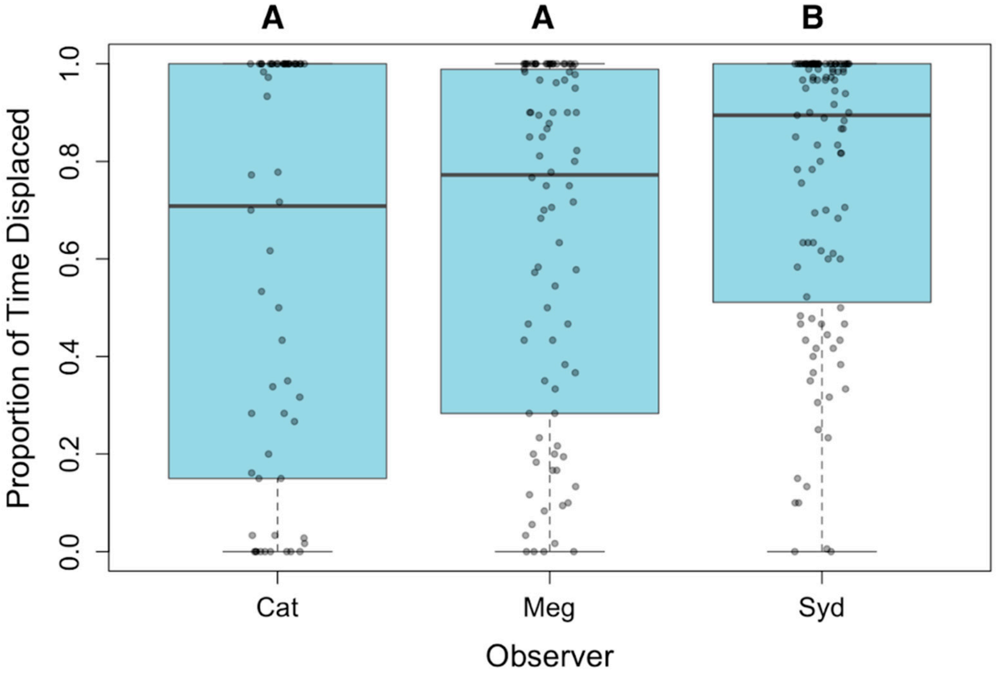

Figure 2. Marginal means (±95% confidence intervals) of time displaced across observers for dusky damselfish. Names of observers include Sydni, Megan, and Catherine. Different letters indicate significant differences in the main effect of treatment time, evaluated by a Bonferroni contrast.

3.3. Treatment Explained Significant Variation in FID

Our final dataset included 242 trials with acceptable FID values. For these trials, the fish were at an average depth of 104.0 ± 23.4 cm, an average starting distance of 252 ± 27.4 cm, had an average of 1.68 ± 1.30 conspecifics around them, were in areas with an average of 78.1 ± 19.0% hard substratum cover, and were an average of 11.5 ± 2.65 cm long.

After controlling for the significant effect of starting distance and size, as well as the non-significant effects of depth, hard substrate percent, and the number of conspecifics, we found significant main effects of treatment and human presence on FID (Tables 8 and 9). Post hoc comparisons for the different treatments revealed a significant difference between the 10 s and 180 s treatments. The difference between the control and 180 s treatments also had a significant uncorrected p-value; however, its corrected p_{Tukey} was insignificant ($p = 0.016$, $p_{\text{Tukey}} = 0.075$). There were no other significant differences between the treatments. At low human presence sites, across all treatments, FID increased with increasing starting distance. At both sites, the 10 s treatment had the highest mean FID, with the 0 and 60 treatments insignificantly below and the 180 s treatment significantly below (Figure 3).

Table 8. Omnibus results from a general linear model containing human presence as a variable examining factors explaining the variation in flight initiation distance (FID) of damselfish. The model also includes treatment duration, starting distance, fish size, depth, number of conspecifics, and the percentage of hard substrate (model $p < 0.001$, adj. $R^2 = 0.192$) (η^2p = partial eta squared).

	p	η^2p
Treatment (s)	0.024	0.040
Starting Distance (cm)	<0.001	0.060
Size (cm)	<0.001	0.058
Depth (cm)	0.138	0.009
Number Cons	0.837	0.000

Hard Sub. %	0.349	0.004
Human Presence	0.021	0.033

Table 9. Parameter estimates result from a general linear model that includes human presence (reference "Low") as a variable to explain variation in flight initiation distance (FID). The model also includes treatment duration (reference 0 s control), percentage of hard substrate, fish size, number of conspecifics, depth, starting distance, and people or not (reference "N") (model $p < 0.001$, adj. $R^2 = 0.192$).

Coefficients	**Estimate**	**SE**	***p***
Intercept	4.191	0.017	<0.001
Treatment 10 s	0.021	0.043	0.626
Treatment 60 s	−0.027	0.043	0.530
Treatment 180 s	−0.102	0.042	0.016
Hard Sub. %	−0.001	0.001	0.349
Size (cm)	0.025	0.006	<0.001
Number of Conspecifics	0.003	0.012	0.837
Depth (cm)	−0.001	0.001	0.138
Starting Distance (cm)	0.002	0.001	<0.001
Human Presence	−0.099	0.035	0.006

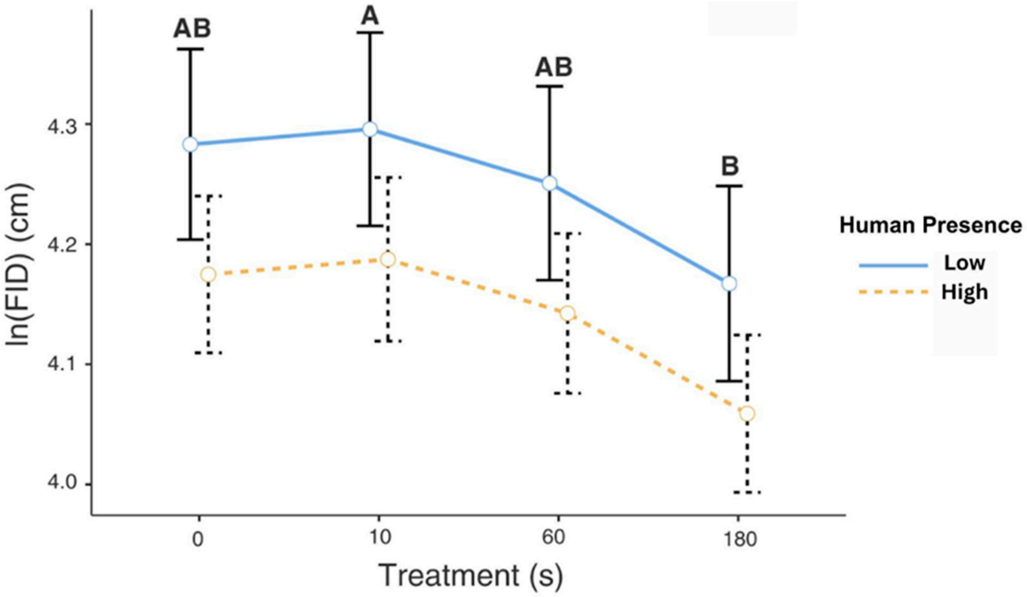

Figure 3. Marginal means (±95% confidence intervals) of ln(flight initiation distance (FID)) in cm across treatments for dusky damselfish in sites with and without human presence. Different letters indicate significantly different responses, as determined by Tukey contrasts. Solid blue illustrates sites with few people; dashed yellow illustrates sites with more people. There was no significant interaction between treatment and location (see text).

3.4. Treatment Explained Significant Variation in Post-Flush Latency to Return

Our final dataset included 240 trials with acceptable latency-to-return measurements. For these trials, the fish were at an average depth of 104 ± 23.5 cm, had an average of 1.64 ± 1.19 conspecifics around them, were in areas with an average hard substrate cover of 77.8 ± 19.0%, and were an average of 11.5 ± 2.63 cm long.

After controlling for the significant effect of number of conspecifics and the non-significant effects of size, hard substrate percent, and depth, we found significant main effects of treatment and human presence on post-flush latency to return (Tables 10 and 11). Post hoc comparisons among the treatments revealed a significant difference between the 10 s and 180 s treatments. The difference between the 0 s and 180 s treatments also had a significant uncorrected *p*-value; however, its Tukey corrected *p*-value was not significant ($p = 0.033$, $p_{Tukey} = 0.141$). The contrast between the 60 s and 180 s treatments also had a significant uncorrected *p*-value, but not after accounting for multiple comparisons ($p = 0.011$, $p_{Tukey} = 0.054$). There were no significant differences between the other treatments.

Table 10. Omnibus results from the general linear model containing human presence as a variable examining factors explaining the variation in post-flush latency to return time. The model also includes the treatment duration, fish size, depth, number of conspecifics, and percentage of hard substrate (model $p < 0.001$, adj. $R^2 = 0.103$) (η^2p = partial eta squared).

	p	η^2p
Treatment (s)	0.029	0.038
Size (cm)	0.305	0.005
Depth (cm)	0.732	0.001
Number Cons.	0.005	0.034
Hard Sub. %	0.597	0.001
Human Presence	<0.001	0.064

Table 11. Parameter estimates from the general linear model containing human presence (reference "Low") as a variable to explain the variation in post-flush latency to return time. The model also includes treatment duration (reference 0 s), fish size, percentage of hard substrate, depth, and number of conspecifics (model $p < 0.001$, adj. $R^2 = 0.103$).

Coefficients	Estimate	SE	*p*
Intercept	3.169	0.052	<0.001
Treatment 10 s	0.069	0.135	0.607
Treatment 60 s	0.061	0.134	0.651
Treatment 180 s	−0.286	0.133	0.033
Size (cm)	0.020	0.020	0.305
Hard Substrate %	−0.001	0.003	0.597
Depth (cm)	0.001	0.002	0.732
Number of Cons	−0.120	0.042	0.005
Human Presence	−0.438	0.110	<0.001

Across all treatments, the latency to return decreased as treatment time increased. This difference in decrease was significant when comparing the 10 s and 180 s treatments (Figure 4). Between sites with high and low human presence, sites with high human presence have lower return latency when comparing the same treatment. At both sites, the 10 s treatment had the highest mean latency to return, with the control and 60 s treatments not significantly lower, and the 180 s treatment significantly lower (Figure 5).

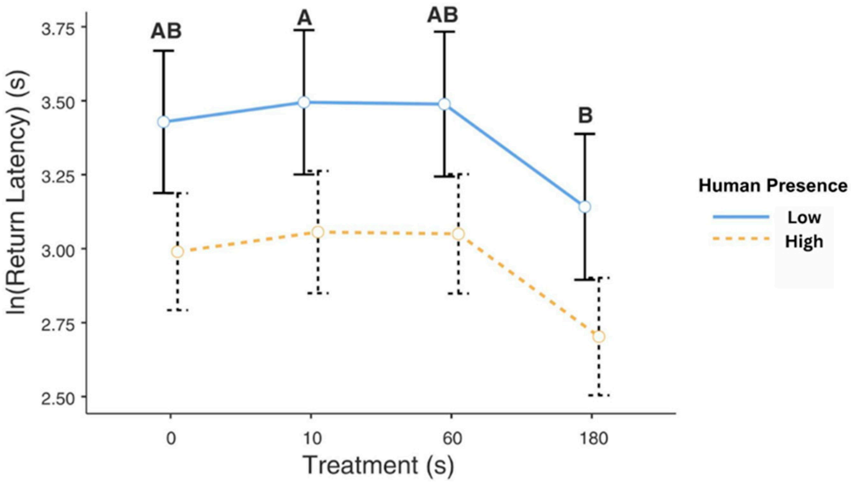

Figure 4. Marginal means (±95% confidence intervals) of proportion of post-flush latency to return time across treatments for dusky damselfish in sites with and without human presence. Different letters indicate significant differences in the main effect of treatment time, evaluated by Tukey contrasts. Solid blue illustrates sites with few people; dashed yellow illustrates sites with more people. There was no significant interaction between treatment and location (see text).

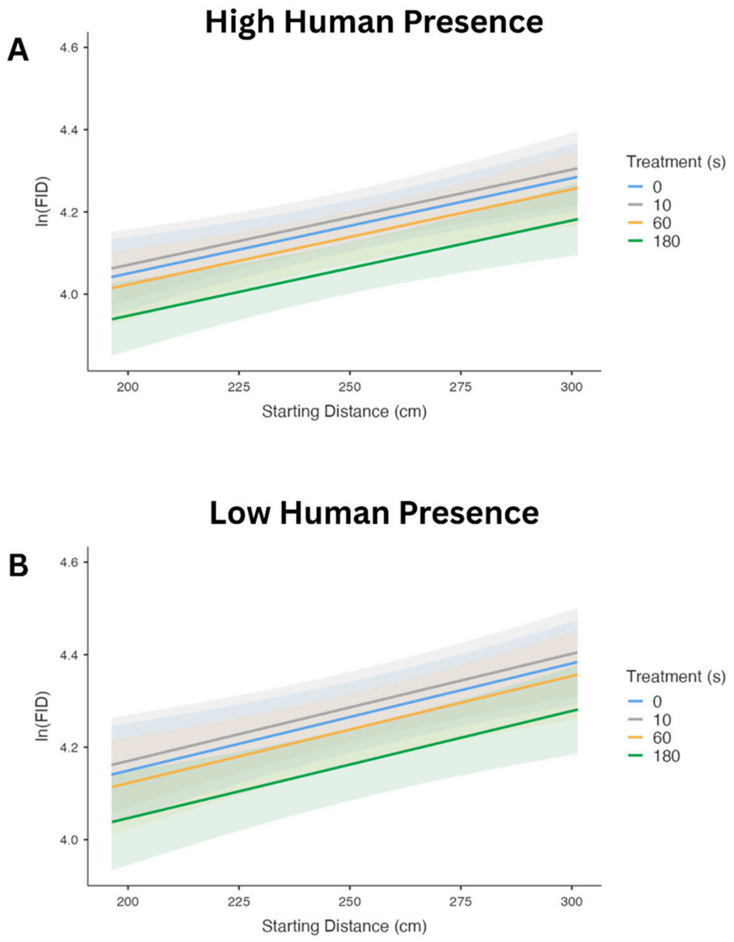

Figure 5. High (**A**) vs. Low Human Presence (**B**) Sites: Interaction plot of marginal mean ln(flight initiation distance (FID)) cm (±95% confidence intervals) and starting distance comparing the relationships of the three different treatment sizes. Each colored line represents a different treatment. Colored bars surrounding the trendlines are 95% confidence intervals.

4. Discussion

These results have potentially important implications for protecting marine environments. In all cases, we found that the level of human presence at a site explained more variation than MPA protection status, suggesting that it is not just the type of human activity that affects fish, such as benign versus fishing activities, but the sheer amount of human exposure alone that more strongly influences risk assessment [27]. Our results indicate that prior experience with humans significantly influences a fish's response to a snorkeler. The patterns we observed suggest that repeated, long-term exposure to benign human disturbance reduces antipredator responses to future threats and decreases the time spent before normal behavior resumes. In less-frequented human sites, the increased antipredator behavior suggests heightened risk assessment and unhabituated fear response to humans. Previous studies have found similar evidence that long-term human exposure can reduce antipredator behavior in fish [30,31].

When fish were exposed to the 10 s, 60 s, or 180 s treatments, they spent significantly more time displaced from their core territory than fish in the control treatment, indicating that any level of human disturbance elicits an immediate antipredator response, which aligns with the results of former studies that demonstrate that fish behavior is altered as a direct response to human presence [12–14]. Such interactions may redirect energy away from fitness-enhancing behaviors, such as foraging or mating, and toward increased vigilance [11,15,16]. However, this initial startle experienced by fish diminished as they spent more time with snorkelers, resulting in o reduced fear responses.

Interestingly, fish exposed to the 180 s treatment spent significantly less time displaced from their core territory during snorkeler exposure than fish subjected to the 10 s treatment, tolerated closer approaches by non-human threats, and had shorter post-flush latencies to return after their flush. These results indicate that damselfish developed tolerance to human exposure and reduced their antipredator behavior in response to longer treatment times. Importantly, this tolerance developed rapidly to humans after short-term interactions lasting no more than 180 s, yet we found that 60 s of human exposure was insufficient to induce tolerance in fish or alter antipredator behavior. This rapid desensitization from our snorkeler treatment reflects changes in antipredator behavior observed at long-term scales in marine systems [30,31], and mirrors similar reduced antipredator responses observed in terrestrial animals exposed to repeated non-threatening human presence [9,25,27–29]. Furthermore, the pattern of short-term desensitization we found here may have important implications for survival, because human presence has been associated with decreased responses to natural predators [9,25]. These findings suggest that even short exposure to humans could compromise fish vigilance and increase vulnerability during subsequent interactions with predators. Similarly, reduced antipredator responses to humans following both short and long-term interactions could increase their susceptibility to fishing or other harmful interactions with ecotourists. Comparable patterns of short-term desensitization could be found across taxa, highlighting the importance of considering human-induced behavioral changes when evaluating the survival and protection of such species.

There was no significant difference between the control treatment and other treatments for either FID or latency to return post-flush. This is likely because the control was not a perfect control, as we were still visible to the fish and influenced its behavior, despite our acclimation period from >2 m away [13]. This finding may also have potential implications for ecotourism, as even in trials where observers remained within 2 m of the fish, their presence still induced such strong behavioral responses comparable to those observed in the float treatments. Hence, even more distant interactions with humans may alter fish behavior. However, we observed that the effects of human presence attenuated as treatment duration increased.

The number of conspecifics also had a significant effect on the proportion of time spent displaced from the core territory during the treatment and on the post-flush latency to return. This pattern may suggest either a "safety in numbers" effect [61,62] or intraspecific competition for territory [63]. Similarly, the percent of hard substrate at a site also affected the proportion of time spent displaced from the core territory during the treatment, likely because greater coral cover could create more refugia for the fish [46].

Fish size explained significant variation in FID, with smaller fish tolerating closer approaches. This did not align with our initial expectations that larger fish should feel more secure due to their size [64,65], and thus allow a closer approach. However, it aligns with previous findings that larger parrotfish (family Scaridae) [66] and dusky damselfish [44,46] had greater FIDs, as well as a meta-analysis on fish FIDs in response to humans [52]. In the field, we saw smaller fish having lower alert distances (the distance at which they become alert to an approaching threat) [16]. This suggests that smaller, younger fish take more risks [46]. This may suggest that awareness of threats is a learned or acquired skill that develops as fish age and grow larger [67], or may reflect that the cost of fleeing is higher for smaller fish [34].

Starting distance was, as expected, significantly associated with FID; fish across all treatments tolerated closer approaches at lower starting distances. This pattern aligns with the idea that threats from farther away are associated with greater FIDs [57,58], possibly to reduce the costs of ongoing monitoring [57].

Notably, we detected significant observer effects. We suggest this may reflect differences in the three observers' heights. Our tallest observer (179.7 cm) affected fish significantly differently than did our shorter two observers (heights: 157.5 cm, 160.0 cm), with fish exposed to the tallest observer spending more time displaced from the core territory during the float. While we cannot conclusively determine the cause of this relationship, predator length is an important determinant of risk, and larger predators are more threatening [68]. Additionally, reef fish adjust the strength of predator avoidance and escape responses based on the size and threatening posture of their predators [69]. Specifically in damselfish, individuals subjected to different-sized predators vary in their FID responses [45]. Previous studies focused on the impact of different-sized threats, yet none have examined the effect of different-sized humans. Taller humans may be more disturbing to fish than shorter humans; this is a novel insight that requires future work.

The implications of these must be further studied, especially since damselfish have a major influence on the health of coral reef communities. They are herbivores that, through their grazing and algal farming, enhance coral health by reducing the accumulation of harmful substrates on coral surfaces and deterring corallivorous fish [70–72]. However, damselfish also indirectly promote algal biomass and productivity [73–75]. Nonetheless, damselfish play a key role in the ecosystems in which they live, shaping community composition and impacting coral reef dynamics. As such, any change in damselfish behavior may significantly impact the coral reef community and its dynamics. Thus, it is ecologically important to determine how damselfish antipredator behavior may change across different magnitudes of human interactions. In addition, the patterns seen in this work may translate to other fish species, suggesting that human-induced changes to antipredator behavior can expand beyond a single species and influence coral reef fish assemblages, which are known to play a major role in coral reef health [76].

Our results have important implications for the protection of marine ecosystems. Fish in coral reefs are increasingly surrounded by tourists [1–4]. As we have demonstrated here, even brief, seemingly benign human interactions can directly inhibit and leave a lasting impact on fish antipredator behavior. While ecotourism may affect behavior, these potentially negative effects may be over-reported or influenced by a researcher's personal opinions [77]. Nonetheless, we suggest that the results of this study could help develop ethical guidelines for ecotourists and inform policy decisions on MPA management [35]. When evaluating the effectiveness of MPAs, our results imply that we should place more focus on the level of human presence in addition to no-take regulations. Our data suggests that behavioral disturbances could be reduced by establishing off-limit zones in sensitive reef areas [78], enforcing tourist capacities at times of the day when fish are more active or vulnerable [79], or limiting the duration of snorkeler interactions with fish [80]. Based on our findings, it may be optimal for a snorkeler to spend a maximum of 60 s with a given fish, so as to prevent changes in antipredator responses. Given that the level of human presence at a site explains more variation in damselfish antipredator behaviors than protection status, our results support the need to manage human activities in MPAs [35] to prevent disruptions and alterations to the fish behaviors, which may have cascading impacts for coral reef communities.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d18050267/s1, Table S1: Omnibus results from a permutation-based linear model examining MPA or not as a factor explaining variation in the proportion of time dusky damselfish were displaced from their territories during snorkeler exposure treatments' Table S2: Parameter estimates from a permutation-based linear model examining MPA or not (reference "N") as a factor explaining variation in the proportion of time dusky damselfish were displaced from their territories during snorkeler exposure treatments; Table S3: Pairwise comparisons for treatments from the permutation-based linear model examining MPA or not as a factor explaining variation in the proportion of time dusky damselfish were displaced from their territories during snorkeler exposure treatments; Table S4: Omnibus results from a general linear model containing MPA or not as a variable examining factors explaining the variation in FID of damselfish; Table S5: Parameter estimates from the general linear model containing MPA or not (reference "N") as a variable to explain the variation in FID; Table S6: Post hoc comparisons for the different treatments from the general linear model containing MPA or not as a variable to explain the variation in FID; Table S7: Omnibus results from the general linear model containing MPA or not as a variable examining factors explaining the variation in post-flush latency to return time; Table S8: Parameter estimates result from a general linear model that includes MPA or not (reference "N") as a variable to explain variation in post-flush latency to return time. Table S9. Post hoc comparisons for the different treatments from the general linear model containing MPA or not as a variable to explain the variation in post-flush latency to return time.

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