Reef fish aggression tracks resource availability throughout coral loss and recovery

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Abstract

Habitat loss caused by anthropogenic climate change poses a significant threat to global biodiversity, and behavioural change is often the first line of defence for affected organisms. However, the potential for altered behaviour to moderate the impact of resource loss remains untested. Using a six-year dataset from three reefs in Japan, we investigated the behavioural responses of 23 butterflyfish species to coral habitat loss and recovery. Aggressive behaviours decreased when resources were depleted, consistent with predictions from the economic defendability model. Once coral cover recovered, aggression returned to predisturbance levels, demonstrating behavioural flexibility potentially capable of preventing energetic deficits in the short-term. These results underscore the importance of behavioural plasticity in species survival during environmental disturbances and highlight potential ramifications for ecological dynamics at broader scales, such as species coexistence. Our results emphasise the need to understand and conserve behavioural adaptive capacities in the face of ongoing global change.

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Keywords: habitat loss, coral bleaching, contests, Chaetodontidae, territoriality

Data availability: https://anonymous.4open.science/r/economic_defendability-DD57/

[anonymised GitHub repository for double blind peer review].

Abstract

Habitat loss caused by anthropogenic climate change poses a significant threat to global biodiversity, and behavioural change is often the first line of defence for affected organisms. However, the potential for altered behaviour to moderate the impact of resource loss remains untested. Using a six-year dataset from three reefs in Japan, we investigated the behavioural responses of 23 butterflyfish species to coral habitat loss and recovery. Aggressive behaviours decreased when resources were depleted, consistent with predictions from the economic defendability model. Once coral cover recovered, aggression returned to pre-disturbance levels, demonstrating behavioural flexibility potentially capable of preventing energetic deficits in the short-term. These results underscore the importance of behavioural plasticity in species survival during environmental disturbances and highlight potential ramifications for ecological dynamics at broader scales, such as species coexistence. Our results emphasise the need to understand and conserve behavioural adaptive capacities in the face of ongoing global change.

Main

Anthropogenic climate change is causing substantial loss of habitat in global ecosystems, with devastating effects on biodiversity [1,2]. Changes in behaviour are often the first response of individuals to disturbance [3–5], yet behavioural responses and their ecological consequences, especially in real-world settings, are poorly understood relative to direct lethal impacts [6]. When faced with acute disturbances, organisms can adopt temporary behavioural changes that increase their chances of survival. [7]. For instance, when resources are depleted, individuals can conserve energy by changing activity levels [8] or reducing territorial behaviour [9]. Despite the significant ramifications for population persistence, species coexistence and wider ecosystem function [10], the mechanisms that underlie these behavioural shifts are unclear. This gap in knowledge hinders our capacity to predict the resilience of populations to environmental change, and to understand the implications for population and community dynamics.

Economic models provide a useful lens for understanding behavioural flexibility [11]. Aggressive behaviour, which functions to defend territories and maintain access to resources, can be dynamically regulated according to the costs and benefits of defence [12]. This dynamic regulation predicts a hump-shaped relationship between aggression and resource availability, where aggression is highest at intermediate resource levels. Decreased aggression of reef fish in response to resource depletion offers partial support for this model [9], but the critical test lies in determining whether aggression returns to pre-disturbance levels following resource recovery. Resolving this question would improve predictions of population resilience to ongoing environmental changes.

An alternative explanation for behavioural change following disturbance posits differences in fixed behavioural phenotypes across individuals within a population. In this case, natural selection can lead to a loss of individuals with an uneconomic level of aggression, which directly impacts on the probability of aggressive encounters within the population. Under such a scenario, a return to pre-disturbance frequencies of behaviour relies on processes that occur over a substantially longer time period, i.e. an increase in the proportion of aggressive individuals either through immigration or reproduction. Reproduction is likely to be delayed or reduced when individuals are energetically compromised following resource depletion [13,14], and a return of aggressive behaviour could be further limited if such behaviours are heritable rather than learned. Thus, reverting back to the original state hinges on several variables, including extant behavioural diversity from which to replenish affected populations, dispersion rates, reproductive rates and the extent of variation in aggressive behaviour within the repertoires of individuals. If behaviour is fixed, the subsequent loss of behavioural diversity following disturbance could affect the potential of the population to adapt to future environmental changes [15]. Therefore, identifying which mechanism is in action can provide vital information on how quickly populations can recover behaviourally from disturbance, if they can recover at all, and the potential ramifications at the community and ecosystem scale.

Coral reef fishes offer an excellent model system with which to explore behavioural responses to disturbance and are particularly vulnerable to environmental change. In particular, butterflyfishes are highly reliant on live coral [16], have small home territories [17], are abundant and easy to identify [18], and their behaviours can reliably be assessed in the field [e.g. 9,14,19]. Butterflyfishes also display a range of territoriality, with a species' levels of aggression positively correlated to their degree of feeding specialisation [20,21]. Here, we use an unprecedented dataset that tracks aggressive behaviour between 23 species of butterflyfishes on three reefs in Japan from 2016-2022. This includes surveys through a full cycle of disturbance and resource recovery, following a mass coral bleaching event in 2016. In the year after this disturbance, corals (the primary food source of butterflyfishes) were significantly depleted throughout the Indo-Pacific (18-65% loss,) leading to a three-fold reduction in aggressive territorial defence [9]. Here, we undertake the first test of the long-term impact of altered resource availability on aggressive behaviour in the field to ask whether the reduction in aggression (1) reverts to pre-disturbance levels, indicating behavioural flexibility, or (2) persists in the population indicating that behaviour is fixed. To ascertain the fit with the predictions of the economic model of defendability, we also tested (3) whether the main food source of the butterflyfishes (Acropora corals) recovered in abundance, and (4) if changes in aggression could be a by-product of potential changes in the relative abundance of *Chaetodon* species caused in response to the bleaching event.

Methods

We surveyed coral reefs on the north coast of Iriomote, Okinawa, Japan over four years (2016, 2017, 2018 and 2022), with a gap in data collection due to Covid-19 travel restrictions. Due to challenges posed by post-covid field work, we sampled substantially less reefs in 2022 than prior years (Supporting information), and have accounted for this unbalance in our analyses. The surveys were conducted across three sites: Nata (24°25'40.1"N, 123°47'41.6"E), Sonai (24°22'53.0"N, 123°44'51.7"E), and Unarizaki (24°25'38.3"N, 123°45'49.3"E). Between the 2016 and 2017 surveys, the reef experienced extensive coral bleaching, with a subsequent decline of live coral[9].

Aggression

To quantify aggression in butterflyfishes we used 5-minute focal follows (n=1177) and scored each encounter (a non-focal fish within 1m of the focal fish), as passive (no response) or aggressive (signalling by flaring fins and or through aggressive posturing, or chasing by one or both individuals). Focal individuals of any butterflyfish (Chaetodontid) species were selected haphazardly based on order of encounter. There was not sufficient replication at the species level across the sampled years, so aggression scores were pooled in each year.

Butterflyfish and coral abundance

We used 50 m belt transects to quantify butterflyfish abundance within each transect, and scored the cover of hard corals (Scleractinia) every 0.5m along the transect tape, across 2 depths (1 and 5 m) each year (n=81). Fish and coral surveys were conducted along the same transect, with the fish surveyor passing first to reduce disturbance to the fish. We recorded the feeding guild of each butterflyfish species, based on those listed in [16, Supporting information].

Statistical Analyses

All analyses were conducted using R [22]. We used mixed linear effects models (lme4 [23]) to analyse the coral and fish abundance, using survey year as fixed and location as a random effect. Butterflyfish community analyses were conducted using a PERMANOVA from the Vegan package [24], with 999 permutations using sequential sums of squares. Location was fitted as the first term in the model, so that that any variation among location is accounted for before testing the effect of years (full model: abundance $\tilde{}$ location + year). Pairwise analyses between years were conducted with the PairwiseAdonis package [25].

Data limitations

We acknowledge the limitations of our dataset, including a reduced sampling effort in 2022 and the challenges of linking correlative data to causal mechanisms. These limitations stem largely from the difficulty of achieving consistent replication at the species level across multiple years. Studying animal behaviour in situ is inherently challenging due to the complex, variable nature of animal behaviours, where the unpredictability of both the species and the environment introduces considerable variability. Additionally, multi-year studies on behaviour are rare, as they require substantial resources and time commitment to track populations over extended periods. While these limitations restrict our ability to conduct species-level analyses of behaviour, this dataset remains one of the only multi-year assessments of behaviour across a species assemblage. As such it provides rare insights into natural behaviour that would be difficult to obtain through laboratory-based studies alone.

See Supporting information for a breakdown of sample effort and detectability rates.

Results

Aggression

The proportion of passive and aggressive interactions differed significantly over the years (Figure 1a, ?-square test, $?^2_{(3)} = 24.8$, P< 0.0001). This difference is driven by a decline in probability of aggression in 2017 compared to 2016 (Pairwise comparison: $?^2 = 23.6$, P< 0.0001). By 2022, six years after significant reduction

in resources due to coral mortality, levels of aggression had returned to those seen before the bleaching event (Figure 1a).

Live coral abundance

Live coral cover was significantly reduced in at least the first two years post-bleaching, and this reduction varied by taxa (Figure 1b, mixed effects model, interaction: year*coral taxa: $\chi^2_{(3,136)} = 12.17$, P= 0.007). The interaction was driven by a 77% decline in mean *Acropora* cover between 2016 and 2017, and a further 7% decline in 2018 (2016 mean *Acropora* % cover \pm SEM: 18.6 \pm 3.92; 2017: 4.29 \pm 0.9; 2018: 3 \pm 0.59, Tukey HSD pairwise test adjusted p-values < 0.001). However, by 2022, six years post-bleaching, mean *Acropora* cover had recovered to pre-bleaching levels and was not significantly different from 2016 (*Acropora* 12.3% \pm 2.48 SEM).

Patterns of aggressive levels and coral cover closely matched each other across all four surveyed years (Supplemental Figure 1).



Figure 1: a) The percent coral cover of *Acropora* spp. and other coral species over the four surveyed years (note irregular survey interval 2018-2022 due to Covid19). Boxplots depict median, interquartile range (25- 75^{th} percentile), and whiskers include values within 1.5 x interquartile range. Black dot and bar on boxplots depict mean coral cover \pm SEM. Letters denote groupings from Tukey's post-hoc pair-wise comparisons, with similar letters denotating non-significant differences. White values are number of encounters. b) The probability of an encounter (i.e. fish <1 m apart) between two fish having an aggressive outcome (i.e. a chase or display). Probabilities have been log transformed to enable visualisation, so that a value of 0 represents a focal follow where 100% of encounters had an aggressive outcome, and a value of -1 (or inf) indicates a

focal follow with 0 aggressive interactions. Black dot and bar on boxplots depict mean coral cover \pm SEM, while boxplots depict median, interquartile range (25-75th percentile), and whiskers include values within 1.5 x interquartile range. Dashed line marks the mass coral bleaching event.

Butterflyfish community composition

The overall abundance of butterflyfishes did not change significantly over the five surveyed years (mixed effects model, fixed effect: year, random effect: site, $\chi^2_{(3)} = 2.35$, P = 0.5, Figure 2a). There was a significant but weak effect of year on community structure (PERMANOVA $F_{(3,73)} = 1.7$, $R^2 = 0.06$, P = 0.03) accounting for 6% of the variation in composition. This result was driven by a significant difference between the 2016 and 2022 communities only (Figure 2c, pairwise adonis, F = 2.64, R² = 0.07, P = 0.02). While these results show an overall shift in the butterflyfish community, this was driven by rare species. Therefore, we also tested whether the community shifted significantly when we included only the five most abundant species (*C. citrinellus, C. lunulatus, C. vagabundus, C. unimaculatus, C. rafflesia*). These species represent at least 70% of the total butterflyfish abundance in each year (2016: 82%, 2017: 75%, 2018: 81%, 2022: 72%), include each feeding guild (facultative corallivore, obligate corallivore, and invertivore respectively), and are responsible for a majority of aggressive interactions. There was no significant difference in the abundance of these dominant species following the bleaching event, suggesting that while the overall community shifted slightly, the majority of species involved in aggressive encounters remained at the same level of abundance (PERMANOVA $F_{(3,70)} = 1.8$, $R^2 = 0.06$, P = 0.06).

The relative abundance of feeding guilds (facultative, obligate coral feeders, and invertivores) did not differ significantly between the four surveyed years (mixed effects model, fixed effects: year and feeding guild interaction; random effect: location, $\chi^2_{(9)} = 8.9$, P = 0.4, Figure 2b).



Figure 2: a) the relative abundance and community change of butterflyfish communities in Iriomote pre- and up to six years post-bleaching. The five most common species in each year are highlighted and labelled with species names. b) relative abundance of the three main feeding guilds of butterflyfish present on Iriomote I. reefs, c) principal component analysis of butterflyfish community structure. Dashed lined indicates the mass coral bleaching event.

Discussion

Here we demonstrate how butterflyfishes respond to the loss and subsequent recovery of their primary food source by adjusting their aggression levels in line with resource availability. We found that this was unlikely to be caused by a reshuffling of the butterflyfish community, or a selective removal of more aggressive individuals, but more plausibly linked to energy conservation during an acute disturbance event. Once coral cover recovered, aggression returned to pre-disturbance levels, demonstrating the importance of behavioural plasticity to maintain species persistence during environmental disturbances. As predicted by models of economic defendability, the drop in the probability of aggressive interactions occurring on Iriomote following bleaching, closely matched the availability of the primary food resource for many butterflyfish species; staghorn Acropora corals. Similarly, as coral cover recovered, in years following the bleaching event, so did aggressive interactions. While we do not have sufficient replication to statistically analyse aggression at the species level across the four years, visual examination of trends suggest the majority of species closely followed the these trends (Supporting information). Engaging in territorial and aggressive interactions carries a significant energetic cost [26], both in terms of energy directly allocated to the behaviour [27], and opportunity cost due to reduced feeding [28]. Thus, a decline in aggressive interactions is likely to lead to lower energy consumption during an ongoing disturbance event. Reductions in energy-intensive behaviours during times of low resource availability may be a successful evolutionary strategy to conserve energy, and species with higher levels of behavioural plasticity tend to have a higher survival during disturbance events [29,30]. As environmental disturbances become more frequent and more severe globally, it is increasingly important to understand how these processes play out in the long-term.

Altered behaviour is invariably linked to a trade-off between energy expenditure (maintenance, growth, reproduction) and energy acquisition, and populations are unlikely to persist on either extreme of this trade-off spectrum. In species or individuals with a high degree of behavioural variability or capacity to adapt their behaviour, we would expect behaviour to always be close to optimum for a given resource availability. For example, urban nesting birds that experienced an increase in availability of nesting and foraging sites during Covid-19 lockdowns were less territorially aggressive [31]. Similarly, male black-throated blue warblers (*Setophaga caerulescens*) that were given a supplemental diet reduced their singing rates, representative of territorial behaviour, in favour of behaviours more directly linked to increased reproductive success, such as mate guarding [32]. In contrast, we would expect strong selective pressure against individuals with limited behavioural flexibility, such that the population and community composition is altered in affected ecosystems [33,34].

The variation in extent and frequency of disturbance will also interact with a species' life history strategy, potentially affecting some species disproportionally. For species with a relatively short lifespan, a severe disturbance event can have a large impact on population dynamics and leave populations with little time to recover between events. However, shorter generation times facilitate more rapid evolutionary adaptation through natural selection. Butterflyfish can live over a decade, with mean maximum age for common species spanning 5-10 years [35], and attain sexual maturity within the first two years of life [36]. The demography of this family of reef fishes suggest they are likely to experience multiple disturbance events throughout their life cycle. Studies of animal behaviour are often limited in spatial and temporal replication making it difficult to tease apart whether it is behavioural plasticity at the level of an individual or within populations, or adaptative selection across generations, that is the underlying mechanism of altered behaviour. By monitoring the abundance and species composition of a community over time we can disentangle whether behavioural changes can be plausibly explained by the selective removal of individuals with maladaptive behavioural traits.

In this study, we found weak evidence of a reshuffling of the butterflyfish community post bleaching, however this pattern was largely driven by rare species. There was no significant shift in the relative proportions of the four most common species in the population, nor an overall change in the abundance of butterflyfishes. We predicted that the degree of feeding preference specialisation would affect how species responded to coral mortality, as highly specialised species are more constrained by resource availability than generalists [37]. Butterflyfishes display a range of dietary preferences, from highly specialised obligate coral feeders that feed exclusively on a small subset of *Acropora* species (e.g. *C. trifascialis*), to facultative coral feeders whose diet consists of over 80% corals (e.g. *C. citrinellus*), through to invertivores (e.g. *C. vagabundus*). However, the relative abundance of these three feeding guilds (facultative, obligate coral feeders, and invertivores) did not differ significantly between the four surveyed years. Combined, these results suggest that a plasticity in behaviour, rather than selective removal of aggressive individuals, species or feeding guilds, has allowed this butterflyfish population to adapt to shifting resource availability and weather the storm of a substantial disturbance event.

Our results follow the classic pattern of the economic defendability model, where individuals must balance the advantages (e.g. energy gained) and disadvantages (e.g. energy lost) associated with competing for the resource to maximise fitness. For example, individuals risk a net loss of fitness if engaging in aggression over an ephemeral or highly mobile resource that is difficult or impossible to defend effectively [11]. Under this model, aggression is predicted to be highest at intermediate resource availability, where resources are limited yet abundant enough to warrant energy investment into aggressive interactions. It follows then that aggression is predicted to be low at both extremes of the resource availability spectrum where resources are either too abundant to require investment in aggressive interactions, or so scarce that such investment is associated with reduced fitness[38]. While Brown's model of economic defendability has been supported in a multitude of systems at varying fixed levels of resource availability (e.g. salmonids[39], herbivorous damselfishes[40] and convict cyclids[41]), our current understanding is largely based on such static snapshots in time. This is the first time the model has been tested in the context of environmental change, using repeated sampling in the field during an ongoing disturbance event.

While a temporary behavioural shift to conserve energy may have allowed this population to weather the storm of a large-scale disturbance event, these findings do not suggest reef fishes are safe from anthropogenic climate change. Only species with adaptable behaviour can access this short-term survival strategy. For example, birds with a capacity to alter migration routes can avoid wintering sites that have suffered habitat loss, while their less flexible counterparts will suffer the consequences of reduced resource availability [42]. Second, a behavioural response to habitat loss hinges on the reliability of cues to assess habitat quality, with incorrect cues leading to maladaptive behaviours (e.g. caught in ecological traps) [43]. Indigo buntings (*Passerina cyanea*) for example, prefer forest edge habitat due to a low abundance of predators in naturally created edges. However, the birds are equally attracted to anthropogenically created edges that contain increased numbers of nest predators, and suffer lower reproductive success as a result [44,45]. Finally, the frequency of disturbance events is likely to increase, reducing the capacity for systems to recover fully between events, limiting the effectiveness of behavioural shifts [46].

Habitat loss remains one of the most pervasive threats against global biodiversity, reshuffling ecosystems and communities and causing a worldwide biodiversity crisis. Here we have demonstrated that a community of butterflyfishes alters their behaviour in line with resource availability by engaging in fewer aggressive interactions when resources are low, and returning to pre-disturbance behaviours as resources recover. The most plausible explanation to understand this change in behaviour is a reduction in energy expenditure during environmental change, to maintain optimal responses following the economic defendability model. While good news for this family of reef fishes benefiting from relatively rapid resource recovery, our findings highlight the vulnerability of individuals, and species, with low behavioural flexibility. Further, behavioural flexibility may not safeguard species experiencing environmental change where the conditions, magnitude of disturbance, or other variables are not as favourable to recovery. Our findings further emphasise the importance of understanding behavioural responses to habitat loss to predict how ecosystems may adapt to future environmental conditions.

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