Received: 26 August 2024 | Revised: 23 October 2024 | Accepted: 24 October 2024
DOI: 10.1111/jfb.15991

REGULAR ARTICLE

JOURNAL OF FISH BIOLOGY fsbi

Comparing remote and hand-held video observation methods for quantifying a cleaning mutualism

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Funding information
Division of Ocean Sciences, Grant/Award Numbers: OCE #1851510, OCE #1851032

Abstract

Field studies of cleaning mutualisms use a variety of methods to quantify behavioral dynamics. Studies in marine systems typically utilize data recorded by human observers on scuba or snorkel or via remote underwater video. The effects of these different methods on cleaner–client behaviors have not been rigorously assessed. We quantified cleaner–client interactions at 13 bluestreak cleaner wrasse (*Labroides dimidiatus*) cleaning stations in Moorea, French Polynesia using hand-held and remote videos. We found that cleaning, cheating, and client posing rates, cleaning duration, and client species richness were all greater in the remote than in the hand-held videos, suggesting that human presence disrupts cleaning interactions by inducing antipredator responses among clients. Some metrics, such as the ratio of cleaner chasing to cleaning behavior and the cleaners' benthic feeding rate, were higher for the hand-held than the remote videos, possibly due to limited access of cleaners to clients in the presence of humans. Other metrics, such as cleaner and client chasing rates, the ratio of cleaning to cheating behaviors, and the duration of cleaner chases, did not differ between video types. Finally, piscivorous clients were far more abundant in the remote than the hand-held videos, suggesting that piscivores are particularly sensitive to human presence, likely because they are targeted by fishers. Overall, our study suggests that human presence can bias studies of cleaning behavior and cleaner–client interactions, and that remote cameras should be used to conduct behavioral studies. These potential biases should be considered when interpreting existing behavioral data.

KEYWORDS
cleaning, French Polynesia, mutualism, video methods

1 | INTRODUCTION

A variety of methods are used to quantify animal behaviors and to understand their causes and consequences. Each method has its own strengths and weaknesses that can lead to biased interpretations of behavioral dynamics if not properly considered. For example, a study of foraging behavior in white capuchins compared continuous vs. interval focal sampling methods and found that while focal interval sampling was 25% more efficient, it yielded lower estimates of movement rates and foraging success than continuous sampling (Rose, 2000). Methodological comparisons can also reveal potential effects of human observers on animal behavior. For example, a study on humbug damselfish (*Dascyllus aruanus* L.) found that some of their behaviors were quantified more efficiently by direct diver observation, while other behaviors were more effectively measured with remote video observations (Branconi et al., 2019). Understanding how these methodological differences shape estimates of different behavioral metrics is crucial for properly interpreting behavioral data and comparing different studies.

In marine cleaning mutualisms a "cleaner" (typically a small fish or shrimp) benefits nutritionally by removing ectoparasites or dead skin from a "client" (typically a larger fish), which benefits from reduced parasite loads (Grutter, 1999; Grutter & Lester, 2002) and tactile stimulation that lowers its stress levels (Losey & Margules, 1974; Soares et al., 2011). Cleaning interactions occur worldwide in temperate and tropical marine environments (Grutter, 2002) among a wide range of cleaner species. Cleaning interactions are most common in the tropics and usually involve wrasses (fishes in the family Labridae), gobies (fishes in the genus Elacatinus), and decapod shrimps (in the families Palaemonidae and Hippolytidae) (Cote, 2000). Of these cleaning species, the most well-known and well-studied is the bluestreak cleaner wrasse *Labroides dimidiatus* (Valenciennes 1839).

Labroides dimidiatus are a model system for studying the behavioral ecology of mutualisms (Bshary & Würth, 2001; Kuwamura, 1984; Potts, 1973) and are found throughout the Indo-Pacific, where they establish cleaning stations in specific locations on coral reefs. Like many mutualisms, cleaning mutualisms can become parasitic (Cheney & Côté, 2005) if cleaners cheat by feeding on a client's healthy tissues, which are often more nutritious than dead skin or ectoparasites (Grutter & Bshary, 2003). To dissuade cleaners from cheating and encourage mutually positive interactions, clients have evolved control mechanisms such as punishment (chasing the cleaner as retaliation for being cheated) and partner switching (leaving the cleaner after being cheated) (Bshary & Grutter, 2005). However, client species vary in their ability to enact these control mechanisms (Bshary & Grutter, 2002). For example, piscivorous clients can inflict more severe punishments than non-piscivorous clients by eating the cleaner rather than just chasing it. Similarly, transient clients (species with large home ranges encompassing multiple cleaning stations) can switch cleaners more easily than can resident clients, whose small home ranges may only cover a single cleaning station. Accordingly, cleaning mutualism dynamics can vary significantly between client species and across different environmental contexts (Bansemer, Grutter & Poulin, 2002). Thus, in situ behavioral observations are essential to document this variation and better understand its causes and consequences (Grutter & Poulin, 1998; Kuwamura, 1976).

Researchers have used a variety of methods to quantify the complex behavioral dynamics of cleaning mutualisms in the field. Historically, most observations of cleaners involved a human observer, either on scuba or snorkel, that followed the cleaner around and recorded their interactions with clients (Kuwamura, 1984; Potts, 1973). However, in recent years, studies have often utilized remote video observations to quantify cleaning dynamics in the absence of an observer (Rose et al., 2020; Titus et al., 2017). Both methods have potential advantages and disadvantages. Specifically, observations by a mobile observer may yield greater overall coverage of cleaning activities than remote video observations because the observer can follow the cleaner across the reef. However, if potential clients alter their behavior in the presence of humans, this could bias the cleaning dynamics quantified by human observers. Numerous studies have shown that human presence can significantly affect the behavior of marine fish by inducing antipredator responses (Samia et al., 2019), yet it is unclear how this might affect cleaner–client interactions. In this study, we quantified interactions between cleaners and clients on 13 cleaning stations in Moorea, French Polynesia using two observational methods: hand-held and remote videos. We then compared multiple behavioral metrics between the two methods to evaluate how they differ in documenting cleaning mutualisms. Our results suggest that studies that rely on observations by divers or snorkelers may be substantially biased.

2 | METHODS AND MATERIALS

2.1 | Study sites

This study was conducted in the Maharepa lagoon on the north shore of Moorea, French Polynesia. We selected 13 cleaning stations, each of which comprised a patch reef (an area of coral surrounded by sand or rubble) occupied by one to three *Labroides dimidiatus*. Cleaning stations varied in area from 9 to 90 m^2 and were distributed over an area of approximately 91,000 m^2. Each cleaning station was at least 67 m away from any other cleaning station included in this study (Figure 1).

2.2 | Collecting fish community data

At each cleaning station, we conducted roving diver fish surveys (Schmitt et al., 2002) to quantify the reef's fish community structure. On snorkel, we censused all fish present on the reef (excluding cryptobenthic species), recording the lengths and abundance of each species. For each survey, we typically recorded transient species first (since they often leave in the presence of a snorkeler) and then resident species (those that stay on a reef despite the presence of snorkelers) to ensure maximal coverage of the fish community. The boundaries of each cleaning station were defined based on prior observation of the cleaner at each study reef. Fish survey duration varied from 20 to 40 min depending on reef size. We conducted five to nine fish community surveys on each cleaning station between June 2022 and July 2023. We used this data to calculate the long-term relative abundance of different client trophic groups on each reef and help contextualize observed patterns in cleaner–client behaviors.

2.3 | Collecting cleaner behavioral data

At each study reef, we recorded cleaner–client interactions using two observational methods: hand-held and remote videos. We conducted

FIGURE 1 Study site and focal cleaner species. Left: The location of the study site (indicated by a red pin) off the north shore of Moorea, French Polynesia. Top right: The location of the 13 replicate cleaning stations (indicated by green pins) within the study site; © Google Earth. Bottom right: Our study species, the bluestreak cleaner wrasse (*Labroides dimidiatus*), photographed by Daniel Cryan in Moorea, French Polynesia.

one hand-held and one remote video observation for each study reef. For the hand-held videos, a snorkeler followed the cleaner wrasse around each reef for 30 min with a video camera (i.e., Go Pro Hero Black 7 or 9) to film cleaner interactions with client fish. During these observations, snorkelers stayed at the surface, minimized excessive movements, and maintained at least 3 m between themselves and the cleaner to reduce potential disruptions to cleaner–client interactions. For the remote videos, a snorkeler placed a camera attached to a dive weight on the seafloor within 2 m of each cleaning station to passively record interactions for around 70–90 min (the camera's battery life) in the absence of any human observers. Cameras were deployed facing the section of the cleaning station with the greatest level of cleaning activity (as determined by prior observations of the cleaners on each reef). All observations were conducted in the early morning from 7:00 to 8:30 AM, when cleaning activity often peaks (Grutter, 1996). The paired videos were collected within 3 days of each other in July 2022 on each study reef to ensure maximum comparability between the two methods.

2.4 | Processing cleaner observation videos

We reviewed the footage from the 26 videos and recorded the cleaner–client behaviors over the entirety of each video (i.e., on reefs with multiple cleaners, we collected behavioral data for all visible cleaner wrasse). In each video, we noted how many individual cleaners were present at any given time (or if no cleaners were visible). We did not attempt to distinguish between individual cleaner wrasse on each reef. Cleaner–client behaviors include those performed by the cleaner wrasse directed towards potential clients and those performed by potential clients directed towards the cleaner wrasse. For all cleaner–client behaviors, we recorded the actor (the species performing the behavior), the recipient (the species receiving the behavior), the start and end time, the number of cleaner wrasse involved, and any other potentially relevant notes.

We described cleaner–client interactions through six categories of stereotyped behaviors: cleaning (the cleaner inspected the client, made physical contact, and did not elicit a negative response from the client), cheating (the cleaner bit the client and provoked a negative reaction), cleaner chasing (the cleaner chased a client fish), client chasing (a client fish chased the cleaner), client posing (a client signaled to the cleaner its desire to be cleaned by altering the presentation of its body, e.g., by flaring its operculum or pointing its head up or down), and benthic feeding (the cleaner fed on benthic substrates). We did not distinguish any additional behaviors since these six categories encompassed the main ecologically relevant cleaner–client behaviors. The negative client responses which indicated a "cheat" included body jolts (flinching reactions to bites by the cleaner), abrupt cessation of the interaction, and, in the most extreme cases, retaliatory chases by the client towards the cleaner. Note that client posing was often concurrent with other cleaner–client behaviors (especially cleaning), and that if multiple clients posed for a cleaner simultaneously, each pose was recorded as a separate behavior. We did not record the number of times cleaners made physical contact with clients during cleaning interactions since this was often not resolvable in the videos (i.e., because the cleaner was too far away or it cleaned the side of the client not facing the camera).

2.5 | Analyzing cleaning behavioral data

We compared the remote and hand-held video methods by calculating multiple behavioral metrics for each video and comparing their mean values for the two methods using a paired *t*-test with a Bonferroni correction; since we ultimately compared 21 metrics between the two observation methods, we used $\alpha = 0.0024$ to determine significance. First, we calculated the percentage of time and total time a cleaner was visible within each video. We then calculated the rates of different cleaner–client behaviors from each video as the total number of cleaning, cheating, chasing (cleaner and client), posing, or benthic feeding behaviors divided by the total time at least one cleaner was visible. Next, we calculated the log ratio of cleaning-to-cheating behaviors and the log ratio of cleaner chasing-to-cleaning behaviors for each video. The former reflects the overall positivity of cleaner–client interactions, while the latter reflects the cleaner's difficulty in initiating interactions with clients (i.e., since cleaners chase clients to initiate cleaning, this metric represents the number of cleaning attempts for each successful cleaning interaction). We calculated log ratios since they are typically less biased and more normally distributed than uncorrected ratios (Hedges et al., 1999). We also calculated the mean duration of cleaning and cleaner chasing (per client interaction) for each video. We did not standardize these metrics by the number of cleaners at each cleaning station since there was not a significant difference in the relative amount of time one, two, or three cleaners were visible between the two video types. Rather we considered these as reef-level behavioral metrics, with cleaner density one of many potential factors contributing to variability between reefs, accounted for by our paired design. Finally, we modelled cleaning as a function of client posing and cleaner chasing and cheating as a function of cleaning to understand the relationships between these different cleaner–client behaviors.

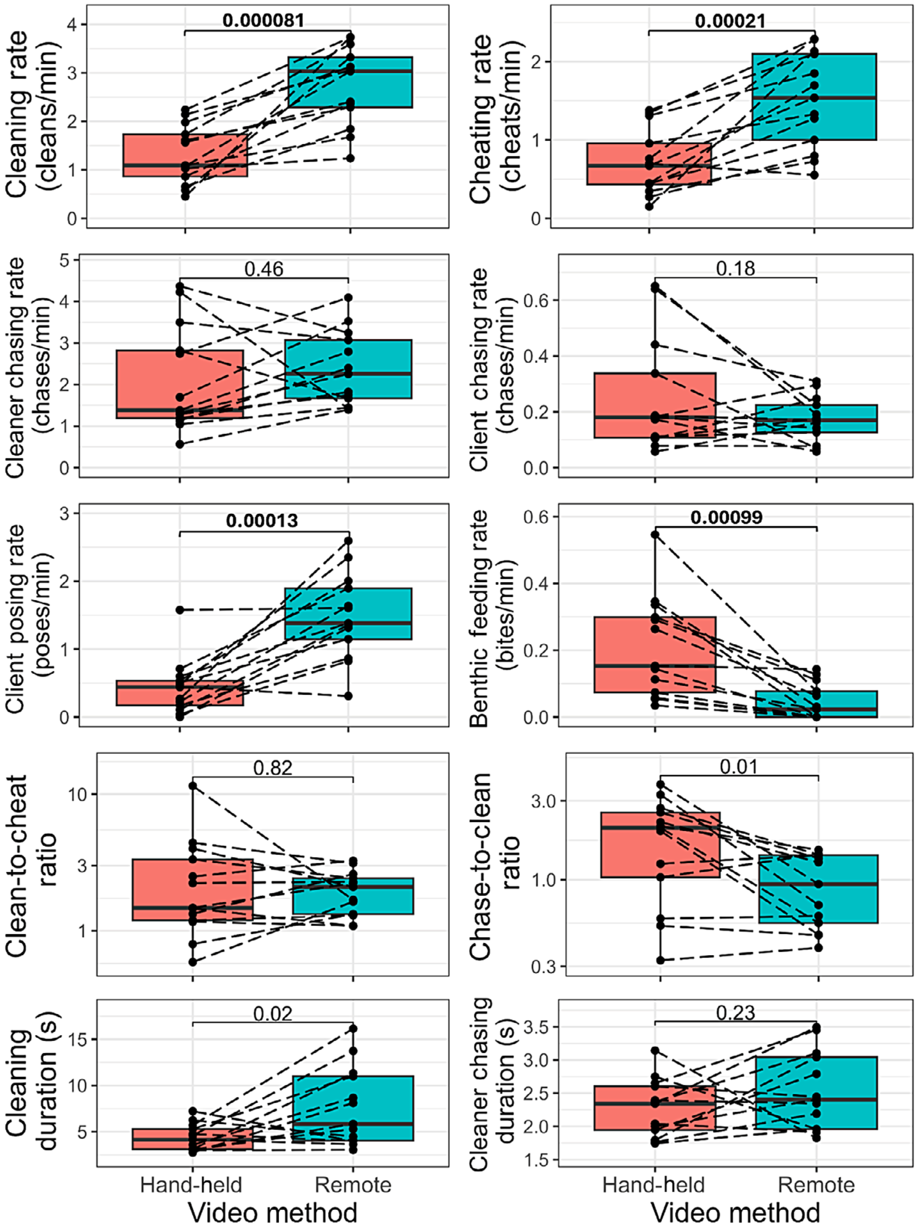


FIGURE 2 Differences in cleaner-client interaction dynamics for hand-held (red) and remote (blue) video methods. Boxplots indicate the median (solid horizontal black lines), the interquartile range (boxes), and 1.5 times the interquartile range (vertical lines). Paired observations are connected by dashed lines ($N = 13$ study reefs for each comparison). *p* values from paired *t*-tests are shown above the two boxplots; bolded *p* values are statistically significant ($\alpha = 0.0024$).

We also compared client communities between the two video methods by calculating several community metrics. First, we calculated the raw client species richness as the number of unique client species participating in any type of cleaner–client interactions for each video. Next, to account for differences in the length of each observation, we constructed two types of rarefaction curves: (1) we derived client species accumulation curves as a function of time for each video and calculated the observed client richness at 30 min (i.e., the minimum duration of the videos); and (2) we constructed accumulation curves based on the number of client interactions and calculated the observed richness after 71 interactions (the minimum in the dataset). We then assigned trophic roles (i.e., piscivore, invertivore, corallivore, omnivore, herbivore, planktivore) to each client species based on natural history information available on FishBase (Froese & Pauly, 2024) and calculated the relative interaction frequency for each trophic role for each video. We then compared these relative interaction frequencies between the two video types using a series of paired *t*-tests, with the same Bonferroni correction and $\alpha = 0.0024$. Here the "client community" refers specifically to the fish observed interacting with the cleaner and is a subset of the broader fish community that we quantified with the roving diver fish surveys. Finally, to help contextualize the patterns we observed in cleaner–client behaviors, we calculated the relative abundance of different trophic groups for the broader fish community from the roving diver fish survey data.

3 | RESULTS

There were several significant differences in behavioral metrics between the hand-held and remote videos. Cleaner wrasse were visible for a significantly greater percentage of time during the hand-held videos than during the remote videos (82 ± 4% vs. 52 ± 5% [mean ± standard error, SE], $t_{12} = 4.73$, $p = 0.001$), likely due to the mobile nature of these observations. However, due to the greater overall length of the remote videos, cleaner wrasse were visible for a significantly greater amount of total time in the remote than in the hand-held videos (39.1 ± 3.2 vs. 25.1 ± 1.2 min [mean ± SE], $t_{12} = 4.32$, $p = 0.001$). Cleaning and cheating rates were both over two times greater for remote than for hand-held videos (2.7 ± 0.2 vs. 1.3 ± 0.2 cleans/min [mean ± SE], $t_{12} = 5.83$, $p = 0.001$ and 1.5 ± 0.2 vs. 0.7 ± 0.1 cheats/min [mean ± SE], $t_{12} = 5.23$, $p = 0.001$), suggesting that human presence likely depressed the rate of interactions. Similarly, client posing rates were nearly four times greater for remote than for hand-held videos (1.5 ± 0.2 vs. 0.4 ± 0.1 poses/min [mean ± SE], $t_{12} = 5.52$, $p = 0.001$), again indicating a behavioral shift in the presence of humans. Cleaner chasing rates were not significantly different between the hand-held and remote videos (2.1 ± 0.4 vs. 2.4 ± 0.2 chases/min [mean ± SE], $t_{12} = 0.76$, $p > 0.05$); nor were client chasing rates (0.25 ± 0.06 vs. 0.17 ± 0.02 chases/min [mean ± SE], $t_{12} = 1.42$, $p > 0.05$). Finally, benthic feeding rates for cleaners, an alternative foraging strategy to cleaning, were five times greater for hand-held than for remote videos (0.21 ± 0.04 vs. 0.04 ± 0.01 bites/min [mean ± SE], $t_{12} = 4.33$, $p = 0.001$) (Figure 2).

The log ratio of cleaning to cheating behaviors, which reflects the overall positivity of cleaner–client interactions, was not significantly different between the hand-held and remote videos (0.3 ± 0.1 vs. 0.28 ± 0.05 $\log_{10}$(cleans/cheat) [mean ± SE], $t_{12} = 0.23$, $p > 0.05$). The log ratio of cleaner chasing to cleaning behaviors, which reflects the cleaners' difficulty in attracting clients, was greater for the hand-held than for the remote videos (0.18 ± 0.09 vs. −0.07 ± 0.06 $\log_{10}$(chases/clean) [mean ± SE]), although this difference was not statistically significant ($t_{12} = 3.04$, $p = 0.01$). The mean duration of cleaning (per client interaction), an indicator of the overall strength

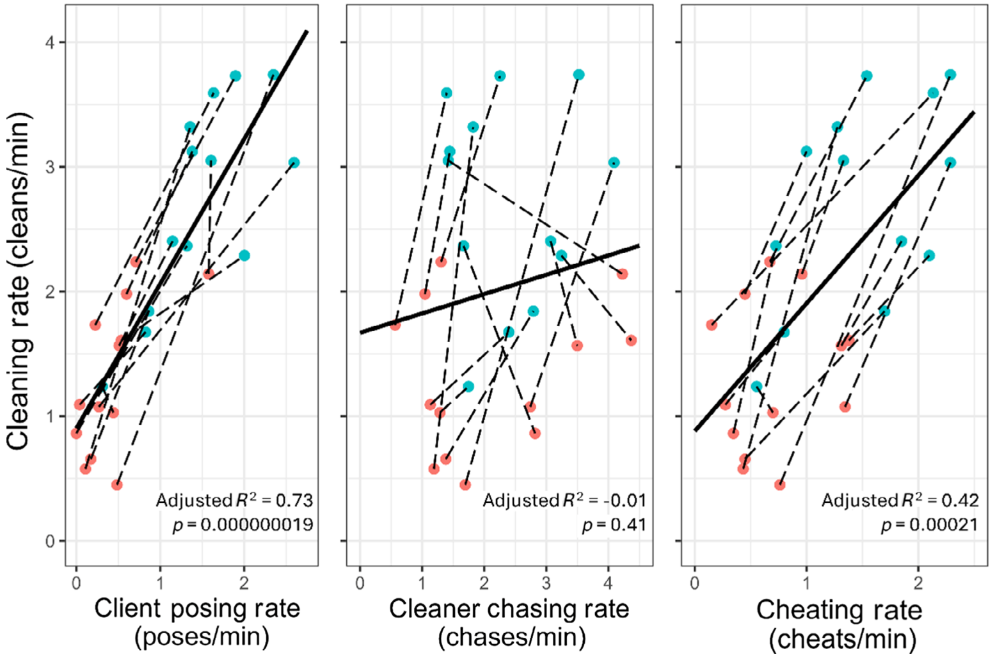


FIGURE 3 Relationships between cleaning and other cleaner–client behaviors. Cleaning rate was significantly positively correlated with client posing rate and cheating rate, but not significantly correlated with cleaner chasing rate ($\alpha = 0.0024$). Solid black lines are the predicted mean values for each relationship, dashed lines connect the paired hand-held (red) and remote (blue) video observations on each of the 13 reefs.

of cleaning interactions, was greater for the remote than for the hand-held videos (7.6 ± 1.2 vs. 4.4 ± 0.4 s [mean ± SE]) although again these differences were not statistically significant ($t_{12} = 2.69$, $p = 0.05$). The mean duration of cleaner chasing (per client interaction) did not significantly differ between the two observation methods (2.3 ± 0.1 vs. 2.5 ± 0.2 s [mean ± SE], $t_{12} = 1.25$, $p > 0.05$) (Figure 2). Finally, cleaning rates were positively correlated with client posing rates (adjusted $R^2 = 0.73$, $F_{1,24} = 67.9$, $p = 0.001$) but not significantly correlated with cleaner chasing rates (adjusted $R^2 = -0.01$, $F_{1,24} = 0.70$, $p > 0.05$), which suggests that client behavior plays an important role in limiting cleaning interactions. Similarly, cleaning rates were positively correlated with cheating rates (adjusted $R^2 = 0.42$, $F_{1,24} = 19.06$, $p = 0.001$) (Figure 3).

Raw client species richness for the remote videos was 81% greater than that observed in the hand-held videos (22.1 ± 1.2 vs. 12.2 ± 0.9 species [mean ± SE], $t_{12} = 7.61$, $p = 0.001$), largely due to the longer overall duration of these videos. However, when controlling for the disparity in sampling effort, this difference was greatly reduced and no longer statistically significant. Client species richness was only 31% greater in the remote videos when controlling for duration of the video (15.1 ± 1 vs. 11.5 ± 0.9 species at 30 min [mean ± SE], $t_{12} = 3.28$, $p = 0.01$), and only 23% greater when controlling for the number of cleaner–client interactions (11.3 ± 0.6 vs. 9.2 ± 0.7 species at 71 total interactions [mean ± SE], $t_{12} = 2.29$, $p = 0.05$) (Figure 4). Client community composition was similar between the two video types, but the relative frequency of interactions with piscivores was over eight times greater in the hand-held than remote videos (13.9 ± 2.7 vs. 1.7 ± 0.9% of client community [mean ± SE], $t_{12} = 5.32$, $p = 0.001$), while no other client trophic group exhibited a significant difference in their relative interaction frequencies. Piscivores comprised only 8% of the total fish community (Figure 5), thus piscivores were over-represented as clients in the remote videos but under-represented in the hand-held videos.

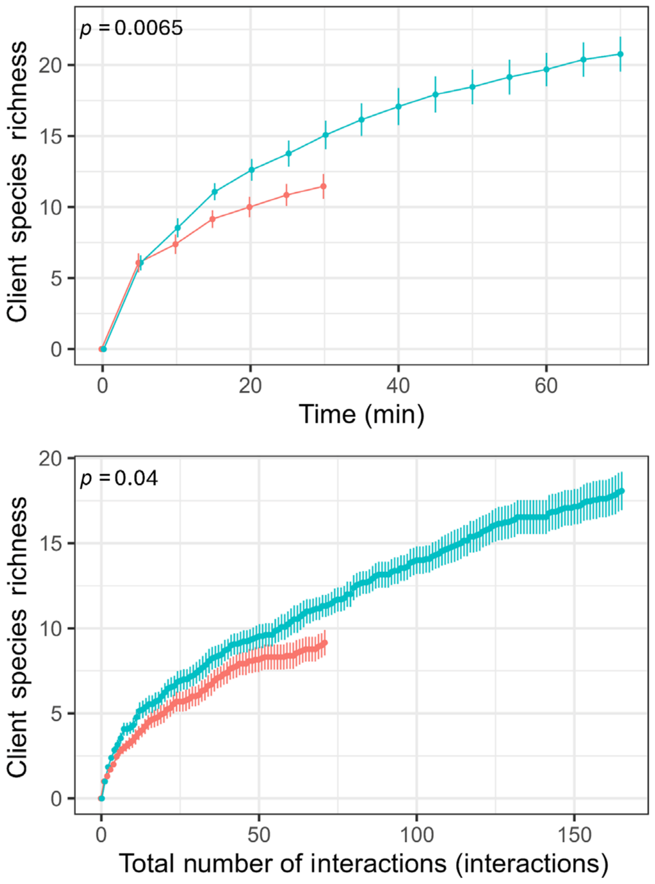


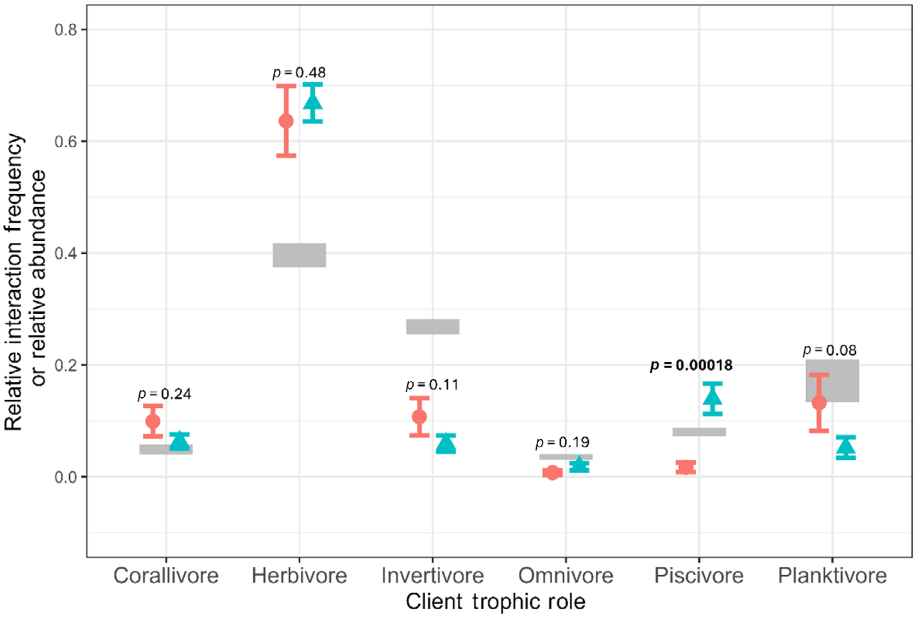
FIGURE 4 Client species accumulation curves for hand-held (red) and remote (blue) video methods. Client species richness was 31% greater for the remote than for the hand-held videos after 30 min (the minimum duration of the hand-held videos) and 23% greater for the remote videos at 71 interactions (the minimum number of total interactions in the 26 videos), although differences were not statistically significant ($\alpha = 0.0024$). Error bars are the mean ± standard error, $N = 13$ study reefs.

4 | DISCUSSION

Cleaning, cheating, and client posing rates were greater in the remote videos than in the hand-held videos. This pattern is probably driven by the presence of a human observer in the hand-held videos, who likely discouraged clients from interacting with cleaners. Human presence is widely known to induce behavioral changes in fishes, mainly through heightened antipredation responses (Samia et al., 2019). If potential clients view a snorkeler (or diver) as a possible threat, they may be less inclined to interact with cleaners since doing so could put them at greater risk of capture. Additionally, transient clients may leave a cleaning station entirely when snorkelers are present, while resident clients may exhibit heightened wariness, both of which would lower cleaner–client interaction rates. This may be especially true for client posing rates, since posing involves a fish altering the position or orientation of its body (e.g., by opening its mouth, flaring its fins/operculum, turning upright/sideways, etc.), which may make the client more vulnerable to predation. This could also explain why client posing rates were almost four times greater in the remote than hand-held videos, while cleaning and cheating rates were only two times greater.

This interpretation that cleaner–client interactions were adversely affected by human presence is further supported by the observation that many piscivorous client species were not recorded at all in the hand-held videos, and that the relative interaction frequency for piscivores in the remote videos was eight times greater than in the hand-held videos. Piscivores are especially sensitive to the presence of humans, likely because they are frequently targeted by fishers (Russ & Alcala, 1996; Stallings, 2009). Indeed, piscivores were relatively rare in the fish surveys, comprising only a small portion of the overall fish community. However, the use of human observers in conducting these fish surveys could itself negatively bias estimates of piscivore abundance so this may be an underestimate of piscivores' actual community composition. Overall, our results strongly suggest that human presence can disrupt cleaning interactions by inducing client fear responses, and that certain species, like piscivores, are especially susceptible.

FIGURE 5 Relative interaction frequencies for different client trophic groups for hand-held (red) and remote (blue) video methods. Piscivores were cleaned more often in remote videos, but other trophic groups did not significantly differ in their relative interaction frequencies for the remote vs. hand-held videos ($\alpha = 0.0024$). Grey crossbars indicate the long-term relative abundance (± standard error [SE]) of each client trophic group across the study reefs. Error bars are the mean ± SE, $N = 13$ study reefs.



Another important methodological difference between the two video types is that the remote videos had a fixed frame of view while the hand-held videos had a mobile frame of view. This explains why cleaners were present for an average of 82% of time in the hand-held videos but only 52% of time in the remote videos. It is noteworthy, however, that the remote videos were recorded facing the section of the cleaning station where we had previously observed the most cleaning activity. This was done to maximize our chance of observing cleaner–client interactions, but by only observing the high-activity portions of cleaning stations, the behavioral estimates from the hand-held videos might be biased. The strength of this bias will depend on the spatial variation in cleaner–client interactions (e.g., inside vs. outside the remote frame of view). Although we lack quantitative data on the fine-scale distribution of cleaning interactions around cleaning stations, our observations suggest that while some areas are clearly preferred, cleaners still often roam throughout their cleaning stations and interact with clients opportunistically.

Spatial variation in cleaner behaviors may also explain the observed patterns in benthic feeding. Benthic feeding is relatively rare in *Labroides dimidiatus* (Côté, 2000; Potts, 1973). If benthic feeding and cleaning occur on different portions of the reef, then the limited frame of view of the remote camera might have missed most benthic feeding events, leading to artificially low benthic feeding rates in the remote videos. Alternatively, this behavior could be caused by human observers altering client fishes' behavior. Specifically, if the presence of a snorkeler induced fear responses in the clients, then the cleaners may have responded by temporarily shifting to another foraging strategy. This partial abandonment of cleaning mutualisms in favor of benthic feeding has been observed previously in *Labroides dimidiatus* living in strongly tidal environments where access to clients is limited (Dunkley et al., 2020). Unfortunately, we do not have data to discriminate between these two hypotheses, nor are they mutually exclusive (i.e., both may contribute to the pattern). Overall, it is clear that methodological differences between the two video types lead to stark differences in certain behavioral metrics.

We gained additional insights into cleaner behavioral dynamics by examining the relationships between different cleaner–client behaviors across the two video types. For example, there was a significant positive correlation between cleaning rates and client posing rates. This is unsurprising, given that clients pose to signal their intent to be cleaned (thus greater posing rates should lead to greater cleaning rates). By contrast, cleaning rates and cleaner chasing rates were not significantly correlated, suggesting that increased chasing by cleaners does not necessarily lead to more cleaning. Together, these results suggest that clients are choosy when interacting with cleaners, preferring to be cleaned on their own terms (i.e., by posing to initiate cleaning) rather than under duress (i.e., after being chased by a cleaner). High levels of choosiness have previously been documented among clients of *Labroides dimidiatus* and serve as partner control mechanisms to reduce cheating by cleaners (Bshary & Noë, 2003). Interestingly, cleaning rates were also positively correlated with cheating rates in our videos, suggesting a constant ratio of cleaning to cheating (e.g., for every two cleans there is one cheat) and that clients may tolerate high cheating rates if cleaning rates are also high. Cleaners that cheat frequently and rarely clean no longer provide a net benefit to their clients and are likely avoided altogether. Altogether, these results suggest that client choosiness plays an important role in shaping overall behavioral dynamics.

Our study revealed that remote and hand-held videos can lead to different interpretations of cleaner–client interactions due to the effects of human observers and differences in the camera's frame of view. Although both factors likely contribute to differences in behavioral metrics, we suspect human presence in the hand-held videos is the main driver and that the hand-held videos are substantially biased by this effect. Field-based behavioral studies of *Labroides dimidiatus* conducted by human observers on scuba or snorkel are common in the literature (Bshary & Würth, 2001; Dunkley et al., 2020; Grutter, 1996; Kuwamura, 1984; Ros et al., 2011; Slobodkin & Fishelson, 1974). Yet the effects of human presence on cleaning interactions often receive little consideration, typically referenced only when justifying methods intended to reduce disruptions to cleaning, such as maintaining a minimum distance from the cleaner and allowing a short acclimation period. While these measures likely help, they probably do not fully ameliorate the disruptive effects of human presence. Our results suggest that human observers can have a significant impact on behavioral dynamics and should be actively considered when designing behavioral studies and interpreting the resulting data. The magnitude of these biases may also vary among localities, e.g., human-induced effects (and the associated biases) may be minimal in no-take marine reserves, where fish perceive little threat from humans, but large in areas open to fishing, where fish perceive greater risk. Indeed, one study found that cleaners in a no-take marine reserve interacted with more large client fish, including commercially targeted species, than cleaners at a nearby site open to fishing (Silvano et al., 2012). Additionally, our study highlights the context-dependent nature of cleaning mutualisms and the complex behavioral dynamics governing these interactions. We suggest that future studies of cleaning mutualisms should limit the use of human observers, and other studies should examine how variation in predation risk affects the benefits and dynamics of cleaner–client interactions.

AUTHOR CONTRIBUTIONS

D.M.C. developed the idea for the study, collected the field data, oversaw the data processing, directed the data analysis, and led the writing process. J.F. processed the video data, assisted with data analysis, and helped write the manuscript. C.W.O. provided funding and other material support for the project and advised D.M.C. on the data collection, analyses, and writing.

ACKNOWLEDGEMENTS

All work was conducted under approved permit by the Government of French Polynesia and the UGA Institutional Animal Use and Care Committee. We thank the National Science Foundation (OCE #1851510, 1851032), the UGA Odum School of Ecology, a CURO research award (to J.F.), and the UGA Graduate School Fellowship and grant (to D.M.C.) for funding that helped support this research, the staff of Gump Research Station for logistical support, and members of the Osenberg Lab for constructive feedback.

FUNDING INFORMATION

We thank the National Science Foundation (OCE #1851510, 1,851,032), the UGA Odum School of Ecology, a CURO research award (to J.F.), and the UGA Graduate School GREAT Fellowship and summer research grant (to D.M.C.) for funding that helped support this research.

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How to cite this article: Cryan, D. M., Freeze, J., & Osenberg, C. W. (2025). Comparing remote and hand-held video observation methods for quantifying a cleaning mutualism. *Journal of Fish Biology*, *106*(3), 775–783. https://doi.org/10.1111/jfb.15991