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Using Drone Footage to Analyze the Effect of Diver Presence on Juvenile Manta Ray Behavior

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Highlights

What are the main findings?

- Diver presence significantly influenced juvenile manta ray behavior in a nursery habitat, leading to an increase in avoidance behaviors and a higher likelihood of having their cephalic fins unfurled.
- Individual mantas showed a significant difference in behavioral response to diver presence.

What are the implications of the main findings?

- These findings indicate that marine tourism could have a negative effect on juvenile manta rays by increasing the energetic and time costs of mantas performing avoidance behaviors in the presence of divers and reducing energy acquisition for natural behaviors such as feeding, transiting, and socializing.
- Our results show that quantifying the behavioral responses and energetic costs of juvenile manta rays to human presence is critical for developing sustainable management practices, particularly for populations that may be more vulnerable to the effects of marine tourism activity.

Abstract

Manta ray tourism has become a multi-million-dollar industry proposed as a conservation tool in recent decades; however, its impacts remain unclear. We use drones and Markov models to quantify the effects of diver presence on a juvenile population of the recently described Atlantic manta ray (*Mobula yarae*) off the coast of Florida. We contrast diver effects on behavioral states (avoidance, feeding, and neutral), examine the responses of individual manta rays, and estimate the energetic costs of diver presence. Diver presence significantly influenced manta ray behavior. Manta rays spent 37% of their time avoiding divers, with neutral and feeding manta rays having an increased probability of transitioning to avoidance states in the presence of divers. We found a significant difference in the proportion of time individual manta rays spent in avoidance, with some individuals being highly avoidant (up to 70%), while others were less affected by diver presence (<20% avoidance). While wingbeat frequency did not change in the presence of divers, manta rays with divers spent significantly more time with their cephalic fins unfurled. Our findings suggest that tourism could negatively impact this small, vulnerable population, making it unsuitable for development. We recommend similar behavioral and kinematic assessments to guide sustainable wildlife tourism management.

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Keywords: ethology; *Mobulidae*; wildlife tourism; endangered species; Florida

1. Introduction

The growth of marine tourism over the past few decades has had profound direct and indirect impacts across local communities and conservation efforts around the world. As a developing industry, marine tourism has created economic support in coastal communities, while also providing an opportunity for sustainable natural resource management for marine species [1]. However, the increased demand for close experiences with charismatic megafauna has made quantifying the effects of marine tourism on both target and non-target species a critical management concern [2]. The current rate of marine tourism activity is exceeding the ability of tourism operations to implement safe and suitable management practices [2,3]. It is crucial to develop sustainable tourism initiatives, especially when imperiled species are involved

Previous studies on various marine megafauna species have indicated that tourism can have negative effects on species' natural behavior [2,4–7]. Some species of dolphins (*Tursiops* spp.), for example, are known to experience a significant reduction in time spent foraging, socializing, and resting when interacting with boats [8–13]. A recent study utilized drones to analyze a whale shark population subjected to frequent tourism interactions, evaluating changes in their behaviors with and without human presence. The results suggest that the increased energy expenditure required for avoidance behaviors may have long-term consequences on populations subjected to frequent tourism activity [14]. Impacts on behavioral budgets caused by wildlife tourism are still poorly understood and can reduce time allotted for energy acquisition, leading to long-term effects on population dynamics related to fitness, reproduction, and physiological stress [14,15].

Manta rays are of particular interest in marine tourism due to their social, somewhat predictable nature and their tendency to gather at coastal aggregation sites [1]. As filter feeders, manta rays often aggregate in areas of high prey abundance where zooplankton is concentrated by tides or currents [16], as well as cleaning stations, where fish remove parasites and dead skin off manta rays [17,18]. While aggregative behavior is beneficial for tourism, it increases the vulnerability of manta rays to human disturbance. Manta rays exhibit one of the most conservative life history strategies (e.g., low fecundity, late maturity) of all elasmobranchs, making manta rays particularly susceptible to overexploitation [19]. Manta ray populations are experiencing alarming declines worldwide [20] largely caused by overfishing, both as bycatch [21], and targeted harvest for meat and the gill plate trade [22].

Tourism has been promoted as a potential sustainable strategy for reducing manta ray exploitation and supporting local communities [23]. Manta ray tourism exists across more than 25 countries and contributes an estimated 140 million USD annually to the global economy [17]. Despite the rapid growth of manta ray tourism, there is a lack of knowledge regarding how tourism interactions influence manta ray natural behavior, population dynamics, and overall health. Manta rays are highly intelligent and exhibit complex inter- and intraspecific social behaviors [24,25], raising questions about the potential influence of individual personalities on behavioral responses to human presence. One of the first studies addressing the effects of tourism on manta rays used underwater video footage to document manta ray behavioral responses to divers and snorkelers at popular dive sites in Mexico [26]. Since the authors used opportunistic footage collected during active tourism operations, they were unable to evaluate the behavior of manta rays in the absence of divers. While diver-collected footage provides valuable insights about the disturbed

behavior of manta rays, quantifying undisturbed behavior remains essential for comparison with tourism-exposed individuals. In contrast, a recent study used drones to track traveling, feeding, and resting manta rays in Florida, establishing behavioral baselines and associated energetics for undisturbed manta rays [27], but lacked a direct comparison with disturbed manta rays.

Occurrences of juvenile manta ray seasonal aggregations on the coast of Florida have raised questions about their potential for wildlife tourism and management options [28]. Juvenile manta rays in the south Florida nursery habitat belong to the recently described third species of manta ray, *Mobula yarae* [29]. While manta ray tourism does not yet exist in Florida, many stakeholders have proposed initiating tourism operations [30]. Understanding how this vulnerable population of juvenile manta rays would respond to tourism is key for conservation in the region. In this study, we aim to evaluate the behavioral responses of the juvenile manta ray population in Florida to divers. Using drone technology and ethological analysis, we quantify the differences between undisturbed (without divers) and disturbed manta ray (with divers) behavior for the first time, incorporating individual variation and possibly elucidating personalities. Our specific objectives are to: (1) quantify how the presence of divers affects the natural behaviors of manta rays; (2) determine if individual manta rays show different responses to divers; (3) examine the behavioral responses of manta rays to divers based on their kinematics (wingbeat frequency and cephalic fin movements). While the divers in this study were researchers collecting data, they serve as a proxy for how manta rays may react to tourists.

2. Methods

2.1. Study Site

Aerial footage was collected opportunistically on Florida Manta Project boat surveys on the Atlantic coast of South Florida from October 2023 to January 2025 (see detailed methodology in [28]). Boat surveys were conducted between St. Lucie Inlet (27°09′47″ N, 80°09′27″ W) and Boynton Beach Inlet (26°32′44″ N, 80°02′31″ W), Florida, USA (see Figure 2 in [28]). This area has been described as a nursery habitat for juvenile manta rays [28] who feed and cruise in the shallow, nearshore waters. Manta rays are seen year-round in the nursery habitat, but most sightings are between July and December [31]. No reef cleaning stations have been located for manta rays in Florida and they are rarely observed by SCUBA divers [31]. These manta rays often encounter boats and fishers, with boat strikes and fishing line entanglement observed regularly [28]. However, while these manta rays sometimes encounter snorkelers, people swimming with manta rays in the nursery habitat is not a common practice [31]. All manta rays in this study were confirmed to be juvenile by small size ($\leq$3 m) and/or immature claspers that did not extend past pelvic fins.

2.2. Video Collection

We used a drone (DJI Mavic Pro 2 and DJI Mavic 3, Shenzhen Dajiang Baiwang Technology Co., Ltd., Shenzhen, China) with a polarizing filter to collect videos of manta rays swimming. Drone flights were conducted approximately 200 m from the shore at altitudes of approximately 100 m to maximize our search area. When a manta ray was located, we lowered the drone (>15 m) such that all parts of the animal's body were clearly visible in the field of view. No noticeable changes in manta ray behavior were observed while lowering the drone altitude. Other studies have found that drone altitude did not affect stingray behavior [32]. We then recorded a video of the manta ray swimming in its 'natural state' or 'without diver' (i.e., before a diver entered the water or the boat approached) for ~ one minute. For each clip, the manta ray's natural behavior was classified

as 'traveling', 'feeding' or 'resting' (see Fong et al. [27] for description of behaviors). After filming of the natural or without diver behavior was complete, the boat was positioned ahead of the manta ray's direction of travel and then either placed in neutral or the engine turned off. Next, the drone filmed while a researcher (snorkeler) entered the water, swimming towards the manta ray and making a dive under the manta ray to collect a photograph of the unique spot pattern on the manta rays' ventral surface (with diver). Time between filming without a diver and with a diver taking videos averaged 6 min (±SD 4.6 min). We attempted to get with and without diver footage of most manta rays observed on boat surveys during the study period. However, sometimes logistics (e.g., a manta ray about to swim into a vessel exclusion zone) or other research priorities (e.g., tagging) prevented collecting footage. Not all footage was usable for behavioral analysis (see below).

2.3. Video Analysis

We analyzed videos by hand using Windows Media Player in one-second intervals. All videos were analyzed by a single observer (MGG). Observations were corroborated by the researcher (JP), who collected the videos in the field. We shared a subsample of ten random videos with a researcher (AO) who had not seen the videos to check for observer bias on individual behaviors and behavior states. We only analyzed footage where visibility allowed us to count individual wingbeats, assess cephalic fin positions (furled or unfurled), and identify changes in manta ray behavior. We considered cephalic fins as "unfurled" if at least one cephalic fin was open and visible during a frame. When cephalic fins were not visible, their position was recorded as "unknown". We recorded 62 videos of manta rays feeding or transiting independently before encountering a diver (without a diver). The remaining 100 videos documented interactions where divers attempted to collect photo identification samples from individual manta rays (with a diver). Our analysis included 162 drone video clips, ranging in length from 23 to 255 s (mean + SD: 68.88 + 41.58). In total, our dataset contained 3.16 h of drone footage. When possible, each clip was assigned to individual manta rays according to their photo ID.

We constructed ethograms using one-second intervals as a sampling unit. We recorded wingbeats, cephalic fin movements (opening and closing), and behavioral changes on a second-by-second basis. We identified individual behaviors based on the catalog previously established for the species by Gómez-García et al. [26] and the kinematic description of behaviors published by Fong et al. [27]. Our analysis included six previously documented manta ray behaviors: 1. acceleration, 2. course changes, 3. defensive/avoidance movements, 4. directional swimming, 5. feeding, and 6. resting. We observed four instances of non-feeding somersaults, described as "avoidance somersaults" by Gómez-García et al. [26], and recorded them as "avoidance" for simplicity. To simplify modeling and improve interpretability, we grouped behaviors into three broader behavioral states: Avoidance, Feeding, and Neutral (Table 1). Feeding behaviors are predominantly ram feeding at the site, and hard to confidently determine through drone footage. We relied on cephalic fin positions (unfurled, mouth open) as well as on-site observatory to determine if a video showed a manta ray feeding or not, but caution must be taken for possible errors regarding feeding occurrence. It is worth noting that divers may have been present in the water, but not recorded as "present" until they appeared in the video frame. We recorded diver presence in our ethograms as soon as divers were visible in the video frame to reduce observer bias as much as possible.

Table 1. Behavior catalog of the juvenile manta ray population observed in West Florida. We show grouped individual behaviors under the "Behavioral State".

Behavior	Behavioral State	Description
1. Acceleration	Avoidance	The focal manta ray suddenly increases its speed. Speed increase is accompanied by noticeably wider and quicker wingbeats. Or the manta ray performs a single wing beat, leaving its fins curved upwards in an "Omega-like" shape (ω)
2. Defensive/Avoidance movements		Focal manta ray changes direction suddenly in response to a source of stimuli (A diver, fish, another manta ray, a boat, etc.). Sometimes the manta ray can perform a downwards somersault, "avoidance somersault", exposing its ventral side towards the stimuli and swimming away.
3. Course Changes	Neutral	Focal manta ray gradually changes its course either in a wide or sharp turn without significantly increasing its current speed or performing sudden movements
4. Directional swimming/traveling		Focal manta ray remains swimming in a straight or semi-straight line. Also called "transiting" or "cruising".
5. Resting		Focal manta ray appears to be immobile, typically facing into a current. Pectoral fins are moving slightly. Wingbeat frequency varies. Sometimes the manta ray sinks noticeably due to the lack of horizontal movement.
6. Feeding	Feeding	Focal manta ray appears to be feeding. Cephalic fins must be unfurled. Manta ray can feed while swimming in a straight line or in circles with frequent turns to remain in the same area or performing backwards somersaults.

We calculated the proportion of time each manta ray spent in each behavior or behavioral state by dividing the duration of each behavior by the total length of the ethogram. Similarly, we calculated the proportion of time the cephalic fins remained open or closed during each behavior for every ethogram.

Markov models are a statistical tool that models the changes in a sequence of events by estimating the provability of the event or "state" to remain constant or transition to a different state [33,34]. By using transition matrices, ecologists can examine the changes in animal behaviors under different scenarios and evaluate causes of the observed behavioral transitions [12,26]. We modeled the behavioral sequence of manta rays for each ethogram to evaluate the effects of diver disturbance using a discrete-time stochastic first-order Markov chain:

$$\gamma_{ij} = Probability\ (S_t = j | S_{t-1} = i)$$

where entries for the 3×3 transition matrix were defined by the probability of transitioning from state (S) i to state j at time t (seconds). Initial state distributions were calculated using our field observations for each i behavior state by

$$\delta_i = Probability\ (S_1 = i).$$

To assess the effect of diver presence on natural manta ray behavior (Objective 1), we modeled the entries of a transition matrix Γ using a multinomial logit link function. We treated the transition probabilities of manta ray behavioral states as response variables and diver presence/absence as a binomial categorical predictor, where $w_t = 0$ indicated no divers at time t and $w_t = 1$ indicated diver presence following the next formulation:

$$\gamma_{ij}{}^{(t)} = \frac{exp\ (n_{ij})}{\sum_{k=1}^{N} exp\ (n_{ik})}\ \eta_{ij} = \{\beta_0^{ij} + \beta_1^{ij} w_t,\ if\ i \neq j\ 0,\ otherwise$$

This approach generated two sets of transition probability matrices: Γ^1 for manta rays in the absence of divers and Γ^2 for manta rays interacting with divers. Each non-diagonal entry represents the probability of a manta ray transitioning to a different behavioral state in the next step (one second later), while each diagonal entry indicates the probability of remaining in the same state. Thus, a transition probability does not reflect the likelihood of an individual recorded initially in state 1 eventually moving to state 2; rather, it represents the probability that an individual in state 1 at a given time step will transition to state 2 in the next.

We implemented a model within a Bayesian framework using the rstan package [35] in the R programming environment [33]. We chose β_0 and β_1 following [34,36] and their successful application in analyzing behavioral effects in marine species [26,37]. To account for uncertainty in the statistical distribution of manta ray behavior, we specified diffuse prior distributions for β_0 and β_1 as follows:

$$\beta_0 \sim N(0,1)\ \beta_1 \sim N(0,1)$$

We tested model convergence by inspecting posterior trace plots. We further assessed the effect of diver presence on manta ray behavior by analyzing the distribution of beta coefficients. A covariate effect was considered significant if the 95% credible interval did not include zero across all posterior draws, indicating a consistent pattern across posterior samples [38].

To assess Objective 2 (individual manta ray response to divers), we looked for significant differences in the proportion of time spent at each behavior according to diver presence/absence and individual manta ray ID using analysis of variance (ANOVA) and Tukey tests as needed. Similarly for Objective 3, we evaluated the proportion of time cephalic fins remained open or closed by diver presence and behavior. Additionally, we evaluated the number of wing beats per behavior following Fong et al. [27] methods. Finally, we compared wingbeat frequencies of manta rays before and after encountering divers using paired *t*-tests by averaging wingbeat frequencies of individual manta rays with ethograms before and after encountering divers.

3. Results

Data Analysis

We analyzed 162 ethograms and were able to successfully identify 27 individual manta rays through photo identification (93% of samples with ID, 10 ethograms with unidentified individual manta rays). The frequency of individuals through multiple ethograms ranged from 1 to 17 (5.62 + 4.39). Note that more than one ethogram could have been taken for the same manta ray in a single sampling day. A juvenile male, identified by the Florida Manta Project as Manta 188, was the most observed manta ray, appearing in 7 ethograms prior to diver interaction and 10 ethograms during diver interactions (Supplementary Table S1). The observer bias analysis showed an agreement between observers of 88% for individual behaviors and 89% for behavior states. Most disagreements were caused when distinguishing "avoidance" from other behaviors.

The average time at each behavior state for manta rays without divers was 52% for feeding and 48% for neutral. The proportion for manta rays with divers was 37% for avoidance, 17% for feeding, and 45% for neutral states (Figure 1). Manta rays displayed a higher number of individual behaviors when interacting with divers (Supplementary

Figure S1). The average proportion of behaviors in the "avoidance" state was 67% avoidance movements and 33% acceleration.

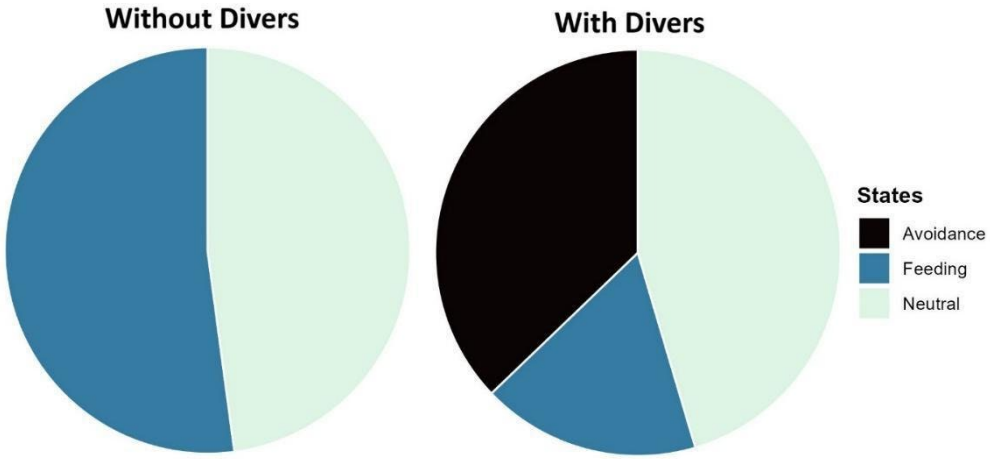


Figure 1. Proportion of time manta rays spend at each behavior state on average. The left plot corresponds to videos of manta rays without divers. The right plot corresponds to videos of manta rays with divers.

We show a summary of the important results and statistical significance in Table 2. The proportion of time manta rays spent on each behavior and state was significantly different with or without divers. Paired comparisons of specific behavior differences and significant results are shown in the Supplementary Table S2. For behavior states, paired comparisons showed significant differences in the percentage of time spent at feeding and avoidance states, and neutral and feeding states when in presence of divers (Table 3).

Table 2. Results of analysis of variance (ANOVA) tests for different responses and predictor variables of manta ray behavior. Asterisks (*) show significant results ($p < 0.05$). Post hoc test results are shown in the Supplementary Material.

Response	Predictor	Divers	*p*
% time	Behavior	No *	<0.01
		Yes *	<0.01
% time	States	No	0.62
		Yes *	<0.01
% time	Lobes	No *	0.016
		Yes *	<0.01
% time	Lobes (excluding feeding)	No *	<0.01
		Yes *	<0.01
Wingbeat	States	No *	<0.01
		Yes *	<0.01

Table 3. Paired comparisons between % of time spent at each behavior state. Diver presence/absence is shown under "Divers". Asterisks (*) show significant results ($p < 0.05$).

Paired Comparison States	Divers	*p*
Neutral-Feeding	No	0.91
Feeding-Avoidance	Yes *	<0.01
Neutral-Avoidance	Yes	0.09
Neutral-Feeding	Yes *	<0.01

Markov models achieved convergence and showed expected variability, with no clear pattern for negative or positive beta values according to covariate effects (Supplementary Table S3). The initial state distribution, derived from the mean posterior draws for each behavioral state, showed that neutral behavior (State 3) was the most likely starting behavior (57% probability), followed by feeding (State 2, 40%) and avoidance (State 1, 3%). Diver presence/absence significantly influenced 8 out of the 18 transition probability distributions (Figure 2). Specifically, diver presence had a significant effect only on transitions from feeding to avoidance and from neutral to avoidance. We observed the opposite effect for diver absence over the same transitions. In other words, diver presence caused a significant increase in transition probabilities to avoidance states in feeding or transiting manta rays, while their absence significantly reduced the probability of these transitions occurring. Other significant transitions influenced by the absence of divers are detailed in the Figure 2 and Supplementary Table S3.

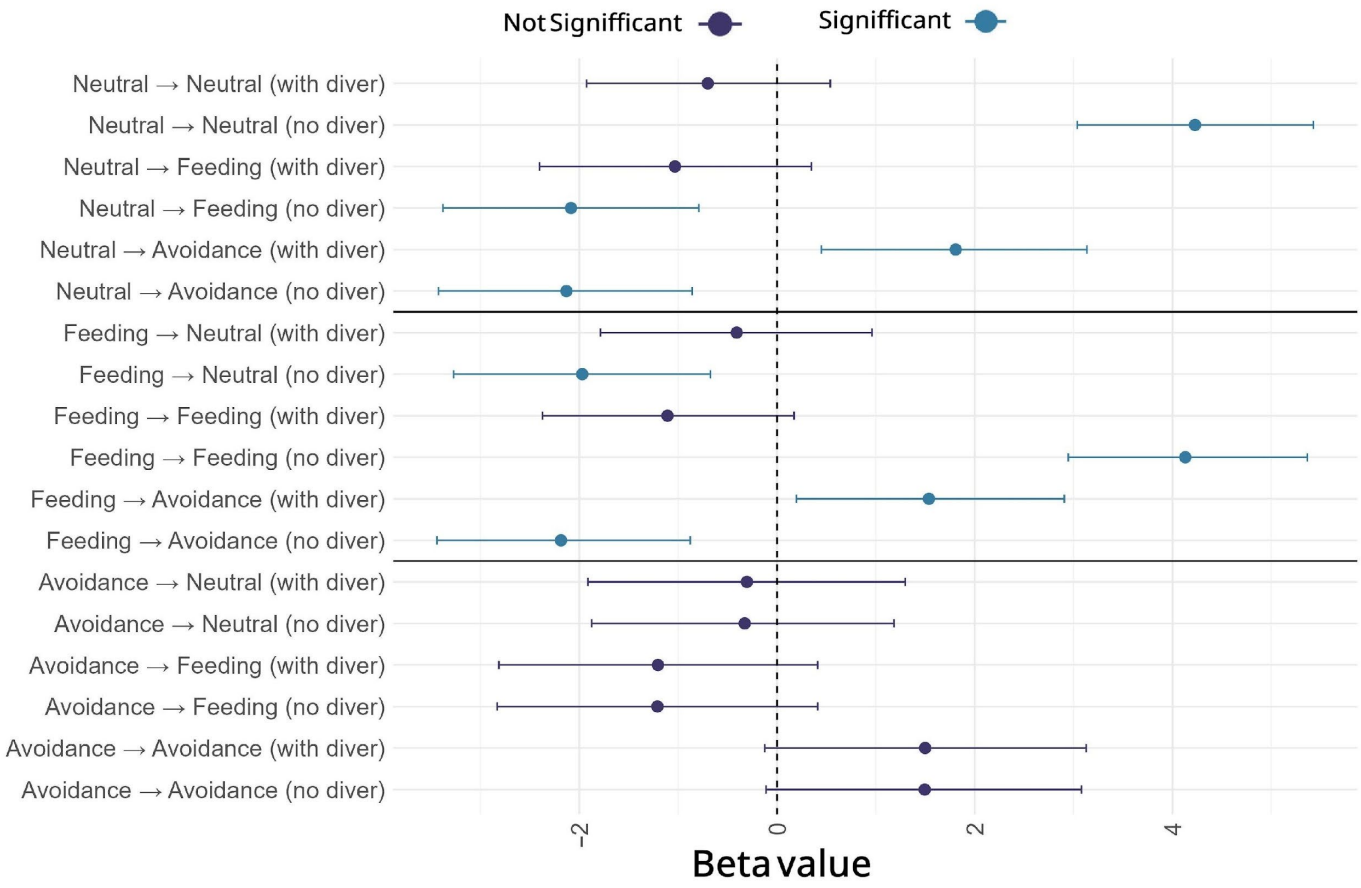


Figure 2. CI plot of Bayesian model output. The Y axis shows the transition probability matrix entry. Covariate effect (diver presence) is shown in parentheses. The X axis shows model output as beta values. Error bars represent the 95% credible intervals. Transitions whose 95% credible interval posterior distribution did not cross 0 can be considered significant. Significant transitions are shown in light blue.

At the individual level, the proportion of time spent in avoidance with divers was significantly different between individuals, with some spending around 70% of their interactions in avoidance while others spent below 20% (Figure 3). No other behavioral states exhibited significant differences across individuals.

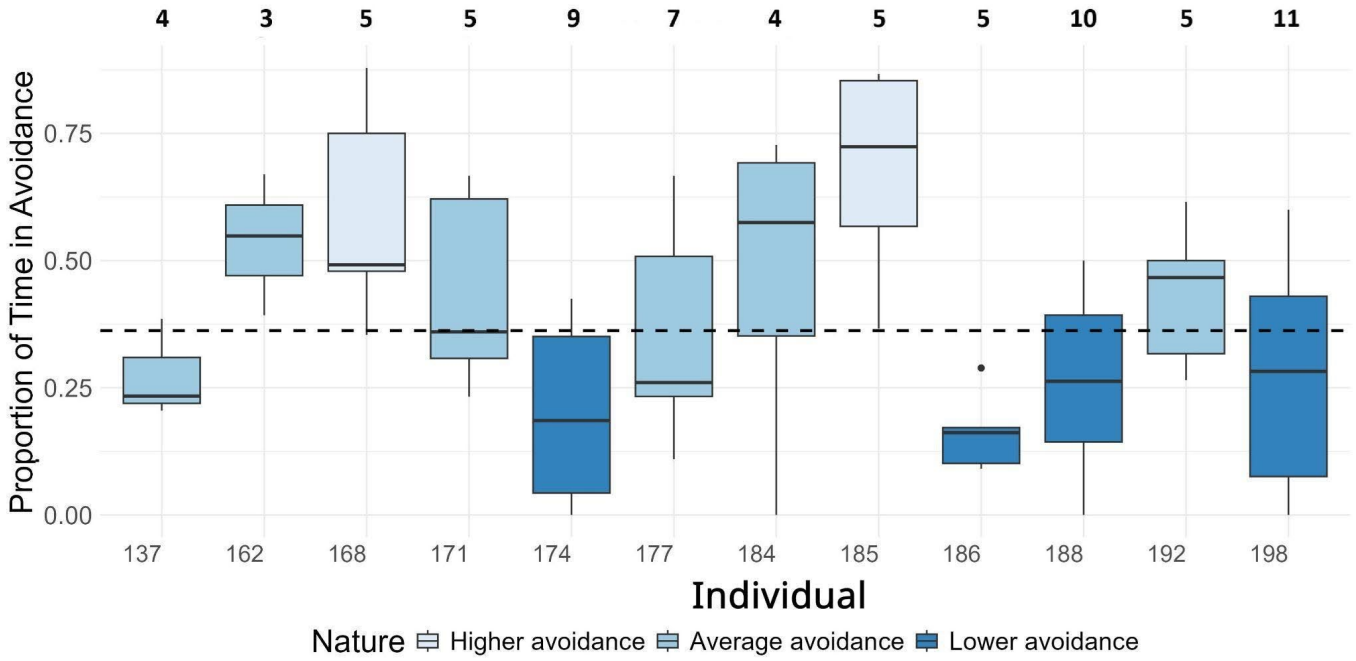


Figure 3. Differences in individual manta ray proportion of time spent at the avoidance behavioral state when in presence of divers. Colors represent whether individuals showed significantly higher avoidance (light blue), lower avoidance (dark blue) or were not different from the mean proportion of time in avoidance (medium blue). Bold numbers at the top show the sample size for each individual manta ray. The mean of the percentage of time spent in avoidance by all manta rays is shown as a black dashed line.

We found significant differences in the proportion of time lobes remained open or closed in the presence of divers ($p < 0.01$). Manta rays kept their cephalic fins unfurled more frequently in the presence of divers when in neutral or avoidance states (Figure 4a). This effect persisted even after excluding feeding manta rays (cephalic fins always unfurled, Table 2) from the analysis. When comparing individual behaviors, manta rays with divers spent more time with their fins furled during directional swimming but more time with fins unfurled during both course change and feeding (Figure 4b). In contrast, manta rays without divers spent more time with their cephalic fins furled during directional swimming and resting behaviors and exclusively unfurled during feeding (Figure 4b).

Wingbeat frequency varied significantly by behavior and behavior state, especially in the presence of divers (Supplementary Table S4). Manta rays with divers showed the highest wingbeat frequency during feeding (0.35 + 0.1 Hz), followed by avoidance (0.28 + 0.16 Hz) and neutral (0.25 + 0.11 Hz) states (Table 1, Figure 5). Manta rays without divers also showed the highest frequency during feeding (0.40 + 0.07 Hz), followed by neutral (0.23 + 0.1 Hz) (Figure 6). Wingbeat frequencies between individual behaviors also showed significant differences between certain paired comparisons (Supplementary Table S4). Course change wingbeat frequencies overlapped with most other individual behaviors, with and without divers, and only overlapped with directional swimming without divers (Figure 5). Regarding the comparison of wingbeat frequency with and without divers, we used 25 out of 26 individual manta rays, which had ethograms from before and after encountering a diver. The average wing beat frequency was not statistically different for manta rays before and after encountering divers ($t = -0.27$, $df = 24$, $p = 0.78$).

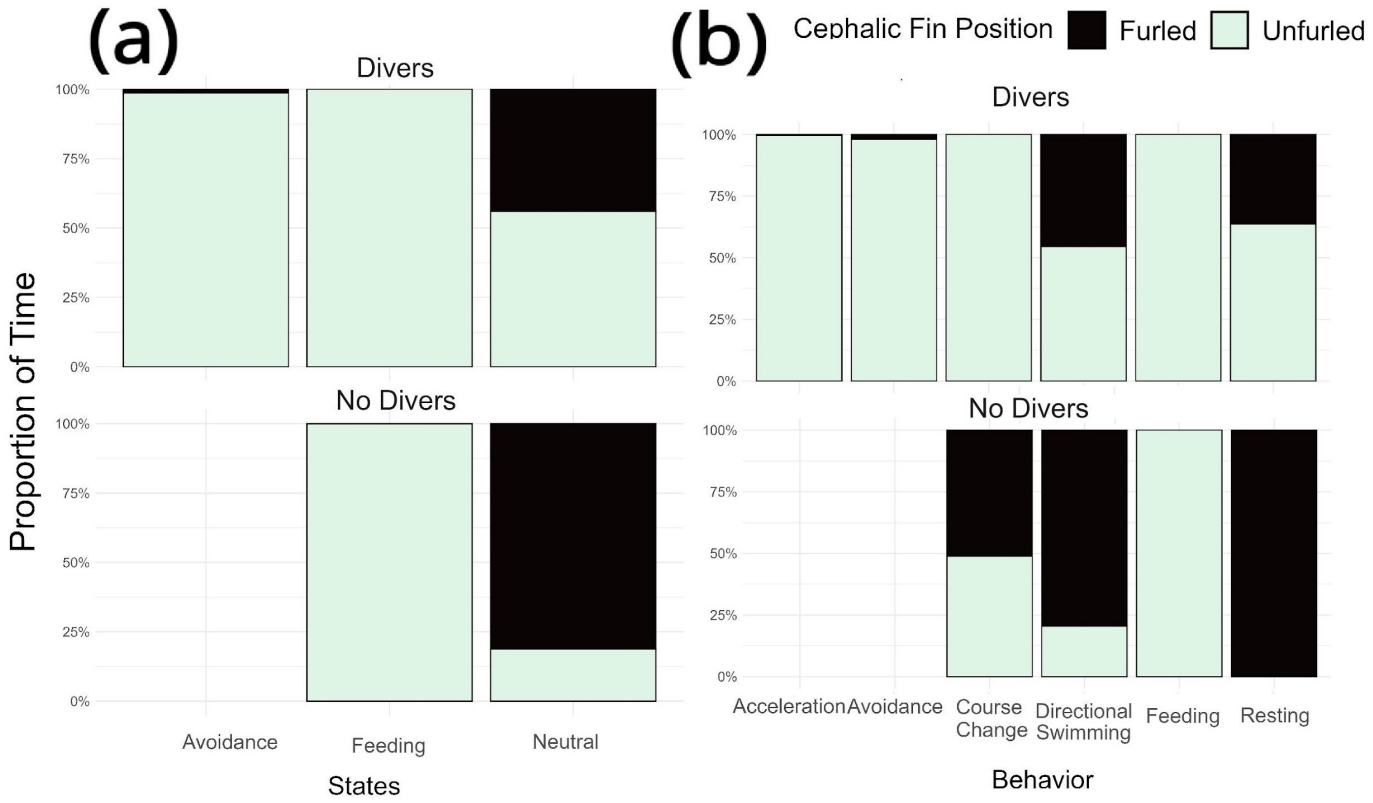


Figure 4. Proportion of time manta rays spend with their cephalic fins furled (dark color) and unfurled (light color) by behavior state (plot (**a**)) and individual behavior (plot (**b**)).

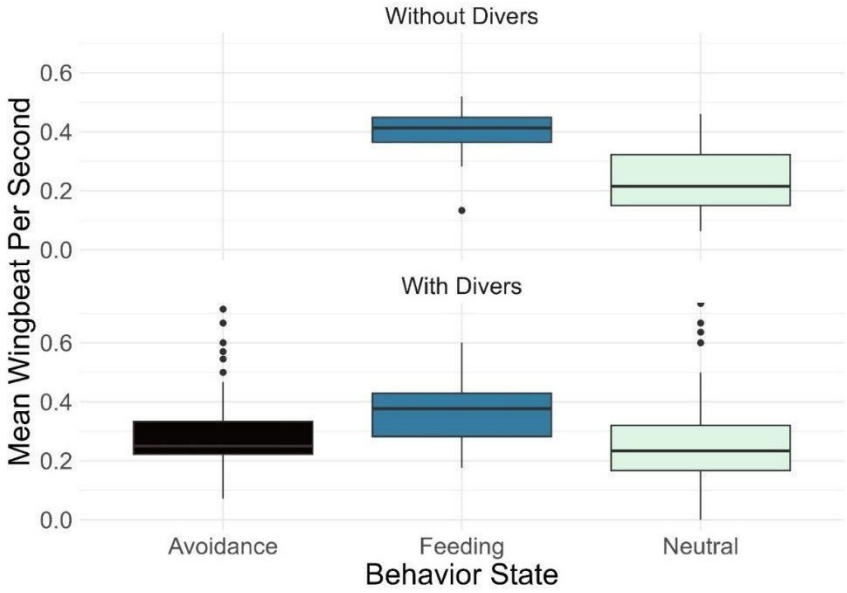


Figure 5. Mean wingbeat frequency by behavioral state. Results for manta rays recorded without divers are shown on top. Manta rays recorded while interacting with divers are shown on the bottom. The x axis shows the observed behavioral state, the y axis the mean wingbeat per second.

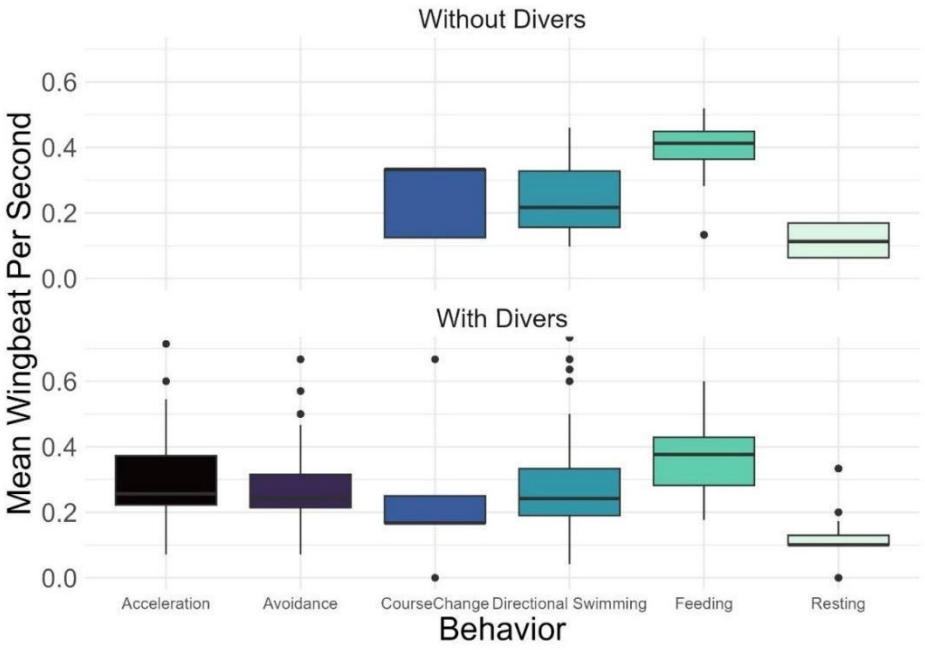


Figure 6. Mean wingbeat frequency by manta ray behavior. Results for manta rays recorded without divers are shown on top. Manta rays recorded while interacting with divers are shown on the bottom.

4. Discussion

Here, we use drone-gathered data in combination with analytical techniques and behavioral models to provide insights into the potential effects of wildlife tourism on juvenile manta rays in southeastern Florida. Drone technologies offer a unique opportunity to evaluate elasmobranch behaviors that are otherwise difficult to observe in the wild [39–41].To the best of our knowledge, this is the first study that directly compares natural versus disturbed manta ray behavior. We found that diver presence significantly alters juvenile manta ray natural behavior in a nursery habitat. This behavioral change was seen in the increased time manta rays spent in avoidance behaviors and the cessation of natural behaviors, such as feeding. Similar patterns for disturbed animals have been seen in dolphins [12] and whale sharks [14] during human encounters.

We only recorded divers as 'present' once they appeared in the video frame with the manta ray. This was to ensure we were capturing behavioral responses of manta rays to active divers. Thus, our results represent a minimum avoidance response to divers (37%), since manta rays may have begun avoidance behavior before the diver entered the frame. Future studies could fly at a higher altitude to capture a wider field of view; however, for our study we wanted to accurately quantify cephalic fin movements which required a lower flight altitude. Future studies could quantify how avoidance response to divers varies with approach distance, while taking into account confounding variables, such as in-water visibility and individual variation in manta behavior.

Individual variation played a significant role in behavioral response, with certain manta rays spending more time in avoidance behavior states than others. Florida Manta Project researchers have noticed differences in individual manta ray response to divers, with some individuals being more 'friendly' and others being highly avoidant [31]. Previous studies examining the role of personality in juvenile lemon sharks and Port Jackson sharks found consistent, individual variation in boldness, shyness, sociability, and stress reactivity, highlighting persistent behavioral traits across timescales [42–44]. These studies also suggest that baseline personality differences between juvenile sharks influence how quickly individuals become habituated to a stimulus, with bolder individuals habituating more quickly than those who were shyer [42]. Larger individuals with long-term exposure

to tourism may display less acute responses to divers due to acclimatization [26]. Further experimental studies on individual responses, coupled with direct measures such as hormonal stress [45], would help clarify the role of personality in manta ray behavioral responses.

Our study was conducted with researchers trained in understanding manta ray behavioral responses and who only interacted with manta rays in the water in groups of one to two people. Despite having extensive training and knowledge in manta ray behavioral ecology, researchers actively approached manta rays to gather specific data instead of engaging in passive interactions, a key component of reducing negative behavioral responses of manta rays to diver presence [46]. It is important to acknowledge that researchers in our study were acting as proxies for how manta rays could react to tourists in case tourism is implemented in the area. In many ways, researchers can be more invasive than tourists, having to approach quickly and closely to collect a ventral identification photo of the focal animal. At the same time, researchers approach in small groups of one to two divers, with less disturbance (e.g., kicking and splashing). They also know when to end an encounter if the animal is showing signs of stress. In contrast, tourist groups are typically larger, less experienced in the water and likely would enter the water repeatedly regardless of the animal's stress level. Therefore, we advise similar studies to keep our assumptions in mind when interpreting our results for different areas or species. Future research could investigate the effects of passive versus active interactions, the number of people in the water, the distance at which manta rays react to divers and the direction divers take to approach manta rays (i.e., front, side, behind) in relation to individual manta ray personalities.

Our study used leading frameworks for assessing energetic costs of tourism on manta ray behavior by using wing beat frequencies and cephalic fin movements [25,27]. Compared to the observational methods used in [25], our study provides a unique opportunity to view manta ray behavior before and after the presence of a diver using drone footage, allowing us to fully compare behavioral transitions from disturbed versus undisturbed states. Our results showed that diver presence significantly increased the amount of time manta rays spent with their cephalic fins unfurled, a behavior typically associated with feeding [26,47]. Manta rays may use their cephalic fins outside of feeding, with previous results determining that manta rays use their cephalic fins as sensory organs or for communication when engaging with conspecifics, cleaner fish, and human divers [25]. Our observations of an overall increase in the amount of time manta rays spent with their cephalic fins unfurled in the presence of divers could indicate that manta rays are engaged in an increased awareness and sensory state by examining a novel stimulus in their environment.

Similarly, our study found a significant effect of diver presence on wingbeat frequency in specific behavior states, particularly by increasing avoidance and acceleration behaviors. Acceleration and avoidance are high-cost behaviors, suggesting that human presence may put additional pressure on manta ray energy expenditure when they are already performing behaviors that require more energy [2,48]. However, previous studies in energy acquisition and disturbance of marine animals by tourism suggest that the higher energetic cost for animals stems not from the increased energetic demand of avoiding tourists, but rather from the reduction of energy acquisition by interrupting feeding [48]. Our results show evidence of interrupted feeding and clear behavioral differences in disturbed and undisturbed animals, suggesting wildlife tourism may have a negative effect on juvenile manta rays in coastal Florida. Further studies quantifying the energetic costs of tourism for manta rays, including elevated respiration and hormonal stress [45] would improve our understanding of tourism impacts. We suggest researchers and managers carefully consider the importance of our study site as a foraging ground for juvenile manta rays when developing research projects and management plans.

Previous studies have shown that manta ray populations have different responses to diver interactions according to their aggregation sites, with larger adult populations in cleaning stations being less affected than feeding or transiting manta rays [26]. For example, the manta ray population at the Revillagigedo Archipelago in Mexico, often observed at cleaning stations with good visibility, have a significantly reduced response to diver presence (7% avoidance response). In contrast, transiting manta rays from Banderas Bay, Mexico showed a higher proportion of avoidance behaviors that could be attributed to poor visibility, habitat use, or anthropogenic disturbances caused by the heavy boat traffic in the site [49]. Juvenile manta rays along the coast of southern Florida already face similar anthropogenic threats such as fishing line entanglement and boat strikes due to their proximity to shore [28] and showed a similar proportion of avoidance behaviors (37% in this study, 30% in Banderas Bay). Their strong site fidelity, often tied to urbanized areas, makes them especially vulnerable to additional pressures from tourism. Tourism can discourage manta rays from using key foraging grounds [20], which may be particularly harmful for juveniles repeatedly returning to disturbed habitats. Surveys indicate that only 30–50 individuals use this area annually [50], suggesting that sustained exposure to tourism could have long-term impacts on this small, resident population.

Given the avoidance responses to human interactions (this study), the increased effects of disturbances on juveniles within populations [51,52], and the life history traits of the manta rays [19], we do not suggest marine tourism as an effective management strategy for manta rays in Florida currently. Researchers in Florida have been consistently approached by the public inquiring about manta ray tourism operations, including individuals who suggest establishing unregulated light systems for attracting feeding manta ray at night, similar to tourism operations in Hawai'i [31,53]. A multidisciplinary framework was recently established for assessing the sustainability and appropriateness of wildlife tourism, which evaluates tractability, socioeconomic values, animal welfare and ecosystem impacts [54]. Our study can help assess factors within the animal welfare section, such as if foraging and energy budgets are affected. Future inquiries into sustainable tourism for marine megafauna, especially those that are endangered, should carefully consider this framework and how natural behaviors may be impacted.

5. Conclusions

We demonstrated that diver presence can have a significant effect on juvenile manta ray behavior and kinematics in Florida nursery habitat by comparing undisturbed and disturbed manta rays using drone technology. Our analysis showed evidence of increased manta ray avoidance responses to divers, with individual variation playing a role in the amount of time spent in avoidance and returning to natural behaviors, such as feeding and transiting. These results suggest that tourism activity can have implications for juvenile manta ray energy acquisition by reducing time spent feeding, restricting site fidelity, and reducing overall fitness. The use of drones is a novel approach to quantifying behavioral responses in marine megafauna, providing an opportunity to make direct comparisons of undisturbed and disturbed animals. Despite the advantages of capturing behavioral gradients, there are existing limitations to the use of drones. These include the inability to document subsurface behaviors or oceanographic factors influencing behavior, and limitations on continuous observation due to drone flight duration. Similar studies could be conducted at deeper manta ray aggregation sites (e.g., cleaning stations) by deploying remote underwater 360° cameras and comparing cleaning behavior in the absence and presence of divers. We encourage researchers and managers to consider and measure the effects of tourism on natural behavior. By doing so, long-term sustainable tourism practices can be

developed by allowing stakeholders to distinguish areas and populations where tourism operations could have minimal behavioral impacts on endangered marine megafauna.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/drones9110781/s1. Table S1: Individual manta ray ethogram sample sizes; Figure S1: Proportion of time mantas spent at each behavior; Table S2: Paired comparisons between individual manta behavior; Table S3: Outputs of transition matrix models; Table S4: Paired comparisons of wingbeat frequency between individual manta behaviors; Supplementary Video shows five ethograms and how the behaviors were analyzed second by second, can be downloaded at https://www.youtube.com/watch?v=oH6SAtd2VsU.

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